GROWTH AND MORPHOMETRY OF THE PYGMY WHITEFISH (PROSOPIUM COULTERI) IN BRITISH COLUMBIA

by

PETER JAMES MCCART

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Institute of Fisheries
Department of Zoology
The University of British Columbia
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ABSTRACT

The present study is, in part, a description of meristic variation in the pygmy whitefish, Prosopium coulteri, of British Columbia fish with those of other areas. The species was shown to be highly variable meristically both within and between populations. There are indications in some characters of a north-south cline of meristic counts. One character (gill raker counts) seems to form a V-shaped curve of variation.

The major part of the study is a comparison of the growth and relative growth of fish from four British Columbia lakes. The two "giant" forms from MacLure and McLeese Lakes are more like one another in relative growth than like either of the two dwarf forms inhabiting Cluculz Lake or Tacheeda Lake.

The possible relationship between growth, form and environment is discussed.

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INTRODUCTION

The pygmy whitefish, *Prosopium coulteri* (Eigenmann and Eigenmann), is a small coregonine fish widely distributed throughout the lakes and rivers of the North American Cordillera from the Columbia River drainage northward to Alaska. In addition, a relict population is known to inhabit Lake Superior (Eschmeyer and Bailey, 1954). Aside from a few populations in the Columbia River basin, the pygmy whitefish of British Columbia has never been adequately described. The present study is, in part, a description of meristic variation within the species in British Columbia and a comparison of British Columbia fish with those of other areas.

Typically, the pygmy whitefish is characterized by a very slow growth rate and small size at maturity. There is, however, within the province of British Columbia, considerable disparity in the size at maturity of fish from different populations. The sizes attained by fish in MacLure and McLeese Lakes greatly exceed those reported for any other population. The major part of this study is a comparison of the age and growth of the MacLure and McLeese lake populations with the more typical "pygmy" growth form of fish from Cluculz and Tacheeda Lakes. An attempt has been made to correlate these differences in growth rate with factors in the physical and biotic environment. In addition, the relative growth of body parts of fish in the four populations has been analyzed to discover whether there exists any relationship between this and growth rate.

MATERIALS AND METHODS

Field Data

During the summer of 1962, pygmy whitefish were collected in four lakes in British Columbia: Tacheeda Lake in the MacKenzie River drainage; MacLure Lake in the Skeena River drainage; and two lakes, Cluculz and McLeese, in the Fraser River drainage basin.

All fish were taken in monofilament gillnets approximately fifty feet in length. These were of two kinds: eight-foot deep nets ranging in size from ½ inch to 2½ inches, and twenty-five-foot deep nets of 1½, 2, and 2½ inches stretch measure. Nets were fished at known depths for periods of from four to thirty-six hours; generally about twelve hours. The approximate position of each fish in the net was recorded at the time of removal.

After being removed from the net, the fish were slit to hasten the preservation of stomach contents and then placed in a forty per cent solution of formalin.

Other field data include temperature profiles for each lake recorded at irregular intervals using an Electronic thermometer manufactured by Applied Research Associates, Austin, Texas; and two series of oxygen determinations made during August at MacLure and Cluculz Lakes.

Counts and Measurements

Counts and measurements were made after the fish had been washed and transferred to forty per cent isopropyl alcohol.

Specimens examined

The specimens examined are from the collections of the Institute of Fisheries Museum, University of British Columbia, or are from as yet uncatalogued collections made by the author during the summer of 1962 (the latter are designated by numbers prefixed with the letter "s"). Collections which were examined in whole or in part are listed below in Table 1.

Counts

The definition of various counts was that of Hubbs and Lagler (1957). Wherever necessary a binocular microscope was used as an aid in counting.

a) lateral line scales. The count was terminated at the end of the hypural plate, the position of which was determined by the crease formed when the tail of the fish was sharply bent. In most cases there were only two or three lateral line scales beyond this point. Gaps where scales had been removed by gill net strands or otherwise lost were bridged by the enumeration of empty scale pockets.

Table 1. Collections examined

Locality	Collection Numbers
Alaska	
Brooks Lake	BC 58 - 418
Aleknagik Lake	BC 60 - 399, BC 62 - 967
MacKenzie Drainage	
Dease Lake	BC 56 - 477
Tacheeda Lake	S94, S95, S154, S177
Skeena Drainage	
MacLure Lake	S172A, S172B
	S69, S72, S179
Fraser Drainage	
Moose Lake	BC 57 - 384
	BC 57 - 385
	BC 57 - 386
Yellowhead Lake	BC 57 - 390, BC 57 - 391
McLeese Lake	S83, S84, S86, S88, S89, S157, S160
Cluculz Lake	S104, S143, S178
Columbia River Drainage	
Kicking Horse River	BC 56 - 493
Blaeberry River	BC 56 - 472
Kinbasket Lake	BC 56 - 476
Laird Creek	BC 56 - 189
Lake Superior	
Keewenaw Bay	BC 55 - 387
	BC 57 - 416

b) gill rakers. Counts were made of all gill rakers, including rudimentary ones, on the first arch on the left side. In all but a few cases it was not necessary to remove the gill arch.

c) pyloric caeca. Because of the small number of caeca found in individual fish, it was not necessary to remove each caecum at the time of enumeration. The digestive tract was severed just anterior to the stomach and then removed from the body cavity for examination. The digestive tract was left attached at its posterior end to prevent its separation from the specimen.

d) dorsal and anal rays. All anterior unbranched rays were included in this count. The last double ray, divided near the base, was counted as one.

e) vertebrae. All vertebral counts were made from X-ray negatives produced by a General Electric Model "D" machine using Type "M" Industrial Kodak film. Exposures averaged about 1600 milliampere seconds at a distance of fifty-five inches. The hypural vertebrae were included in the counts. Plate 14, Diagram H in Norden (1962) was used as a guide.

f) pectoral and pelvic rays. Although both left and right fins were counted, the two did not appear to differ significantly and only the counts for the left pectoral and left pelvic fins are included here. All rays, branched and unbranched, were counted.

Measurements

Measurements of standard length and various body parts were made to the nearest tenth of a millimeter using a pair of dial-reading calipers. In a few cases, where the standard length of a fish exceeded the 200 mm capacity of the calipers, measurements were made with dividers and a rule. All measurements were made exactly as described in Hubbs and Lagler (1957). The exceptions were:

a) body depth. This measurement was taken as the distance from the anterior base of the dorsal fin to the anterior base of the pelvic fin. This was done so as to eliminate discrepancies arising from distention due to expansion of the swim bladder or from slitting.

b) length of eye. The length of the eye was measured as indicated in Figure 1. This measurement is the midline distance from the posterior margin of the eyeball to the anterior fold of the vestigial adipose eyelid (as identified by K. W. Stewart, personal communication). It was felt that this method of measurement would give more easily reproducible results than the usual measurement of length of orbit.

Measurements were also made of the height of the dorsal and anal fins. The length of the dorsal and anal base, the length of the left pectoral and pelvic fins, head length, inter-orbital width, predorsal length, and length of the upper jaw.

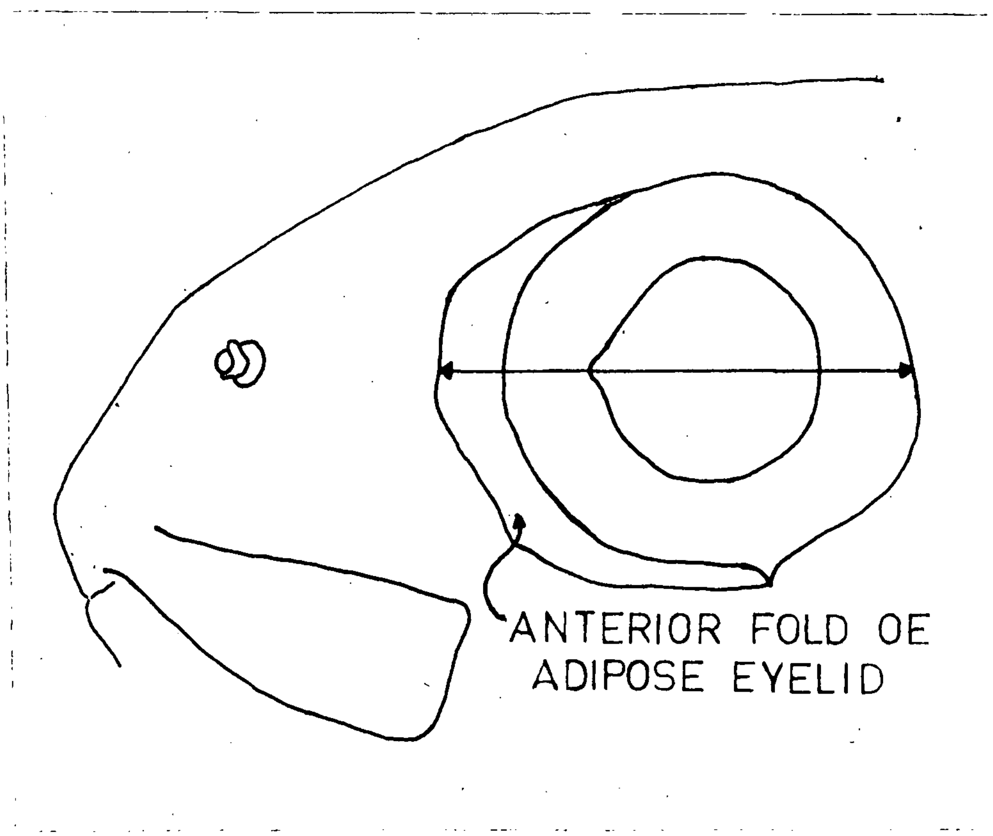


Figure 1. Diagram of eye measurement

Age and Growth

All fork lengths, weights, and scale samples were taken from preserved fish. Sex and state of maturity were determined at the same time. Fork lengths were determined using a measuring board.

The scales were removed from an area lying between the dorsal fin and the lateral line. The scales were then cleaned by gentle scraping and sandwiched between two slides which were then taped together. Scales mounted in this way have been kept for as long as nine months without showing any signs of drying, cracking, or wrinkling. Measurements of annuli were made at a magnification of X43.8 using and Bausch and Lomb slide projector. A simple nomograph was used in back calculation.

Food Studies

The amounts of various food items present in the diets of pygmy whitefish were determined by emptying the contents of the stomachs into a squared petri dish. The food items were then separated into groups and a visual estimate recorded of the relative proportions of the various foods represented. Because of the small size of most stomach samples, the contents of from five to ten stomachs were combined in making the estimate. Only the stomachs of large MacLure Lake fish were examined individually.

The Habitat

Table 2 presents the available physical, chemical, and biological data for each of the four lakes. Figures 2 to 5 illustrate the contour characteristics of the lakes and the main netting areas. Their geographical position is shown in Figure 6. None of the lakes has been the subject of intensive limnological investigation.

The lakes fall into two groups. Tacheeda and Cluculz are both relatively deep lakes with a low to moderate content of dissolved solids (TDS). This fish fauna is dominated by salmonid species (seven in Cluculz Lake and six in Tacheeda). The other two lakes, McLeese and MacLure, are smaller, shallower, and have considerably higher TDS values. In each case only two salmonids are present, Salmo gairdneri and Prosopium coulteri.

Northcote and Larkin (1956) have demonstrated a significant relationship between lake productivity and total dissolved solid content of British Columbia lake waters. Lake productivity was shown to increase with increasing TDS. Field observations would indicate that their generalization holds true in this case and that Cluculz and Tacheeda are indeed less productive than McLeese and MacLure.

Within the groups, Tacheeda appears to be less productive than Cluculz and McLeese less productive than MacLure. Data are meagre, however, and this ranking is largely subjective.

Table 2. Limnological data and fish complement of four British Columbia lakes

	CLUCULZ	MACLURE	MCLEESE	TACHEEDA
Elevation	2500'	1800'	2400'	2382'
Maximum Depth	200'	73'	152'	195'
Mean Depth	97'	36.4'	53.6'	57.4'
Total Dissolved Solids	118 ppm	208 ppm	250 ppm	52 ppm
Surface Area	6223 acres	785 acres	841 acres	1460
Trout and Char				
Salvelinus namaycush	x			x
S. malma	x			x
Salmo gairdneri	x	x	x	x
Oncorhynchus nerka	x			
Whitefish				
Prosopium coulteri	x	x	x	x
P. williamsoni	x			x
Coregonus clupeaformis	x			x
Suckers				
Catostomus macrocheilus	x		x	
C. commersoni	x			x
C. catastomus	x	x	x	x
Minnows				
Richardsonius balteatus	x	x	x	x
Ptychocheilus oregonensis	x	x	x	x
Mylocheilus caurinum	x	x	x	x
Sculpins				
Cottus asper	x	x		x
Burbot				
Lota lota	x	x		

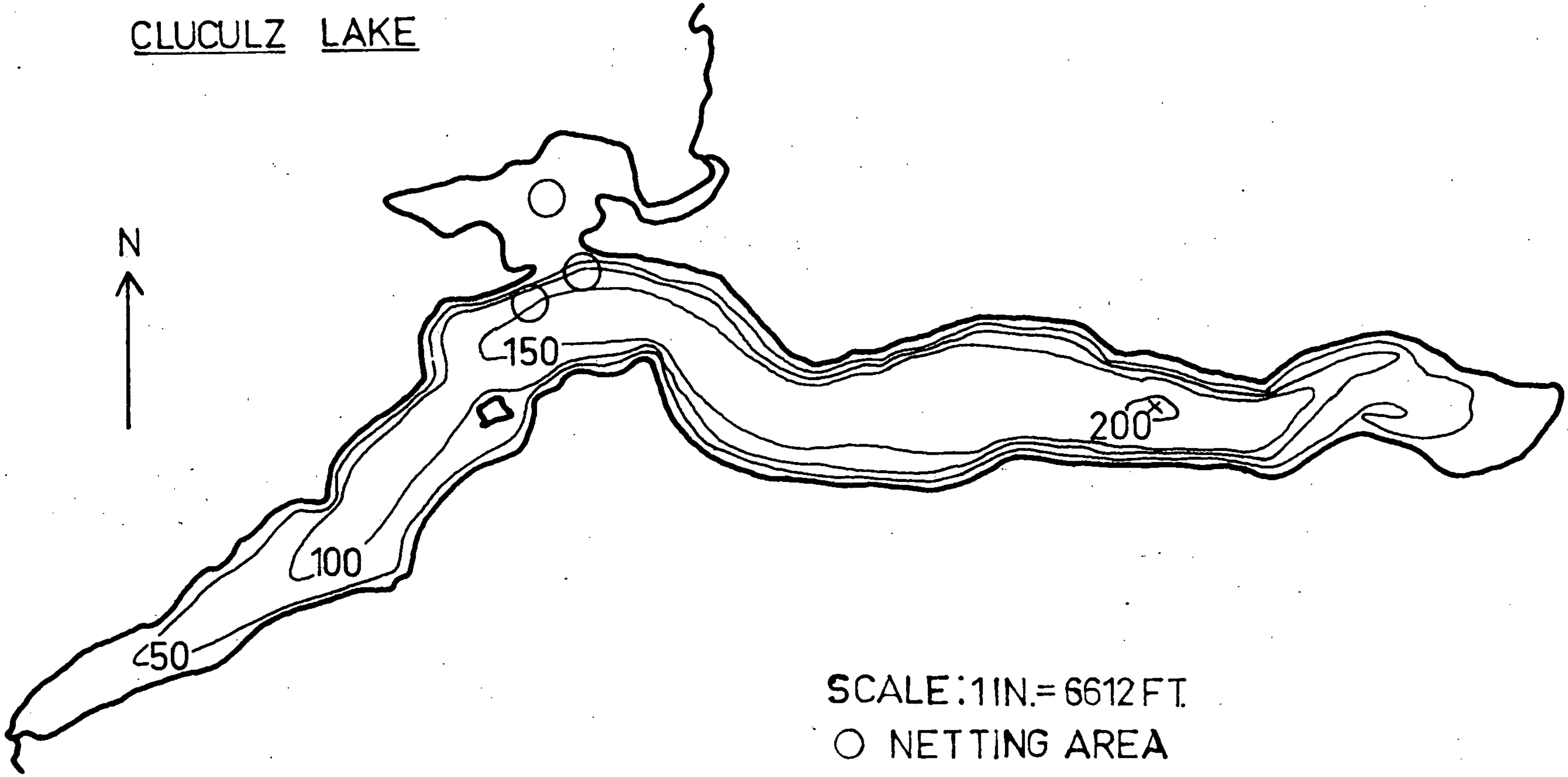


Figure 2. Contour map of Cluculz Lake

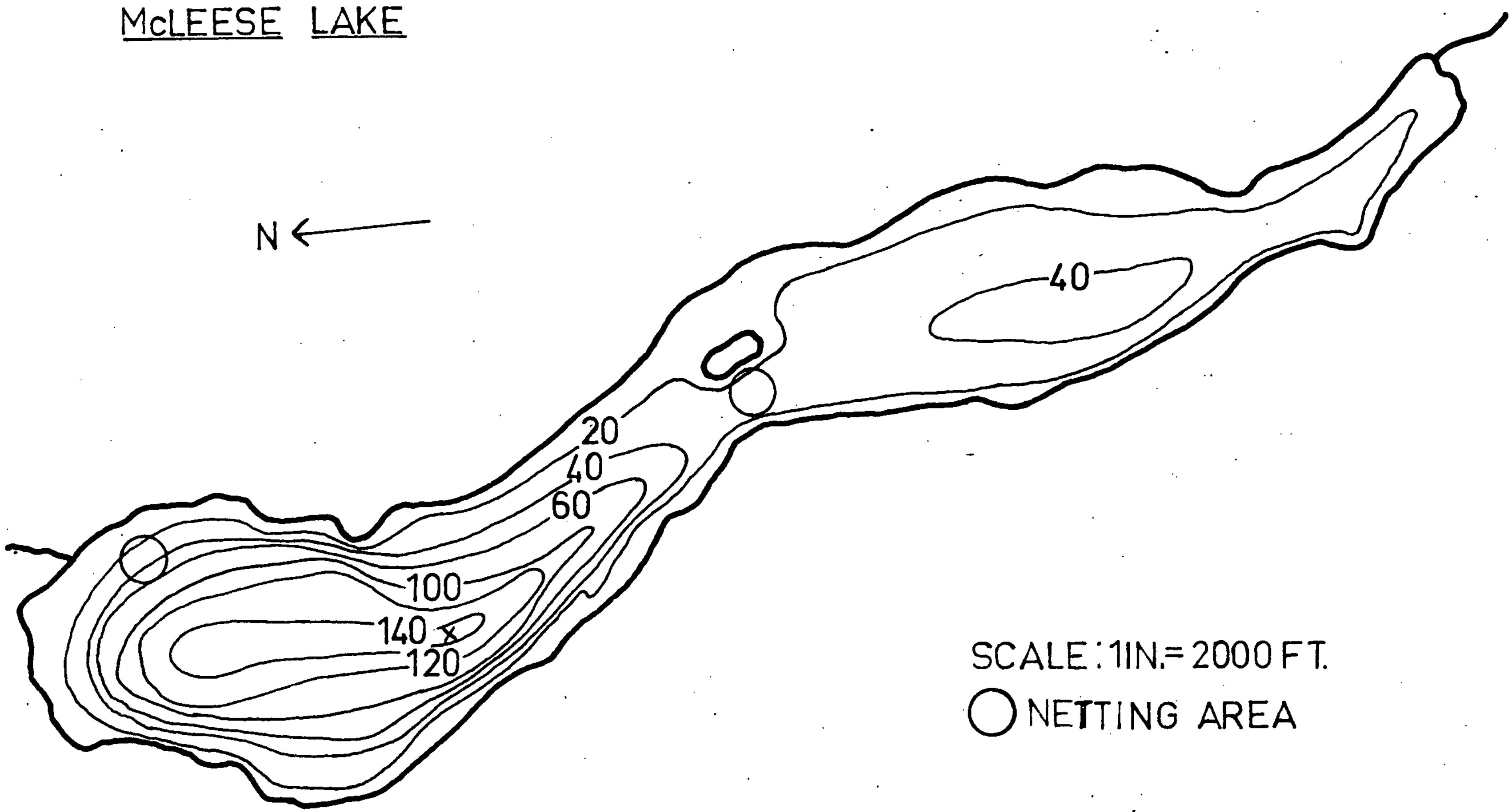


Figure 3. Contour map of McLeese Lake

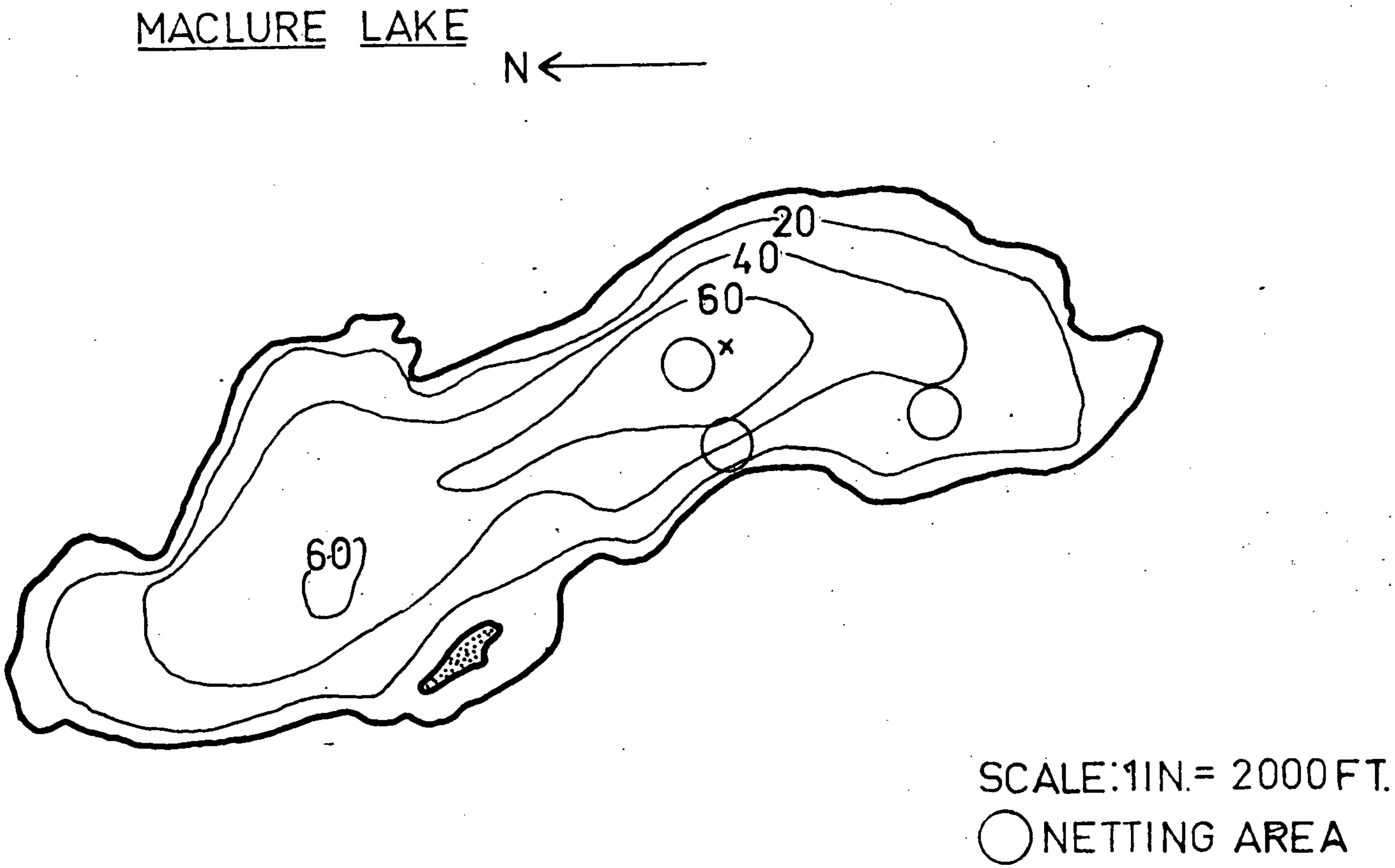


Figure 4. Contour map of McLure Lake

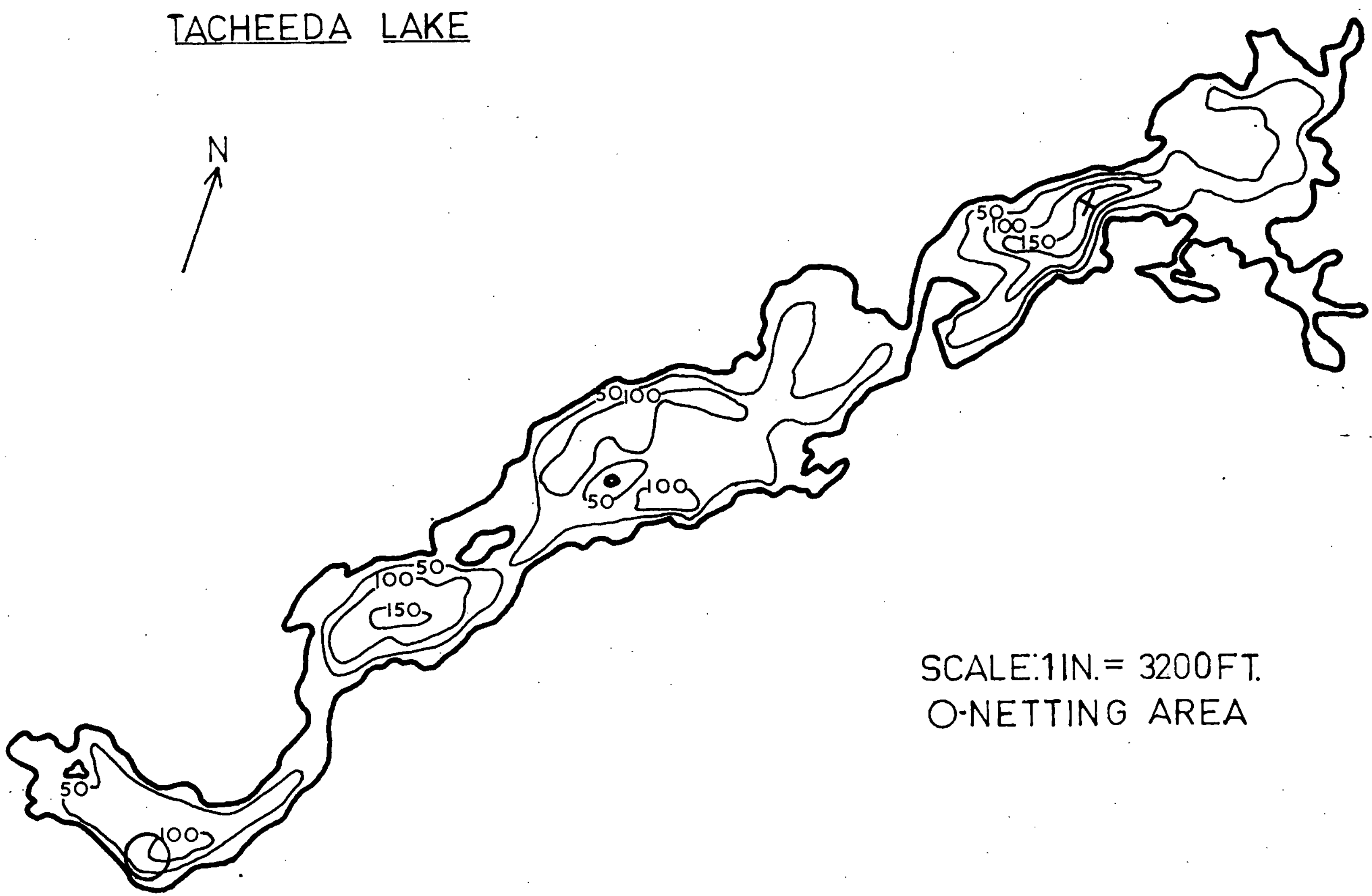


Figure 5. Contour map of Tacheeda Lake

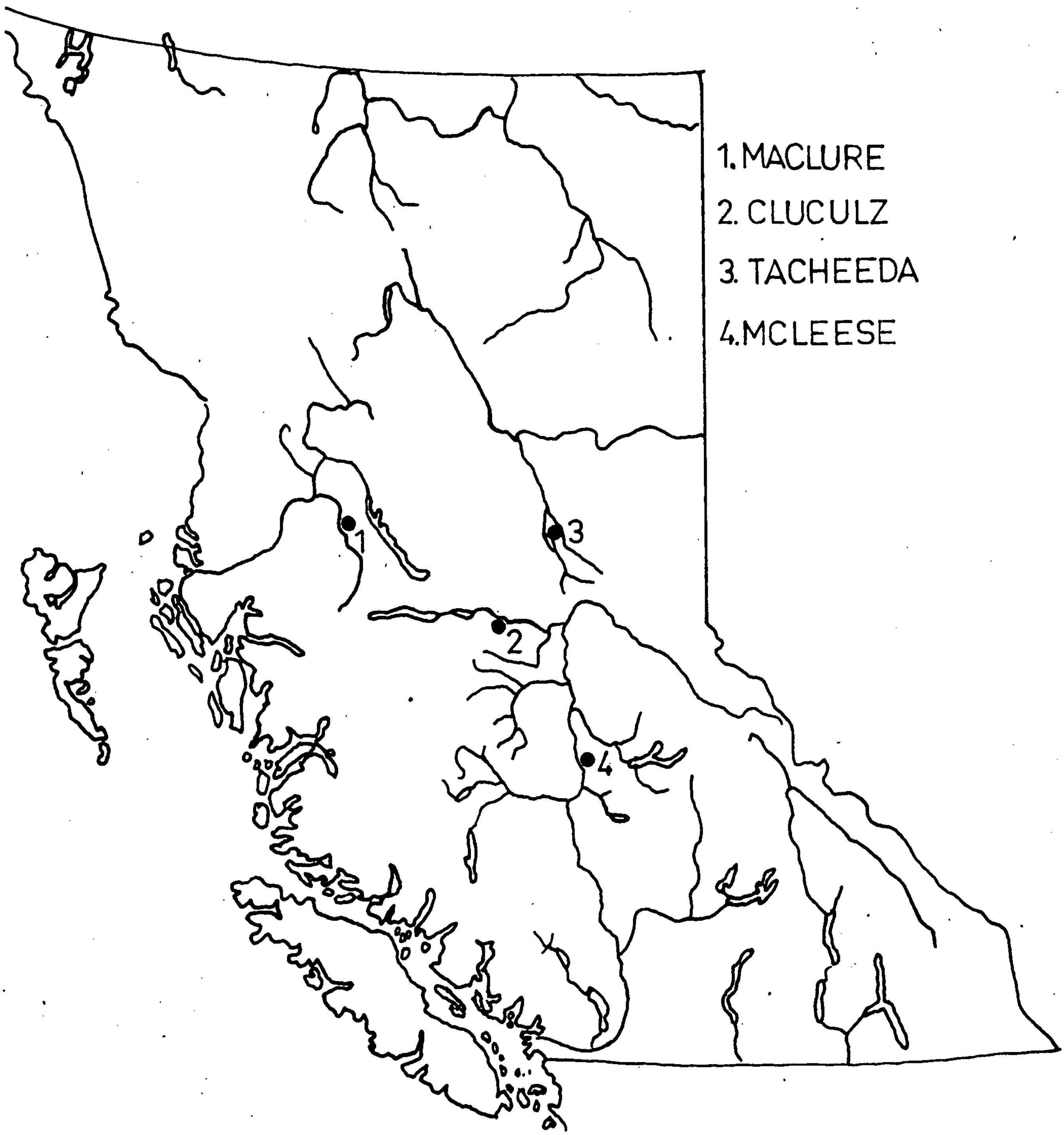


Figure 6. Map of British Columbia showing location of the four study lakes

RESULTS

Meristics

Whitefishes (Coregonidae) are notorious for the high degree of meristic variability found within and between populations of the same species. In this respect the species making up the genus Prosopium are not different from others. The meristic counts of the six species of Prosopium are compared in Table 3. Of the six, three (P. spilonotus, P. gemmiferum, and P. abyssicola) are endemic to Bear Lake, Idaho and Utah, and presumably constitute single, homogeneous populations. The samples counted were small (Snyder, 1919). For these reasons the small range of counts is not unexpected. The other three species, which range over a much wider area, show considerable variability.

In general, pygmy species of a group tend to have fewer parts than closely related larger fishes. Barlow (1961) has demonstrated a reduction in the number of fin rays and scales in a dwarf species of the goby Gillichthys. Myers (1958), generalizing about fishes of minute size, notes, among other

Table 3. Range of meristic counts in six species of *Prosopium*

	WILLIAMSONI	SPILONOTUS	CYLINDRACEUM	ABYSSICOLA	GEMMIFERUM	COULTERI
	Holt (1960)	Snyder(1917)	J.D.McPhail (pers.comm.)	Snyder(1917)	Snyder(1917)	This study
Number of Specimens	357	22	8 + 4 + 10	10	10	229
Lateral line scales	73 - 92	74 - 81	83 - 107	69 - 76	71 - 77	50 - 72
Gill rakers	17 - 25	18 - 22	14 - 21	18 - 23	41 - 44	12 - 20
Pyloric caeca	50 - 146	135 - 140	50 - 130	73 - 78	81 - 86	13 - 33
Dorsal rays	11 - 14	10 - 12	13 - 15	10 - 11	9 - 11	10 - 13
Anal rays	10 - 13	9 - 11	11 - 13	9 - 11	11 - 12	10 - 14
Vertebrae	53 - 61		59 - 65			50 - 55
Pectoral rays	14 - 18					13 - 18

trends, a reduction in the number of scales and a similar but less striking reduction in the number of fin rays.

Of the six species, P. coulteri is distinguished by its small number of lateral line scales, gill rakers, and, most important in the opinion of Eschmeyer and Bailey (1954), its very low pyloric caeca count. Although counts of vertebrae are not available for the three Bear Lake whitefishes, it is not unlikely that the low numbers characteristic of pygmy whitefish are also distinctive. The numbers of fin rays do not appear to be significantly different from those of other species.

The only review of meristic variation in Prosopium coulteri is Eschmeyer and Bailey's 1954 paper reporting the discovery of a relict population of the fish in Lake Superior at a distance of over 1100 miles from the nearest population in the Columbia River basin. The authors did not examine British Columbia fish from outside of the Columbia River system and there is, consequently, a considerable hiatus in their discussion of geographic variation from southern British Columbia to Alaska. This work presents counts for additional Columbia populations as well as data for fish from the Fraser, Skeena and Mackenzie basins in British Columbia. In addition, counts were made on pygmys from Brooks Lake and Lake Alegnagik, Alaska, and Lake Superior. These counts are presented in tables 4 to 9. In every case, an analysis of variance indicates a significant difference between the means of the populations (the F values are included with the tables).

Table 4. Frequency distribution of lateral line scale counts in *Prosopium coulteri*

LOCATION	LATERAL LINE SCALES																								
	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	N	Mean	SD
Alaska																									
Brooks Lake	--	1	3	2	2	4	3	3	1	1	--	--	--	--	--	--	--	--	--	--	--	--	20	54.85	2.21
MacKenzie Drainage																									
Dease Lake	--	1	1	--	3	2	3	4	2	--	1	--	1	--	--	--	--	--	--	--	--	--	20	56.10	2.62
Tacheeda Lake	--	--	1	--	1	1	3	4	4	1	2	1	2	--	--	--	--	--	--	--	--	--	20	57.65	3.56
Skeena Drainage																									
MacLure Lake	--	--	--	--	--	--	--	--	2	3	2	2	3	2	2	4	--	--	--	--	--	--	20	61.75	2.45
Fraser Drainage																									
Moose Lake	--	--	--	--	--	1	1	1	--	1	4	1	1	3	5	--	1	1	--	--	--	--	20	61.60	3.22
Yellowhead Lake	--	--	1	--	2	1	--	2	--	2	2	1	--	--	--	--	--	--	--	--	--	--	11	57.09	2.98
McLeese Lake	1	1	1	2	1	5	6	1	1	--	1	--	--	--	--	--	--	--	--	--	--	--	20	54.95	2.33
Cluculz Lake	--	1	--	2	2	1	--	2	1	2	3	3	2	2	--	--	2	--	--	--	--	--	22	58.59	3.91
Columbia Drainage																									
Kicking Horse R.	--	--	--	--	--	--	--	1	--	1	1	5	--	2	--	--	1	--	1	--	--	--	12	61.75	2.95
Blaeberry River	--	--	--	--	--	--	1	1	1	2	--	3	3	2	--	1	2	--	1	2	--	1	20	62.90	4.16
Kinbasket Lake	--	--	--	--	1	--	1	--	1	4	5	2	2	2	1	1	--	--	--	--	--	--	20	60.25	2.59
Laird Creek	--	--	--	--	1	4	2	3	2	3	2	1	1	1	--	--	--	--	--	--	--	--	20	57.80	2.54

Table 5. Frequency distribution of pyloric caeca counts in Prosopium coulteri

LOCALITY	PYLORIC CAECA 13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	N	Mean	SD
Alaska																								
Brooks Lake	--	--	--	7	4	2	2	4	--	--	--	1	--	--	--	--	--	--	--	--	--	20	17.90	2.13
MacKenzie Drainage																								
Dease Lake	--	--	--	--	2	6	2	3	2	1	1	3	--	--	--	--	--	--	--	--	--	20	19.95	2.25
Tacheeda Lake	1	--	--	--	--	--	3	1	3	7	4	--	1	--	--	--	--	--	--	--	--	20	21.20	2.46
Skeena Drainage																								
MacLure Lake	--	--	--	3	2	2	3	2	4	4	--	--	--	--	--	--	--	--	--	--	--	20	19.35	2.16
Fraser Drainage																								
Moose Lake	--	--	--	--	1	1	1	3	4	2	6	1	--	1	--	--	--	--	--	--	--	20	21.50	2.14
Yellowhead Lake	--	--	1	--	3	1	3	--	--	1	--	1	1	--	--	--	--	--	--	--	--	11	19.27	3.13
McLeese Lake	--	4	1	1	2	1	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	11	16.09	2.02
Cluculz Lake	--	1	--	--	1	5	3	2	1	--	4	1	--	--	1	--	--	--	--	--	--	19	20.10	3.07
Columbia Drainage																								
Kicking Horse R.	--	--	--	--	--	2	--	--	1	1	4	1	--	1	--	1	--	--	--	--	1	12	23.50	4.12
Blaeberry River	--	--	--	1	--	1	4	5	--	4	3	1	--	1	--	--	--	--	--	--	--	20	20.85	2.35
Kinbasket Lake	--	--	--	--	1	--	--	4	4	3	3	2	--	1	1	--	--	--	--	--	--	19	21.95	2.32
Laird Creek	--	--	--	--	1	2	1	2	1	3	1	2	2	1	--	2	1	1	--	--	--	20	23.05	3.85

F = 88.42

Table 6. Frequency distribution of gill raker counts in *Prosopium coulteri*

LOCALITY	GILL RAKERS 12	13	14	15	16	17	18	19	20	N	Mean	SD
Alaska												
Brooks Lake	--	--	--	1	12	5	1	--	--	19	16.32	0.66
MacKenzie Drainage												
Dease Lake	--	--	--	--	2	9	7	1	1	20	17.50	0.95
Tacheeda Lake	--	2	12	4	2	--	--	--	--	20	14.30	0.78
Skeena Drainage												
MacLure Lake	--	1	12	7	--	--	--	--	--	20	14.30	0.56
Fraser Drainage												
Moose Lake	2	9	2	6	1	--	--	--	--	20	13.75	1.17
Yellowhead Lake	--	2	8	1	--	--	--	--	--	11	13.90	0.55
McLeese Lake	--	--	--	7	10	3	--	--	--	20	15.80	0.69
Cluculz Lake	1	8	8	2	1	--	--	--	--	20	13.70	0.92
Columbia Drainage												
Kicking Horse R.	1	--	4	5	1	1	--	--	--	12	14.66	1.24
Blaeberry River	--	3	11	6	--	--	--	--	--	20	14.15	0.69
Kinbasket Lake	3	4	11	2	--	--	--	--	--	20	13.60	0.89
Laird Creek	--	--	1	7	9	3	--	--	--	20	15.70	0.79

F = 41.76

Table 7. Frequency distributions of pectoral and pelvic ray counts in *Prosopium coulteri*

LOCALITY	LEFT PECTORAL RAYS 13	14	15	16	17	18	N	Mean	SD	LEFT PELVIC RAYS 9	10	11	N	Mean	SD
Alaska															
Brooks Lake	--	5	7	7	1	--	20	15.20	0.89	5	15	--	20	9.75	0.46
MacKenzie Drainage															
Dease Lake	8	12	--	--	--	--	20	13.60	0.51	1	19	--	20	9.95	0.23
Tacheeda Lake	--	1	7	7	5	--	20	15.80	0.88	4	16	--	20	9.80	0.40
Skeena Drainage															
MacLure Lake	--	1	13	6	--	--	20	15.25	0.56	--	15	5	20	10.25	0.46
Fraser Drainage															
Moose Lake	--	--	6	14	--	--	20	15.70	0.51	2	17	1	20	9.95	0.40
Yellowhead Lake	--	--	3	8	--	--	11	15.27	0.45	1	10	--	11	9.91	0.32
McLeese Lake	--	7	12	1	--	--	20	14.70	0.56	4	16	--	20	9.80	0.40
Cluculz Lake	--	--	6	11	2	--	19	15.79	0.62	2	17	1	20	9.95	0.40
Columbia Drainage															
Kicking Horse R.	--	2	6	4	--	--	12	15.17	0.74	6	6	--	12	9.50	0.52
Blaeberry River	--	1	13	5	1	--	20	15.30	0.69	5	15	--	20	9.75	0.46
Kinbasket Lake	--	--	13	6	1	--	20	15.40	0.61	1	18	1	20	10.00	0.32
Laird Creek	--	1	--	6	7	6	20	16.85	1.05	2	16	2	20	10.00	0.46

F = 23.000

Table 8. Frequency distributions of dorsal and anal fin ray counts in <u>Prosopium coulteri</u>

LOCALITY	DORSAL FIN RAYS							ANAL FIN RAYS							
	10	11	12	13	N	Mean	SD	10	11	12	13	14	N	Mean	SD
Alaska															
Brooks Lake	5	10	5	--	20	11.00	0.73	--	4	10	6	--	20	12.10	0.73
MacKenzie Drainage															
Dease Lake	5	13	2	--	20	10.85	0.61	--	15	5	--	--	20	11.25	0.46
Tacheeda Lake	--	8	12	--	20	11.61	0.51	--	3	10	7	--	20	12.20	0.68
Skeena Drainage															
MacLure Lake	1	16	3	--	20	11.10	0.46	--	6	14	--	--	20	11.70	0.46
Fraser Drainage															
Moose Lake	--	5	14	1	20	11.80	0.56	--	1	7	9	3	20	12.70	0.83
Yellowhead Lake	1	3	6	1	11	11.64	0.84	1	--	2	8	--	11	12.54	0.95
McLeese Lake	--	7	11	2	20	11.75	0.65	--	6	10	4	--	20	11.90	0.73
Cluculz Lake	--	17	3	--	20	11.85	0.40	--	--	11	7	2	20	12.55	0.69
Columbia Drainage															
Kicking Horse R.	--	5	7	--	12	11.58	0.52	--	3	6	3	--	12	12.00	0.74
Blaeberry River	--	6	14	--	20	11.70	0.51	--	4	13	3	--	20	11.95	0.61
Kinbasket Lake	--	2	15	3	20	12.05	0.51	--	--	8	11	1	20	12.65	0.61
Laird Creek	1	10	8	1	20	11.45	0.69	--	--	3	11	6	20	13.15	0.69
	F = 6.94							F = 10.87							

Table 9. Frequency distributions of vertebral counts in *Prosopium coulteri*

LOCALITY	VERTEBRAE 50	51	52	53	54	55	N	Mean	SD
Alaska									
Brooks Lake	1	10	7	2	--	--	20	51.50	0.76
MacKenzie Drainage									
Dease Lake	--	5	15	--	--	--	20	51.75	0.46
Tacheeda Lake	--	7	9	3	--	--	19	51.79	0.71
Skeena Drainage									
MacLure Lake	--	2	10	5	3	--	20	52.45	0.89
Fraser Drainage									
Moose Lake	--	--	4	9	6	1	20	53.20	0.83
Yellowhead Lake	1	2	4	4	--	--	11	52.00	1.00
McLeese Lake	--	1	10	9	--	--	20	52.40	0.61
Cluculz Lake	--	2	8	6	4	--	20	52.60	0.95
Columbia Drainage									
Kicking Horse River	--	--	1	6	5	--	12	53.33	0.67
Blaeberry River	--	--	2	17	1	--	20	52.95	0.40
Kinbasket Lake	--	4	4	8	4	--	20	52.60	1.05
Laird Creek	1	3	9	7	--	--	20	52.10	0.86

F = 9.67

A notable feature of the meristic characters of Prosopium coulteri is the extreme ranges of counts even within a single population. In the Blaeberry River sample, for instance, there was a twenty-nine per cent difference between the lowest and highest numbers of lateral line scales. In the Kicking Horse River fish, there was a difference of forty-one per cent and eighty-three per cent respectively between the lowest and highest gill raker and pyloric caeca counts. The difference between populations is, of course, even greater: forty-two per cent for lateral line scales; sixty-six per cent for gill rakers; and 151 per cent for pyloric caeca. Thus, the size of the sample is small in comparison with the variation. In most cases the range of counts of any one character for a single population overlaps the means of all populations. As a result, without larger samples from each locality, any conclusions based on a comparison of means can only be tentatively accepted. Where possible, at least twenty individuals from each population were counted. Considering that all together only seventeen populations are represented spread over a third of North America, the tenuity of any conclusions is even more obvious.

Table 10 presents the means for several meristic characters of seventeen populations. Figures for five of these populations have been taken in whole or in part from Eschmeyer and Bailey (1954). These are indicated by an asterisk (*). Only means of samples of ten fish or more are included. (Means for the pectoral and pelvic rays were arrived at by halving their figures which totalled the left and right fins). The

Table 10. Means of meristic counts for various populations of *Prosopium coulteri*

LOCALITY	LAT°N	LONG	MAT	LLS	GR	PC	VERT	DR	AR	P_1R	P_2R
Alaska											
Brooks Lake	58	157	30-35	54.85	16.32	17.90	51.50	11.00	12.10	15.20	9.75
*Aleknagik Lk	60	159	30-35	61.77	13.70	23.00	52.57	11.12	11.70	14.75	9.85
*Chignik Lk	56	159	30-35	63.75	14.56			11.56	12.75	15.19	9.64
MacKenzie River Drainage											
Dease Lake	59	130	30-35	56.10	17.50	19.95	51.75	10.85	11.25	13.60	9.95
Tacheeda Lake	55	123	30-35	57.65	14.30	21.20	51.79	11.61	12.20	15.80	9.80
Skeena River Drainage											
MacLure Lake	55	127	35-40	61.75	14.30	19.35	52.45	11.10	11.70	15.25	10.25
Fraser River Drainage											
Cluculz Lake	54	123	35-40	58.59	13.70	20.10	52.60	11.85	12.55	15.70	9.95
Moose Lake	53	120	35-40	61.60	13.75	21.50	53.20	11.80	12.70	15.70	9.95
Yellowhead	53	119	35-40	57.09	13.90	19.27	52.00	11.64	12.54	15.27	9.91
McLeese Lake	53	122	40-45	54.95	15.80	16.09	52.40	11.75	11.90	14.70	9.80
Columbia River Drainage											
Kinbasket R	52	118	35-40	60.25	13.60	21.95	52.60	12.05	12.65	15.40	10.00
Blaeberry R	52	118	35-40	62.90	14.15	20.85	52.95	11.70	11.95	15.30	9.75
Kicking Horse	51	117	35-40	61.75	14.66	23.50	53.33	11.85	12.00	15.17	9.50
Laird Creek	50	117	40-45	57.80	15.70	23.05	52.10	11.45	13.15	16.85	10.00
*Bull Lake	49	116	40-45	60.70	16.71			11.83	12.57	15.89	9.88
*Lake MacDonald	49	114	40-45	59.20	17.20			11.40	12.54	16.00	9.67
*Lake Superior	48	87	35-40	57.14	18.28	17.60	53.09	10.90	13.20	14.62	10.28

* Counts wholly or partly from Eschmeyer and Bailey (1955) M.A.T. Mean Annual Temperature

table also includes the approximate latitude and longitude of the locality and the range of mean annual temperature. Mean annual temperature was chosen to represent climatological conditions first, because the wide geographic spread of samples must inevitably mean considerable variation in developmental rates and hatching times; and secondly, because the exact period at which various meristic series are laid down in pygmy whitefish is unknown. Some, such as vertebrae, may be determined just prior to hatching (as in *Salmo trutta*, Tåning, 1952). On the other extreme, age group 0 fish may still be without scales toward the end of their first summer of growth. Thus, temperature conditions in no one month would have a meaningful relationship to meristic variation between populations.

If the means of various meristic characters are graphed against the latitude of sample areas (Figs. 7, 8) there appears to be a general tendency toward an increase in parts in the more southerly populations. This tendency is quite apparent in the graphs for anal rays and vertebrae. It *may* be present, but with a higher degree of scattering in pectoral ray and pyloric caeca counts. The number of lateral line scales seems to vary randomly with latitude. Finally, the relation between gill rakers and latitude would appear to be a V-shaped curve with the greatest numbers of rakers at the extremes of latitude and low counts in the middle of the geographic range.

Various authors have reported latitudinal clines of meristic counts in fishes. Jordan (1891) and Hubbs (1925) both reported that northern fishes generally possess more vertebrae than related, more southerly forms. Since then, numerous other examples have been documented involving vertebrae and other meristic characters. Lindsey (1953) and Weisel (1955) for the redside shiner, Tåning (1952) for *Salmo trutta* and Seymour (1959) for *Oncorhynchus tshawytscha* are examples.

Experimental work has shown that meristic series vary as the result of the interaction of both genotypic and phenotypic components. The relation between meristic counts and temperature is most frequently V-shaped with the highest or lowest counts at moderate temperatures (Tåning, 1952, for *Salmo trutta*), but as Lindsey (1962) pointed out:

> "Demonstration of V-shaped rather than simple direct or inverse relationships between meristic counts and temperature sometimes requires rearing at extremes close to the upper or lower temperature tolerances of the species. The inflection in the curve may not be discovered if a narrower range of temperatures is used."

Other environmental factors can also influence meristic counts: salinity, light intensity, oxygen and carbon dioxide tensions have all been studied and shown to affect the formation of parts, presumably by varying the rate of metabolism. Most of these vary with latitude and any one, or all of them might be the cause of a latitudinal cline. However, temperature is usually considered to be the most important. Notice that the northernmost samples do come from the areas with the lowest mean annual temperatures. The southern populations, on the other hand, have the highest mean annual temperatures.

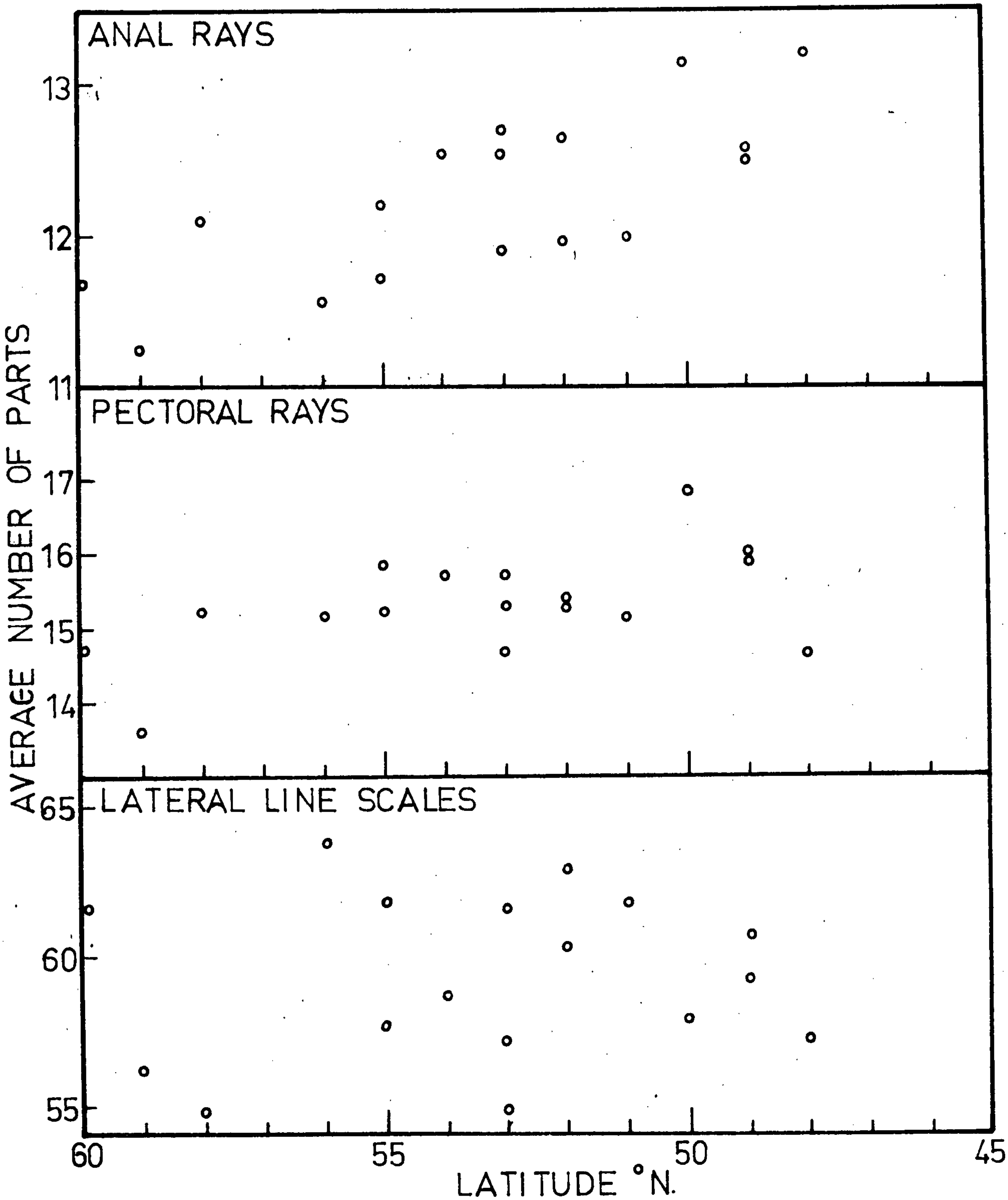


Figure 7. Latitudinal variation in anal rays, pectoral rays, and lateral line scales in *Prosopium coulteri*

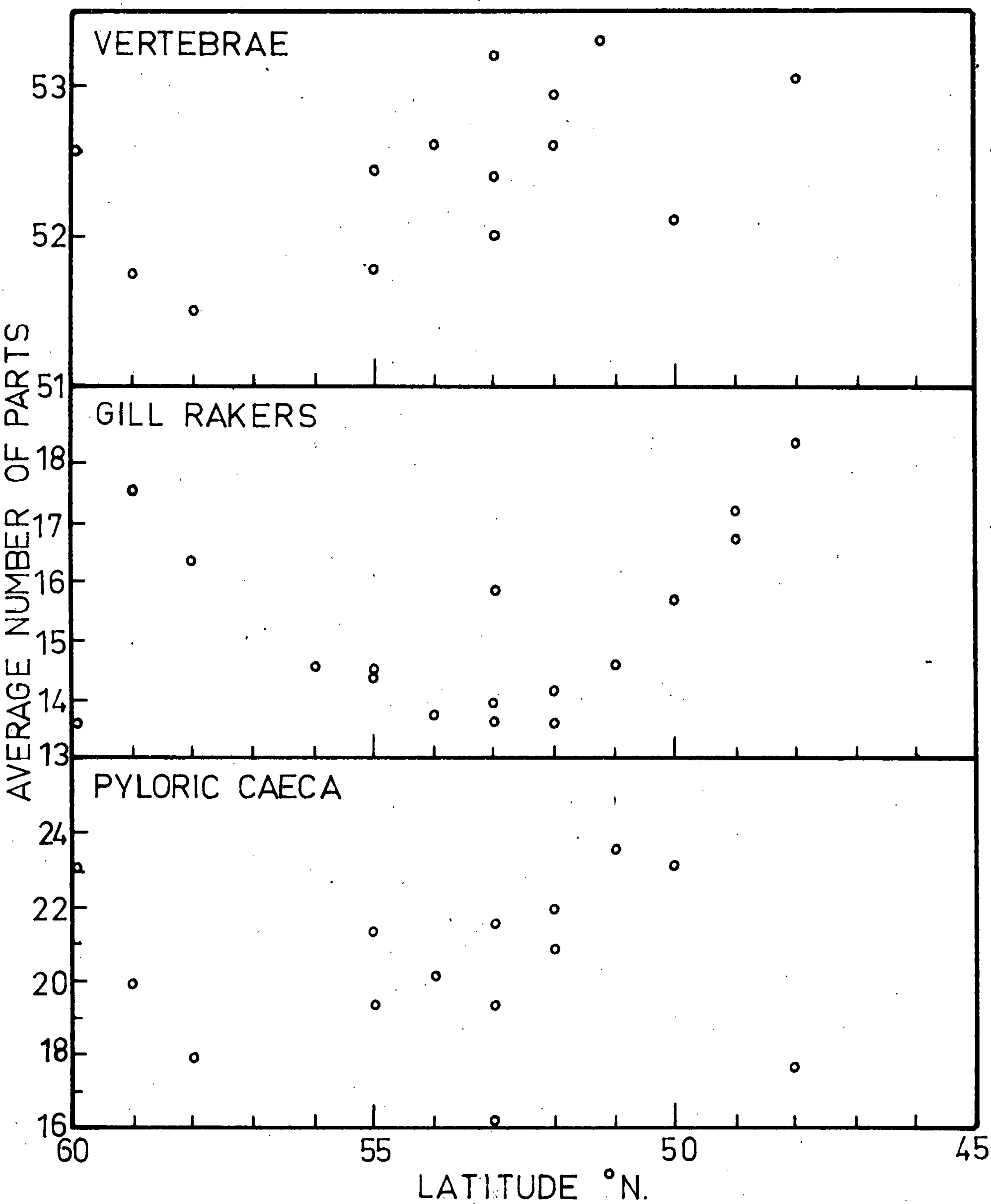


Figure 8. Latitudinal variation in vertebrae, gill rakers, and pyloric caeca in *Prosopium coulteri*

It is unlikely that in nature any one of these environmental factors approaches extreme limits and in most cases only one limb of the V is represented by geographical clines. In salmonids, the usual tendency is for parts to increase with increasing latitude, toward the colder end of the range. The opposite trend seems to be characteristic of most meristic series in the pygmy whitefish. The V-shaped relationship of gill rakers and latitude is exceptional. If this V-shaped curve is real, it may mean that gill raker numbers are more labile to environmental modification than other meristic characters in the pygmy whitefish. This is in contradiction to Svardson's (1950, 1952) opinion that, in whitefish, gill rakers are least modified by environmental influences. On the other hand, the gill raker counts may be largely genetically determined and not the direct result of differences in environment.

Svardson (1952) has demonstrated a relationship between body size meristic counts in Swedish whitefish. Comparing ninety-four populations of Coregonus he found that the number of scales along the body increased with the body size of the population and that whitefish populations with few gill rakers display, on an average, a better growth than populations with numerous gill rakers. On the basis of available data no such relationship can be shown for any meristic series in the pygmy whitefish. Although MacLure Lake pygmys, the fastest growing, have high counts, McLeese Lake fish, which have the second largest adult weight, have one of the lowest scale counts. Seven populations have lower gill raker counts than MacLure Lake fish, eleven have fewer gill rakers than McLeese Lake fish.

Age and Growth

Age and growth calculations were made for a total of 437 fish: 155 from Cluculz Lake; 144 from Tacheeda; 108 from MacLure; and 60 from McLeese. The fish were taken at irregular intervals from May to September, 1962. For most of the summer the smallest nets in use were one inch stretch measure. A half-inch net was available for only a short period in September. As a result, very few fish of a length less than 100 mm were taken and none smaller than 75 mm. Numerous attempts at beach seining of young were unsuccessful, probably because the young, like the adult fish, occupy waters too deep for the usual seining methods. The fish that were taken in gill nets extended, with the exception of thos taken from MacLure Lake, over a very narrow range. The size and age distribution of the sample is given in Tables 11 to 14.

The usual techniques of back-calculation require the use of a scale measurement which has a linear relationship to the length of the fish at all ages. Because young fish were absent from the gill net collections, there was no proof that linear regressions calculated for older fish applied equally to them. Fortunately, a series of seined collections of pygmy whitefish was available from Kinbasket Lake on the Columbia River. These fish ranged in size from 25 mm to 122 mm. Measurements were made of several scale dimensions illustrated in Figure 10.

Two of these measurements show an inflection when the fish has attained a length of about 100 mm. The inflection is

Table 11. Length distribution of age groups of Cluculz Lake <u>Prosopium coulteri</u>

Length interval (cm)	Age Group I		II		III		IV		V		VI	
	M	F	M	F	M	F	M	F	M	F	M	F
8.0 - 8.5	--	1	--	--	--	--	--	--	--	--	--	--
8.6 - 9.0	1	--	--	--	--	--	--	--	--	--	--	--
9.1 - 9.5	1	--	--	--	--	--	--	--	--	--	--	--
9.6 - 10.0	--	--	--	--	--	--	--	--	--	--	--	--
10.1 - 10.5	--	--	--	--	1	--	--	--	--	--	--	--
10.6 - 11.0	--	--	--	2	2	--	--	--	--	--	--	--
11.1 - 11.5	--	--	2	--	7	10	2	3	1	--	--	--
11.6 - 12.0	--	--	--	1	6	17	2	3	1	--	--	--
12.1 - 12.5	--	--	--	--	4	20	5	15	2	--	--	--
12.6 - 13.0	--	--	--	--	--	8	1	12	1	1	--	--
13.1 - 13.5	--	--	--	--	--	1	--	12	--	--	--	--
13.6 - 14.0	--	--	--	--	--	--	--	2	--	2	--	--
14.1 - 14.5	--	--	--	--	--	--	--	--	--	1	--	--
14.6 - 15.0	--	--	--	--	--	--	--	--	--	--	--	--
15.1 - 15.5	--	--	--	--	--	--	--	1	--	2	--	1
15.6 - 16.0	--	--	--	--	--	--	--	--	--	--	--	1
Total Number	2	1	2	3	20	56	10	48	5	6	--	2
Average Length	9.2	8.1	11.3	11.0	11.6	12.1	11.6	12.7	12.2	14.2	--	15.6

Table 12. Length distribution of age groups of Tacheeda Lake <u>Prosopium coulteri</u>

Length Interval (cm)	Age Group I		II		III		IV		V		VI	
	M	F	M	F	M	F	M	F	M	F	M	F
7.0 -- 7.5	--	--	--	--	--	--	--	--	--	--	--	--
7.6 - 8.0	--	--	1	1	--	--	--	--	--	--	--	--
8.1 - 8.5	2	3	1	--	--	--	--	--	--	--	--	--
8.6 -- 9.0	--	--	2	--	--	--	--	--	--	--	--	--
9.1 - 9.5	--	--	1	--	--	--	--	--	--	--	--	--
9.6 - 10.0	--	--	1	1	--	--	--	--	--	--	--	--
10.1 - 10.5	--	--	--	2	1	2	--	--	--	--	--	--
10.6 - 11.0	--	--	1	9	1	7	--	1	--	--	--	--
11.1 - 11.5	--	--	--	2	1	19	--	7	--	--	--	--
11.6 - 12.0	--	--	--	--	--	15	--	6	--	--	--	--
12.1 - 12.5	--	--	--	--	--	2	--	15	--	2	--	--
12.6 - 13.0	--	--	--	--	--	--	--	2	--	4	--	--
13.1 - 13.5	--	--	--	--	--	--	--	--	--	1	--	--
13.6 - 14.0	--	--	--	--	--	--	--	--	--	--	--	1
Total Number	2	3	7	15	3	45	0	31	0	7	0	1
Average Length	8.2	8.4	9.0	10.6	10.8	11.4	--	12.0	--	12.6	--	13.6

Table 13. Length distribution of age groups of MacLure Lake *Prosopium coulteri*

Length (cm)	Age Group																	
	I		II		III		IV		V		VI		VII		VIII		IX	
interval	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
10.0-11.0	--	--	12	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--
11.1-12.0	--	--	6	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--
12.1-13.0	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--
13.1-14.0	--	--	4	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--
14.1-15.0	--	--	6	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--
15.1-16.0	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
16.1-17.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
17.1-18.0	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--
18.1-19.0	--	--	--	--	3	1	2	--	1	--	--	--	--	--	--	--	--	--
19.1-20.0	--	--	--	--	1	4	1	1	--	--	--	--	--	--	--	--	--	--
20.1-21.0	--	--	--	--	--	2	1	--	--	--	1	--	--	--	--	--	--	--
21.1-22.0	--	--	--	--	--	--	7	4	--	--	--	--	--	--	--	--	--	--
22.1-23.0	--	--	--	--	--	--	2	1	--	1	2	--	--	--	--	--	--	--
23.1-24.0	--	--	--	--	--	--	--	3	--	1	1	2	--	--	--	--	--	--
24.1-25.0	--	--	--	--	--	--	--	--	--	5	--	3	--	--	--	--	--	--
25.1-26.0	--	--	--	--	--	--	--	--	--	3	--	4	--	2	--	--	--	--
26.1-27.0	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--
27.1-28.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1
Total Number		0	30	15	4	8	14	9	1	10	4	9	0	3	0	0	0	1
Ave Length	--	--	12.1	11.7	19.2	19.0	21.0	21.9	18.5	24.5	22.5	24.8	--	25.7	--	--	--	27.1

Table 14. Length distritubion of age groups of McLeese Lake *Prosopium coulteri*

Length (cm) interval	Age Group I M	F	II M	F	III M	F	IV M	F	V M	F
10.0-11.0	--	--	1	3	--	--	--	--	--	--
11.1-12.0	--	--	2	1	--	--	--	--	--	--
12.1-13.0	--	--	--	--	--	--	--	--	--	--
13.1-14.0	--	--	--	--	--	--	--	--	--	--
14.1-15.0	--	--	--	--	5	4	--	--	--	--
15.1-16.0	--	--	--	--	3	19	--	--	--	--
16.1-17.0	--	--	--	--	3	10	--	--	--	--
17.1-18.0	--	--	--	--	--	3	1	--	--	--
18.1-19.0	--	--	--	--	--	--	--	--	--	1
19.1-20.0	--	--	--	--	--	--	--	1	--	3
Total number	0	0	3	4	11	36	1	1	0	4
Ave Length	--	--	11.1	10.9	15.3	15.8	17.8	19.4	--	19.4

most marked in the antero-lateral ridge (Fig. 11), but is also present in measurements of the anterior radius of the scale (Fig. 12). The inflection in the anterior radius is more obvious if the measurements of Cluculz Lake fish, which are larger, are graphed along with those of the Kinbasket Lake samples (Fig. 13). The superposition of data in this fashion is subject to error as the scale size-body length relationships are probably not identical in the two populations, but in this case the error is probably small in relation to the magnitude of the inflection. The data can be interpreted as forming two lines: one line extends to about 100 mm and includes most of the Kinbasket Lake

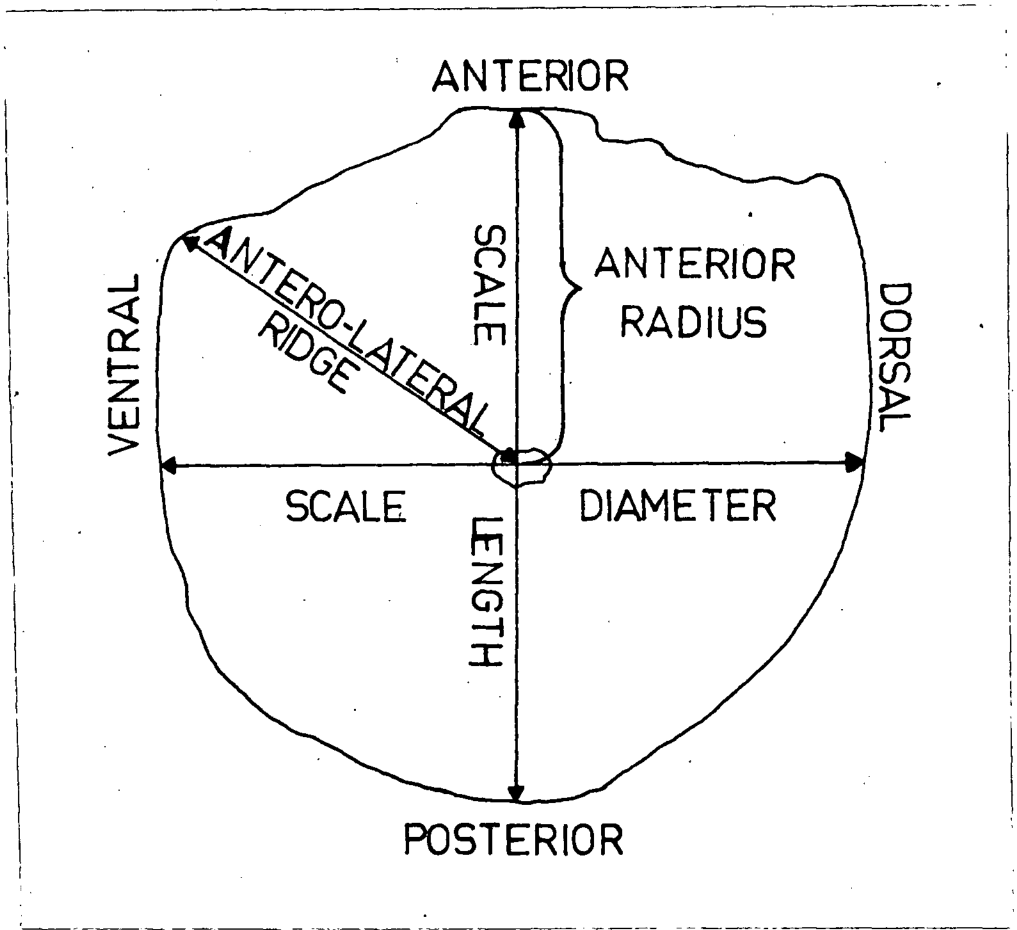
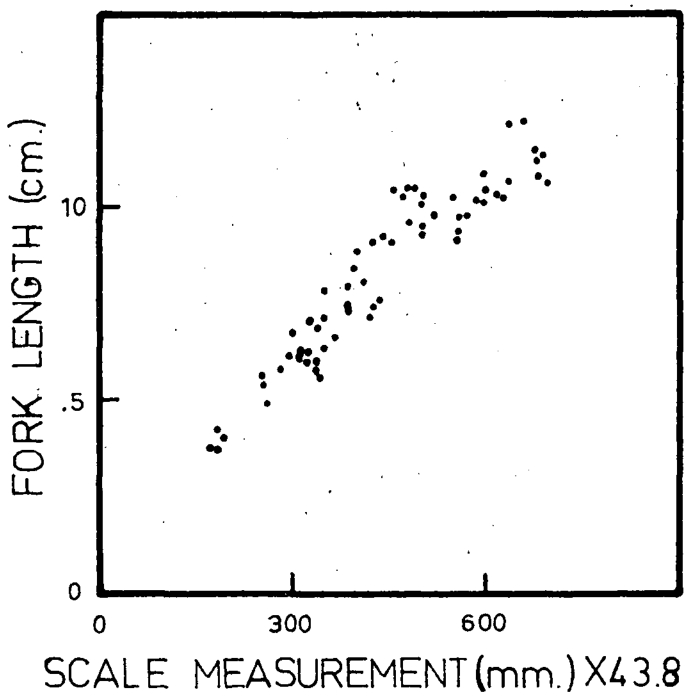


Figure 10. Diagram illustrating scale measurements used

fish and the smallest fish from Cluculz Lake; and the second line includes the majority of Cluculz fish and few largest Kinbasket Lake fish. Obviously, a regression line calculated for fish larger than 100 mm (most of the sample fish) would give an intercept for the scale size-body length relationship which would be far too high for smaller fish. For this reason, neither anterior radius nor antero-lateral ridge measurements were useful in the back-calculation of growth.

The inflection is probably due to changes in relative growth coincident with the attainment of maturity. In both Cluculz and Kinbasket the fish spawn for the first time at the end of their third summer at a length of about 100 mm. As far as

Figure 11. Relation of antero-lateral ridge scale measurement to fork length in Kinbasket Lake fish



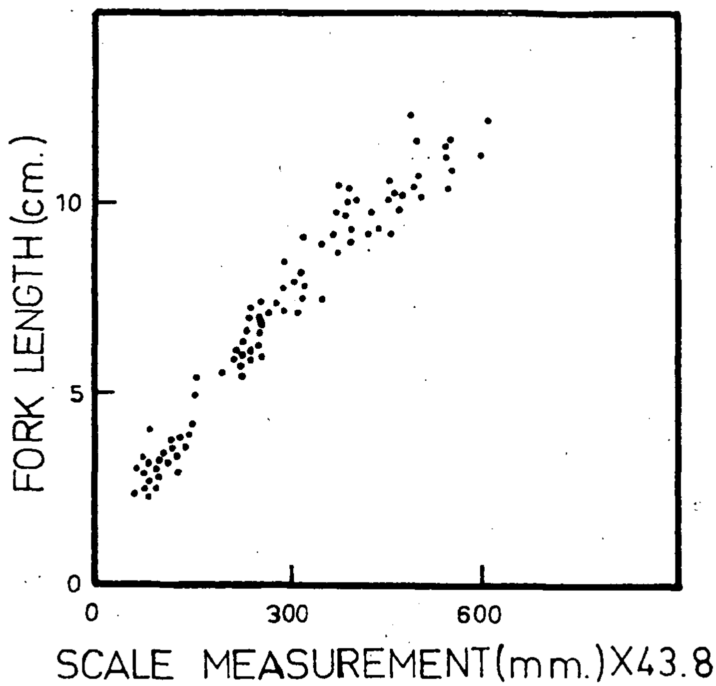


Figure 12. Relation of anterior radius scale measurement to fork length in Kinbasket Lake fish

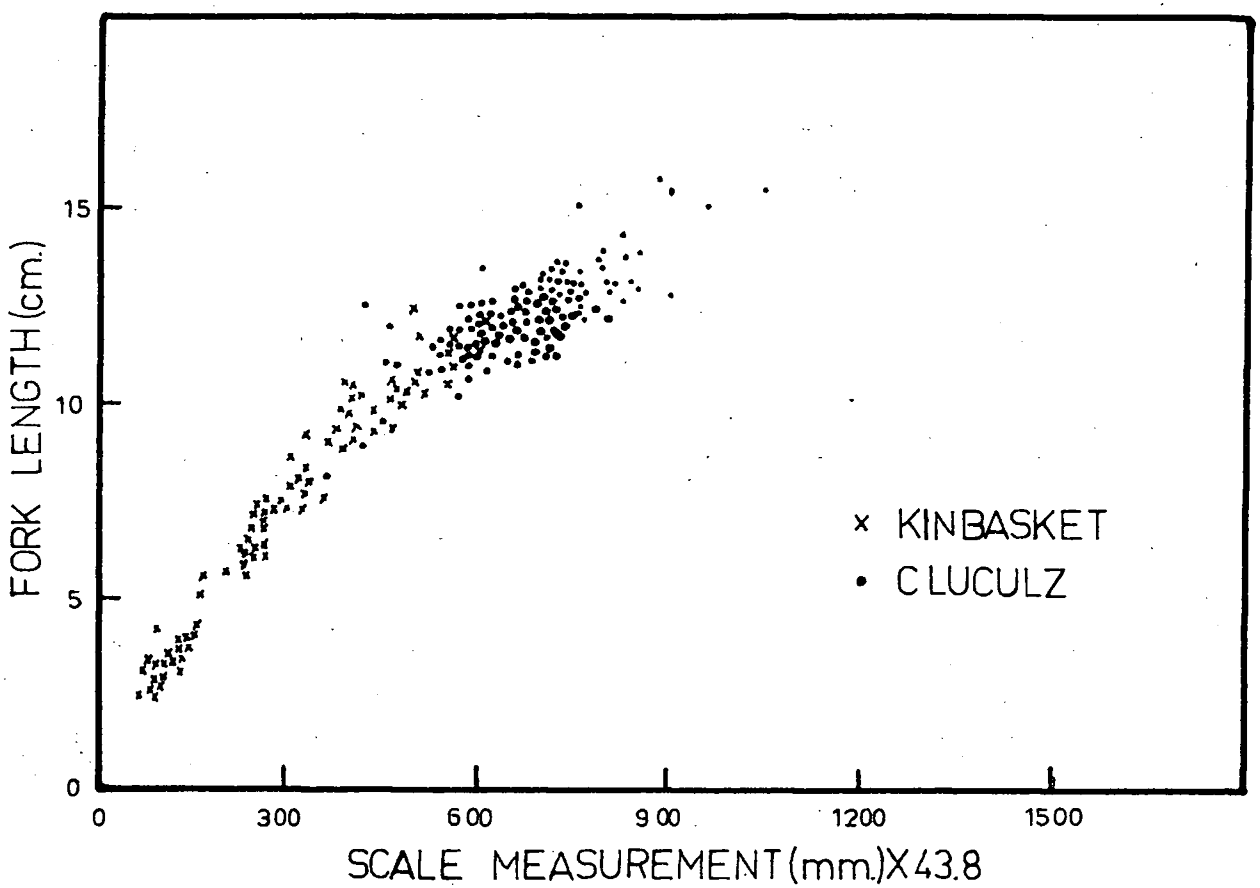


Figure 13. Relation of anterior radius scale measurement to fork length in Kinbasket Lake and Cluculz Lake fish

the author is aware, such inflections have not been previously described for whitefish.

Two other scale measurements, scale length and scale diameter, both showed a straight-line relationship to body length (Figs. 14, 1 5) for Kinbasket Lake. Difficulty in identifying annuli along the posterior margin in older fish precluded the use of scale length, and scale diameter was therefore chosen as the best measurements for the purpose of back-calculation. The scale diameter - fork length relationship is graphed for Tacheeda, Cluculz, McLeese and MacLure Lakes in Figures 16 to 19. In the first three lakes, the sample fish concentrated in a very small segment of the range over which growth occurred -- toward the upper limit. Linear regression of scale diameter against fork length resulted in an apparent intercept which, in each case, was felt to be far too high. Presumably this resulted from differences in intra-class and inter-class correlations. The preponderance of fish from a few year classes seems to have biased the result. The clusters of points do, however, appear to be very nearly in line with the calculated regression for Kinbasket Lake data which includes a considerable range of sizes. The relationships are probably not identical, but in the absence of further data, the intercept calculated for Kinbasket Lake was used in back-calculating the lengths of fish from the other three lakes. Because the MacLure Lake sample extended over a much broader length range, the calculated intercept is probably quite reliable and it was used in back-calculation for the fish from the lake.

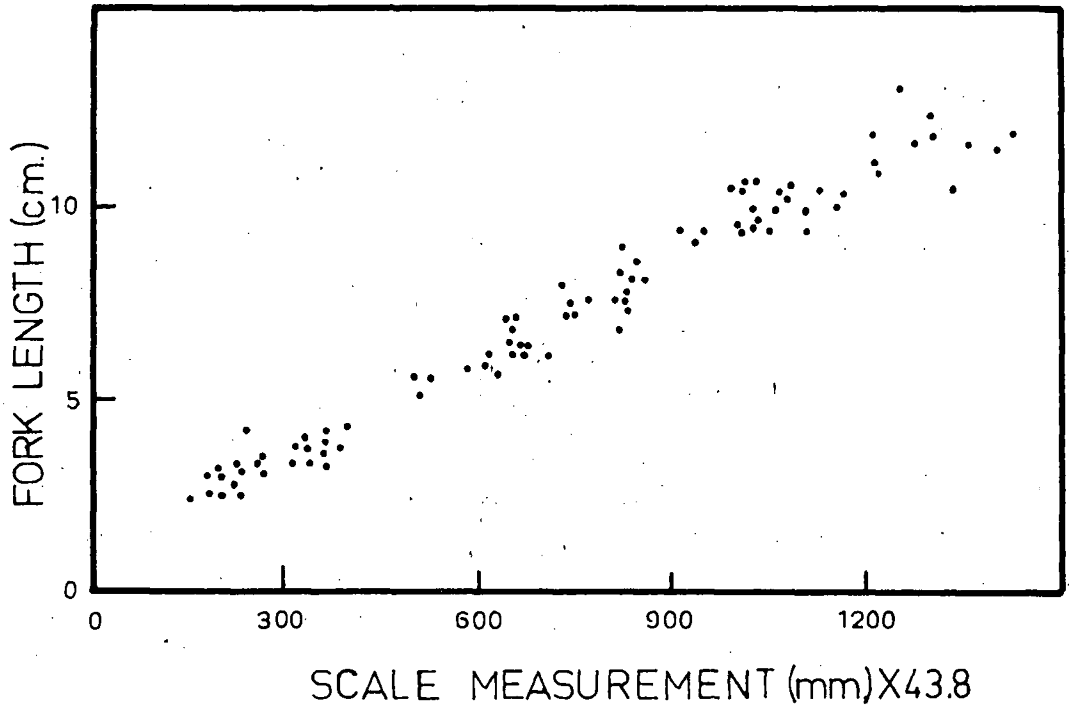


Figure 14. Relationship of scale length to fork length in Kinbasket Lake pygmy whitefish

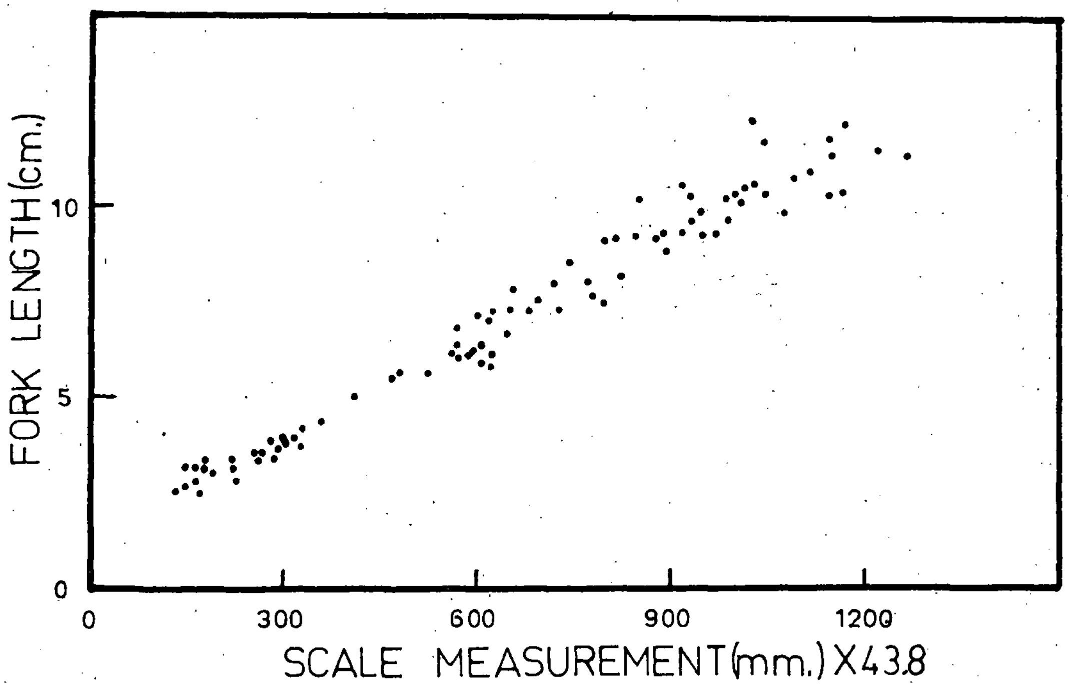


Figure 15. Relationship of scale diameter to fork length in Kinbasket Lake pygmy whitefish

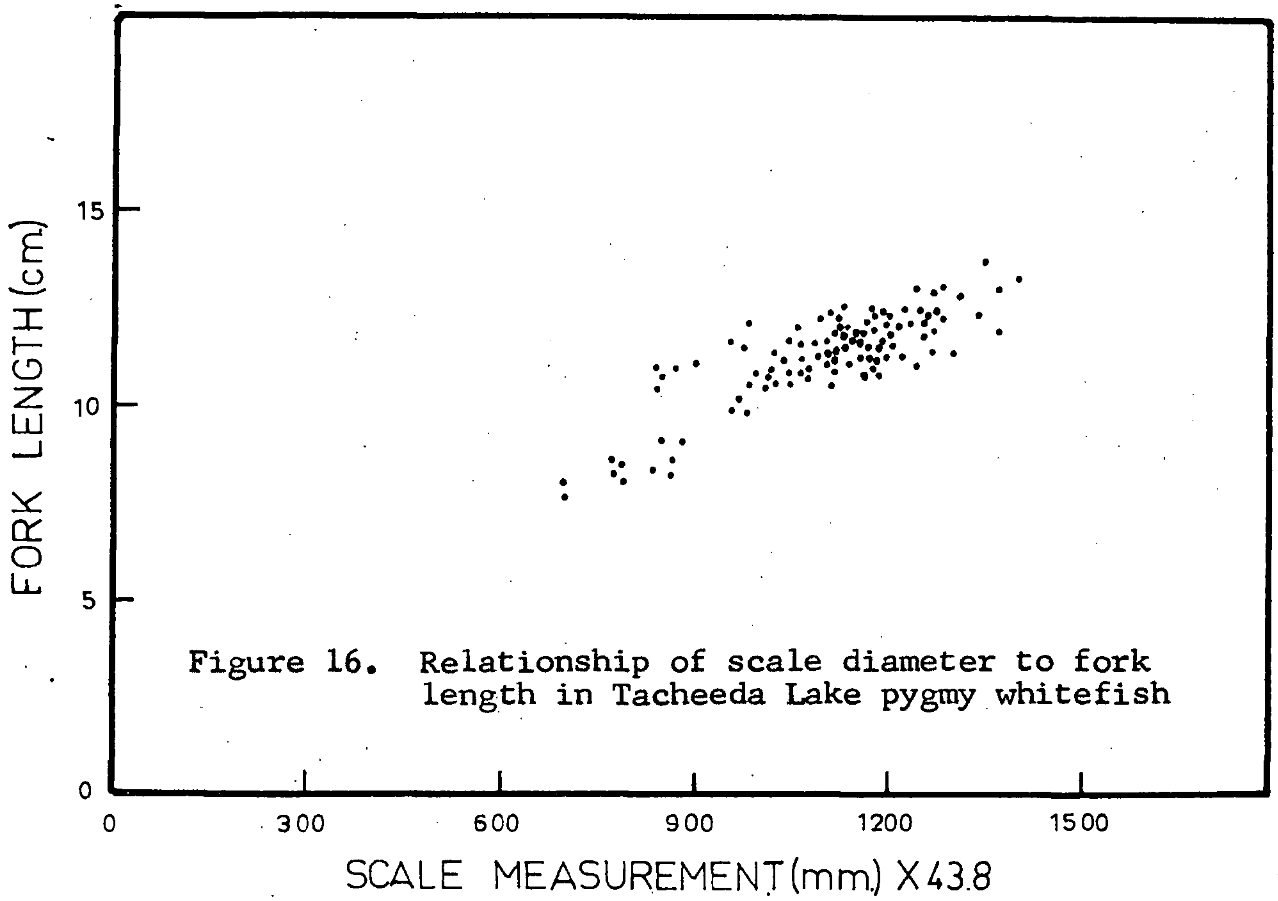


Figure 16. Relationship of scale diameter to fork length in Tacheeda Lake pygmy whitefish

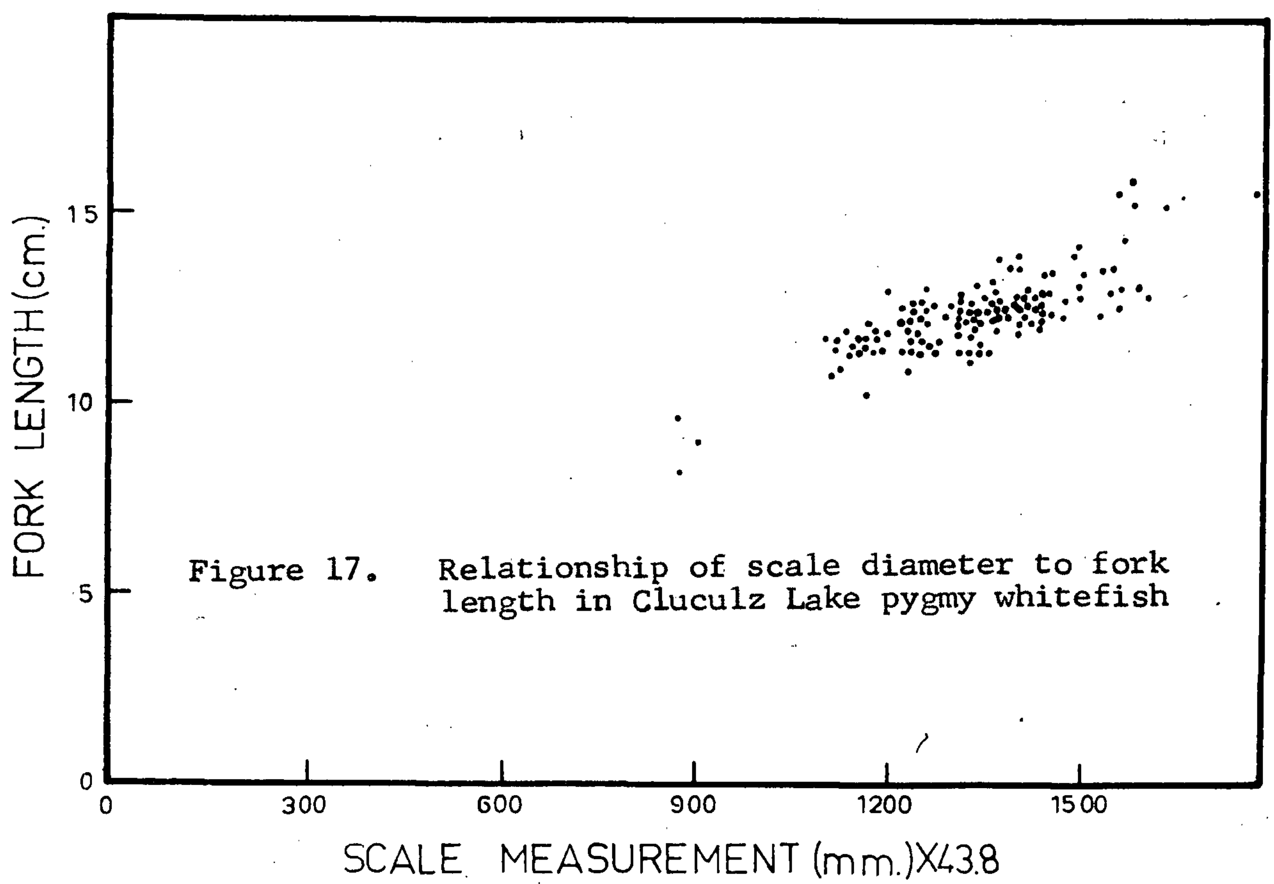


Figure 17. Relationship of scale diameter to fork length in Cluculz Lake pygmy whitefish

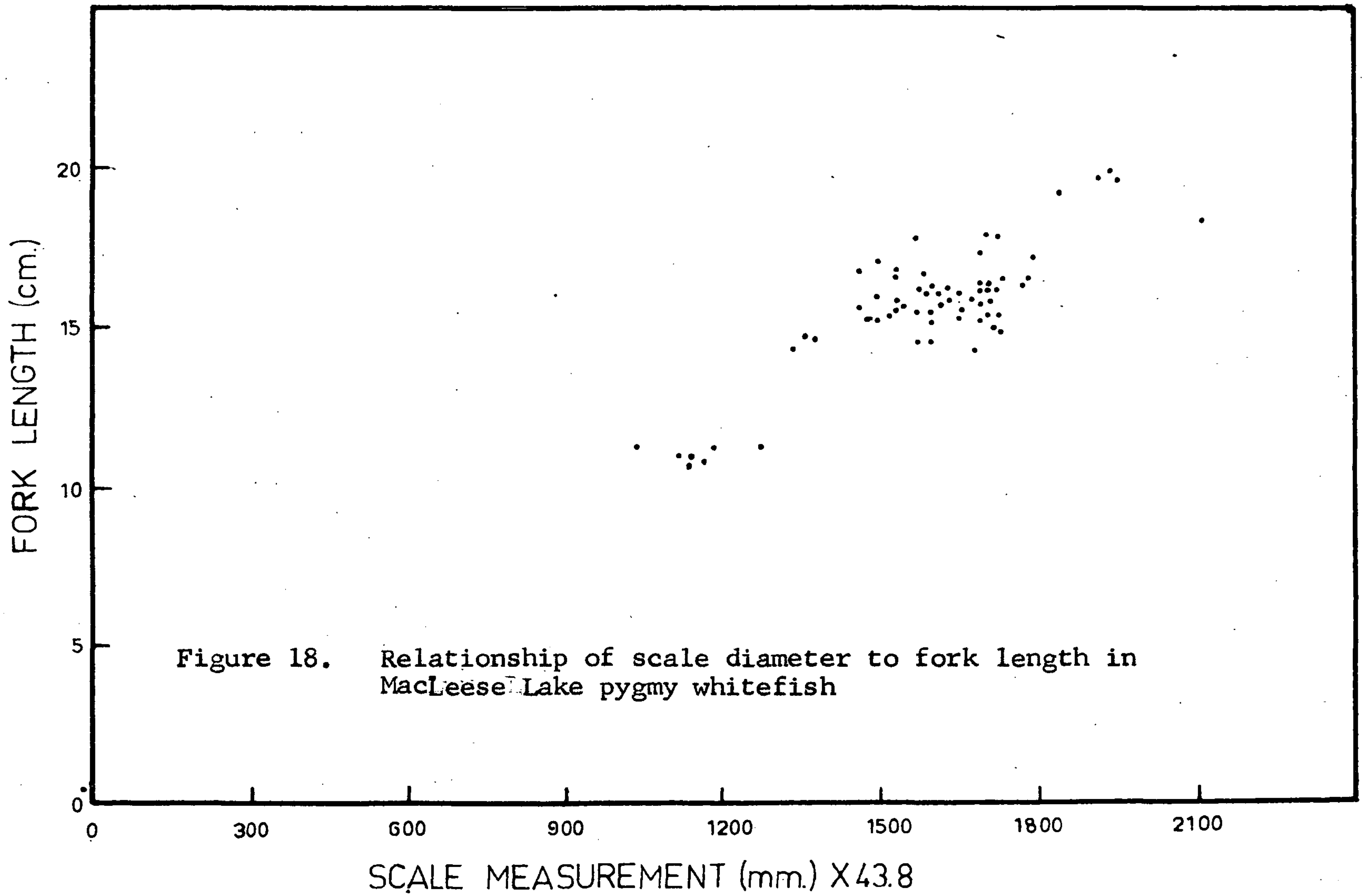


Figure 18. Relationship of scale diameter to fork length in MacLeese Lake pygmy whitefish

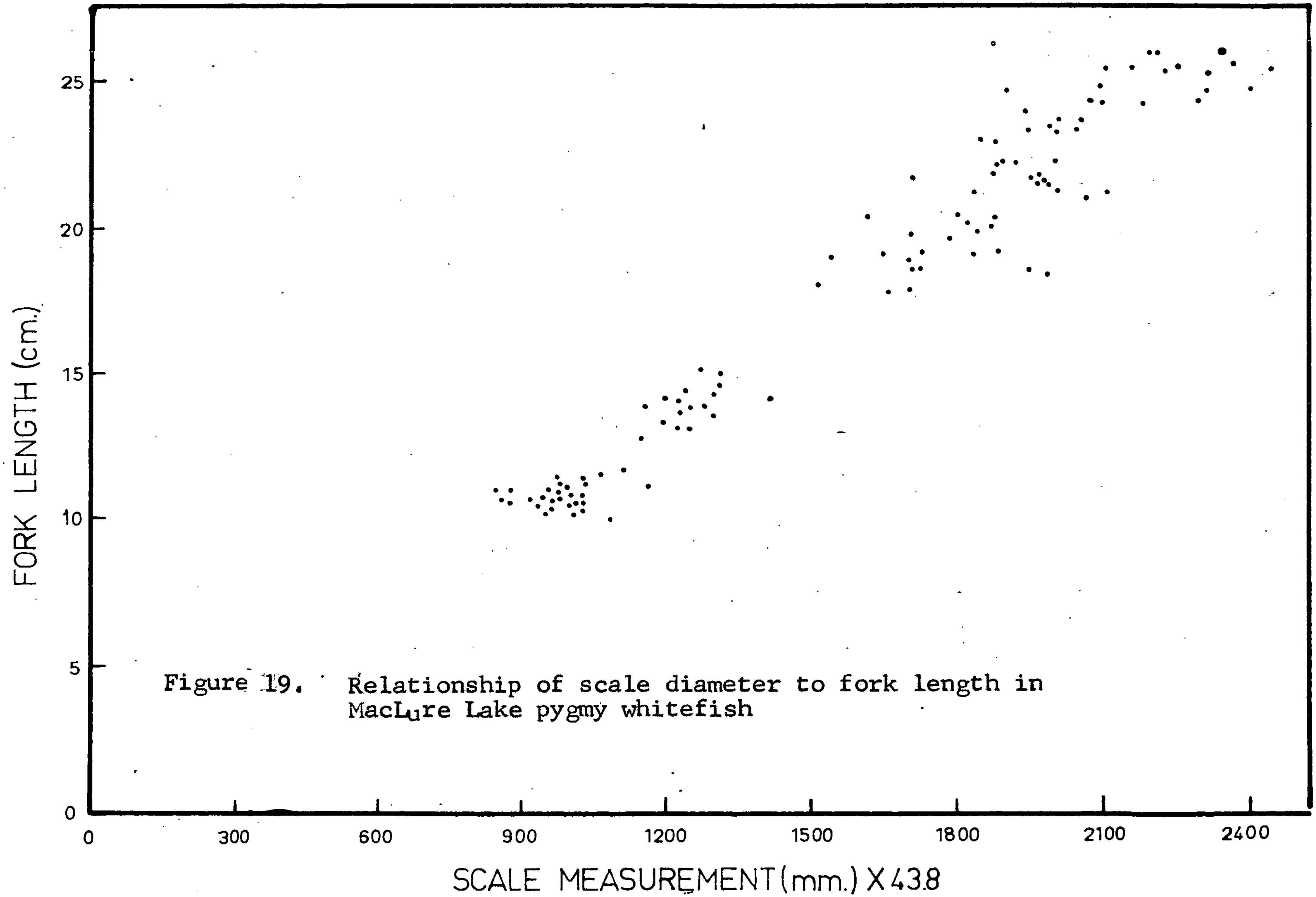


Figure 19. Relationship of scale diameter to fork length in MacLure Lake pygmy whitefish

Table 15. Calculated body-scale relationships for pygmy whitefish from five British Columbia lakes

	MacLure	McLeese	Cluculz	Tacheeda	Kinbasket
Slope of Regression Line	0.010990	0.008544	0.005624	0.006734	0.007972
Intercept of Regression Line	0.388788	2.004891	4.708823	3.788794	1.324125
Standard Error of Estimate	1.313413	1.075486	0.635308	0.637988	0.539005
Correlation	0.971181	0.854798	0.793345	0.838985	0.983139

Data relating to the body-scale relationship of pygmy whitefish from the five lakes is given in Table 15. The regression was machine-calculated from data obtained for every scale. Back-calculation was carried out according to the formula

$$L_n = I + \frac{L_t - I}{S_t} S_n \quad \text{or} \quad \frac{L_n - I}{L_t - I} = \frac{S_n}{S_t}$$

where L_n is the length of the fish at the end of the N^{tn} year of life, I is the intercept of the scale-body relationship, L_t is the length of the fish at capture, S_t is the diameter of the scale at the time of capture and S_n is the diameter of the scale within the N^{th} annulus. In practice the calculation was performed used a simple nomograph.

Eschmeyer and Bailey (1954) do not appear to have used an intercept in back-calculating the growth of pygmy whitefish in Lake Superior. They state that "Growth calculations were by direct proportion". (This in spite of the fact that specimens from lake Superior in the Institute of Fisheries Museum do appear to exhibit an intercept in the scale diameter - fork length relationship (Fig. 20)).

Van Oosten (1929) describes a typical coregonine scale. His description of the annulus was used as a guide in the location and measurement of year marks in the pygmy whitefish under study. No year round samples are available but during 1962 all fish showed evidence of new growth by the end of May, placing the termination of annulus formation somewhere at the end of April or early in May.

In general, annuli were not difficult to place. Exceptions were fishes of advanced age in which increments of growth were very small and annuli consequently very close together and fish from McLeese Lake where the annuli tended to be very indistinct especially early in life. This latter phenomenon may be related to the very rapid early growth of these fish. Any fish scale in which the position of the annuli was still questionable after three readings was discarded. Nevertheless without fish of known age for comparison, aging of fish by the scale method is at best only tentative. False annuli due to spawning stress or other growth checks may be indistinguishable from real ones.

The calculated lengths at various ages are given for the four lakes in Tables 16 to 19. Figures 21 to 24 present the average length at different ages for the males and females of each lake. In each population, male fish grow at about the same rate as females for the first two years of life. After this, there is an increasing disparity in the growth of the two sexes. Presumably this is related to the onset of sexual maturity which differentially affects the sexes. The difference in growth is probably even more pronounced than the figures indicate due to

Table 16. Calculated total length at end of each year of life of each age group and average growth for the combined age groups in Cluculz Lake

AGE GROUP	NUMBER OF FISH		LENGTH AT END OF YEAR					
			1	2	3	4	5	6
I	2	M	6.4	--	--	--	--	--
	1	F	5.3	--	--	--	--	--
II	2	M	5.5	9.6	--	--	--	--
	3	F	5.5	9.1	--	--	--	--
III	20	M	5.0	8.6	10.7	--	--	--
	56	F	5.3	8.9	11.2	--	--	--
IV	10	M	5.1	7.6	10.0	11.2	--	--
	48	F	5.0	8.1	10.6	12.1	--	--
V	5	M	4.7	8.0	9.9	11.0	11.8	--
	6	F	5.2	8.4	10.9	12.7	13.6	--
VI	0	M	--	--	--	--	--	--
	2	F	5.3	8.4	10.8	12.7	14.0	15.2
Grand average calculated length:								
		M	5.1	8.4	10.4	11.1	11.8	--
		F	5.2	8.6	10.9	12.2	13.7	15.2
Increment of average:								
		M	5.1	3.3	2.0	0.7	0.7	--
		F	5.2	3.4	2.3	1.3	1.5	1.5

Table 17. Calculated total length at end of each year of life of each age group and average growth for the combined age groups in Tacheeda Lake

AGE GROUP	NUMBER OF FISH		LENGTH AT END OF YEAR					
			1	2	3	4	5	6
I	2	M	5.8	--	--	--	--	--
	3	F	5.8	--	--	--	--	--
II	7	M	5.7	8.o	--	--	--	--
	15	F	6.1	8.9	--	--	--	--
III	3	M	6.4	8.6	10.0	--	--	--
	45	F	5.8	8.5	10.5	--	--	--
IV	0	M	--	--	--	--	--	--
	31	F	5.8	8.5	10.4	11.4	--	--
V	0	M	--	--	--	--	--	--
	7	F	5.7	7.9	10.2	11.5	12.4	--
VI	0	M	--	--	--	--	--	--
	1	F	6.2	8.4	10.8	11.1	12.1	13.4
Grand average calculated length:								
		M	5.9	8.2	10.0	--	--	--
		F	5.8	8.5	10.5	11.4	12.3	13.4
Increment of average:								
		M	5.9	2.3	1.8	--	--	--
		F	5.8	2.7	2.0	0.9	0.9	1.1

the selective effect of gill net sampling. In Tacheeda Lake, the extreme case, only twelve male fish were taken during the entire summer. There is no reason to suppose that the unequal sex ratio in the sample represents a real situation in the lake. Observations

Table 18. Calculated total length at end of each year of life of each age group and average growth for the combined age groups in MacLure Lake

AGE GROUP	NUMBER OF FISH		LENGTH AT END OF YEAR 1	2	3	4	5	6	7	8	9
I	0	M	--	--	--	--	--	--	--	--	--
	0	F	--	--	--	--	--	--	--	--	--
II	30	M	5.3	8.7	--	--	--	--	--	--	--
	15	F	5.4	8.7	--	--	--	--	--	--	--
III	4	M	4.9	9.5	13.3	--	--	--	--	--	--
		F	5.5	9.0	14.1	--	--	--	--	--	--
IV	14	M	5.2	8.9	14.3	18.8	--	--	--	--	--
	9	F	5.8	8.8	13.8	19.1	--	--	--	--	--
V	1	M	4.7	8.7	13.0	15.6	17.4	--	--	--	--
	10	F	5.5	8.9	15.2	19.9	22.8	--	--	--	--
VI	4	M	4.9	7.8	13.4	17.5	19.8	21.5	--	--	--
	9	F	5.0	8.4	13.5	18.1	20.6	23.2	--	--	--
VII	0	M	--	--	--	--	--	--	--	--	--
	3	F	6.1	8.5	15.0	20.4	22.4	23.9	25.0	--	--
VIII	0	M	--	--	--	--	--	--	--	--	--
	0	F	--	--	--	--	--	--	--	--	--
IX	0	M	--	--	--	--	--	--	--	--	--
	1	F	6.8	10.5	15.6	18.3	21.5	22.5	23.6	25.0	26.2
Grand average calculated length:											
		M	5.2	8.8	13.9	18.4	19.3	21.5	--	--	--
		F	5.5	8.8	14.3	19.2	21.8	23.3	24.6	25.0	26.2
Increment of average:											
		M	5.2	3.6	5.1	4.5	0.9	2.2	--	--	--
		F	5.5	3.3	5.5	4.9	2.6	1.5	1.3	0.4	1.2

Table 19. Calculated total length at end of each year of life of each age group and average growth for the combined age groups in McLeese Lake

AGE GROUP	NUMBER OF FISH		LENGTH AT END OF YEAR				
			1	2	3	4	5
I	0	M	--	--	--	--	--
	0	F	--	--	--	--	--
II	3	M	6.5	9.5	--	--	--
	4	F	7.1	9.5	--	--	--
III	11	M	7.3	11.2	14.6	--	--
	36	F	7.0	10.9	14.8	--	--
IV	1	M	6.6	9.7	13.7	16.7	--
	1	F	6.4	9.8	15.2	17.8	--
V	0	M	--	--	--	--	--
	4	F	6.7	9.5	13.1	16.8	18.5
Grand average calculated length:							
		M	7.1	10.8	14.5	16.7	--
		F	7.0	10.6	14.6	17.0	18.5
Increment of average:							
		M	7.1	3.7	3.7	2.2	--
		F	7.0	3.6	4.0	2.4	1.5

in MacLure Lake indicate that the sexes school together so that it is unlikely that the disporportionate number of females is the result of sampling in areas where females are more likely to be found. Probably, most of the males of any one year class never reach a sufficient size to become liable to capture by a one-inch gill net because of their lower growth rate and greater mortality

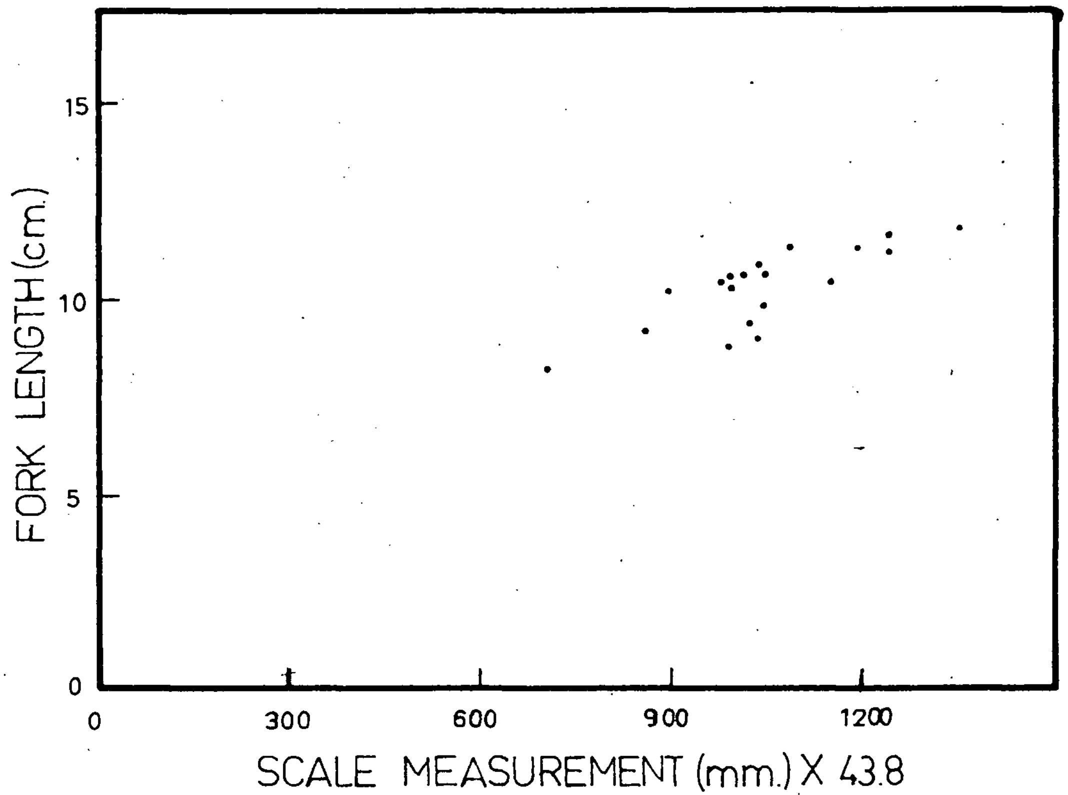


Figure 20. Relationship of scale diameter to fork length in Lake Superior pygmy whitefish

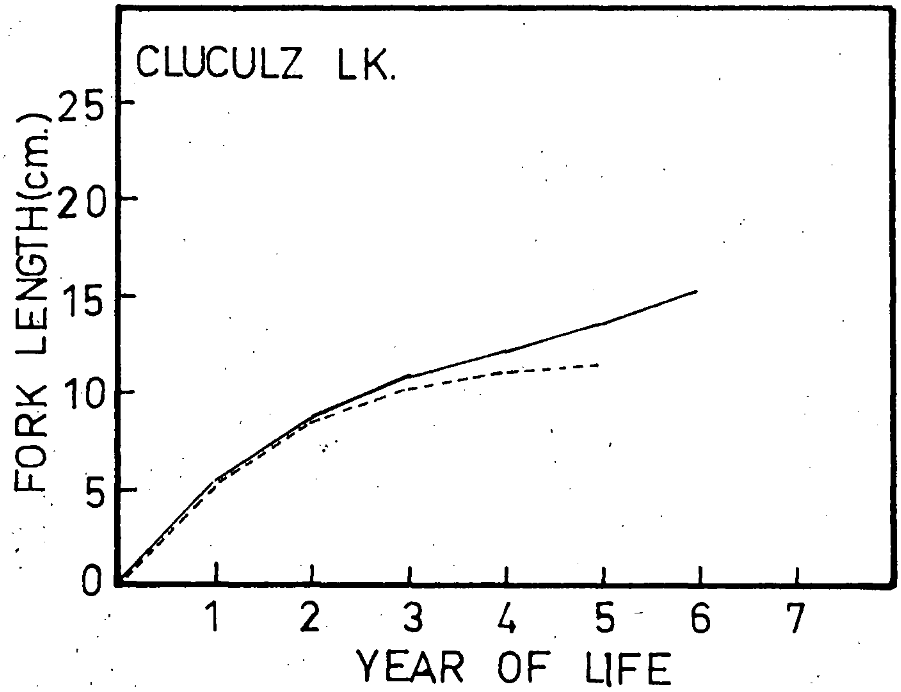


Figure 21. Calculated length at end of each year of growth for Cluculz Lake pygmy whitefish (solid line - females; broken line - males)

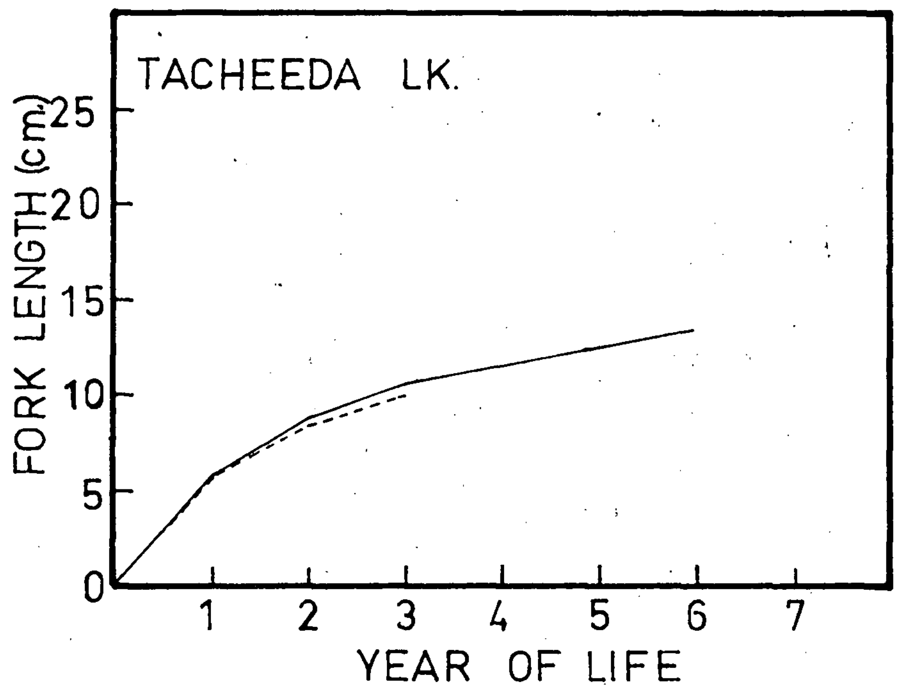


Figure 22. Calculated length at end of each year of growth for Tacheeda Lake pygmy whitefish (solid line - females; broken line - males)

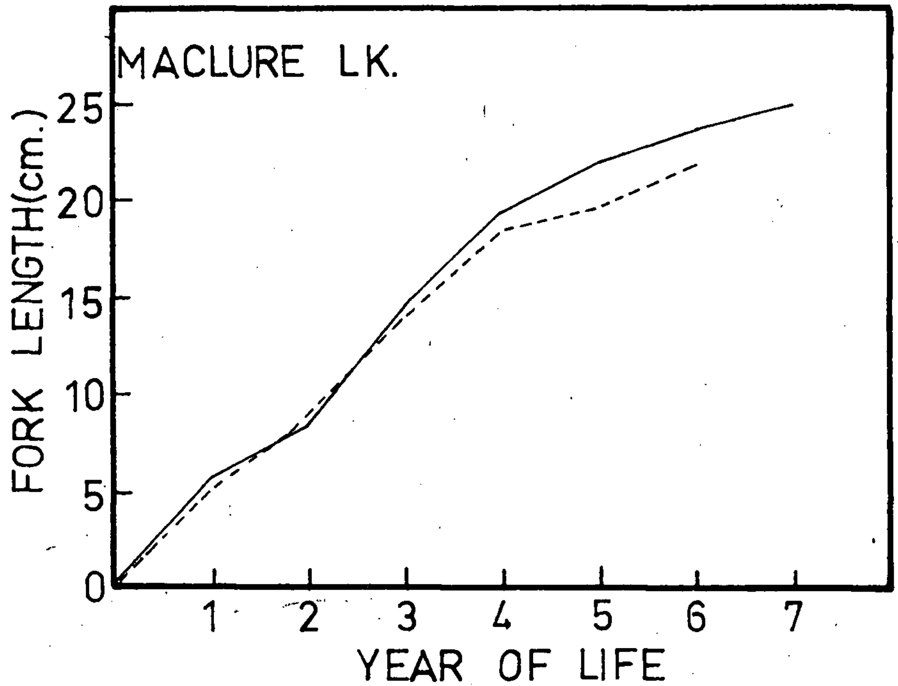


Figure 23. Calculated length at end of each year of growth for MacLure Lake pygmy whitefish (solid line - females; broken line - males)

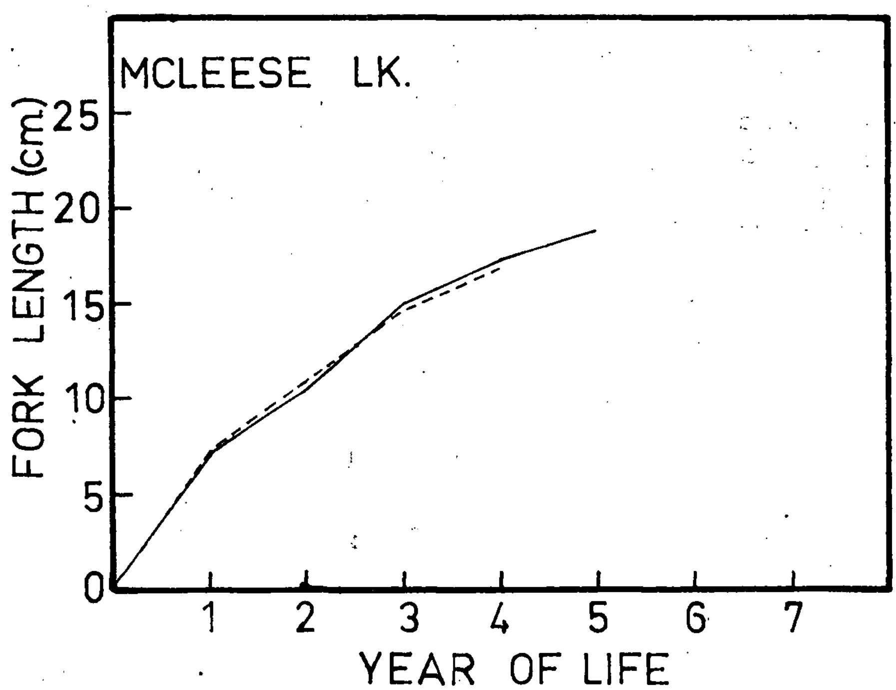


Figure 24. Calculated length at end of each year of growth for McLeese Lake pygmy whitefish

at young ages. Significantly, most of the males were taken during September at a time when they would be approaching their maximum seasonal growth and so coming to a size at which one-inch gill nets would be more effective. This was also the only time at which a half-inch net was used. Thus the one-inch net, the principle means of capture, crops only the faster growing or longer lived males and therefore presents a biased picture of male growth rates. In Tacheeda, which has the slowest growing pygmy whitefish in the four lakes, the female growth rates may be similarly biased as might the calculated growth rates for Cluculz Lake pygmys. By contrast, the fish in McLeese and MacLure Lakes were probably inadequately sampled by the available nets.

Because of the poor representation of males in some samples, comparison of growth in the four populations has been restricted to data for female fish. Table 20 presents data related to the growth in length of fish from four lakes. L_t and L_{t+1} are, respectively, the average length of fish at the beginning and end of each year of growth. The increment is the average increase in length during any year, in other words, $L_{t+1} - L_t$. The instantaneous annual growth rate (i) is defined as

$$\log_{10} L_{t+1} \text{ (in cms)} - \log_{10} L_t \text{ (in cms)}$$

The term, mean size, as used here is the mean size of the population at the midpoint of the growth period if the animals are growing logarithmically. It was calculated as

Table 20. Mean fork length in centimeters and instantaneous annual growth rates of pygmy whitefish in four British Columbia lakes

	I	II	III	IV	V	VI
MacLure:						
L_t	5.4	8.7	14.3	19.2	21.8	23.2
L_{t+1}	8.7	14.3	19.2	21.8	23.3	24.6
Increment						
Mean Size	6.85	11.15	16.60	20.45	22.52	23.94
i	.20713	.21582	.12796	.05516	.02890	.02358
McLeese:						
L_t	7.0	10.6	14.6	17.0		
L_{t+1}	10.6	14.6	17.0	18.5		
Mean Size	8.61	12.44	15.75	17.73		
i	.18021	.13904	.06610	.03672		
Cluculz:						
L_t	5.2	8.6	10.9	12.2	13.7	
L_{t+1}	8.6	10.9	12.2	13.7	15.2	
Mean Size	6.69	9.68	11.53	12.93	14.43	
i	.21850	.10293	.04893	.05036	.04512	
Tacheeda:						
L_t	5.8	8.5	10.5	11.4	12.3	
L_{t+1}	8.5	10.5	11.4	12.3	13.4	
Mean Size	7.02	9.45	10.9	11.84	12.84	
i	.16599	.09177	.03571	.03301	.03719	

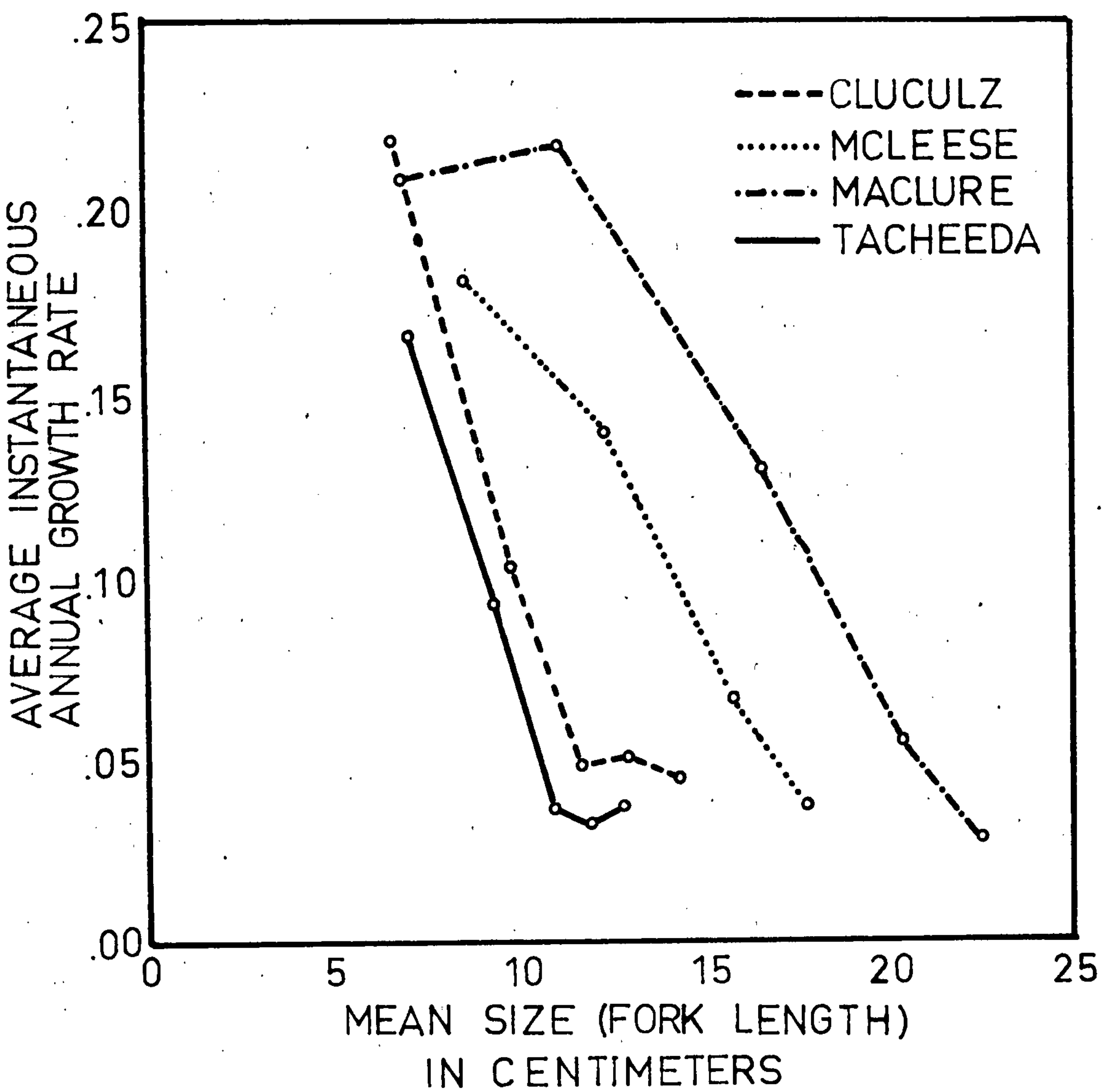


Figure 25. Plot of instantaneous growth rate against specified size for pygmy whitefish in four British Columbia Lakes

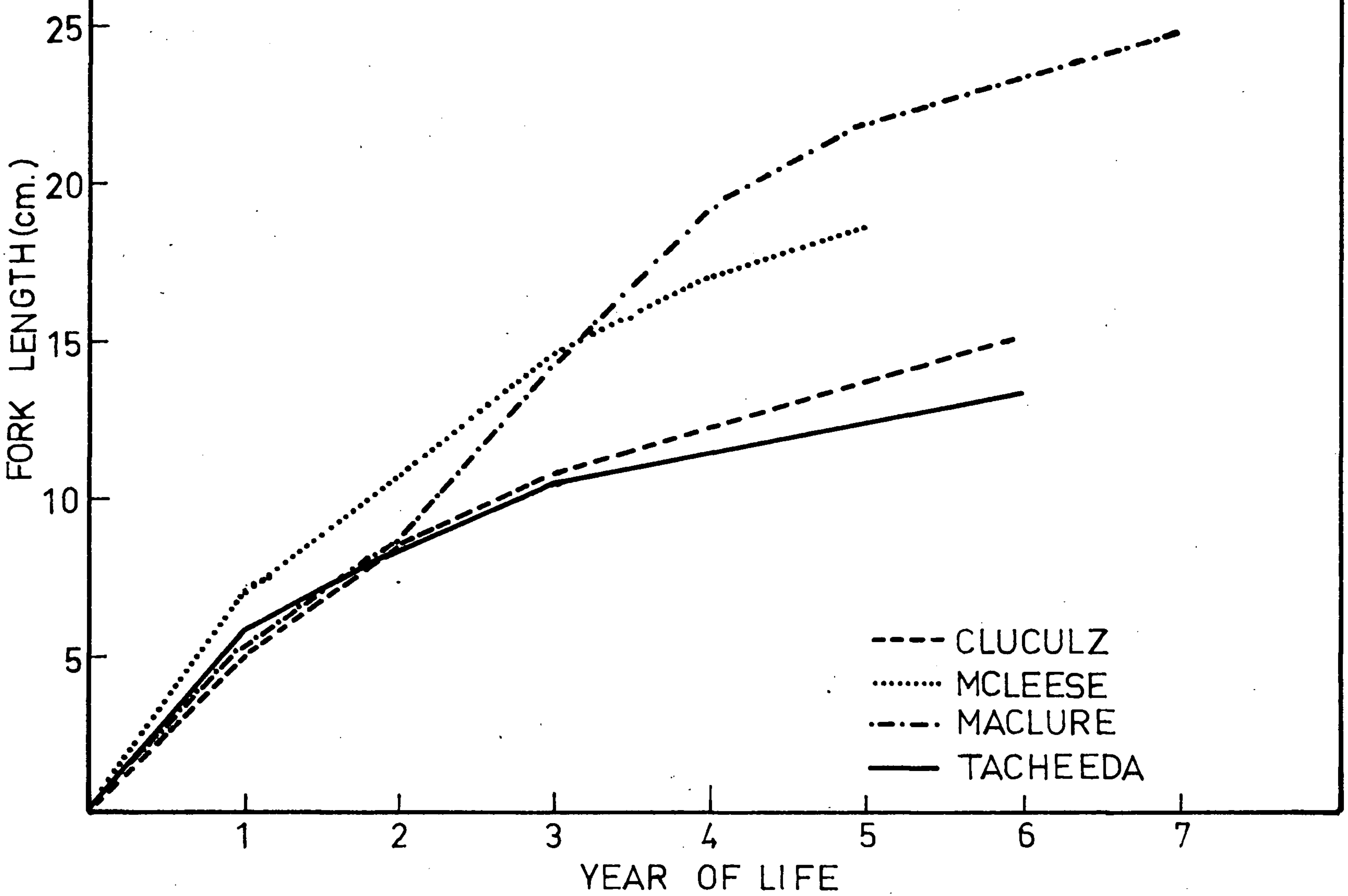
$$\text{antilog}\left(\frac{\log_{10} L_{t+1} + \log L_t}{2}\right)$$

Larkin et al. (1957), comparing the growth of different populations of rainbow trout, state that "...it is desirable to dispense with age as a criterion of growth rate and to restrict comparisons to growth rates of fish of the same size, i.e. plot instantaneous growth rate against specified size." This has been done in Figure 25.

Most fishes attain their highest rate of growth during their first year of life and thereafter the rate of growth undergoes a rapid decline. The graph shows that the expected decline takes place in all four lakes. In Tacheeda Lake, which has the slowest growth rates for fish of comparable size, the decline is very rapid at first, but it seems to be stabilized at about .035 for lengths above 11 cm. Samples of older fish are small, however, and may not be representative. Cluculz Lake fish are growing at a very high rate early in year I, but the rate of growth declines as rapidly as that of Tacheeda fish. The growth of larger fish is also similar in kind to that of the Tacheeda population. Fish above 11.5 cm in length appear to grow at a stable rate of .045 to .050.

McLeese Lake fish show a decreasing rate of growth with increasing size, but the decline is much less precipitous than that in Tacheeda or Cluculz Lake. As a consequence, moderately high growth rates are maintained over a wide range of sizes.

Figure 26. Calculated length at end of each year of growth for female pygmy whitefish in four British Columbia lakes



The MacLure Lake population is exceptional in that during their second year the instantaneous growth rate is increasing and this acceleration continues until the fish have reached a length of over 11 cm, when the inevitable decline sets in. The rate of decline is moderate like that of McLeese Lake pygmys. In Salmo gairdneri, such irregularities in the decline of growth rate with age have been attributed to changes in niche which are a function of size, specifically, a change from plankton-feeding to piscivorous habits (Larkin et al., 1957). Conceivably, the exceptional increase in the growth rate of MacLure Lake pygmy whitefish results from the attainment of some size threshold which makes available to them some hitherto unavailable environmental resource. It is not known what this might be.

Figure 26 compares the lengths of female fish in the four populations at various ages. At the end of the first year of growth, McLeese Lake fish have an average length which is 1.0 to 1.8 cm greater than that of same-age fish in the other three lakes. Instantaneous growth rates for year 0 have not been computed because the initial size of the fish is unknown but the large size of McLeese Lake fish at the formation of the first annulus is undoubtedly the result of a higher growth rate. The size difference is even greater at the end of year I, but only because of the larger initial size of McLeese fish. The growth rate is actually higher in both Cluculz and MacLure Lakes. During their third summer the growth rate of the Cluculz Lake population undergoes the precipitous decline already described, but that of MacLure fish actually increases so that at the formation of the third annulus they are only slightly smaller than those from McLeese. In subsequent years, the MacLure population maintains its growth advantage and the fish are larger than McLeese pygmy whitefish at every age. Similarly, although Tacheeda Lake whitefish are larger than either the MacLure or Cluculz at the end of their first years, their growth rates decline more drastically than any, and in the following years they are always the smallest of the four.

Age at Maturity

Table 21 presents data relating to age at maturity for fish from the four study lakes.

The determinations of state of maturity were made on fish taken four to eight months prior to spawning, so that the data, especially for male fish, may be somewhat in error. In most cases the fish are mature by the end of their third summer (age group II). The exceptions are MacLure Lake where the fish of both sexes are not 100 per cent mature until age group IV and Tacheeda Lake where males are not all mature until age III. In Lake Superior (Eschmeyer and Bailey, 1954) all age group II males were mature but females, like MacLure Lake pygmy whitefish, matured more slowly. In age group II, only twenty per cent were mature and not until age IV were 100 per cent mature. Weisel and Dillon (1954) found numerous age I fish spawning in Bull Lake, Montana. These fish have an extremely rapid growth during their first two years of life and the early age of maturation may reflect this.

In most localities pygmy whitefish spawn sometime during November or December (Eschmeyer and Bailey, 1954) although Kendall (1921) did find an Alaskan population spawning as early as August.

Table 21. Age at maturity of pygmy whitefish in four British Columbia lakes

AGE GROUP	NO. MALES	% MATURE	NO. FEMALES	% MATURE
MacLure				
I	0	0	0	0
II	30	20	15	0
III	4	50	8	75
IV	14	100	9	100
McLeese				
I	0	0	0	0
II	3	100	4	100
III	11	100	35	100
IV	1	100	1	100
Cluculz				
I	2	0	1	0
II	2	100	3	100
III	21	100	56	100
IV	8	100	46	96
Tacheeda				
I	2	0	3	0
II	6	66	17	100
III	3	100	46	100
IV	0	0	31	100

Indications are that the four populations under study spawn, like the majority, in November or December. An exceptional female, five years of age and 12.3 cm in length, collected in Cluculz Lake on July 15, 1962 appeared to be ripe and released eggs freely when squeezed. No other fish in similar condition were collected even as late as September 20, 1962. At the moment, it seems best to regard this fish as physiologically atypical.

Both male and female pygmy whitefish have nuptial tubercles at spawning time (Weisel & Dillon, 1954). These are most pronounced in male fish. Several male fish collected during May in Cluculz Lake still possessed unresorbed tubercules, but these were not apparent later in the summer. New tubercles had not yet formed by mid-September.

Length-Weight Relationship

Figure 27 presents the length-weight relationship of preserved pygmy whitefish from MacLure Lake. The points represent a sample selected to provide a fairly even distribution of sizes. The line has been fitted by eye. Data for fish from the other three lakes appear to fall very nearly on the same line.

Relative growth

Marr (1955) pointed out that the use of body dimensions expressed as *per cent* or *per mille* of standard length could lead to confusing and doubtful conclusions. He recommended instead the wider use of regression analysis of the original data as a tool in the interpretation of a relative growth. In the present study, a series of twelve measurements was made on fish from four lakes (fifty fish each from Tacheeda and McLeese, and fifty-one fish each from Cluculz and MacLure). *Per mille* ratios of body parts to standard length were used only to determine whether there was a significant difference in the length of fins between males and females. Eschmeyer and Bailey (1954) report that Lake Superior males have larger fins than females, but a series of t-tests failed to show any significant sexual dimorphism in the four British Columbia populations. Consequently, the data for the two sexes have been combined.

The data were converted to natural logs and a linear regression of size of body part against standard length was carried out. The results then subjected to an analysis of co-variance. These are summarized in Table 22. With the exception of head length, interorbital width, and a length of orbit, there is no significant difference in the slope of relative growth lines for the four lakes. The adjusted means are, however, significantly different in every case.(The tabled F value is 2.65 at the .05 level, and 3.88 at the .01 level of significance.)

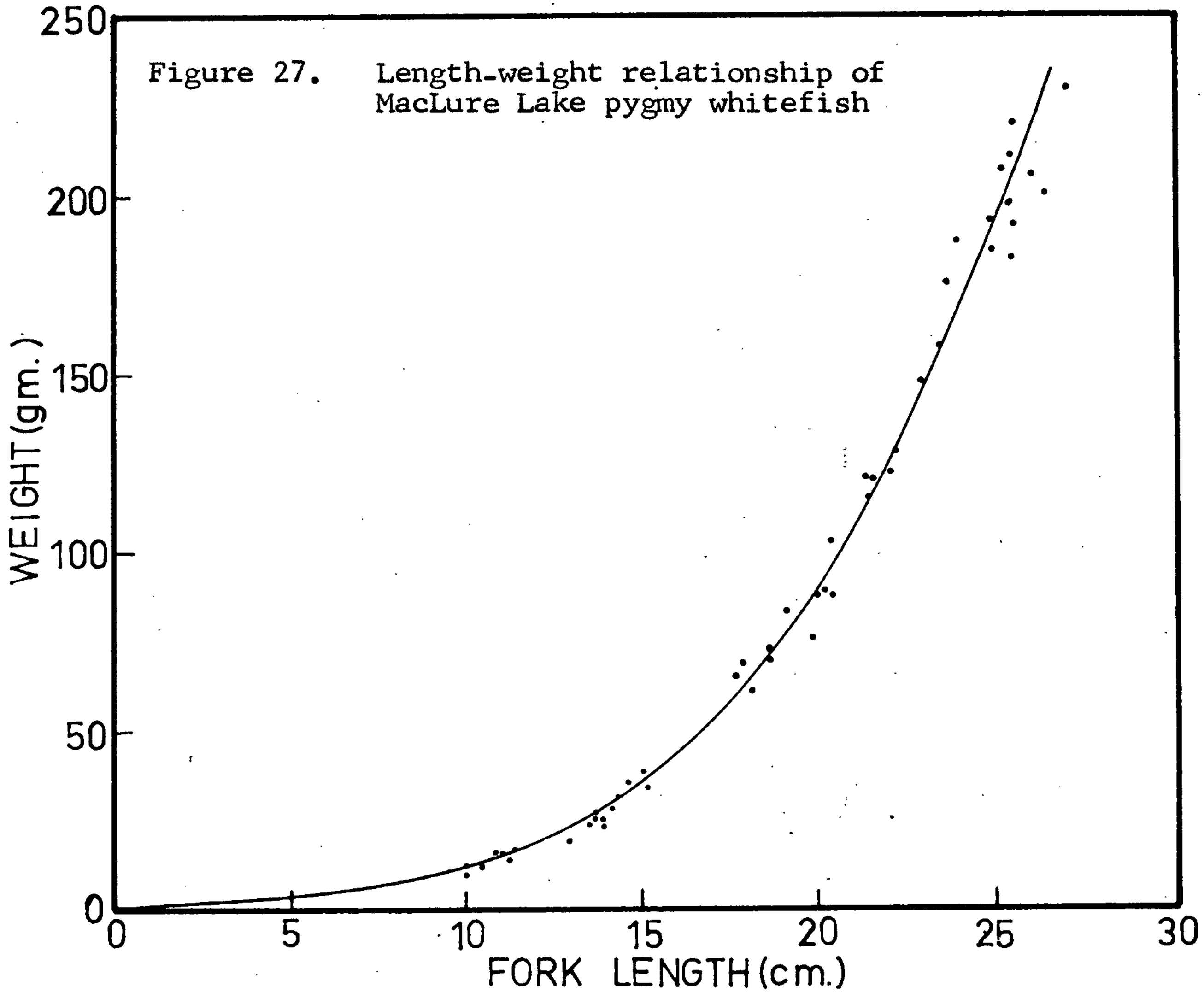


Figure 27. Length-weight relationship of MacLure Lake pygmy whitefish

The meaning of these differences in relative growth is best appreciated from a study of the graphs (Figs. 28 to 39) which relate the common logarithm of various body parts to the common logarithm of standard length. In most cases a distinction can be made between the relative growth of the dwarf Cluculz and Tacheeda fish and that of the larger fish from MacLure and McLeese. The dwarf forms have larger eyes, larger heads, longer maxillaries, shallower bodies, and a narrower interorbital width. In addition, they have proportionately longer paired and median fins. The anal fin, though longer in the dwarf forms, has a narrower base than that of the larger fish. The width of the anal base does not appear to be related to the number of anal rays. The length of the dorsal base may, however, be influenced in this way. The Cluculz and McLeese Lake populations which have the largest number of fin elements also have the broadest fin bases. The predorsal length of the four populations of Tacheeda and Cluculz Lakes have, respectively, the longest and shortest predorsal measurements.

Similar relationships between rate of growth and relative size of body parts have been noted in other whitefishes. Svardson (1950) in a series of transfer experiments involving two species of whitefishes found that in each case the slower growing population had larger heads, shallower bodies, larger eyes and long maxillaries. Koelz (1929) showed that slow growing *Coregonus clupeaformis* raised in the New York Aquarium had larger heads, eyes, snouts and paired fins than the faster growing parent stock in Lake Erie.

Table 22. Data relating measurements of various body parts to standard length for four British Columbia lakes

LAKE	BD	PDL	LDB	LBB	HD	HA	LP	LV	HL	IOW	LO	LUJ
	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	X_{12}
Tacheeda Lake												
Slope	1.148	0.999	0.958	1.135	0.990	1.148	1.103	1.053	1.041	0.987	0.933	0.874
Intercept	-1.991	-0.808	-2.084	-2.610	-1.567	-2.048	-1.881	-1.883	-1.510	-2.744	-2.436	-2.422
Correlation	0.976	0.991	0.895	0.926	0.958	0.955	0.967	0.975	0.970	0.937	0.903	0.917
SE	0.039	0.020	0.074	0.071	0.046	0.055	0.045	0.037	0.040	0.057	0.069	0.059
Cluculz Lake												
Slope	1.091	0.965	0.927	0.838	0.047	1.090	1.039	0.945	0.909	0.915	0.754	0.722
Intercept	-1.857	-0.752	-1.937	-1.830	-1.429	-1.898	-1.702	-1.610	-1.263	-2.564	-2.007	-2.063
Correlation	0.933	0.980	0.906	0.817	0.943	0.943	0.935	0.921	0.954	0.881	0.899	0.814
SE	0.051	0.024	0.052	0.072	0.040	0.047	0.048	0.048	0.035	0.060	0.045	0.063
McLeese Lake												
Slope	1.102	1.018	1.028	1.023	0.937	1.049	1.036	0.991	0.996	1.136	0.795	0.844
Intercept	-1.834	-0.852	-2.161	-2.255	-1.451	-1.881	-1.783	-1.787	-1.466	-2.996	-2.218	-2.392
Correlation	0.982	0.994	0.964	0.960	0.970	0.973	0.973	0.969	0.988	0.968	0.958	0.934
SE	0.035	0.019	0.047	0.940	0.039	0.041	0.040	0.041	0.026	0.048	0.039	0.053
MacLure Lake												
Slope	1.118	1.012	0.975	1.028	0.948	1.069	1.036	0.981	0.913	1.060	0.722	0.816
Intercept	-1.872	-0.855	-2.062	-2.289	-1.513	-1.027	-1.831	-1.812	-1.278	-2.874	-2.061	-2.332
Correlation	0.991	0.998	0.986	0.983	0.993	0.987	0.993	0.990	0.996	0.990	0.980	0.980
SE	0.049	0.022	0.054	0.062	0.035	0.055	0.040	0.045	0.026	0.049	0.047	0.053
Slope F	0.321	1.179	0.567	1.899	1.660	0.057	0.776	1.144	6.479**	3.244*	5.488**	1.122
Adj.Mean F.	12.710	20.506	22.016	79.610	1646.340	27.078	68.995	48.544	38.650	1956.890	54.985	1478.610

2.65 at 5% 3.88 at 1%

Figure 28 Relationship of predorsal length to standard length

Figure 29 Relationship of head length to standard length

Triangles	Cluculz
Crosses	McLeese
Circles	MacLure
Squares	Tacheeda

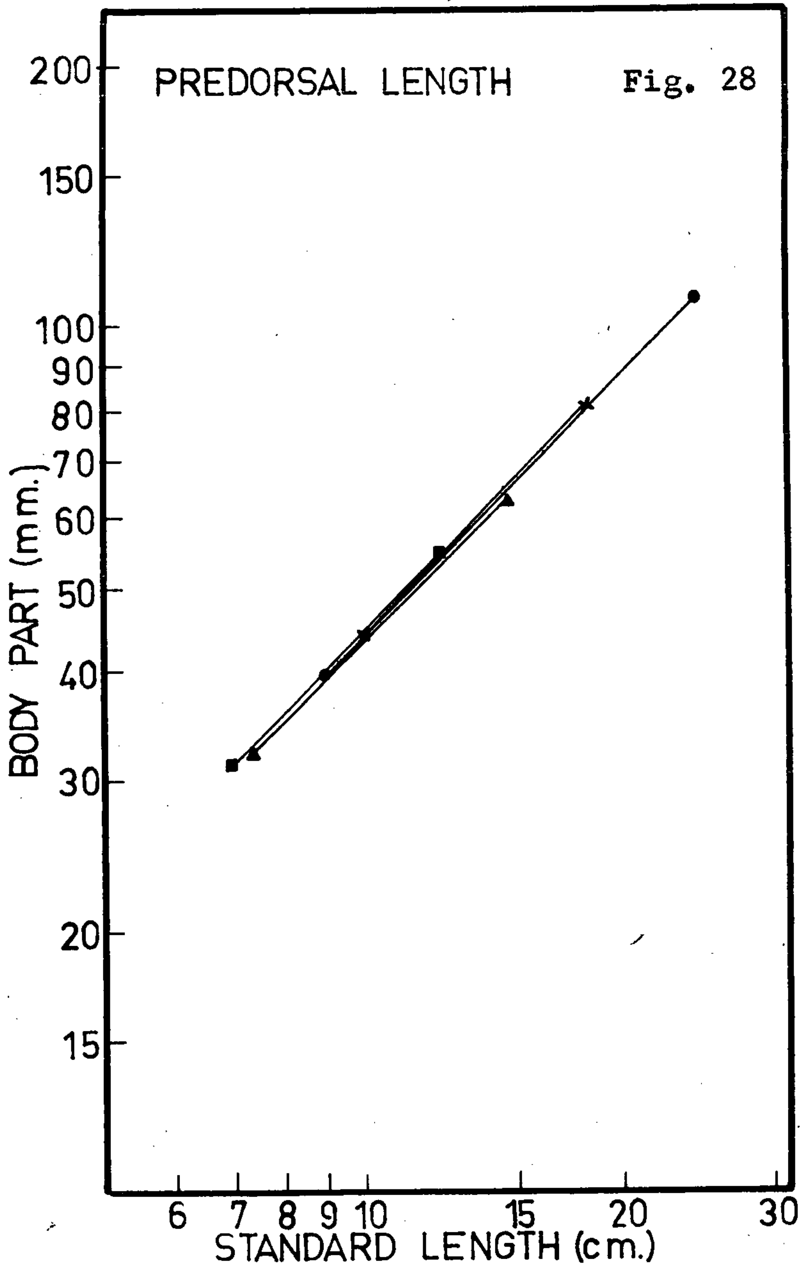

PREDORSAL LENGTH
BODY PART (mm.)
200
150
100
90
80
70
60
50
40
30
20
15
6
7
8
9
10
15
20
30
STANDARD LENGTH (cm.)

Fig. 28

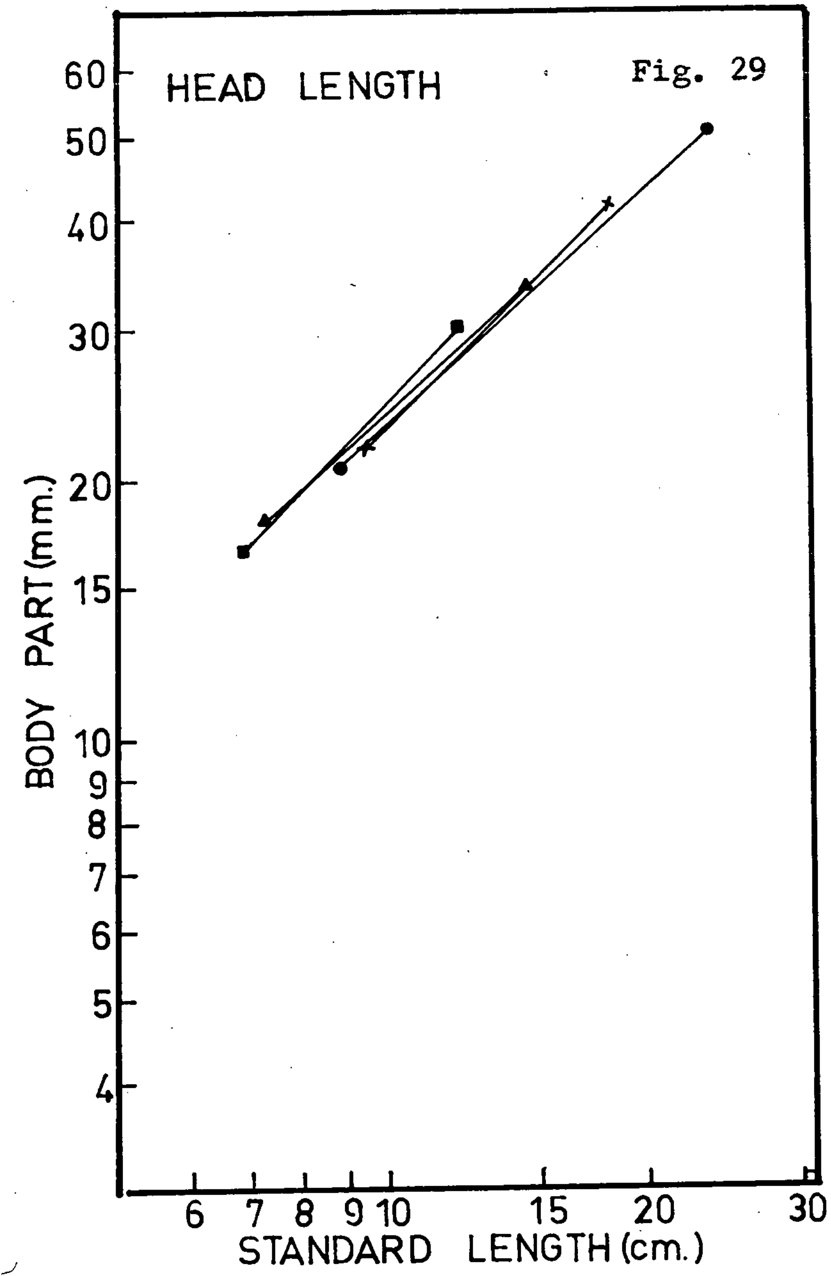
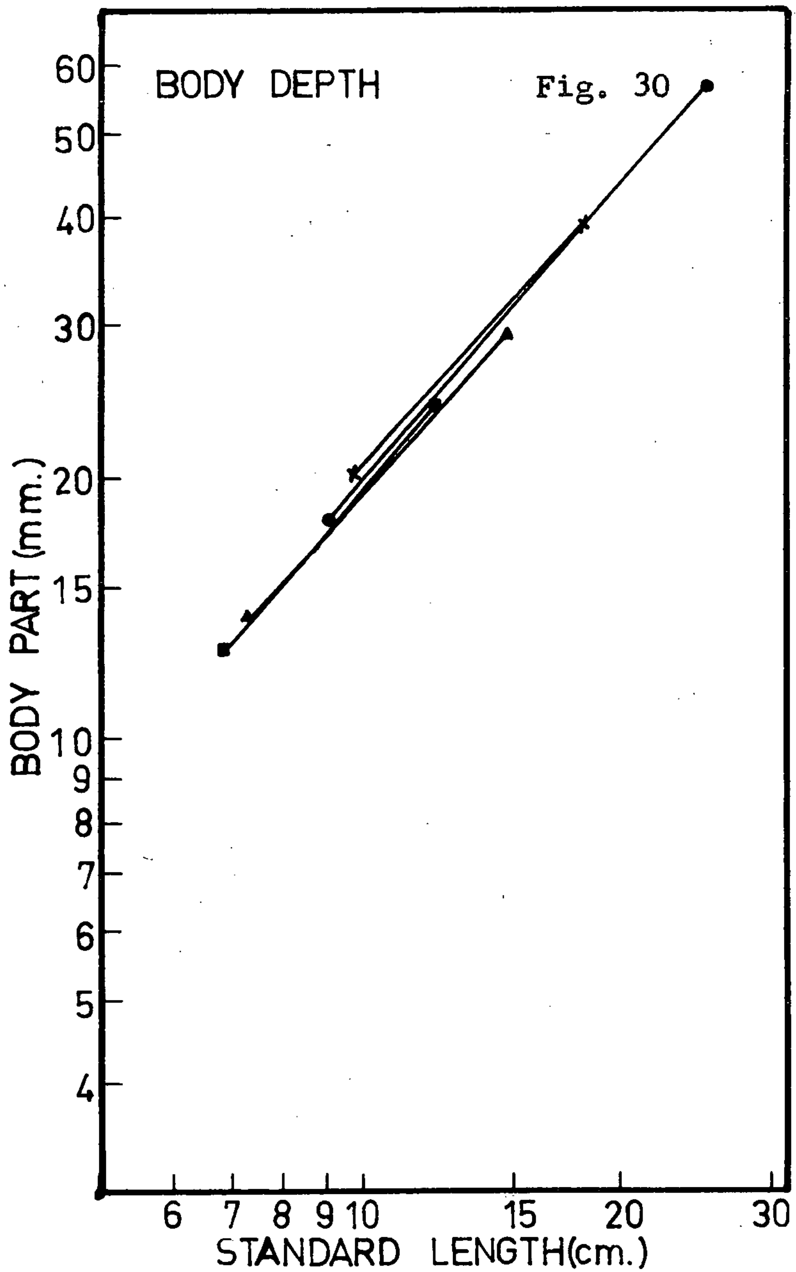

HEAD LENGTH
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30
STANDARD LENGTH (cm.)

Fig. 29

Figure 30 Relationship of body depth to standard length

Figure 31 Relationship of interorbital width to standard length

Triangles	Cluculz
Crosses	McLeese
Circles	MacLure
Squares	Tacheeda


BODY DEPTH
Fig. 30
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6 7 8 9 10 15 20 30
STANDARD LENGTH(cm.)

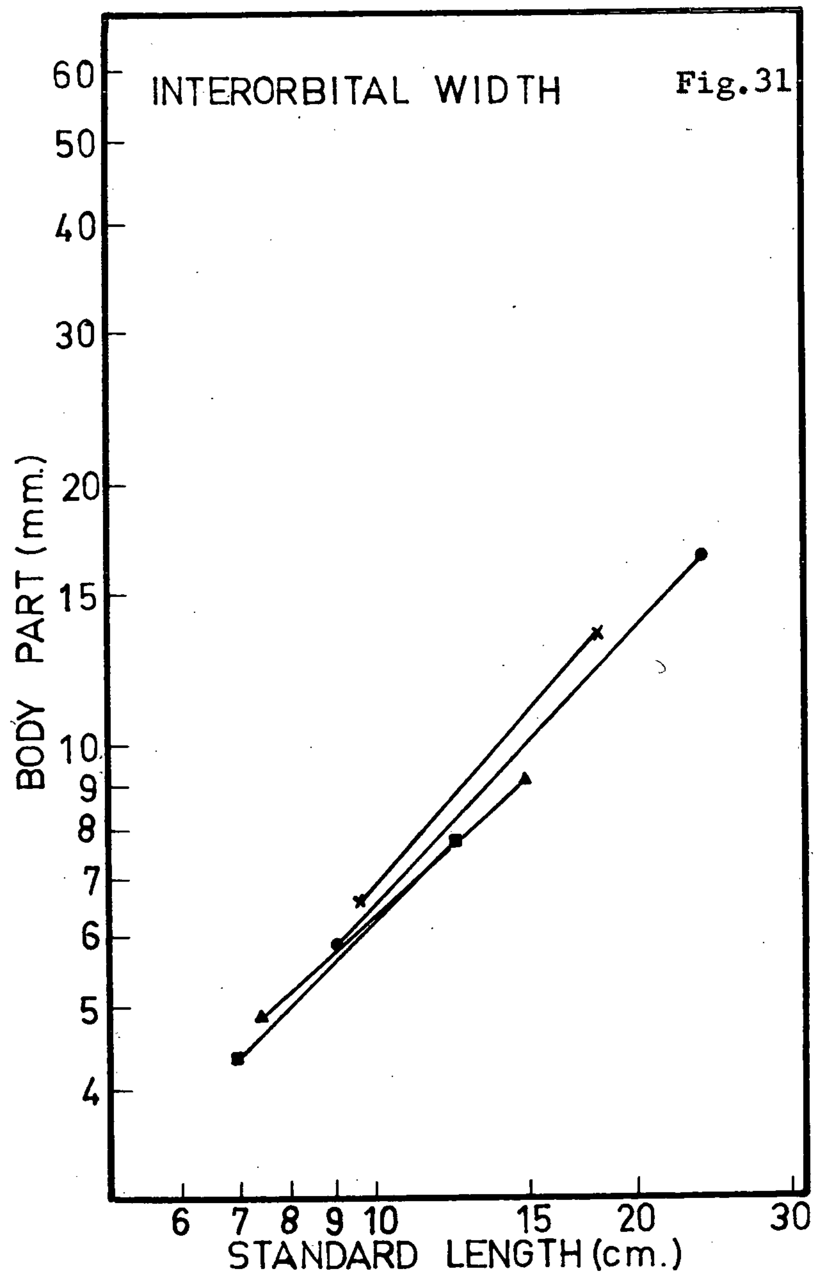
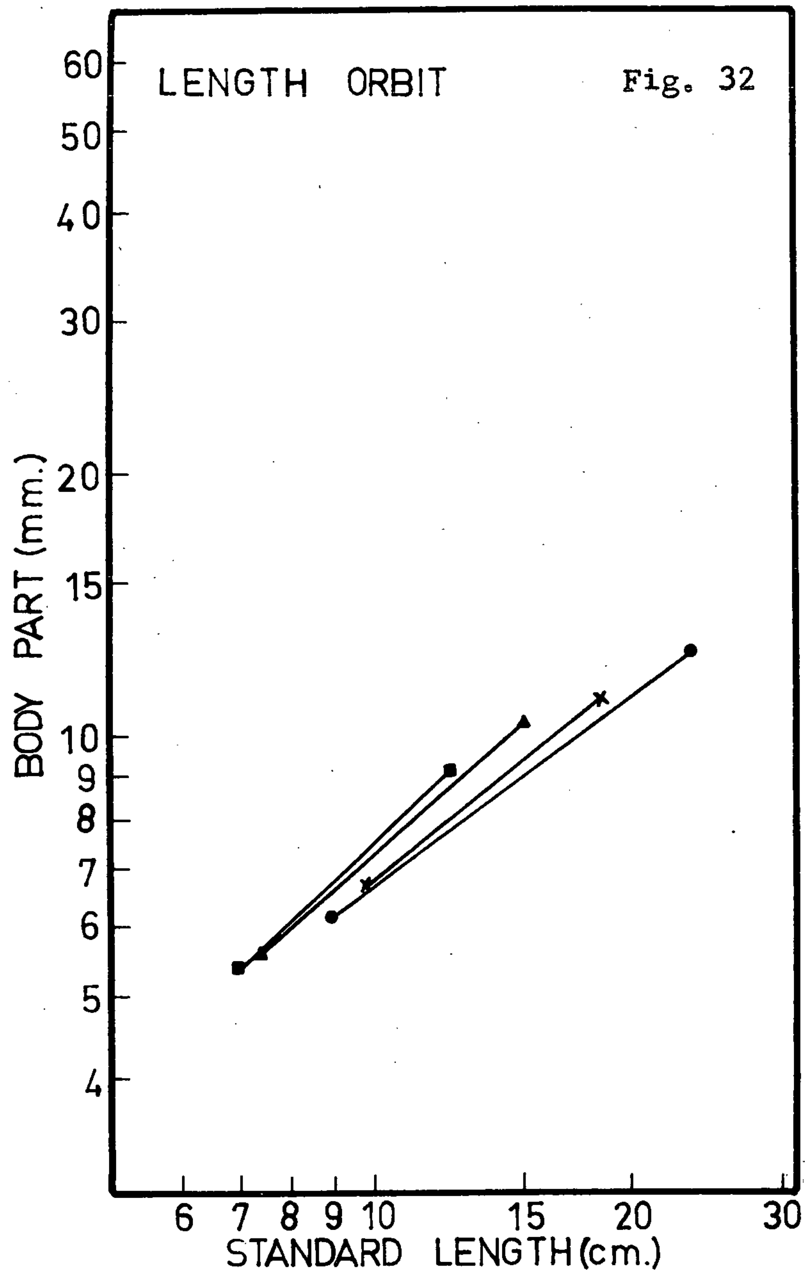

INTERORBITAL WIDTH
Fig.31
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6 7 8 9 10 15 20 30
STANDARD LENGTH (cm.)

Figure 32 Relationship of orbit length to standard length

Figure 33 Relationship of length of upper jaw to standard length

Triangles	Cluculz
Crosses	McLeese
Circles	MacLure
Squares	Tacheeda


LENGTH ORBIT
BODY PART (mm.)
STANDARD LENGTH (cm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30
Fig. 32

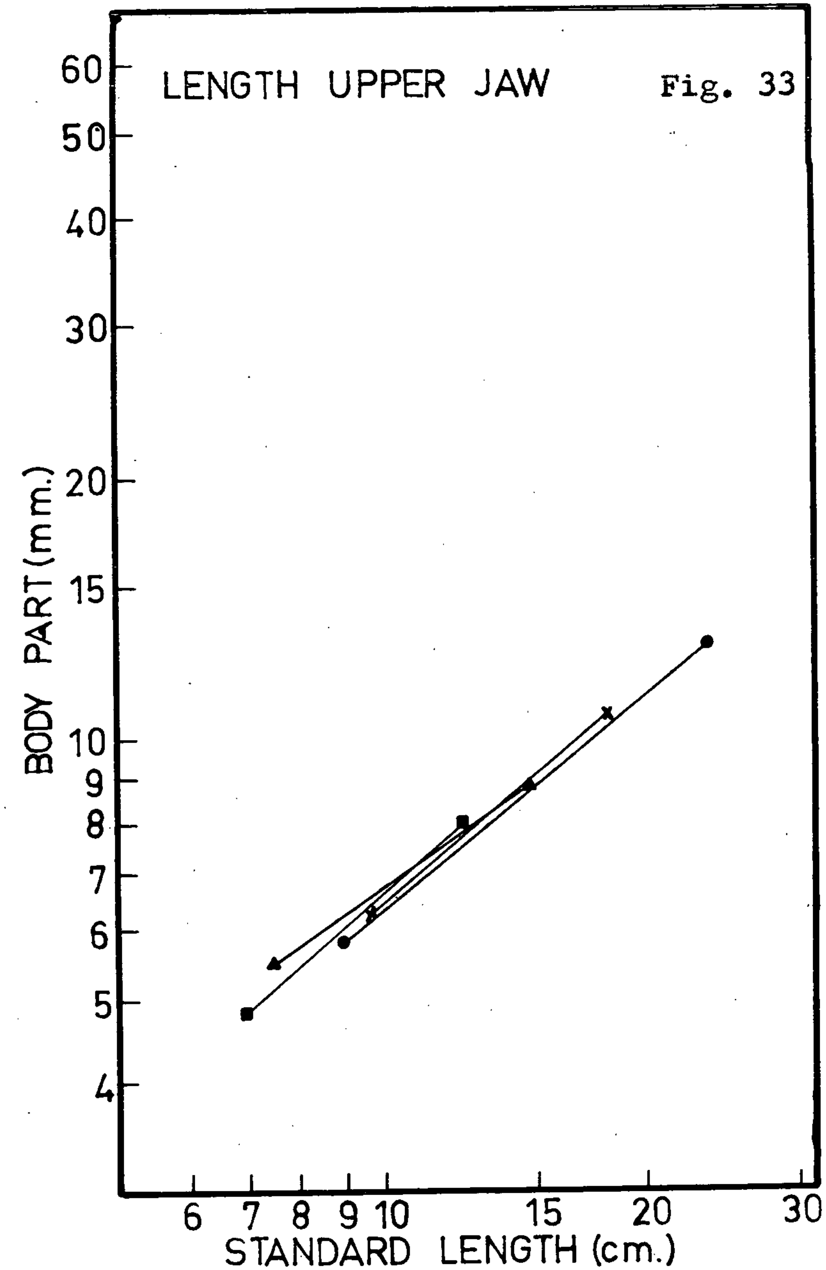
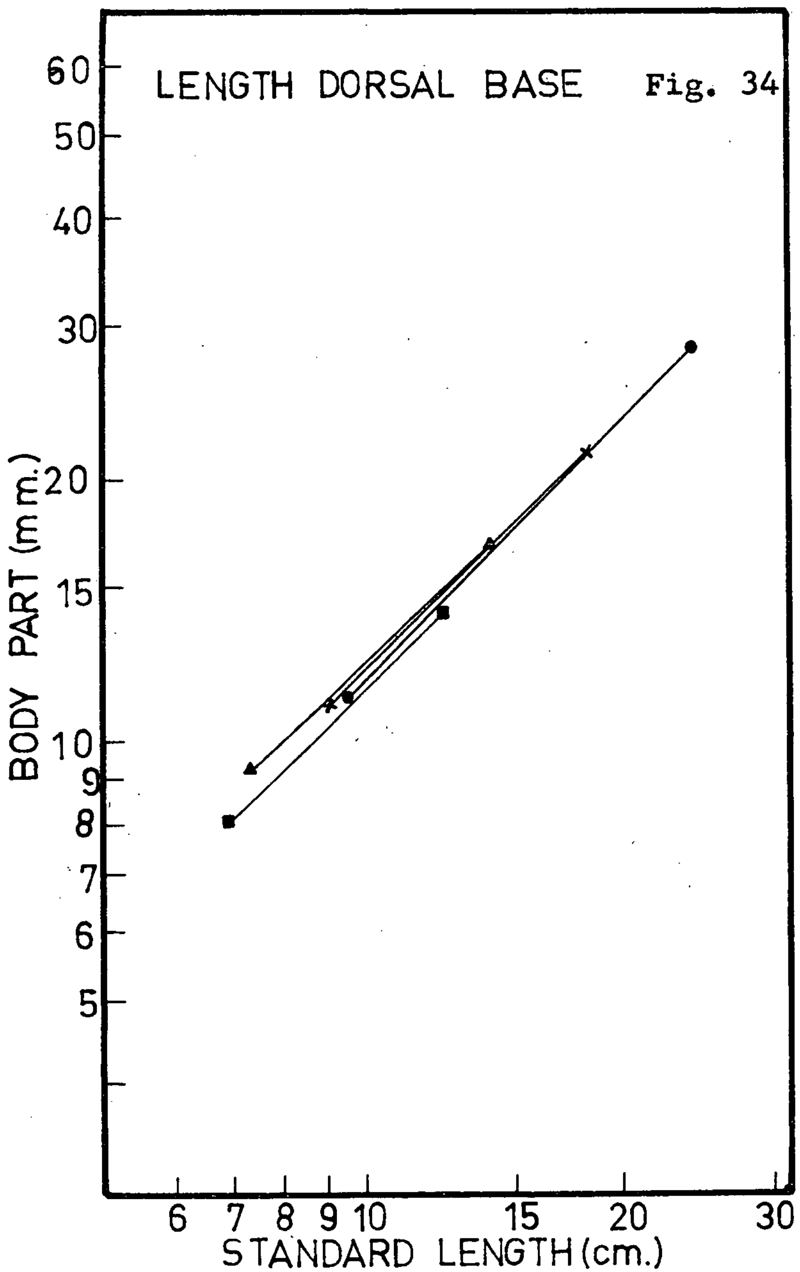

LENGTH UPPER JAW
BODY PART (mm.)
STANDARD LENGTH (cm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30
Fig. 33

Figure 34 Relationship of length of dorsal fin base to standard length

Figure 35 Relationship of length of anal fin base to standard length

Triangles	Cluculz
Crosses	McLeese
Circles	MacLure
Squares	Tacheeda


LENGTH DORSAL BASE
Fig. 34
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
6
7
8
9
10
15
20
30
STANDARD LENGTH (cm.)

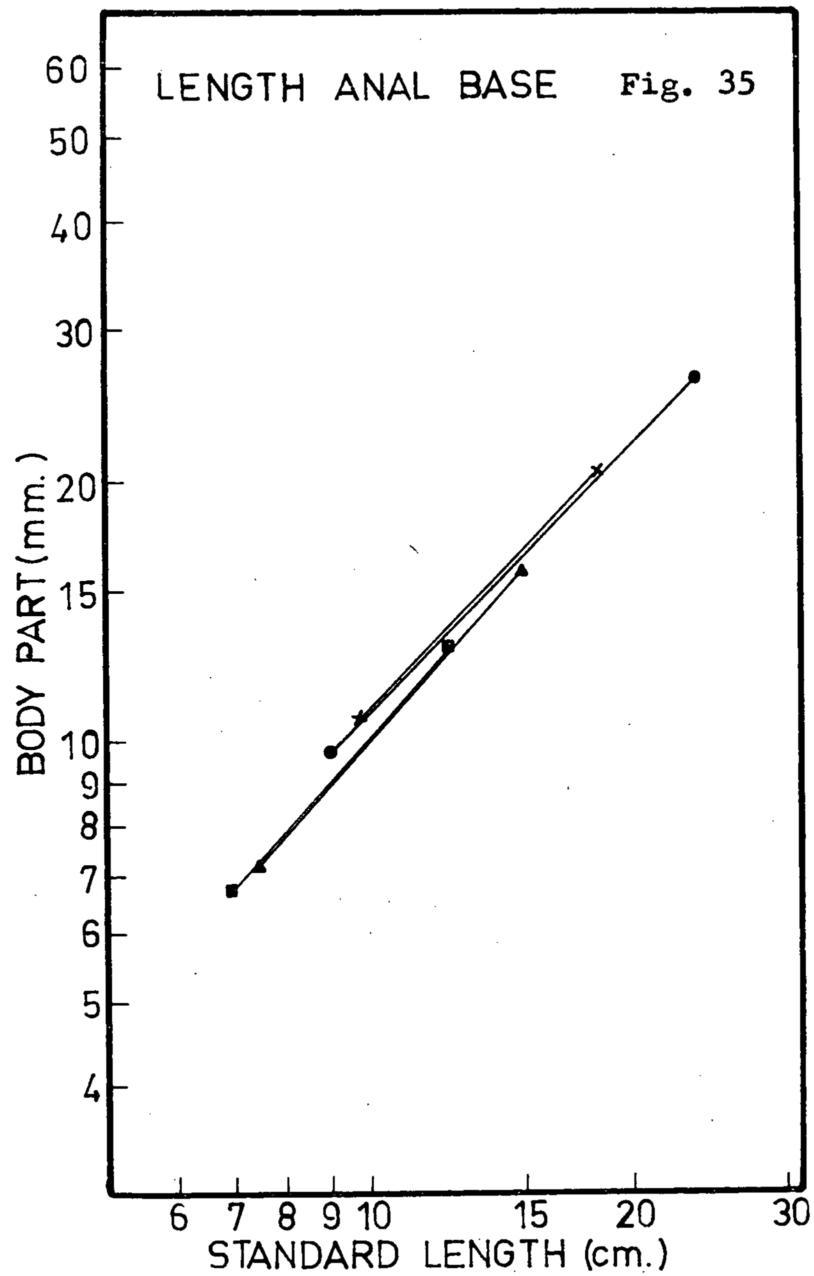
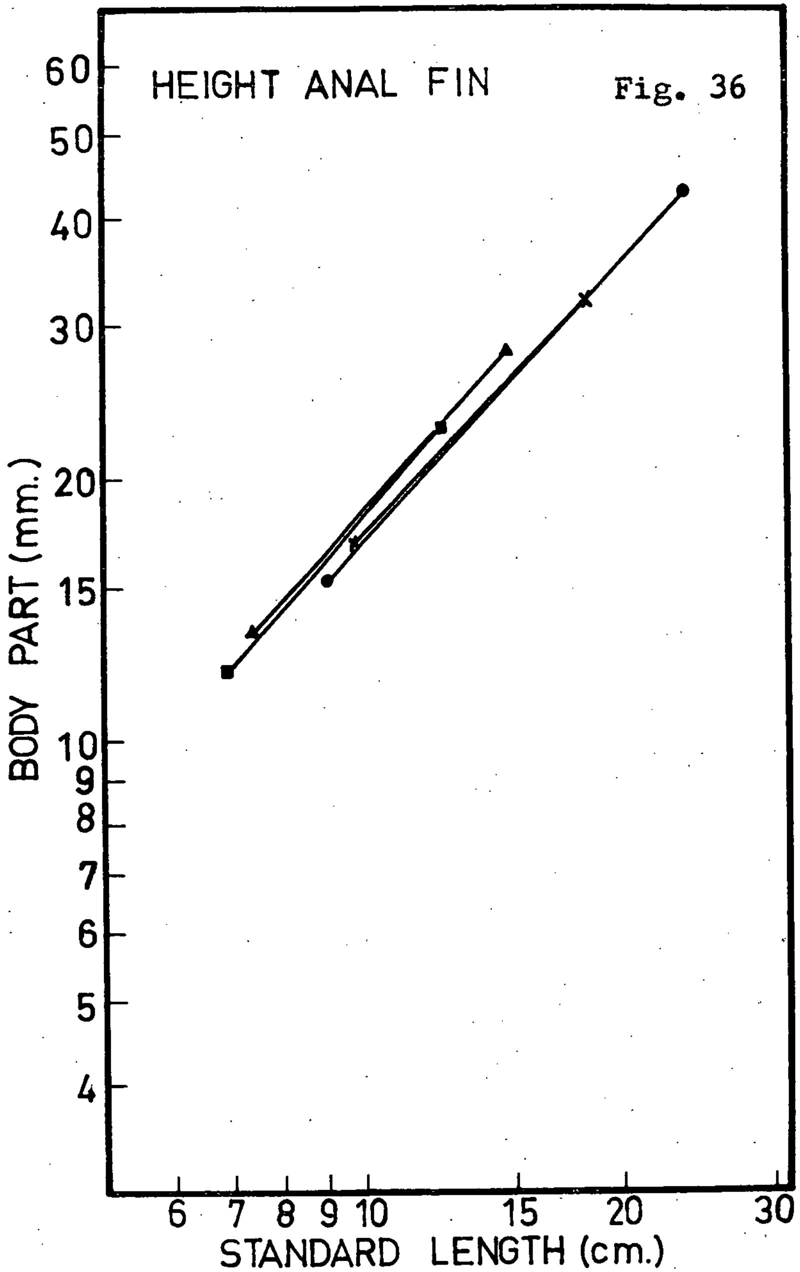

LENGTH ANAL BASE
Fig. 35
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30
STANDARD LENGTH (cm.)

Figure 36 Relationship of height of anal fin to standard length

Figure 37 Relationship of height of dorsal fin to standard length

Triangles	Cluculz
Circles	MacLure
Crosses	McLeese
Squares	Tacheeda


HEIGHT ANAL FIN
Fig. 36
BODY PART (mm.)
STANDARD LENGTH (cm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30

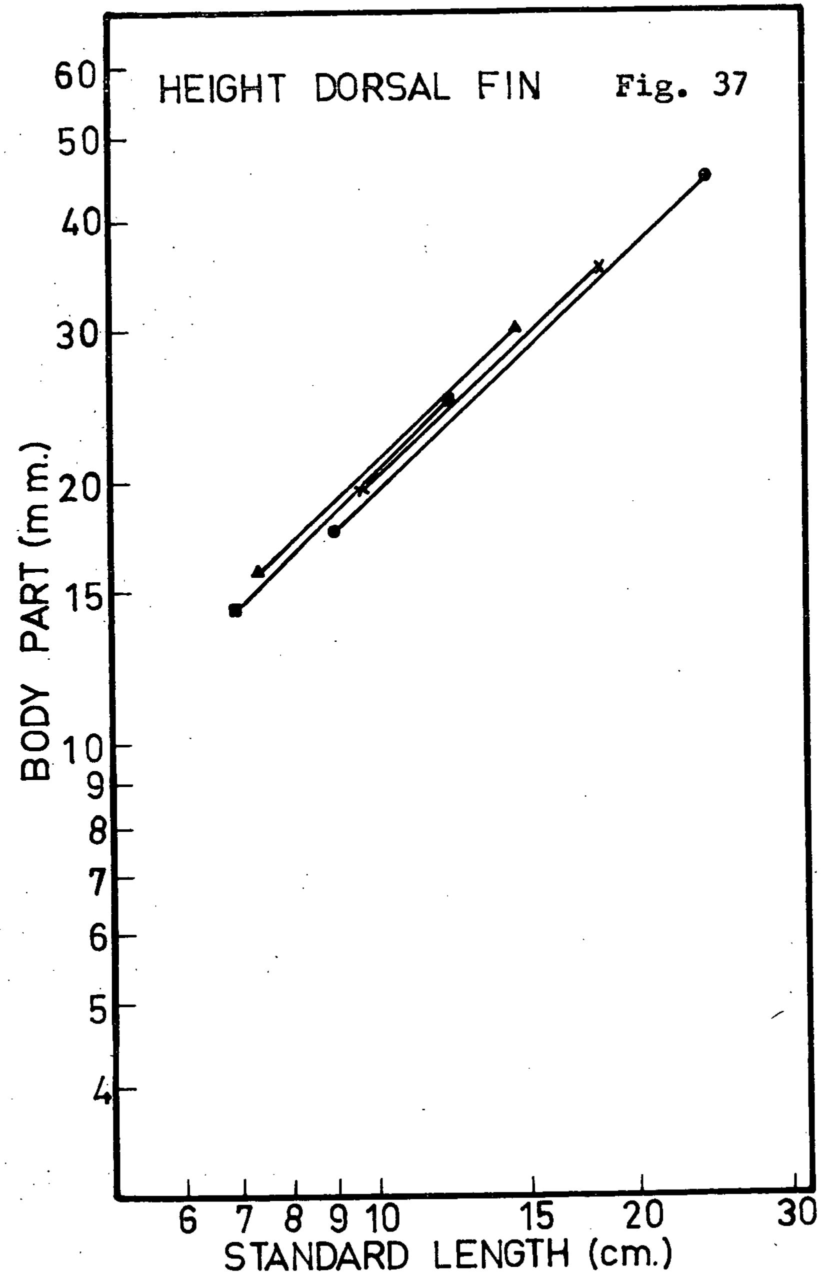
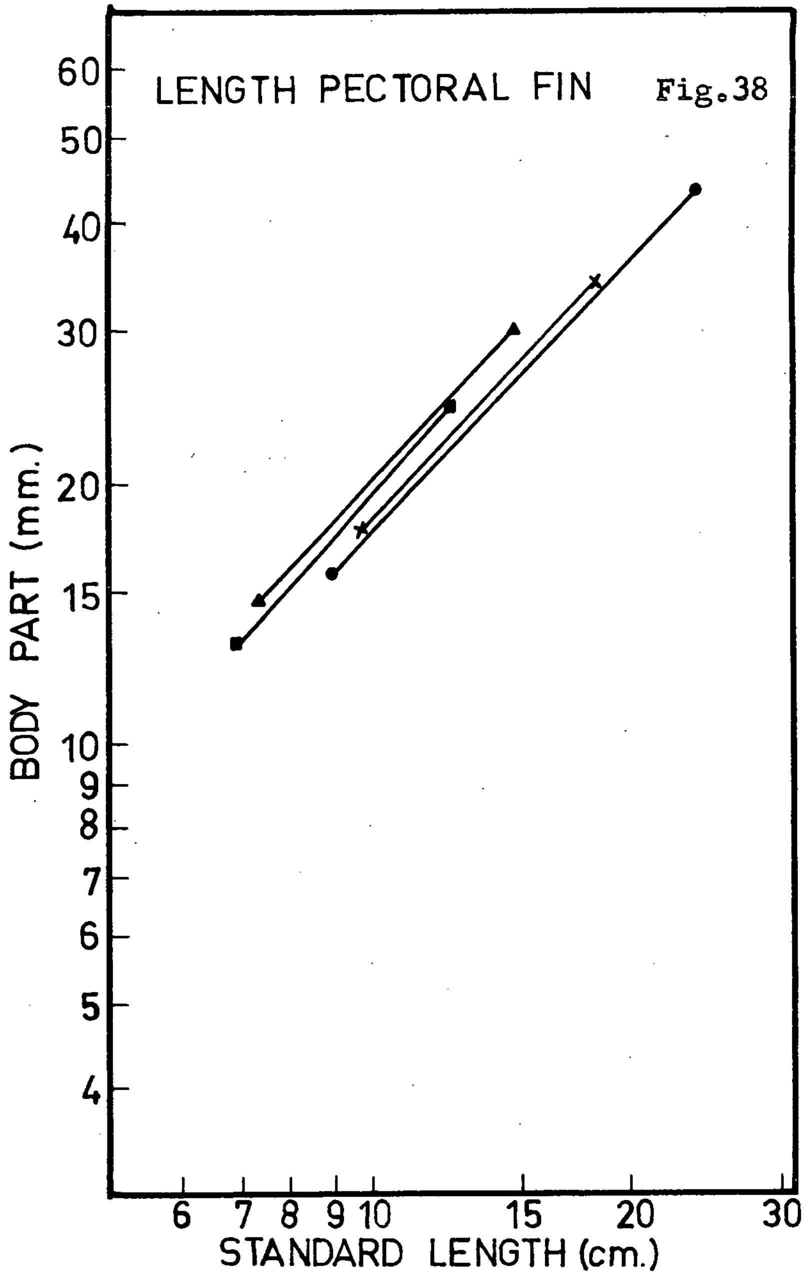

HEIGHT DORSAL FIN
Fig. 37
BODY PART (m m.)
STANDARD LENGTH (cm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30

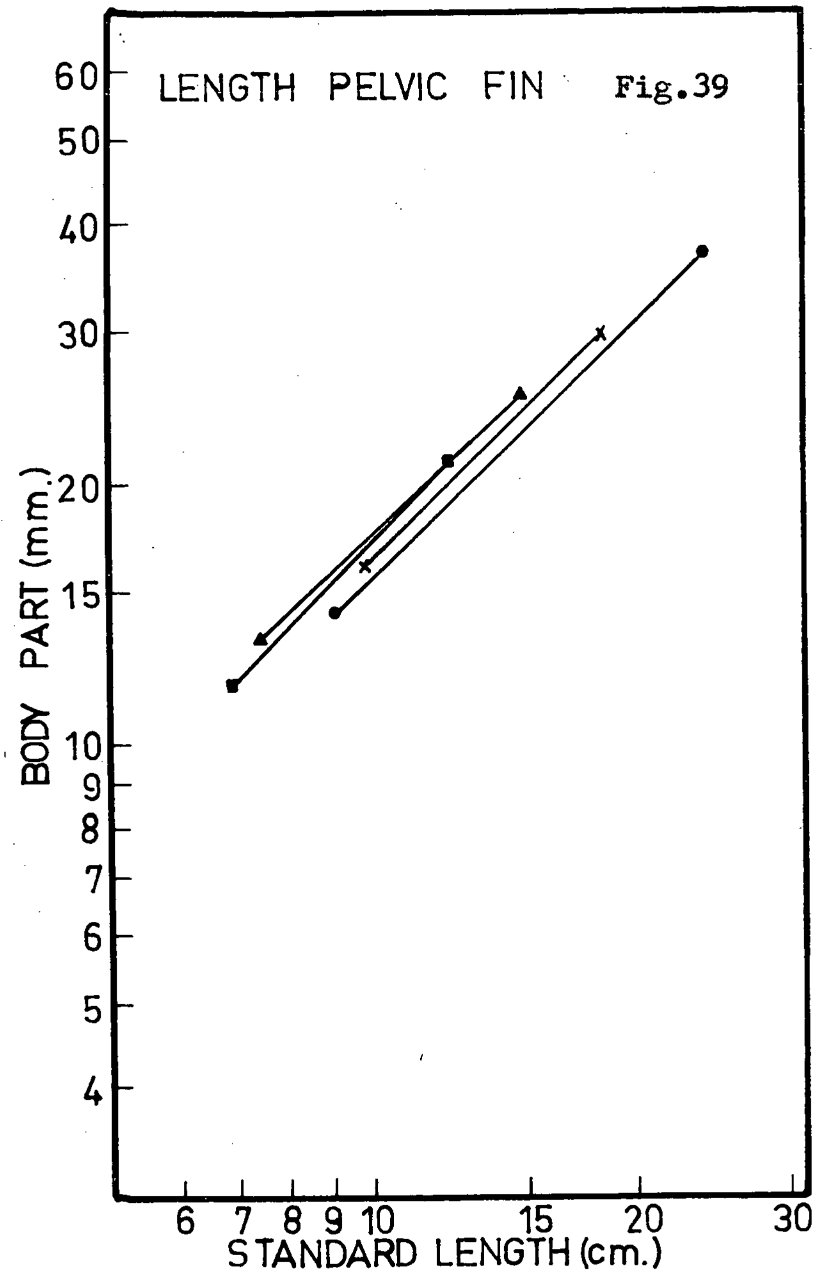
Figure 38 Relationship of length of pectoral fin to standard length

Figure 39 Relationship of length of pelvic fin to standard length

Triangles	Cluculz
Crosses	McLeese
Circles	MacLure
Squares	Tacheeda



LENGTH PECTORAL FIN
Fig.38
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30
STANDARD LENGTH (cm.)



LENGTH PELVIC FIN
Fig.39
BODY PART (mm.)
60
50
40
30
20
15
10
9
8
7
6
5
4
6
7
8
9
10
15
20
30
STANDARD LENGTH (cm.)

Martin (1949), by controlling the growth rates of rainbow trout through variation in temperature and diet, was able to produce differences in body form. He demonstrated that the relative growth of body parts in fishes was characterized by a series of stanzas separated by sharp inflections in the relative growth constant. Generally speaking, there are four distinct stanzas: at the eyed stage, at hatching, at ossification, and at maturity. Martin concluded that "... in general there is no causal connection between body form in fishes and either rate of development of subsequent growth rate, although either of these processes may indirectly affect control of body form through their influence on size at maturity." In most cases the differences between populations of the same species are differences in the intercept of the growth lines rather than in the slope of the lines. Martin was, however, able to produce slope differences in the relative growth of the eyes and head by severely restricting the diet of experimental fish. Interestingly, both these measurements show significant differences in slope in the pygmy whitefish. It is not known whether these differences might also be the result of deficient diet in the dwarf populations.

It is very likely that the relative proportions of body parts in the pygmy whitefish are determined in much the same way as that described by Martin for the rainbow trout and other fish. Unfortunately, no small fish are available from the populations under study so that there is no direct evidence of growth inflections in the pygmy whitefish. Thus, although there are definite differences in the populations of the four lakes, the mechanics of determination are not known.

Depth Distribution

Tables 23 and 24 summarize netting data for the summer of 1962. The tables include the total effort expended in a particular depth stratum and the total catch of fish which resulted. The unit of effort, the net-hour was defined as a single, fifty-foot long, eight-foot deep monofilament nylon net fishing for a period of one hour. Data from twenty-five-foot deep nets were not used because these were not consistently employed. The data for the whole summer are summarized as catch per unit of effort (fish per net-hour) for each depth stratum and the results graphed in Figure 40. For Tacheeda and Cluculz Lakes, data for two other whitefishes, *Coregonus clupeaformis* and *Prosopium williamsoni*, have been included.

The data show two distinct patterns of depth distribution. In both McLeese and MacLure lakes, pygmy whitefish extend from a depth of about fifteen feet downward to depths of seventy and fifty feet respectively. Extensive netting in deeper waters failed to produce a single pygmy whitefish. In the other two lakes, Cluculz and Tacheeda, the upper limit of distribution is about thirty-five feet, and the fish are numerous as far as the limit of netting, 120 feet in Cluculz and 100 feet in Tacheeda lake.

In MacLure and McLeese Lakes the upper limit of distribution may coincide with the depth of the warmer epilimnial water. In the other two lakes the depth distribution during the summer is considerably below that of the thermocline and may be

Table 23. Depth distribution and catch of pygmy whitefish in MacLure and McLeese Lakes during summer, 1962

DATE	DEPTH STRATUM													
MacLure Lake: Eight-foot bottom sets														
	0-10		10-20		20-30		30-40		40-50		50-60		60-70	
	net hrs	no. fish	net hrs	no. fish	net hrs	no. fish	net hrs	no. fish	net hrs	no. fish	net hrs	no. fish	net hrs	no. fish
June 2-6	48	0	36	2	58	9	175	26	40½	8	34½	0	0	0
July 6-10	7½	0	17½	5	81½	172	76	28	72	0	0	0	62	0
July 31	0	0	0	0	7½	8	7½	8	7½	8	0	0	0	0
Sept 20	0	0	0	0	0	0	96	46	0	0	0	0	0	0
Total	55½	0	53½	7	147	138	354	108	120	16	34½	0	62	0
Catch/unit effort	0.000		0.131		0.929		0.305		0.133		0.000		0.000	

DATE	DEPTH STRATUM											
McLeese Lake: Eight-foot bottom sets												
	0-20		20-40		40-60		60-80		80-100		100-120	
June 13-16	29	0	108	9	0	0	0	0	0	0		
July 23	12	0	12	0	12	8	51¼	0	10¼	0		
Sept	0	0	71¼	0	39¼	0	45	0	16¾	0		
Total	41	0	191¼	9	51¼	8	96¼	0	27	0		
Catch/unit effort	.000		.047		.156		.000		.000			

Table 24. Depth distribution and catch of pygmy whitefish in Cluculz and Tacheeda Lakes during summer, 1962 (P - pygmy; M - mountain; L - lake whitefish)

DATE	DEPTH STRATUM																							
	0-20				20-40				40-60				60-80				80-100				100-120			
	net hrs	catch P	M	L	net hrs	catch P	M	L	net hrs	catch P	M	L	net hrs	catch P	M	L	net hrs	catch P	M	L	net hrs	catch P	M	L
Cluculz Lake: Eight-foot bottom sets																								
5/21-31	0	0	0	0	212	19	0	0	22	0	0	0	0	0	0	0	0	0	0	0	--	--	--	--
6/10-24	159	0	27	20	93.5	3	12	6	35	19	0	0	8	10	0	0	0	0	0	0	--	--	--	--
7/13-30	308	0	50	3	217.6	3	32	7	109.8	35	0	0	31	44	0	0	7	1	0	0	28	23	-0	0
Total	467	0	77	23	527	25	44	13	167	54	0	0	39	54	0	0	7	1	0	0	28	23	0	0
Catch per unit effort:																								
	.000 P				.047 P				.323 P				1.385 P				.143 P				.821 P			
	.164 M				.083 M				.000 M				.000 M				.000 M				.000 M			
	.049 L				.025 L				.000 L				.000 L				.000 L				.000 L			
Tacheeda Lake: Eight-foot bottom sets																								
5/18	22	0	0	4	22	0	0	2	22	4	0	0	0	0	0	0	0	0	0	0	--	--	--	--
6/20-1	120.4	0	5	6	73.9	1½	2	8	42.8	9½	0	0	37.5	8	1	0	0	0	0	0	--	--	--	--
7/20-2	61.2	0	43	17	100.5	5	12	18	74.4	29	0	5	17	2	0	0	0	0	0	0	--	--	--	--
9/16	0	0	0	0	10	0	0	0	20	2	0	0	15	7	0	0	20	20	0	0	20	0	0	0
Total	203.6	0	48	27	206.4	6½	14	28	159.2	34½	0	5	69.5	17	1	0	20	20	0	0	20	0	0	0
Catch per unit effort:																								
	.000 P				.031 P				.217 P				.245 P				1.000 P				0.000 P			
	.236 M				.068 M				.000 M				.014 M				0.000 M				0.000 M			
	.137 L				.136 L				.031 L				.000 L				0.000 L				0.000 L			

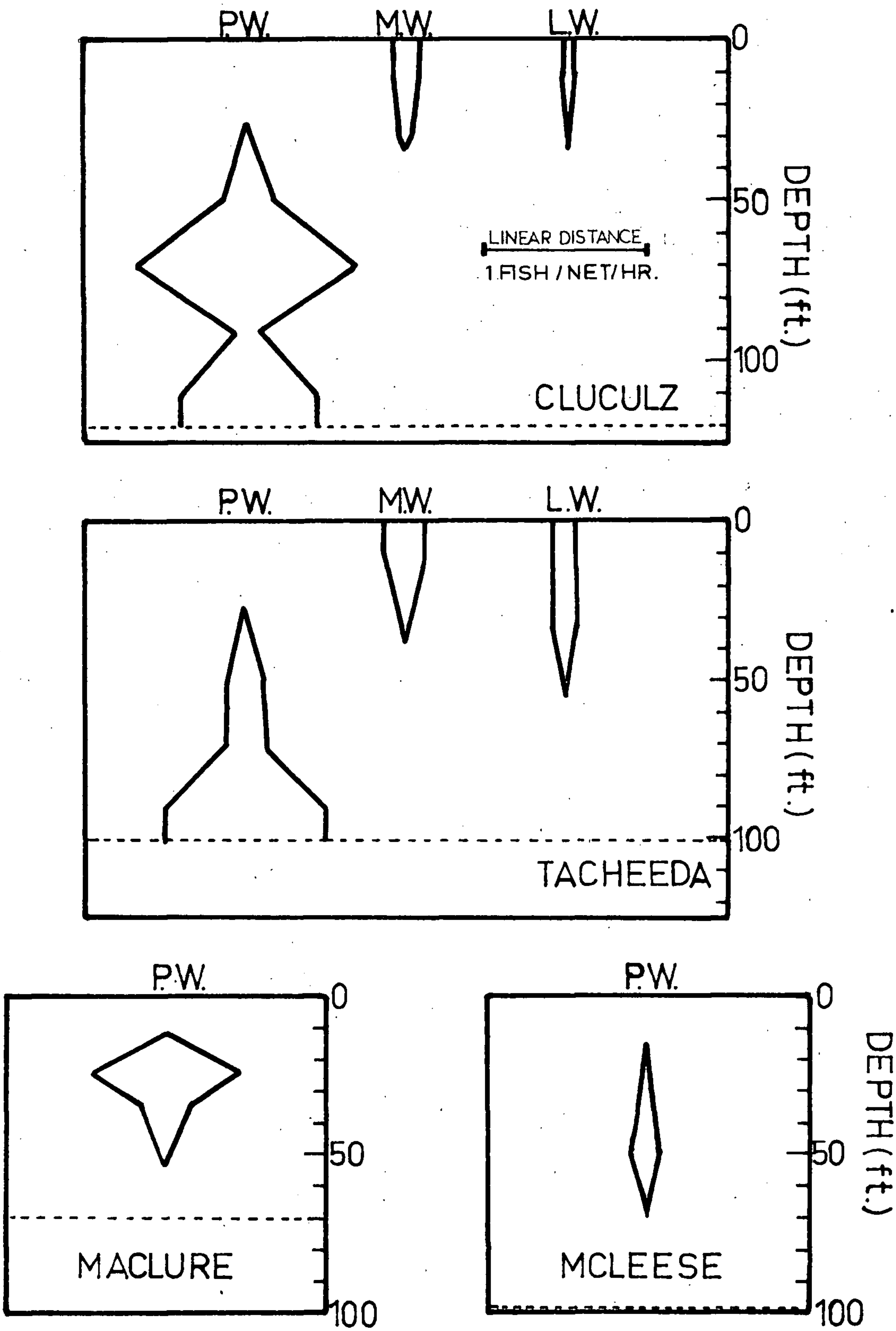


Figure 40. Depth distributions of whitefish in four British Columbia Lakes during Summer, 1962

largely the result of competitive exclusion by the other two whitefish. Both of these Coregonus clupeaformis and Prosopium williamsoni are most abundant inshore and their lower limit of distribution almost exactly coincides with the upper limit of pygmy distribution. The lumping of data partly obscures this. Although all three whitefishes often occurred in the same depth stratum, rarely was another species of whitefish found below a pygmy whitefish in a net. Exceptions were a mountain whitefish taken June 20-21 in the 60 - 80 foot stratum in Tacheeda Lake and four lake whitefish taken in fifty feet of water on July 21 in Tacheeda.

The shallow lower limit of pygmy distribution in MacLure and McLeese Lakes is probably due to low oxygen tensions in the bottom waters. Both lakes have high Total Dissolved Solids values and are quite productive. On July 31, 1962, the waters of MacLure Lake from thirty-three feet to the bottom contained only 2.4 mg/l of Oxygen. No figures are available for McLeese lake, but a similar situation may have prevailed. Both Cluculz and Tacheeda are deeper, more oligotrophic lakes. On July 30, 1962 the water at 105 feet in Cluculz Lake still contained 4.4 mg/l of Oxygen.

There is no evidence of any diurnal vertical or horizontal (inshore-offshore) movements in the pygmy whitefish. There is some evidence, however, of an offshore movement into somewhat deeper water during late spring. In shallow Outlet Bay, Cluculz Lake, numerous pygmys were taken at depths of 25 to 30 feet during May. Nets set in the same area later in the summer failed to take any pygmy whitefish. Residents report similar movements of lake whitefish and lake trout. Mountain whitefish are abundant in the bay at all times. There is no adequate evidence of this sort for the other lakes.

At the depths where it occurs, the pygmy whitefish is by far the most numerous fish. In Cluculz and Tacheeda only the lake trout was commonly taken at such depths. In MacLure Lake there was a zone of overlap between fifteen and twenty feet where the redside shiner (Richardsonius balteatus), peamouth chub (Mylocheilus caurinum) and squawfish (Ptychocheilus oregonensis) were all common, but below this depth,nets contained pygmy whitefish almost exclusively.

Food habits

Only preliminary studies have been carried out on the food of pygmy whitefish in the four lakes. The results are given in Table 25. In each case the three most important foods are cladocerans, chironomid larvae, and Chaeoborus. The relative importance varies considerably, however, even within the same lake. In Tacheeda Lake, for instance, cladocerans made up 90% of the stomach contents on July 23, but on September 21 they represented only 1% of the diet. By contrast, the proportion of chironomid larvae had risen from 2% to 85%. In MacLeese Lake, a similar relationship holds for Chaeoborus and chironomid larvae. In MacLure and Cluculz Lakes, the main constituent of the diet is Cladocera and chironomidae, respectively, on each of three separate dates.

In Lake Superior, Amphipods (Pontoporeia) and ostracods made up 75% of the total stomach contents of pygmy whitefish (Eschmeyer and Bailey, 1954). In Brooks Lake, Alaska, pygmy whitefish had a diet of plankters and few of the smallest insects (mainly chironomid larvae). Cladocerans, copepods, and ostracods were all recorded as present. No amphipods were found although these were present in the stomachs of other species in the lake (Hartman, 1957 and 1958).

The pygmy whitefish is probably an opportunistic feeder, taking whatever foods are readily available at any given time, and the variation in foods eaten in various lakes is not unexpected. What is consistent in the diet from lake to lake is the size of the food organisms. Even the largest MacLure Lake whitefish are restricted to relatively tiny plankters and bottom organisms. By contrast, both Coregonus clupeaformis and Prosopium williamsoni can, and do, feed on much larger organisms, chiefly molluscs and the larger aquatic insects (McHugh, 1939 and 1940; and Godfrey, 1955). P. williamsoni, in particular, rarely takes plankton or other small organisms as an adult.

Hartman (1958) has shown that size of food organisms can be related to the size of the mouth in rainbow trout. Observations indicate that, contrary to expectation, P. williamsoni has a very tiny mouth. The pygmy whitefish, with an intermediate mouth size, has a longer maxillary, greater width between the maxillaries and a larger gape. Of the three, C. clupeaformis has

Table 25. Stomach contents of pygmy whitefish from four British Columbia lakes expressed as estimated percentage of total volume. All fish taken in 1962.

	MACLURE LAKE			MCLEESE LAKE		CLUCULZ LAKE			TACHEEDA LAKE	
Date:	6/4,5	8/1	9/20	6/18	7/24	5/23	6/23	9/18	7/23	9/21
Stomachs examined:	5	10	10	5	5	5	5	5	10	5
Mollusca										
Sphaeriidae	--	--	--	--	--	--	--	tr	--	--
Crustacea										
Ostracoda	--	--	--	--	--	--	tr	tr	--	--
Cladocera	60	91	73	5	10	--	--	--	90	1
Copepoda	--	tr	--	tr	tr	--	--	--	2	tr
Amphipoda	--	--	--	--	--	--	--	tr	--	--
Insecta										
Chironomidae	30	7	2	8	75	60	70	25	2	85
Chaeoborus	--	--	10	82	10	10	--	10	--	3
Unidentifiable	10	2	15	5	5	20	30	65	6	10

the largest mouth in every respect. The choice of food is not, then, strictly a function of mouth size. Mouth shape, may, however, be important. Both C. clupeaformis and especially P. williamsoni have more pointed snouts than P. coulteri with its blunt, broad nose. Pointedness may be advantageous in probing under rocks, sticks, etc. for large insects and snails. The wide mouth of the pygmy may be more efficient in straining mud and water for small bottom animals and plankton.

Plankton feeding species generally have more gill rakers than bottom feeders. In this case the pygmy whitefish (12-20) has not more, but fewer, rakers than either the lake whitefish (23-33) or the mountain whitefish (20-26). (Figures for the last two species are from Carl, Clemens, and Lindsey, 1959).

DISCUSSION

The data give ample evidence of striking differences in the growth form of different populations of pygmy whitefish. It is very difficult, however, to assign specific causes for these differences.

Larkin (1956) has commented on the impermanence of freshwater environments which, in terms of geological time periods, are very short-lived. This is especially true of the temperate regions of the world. As a response to the ephemeral nature of their environment, fishes occupying fresh waters have developed a remarkable plasticity in terms of the habitat and, more particularly, the niche which they can occupy. The variability in meristics, morphometry and growth rate, excemplified in the pygmy whitefish, is a reflection of this ability to adapt to rapidly changing conditions. The differences may be largely the result of environmental modification but the gene complement which permits such a wide range of phenotypic expression must itself be the result of rigorous selection.

The niche that a species occupies in a particular locality is determined by a complex of factors both physical and biotic. The inter-relations of these are not well understood. In fish the distribution and abundance of food organisms and the presence of other competing species are most often mentioned as factors resulting in niche diversity within a single species.

The mountain whitefish provides an example of the direct effect of food abundance on choice of niche. In most areas this whitefish is a shallow water, bottom feeder concentrating its feeding on immature insects. In Morrison Lake, BC, however, the very steep sides severely limit the shallow water areas generally inhabited by such insects and the mountain whitefish has become primarily a plankton feeder (Godfrey, 1955). A similar phenomenon seems to have occurred in Okanagan Lake (McHugh, 1939).

The effects of competition with other species are much more difficult to assess. Mayr (1948) has stated that "So far there is only scanty direct proof for the assumption that populations are kept in check by competition for space and food." Andrewartha and Birch (1954) concluded that the available evidence suggests the competition in natural situations occurs only rarely at best. Much of the difficulty arises because of our inability to control the natural environment. A common technique is to compare two populations of a species; one in which the species occurs alone, and another in which the species occurs together with possible competitors. Unfortunately, "Most of these demonstrations are hampered by the difficulties of ruling out the effects of changes in the environment other than the changes in fish fauna and the difficulties of getting a good measure of the 'adverse effect' on all the competing fish populations." (Lindstrom and Nilsson, 1962). This is very definitely a problem in comparing the pygmy whitefish populations of the four lakes under study, lakes which are quite dissimilar limnologically.

Johannes and Larkin (1961) emphasise another difficulty. In most cases the scientist is presented with a "fait accompli". He is, in fact, studying the results rather than the process of competition and may have little idea of the changes that the advent of a competing species have wrought in the ecology of another. Situations like that at Paul Lake, British Columbia, where there is considerable information available on the growth of the rainbow trout both before and after the introduction of the competing redside shiner are not common. In the present study, the fish fauna of the lakes has probably been stable for long periods of time so that there is no evidence of the causal sequence through which the present conditions developed.

Finally there is the problem of simply defining the term "competition". It has been used in many ways, even including parasitism and predation. Larkin (1956) suggests that the term "competition" be restricted in use to "...the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply." Such competition is generally most severe in closely related species. Significantly, the larger sized MacLure and McLeese Lake populations are the only two in British Columbia where the pygmy whitefish does not co-exist with another species of the genus *Prosopium*. In every other locality, either *P. williamsoni* or *P. cylindraceum* is present and the dwarfed form of *P. coulteri* is the rule.

Nilsson (1955) suggests several possible results of competition. In the first case, severe competition leads to the elimination of one of the species from the area. The severity of competition may be due to a genetic make-up which includes factors for reproductive isolation but not for ecological compatibility. It may also be the result of factors which limit the number of niches available, forcing the two species together. Lindstrom and Nilsson (1962) considered competition between whitefishes to be more severe in a narrow, deep lake with few niches than in a shallower one with a wide littoral zone providing more varied resources. Muira (MS) has shown that in British Columbia's Fraser River drainage the number of species inhabiting lakes increases with the surface area. A similar relationship exists for the four lakes studied in terms of both the total number of species and the number of whitefish species. The two smaller lakes have only a single whitefish species while three species inhabit the larger lakes. In MacLure Lake, at least, the absence of the mountain whitefish is not due to inaccessibility. The lake is connected to the Bulkley River, where these fish occur, by a stream less than two miles long. There appears to be no barrier to movement along the length of the stream. In the case of McLeese Lake, invasion of mountain whitefish from downstream is definitely cut of by an impassable falls on Soda Creek where it drains into the Fraser River.

In the second situation resulting from competition, the two species are able to co-exist without severe competition by either occupying different types of habitat or by obtaining their food and other necessary resources in different ways (i.e. occupying different niches). Brian (1956) suggests that this ecological separation of species can come about in two ways. It may be based on strictly differential habitat selection which is presumably the result of genetic differences or it may be the result of effects that the species in contact have upon one another. The former, Brian termed selective segregation, and the latter interactive segregation.

In Cluculz and Tacheeda Lakes the adult pygmy whitefish very definitely occupies a different niche than either the lake or mountain whitefish. It is a dwarfed fish feeding on plankton and small bottom fauna and inhabiting deep waters. The other two are normal in size, feed on large bottom fauna and inhabit shallower waters. Are these differences in niche the result of selective or interactive segregation? The answer to this question is not clear, but some insight may be gained by a comparison of the two lakes having sympatric whitefish populations with McLeese and MacLure where the pygmy whitefish exists alone.

Nilsson (1955) found that in competitive situations, the trout (Salmo trutta) is mainly a bottom feeder and tends to occupy shallow water. Char (Salvelinus alpinus) in the same lakes feed primarily on plankton and occupy the open, deep waters. Alone, or when bottom insects are superabundant, the char is much more evenly spread over the basin of the lake and moves in to shallow water. Char feeding primarily on plankton grow much more slowly than those with access to bottom fauna. A similar pattern is apparent for the pygmy whitefish. Alone, the pygmy whitefish occupies shallower water and grows to considerably larger sizes than it does when co-existing with other species of whitefish.

There does not, however, appear to be any significant change in food habits from lake to lake. The oft remarked relation between fish size and food size (Lindstrom, 1955) is not shown.

Dahl (1917 and 1926), cited in Nilsson (1955), pointed out that smaller or less available food objects require a greater expenditure of energy by the fish in relation to the quantity of food obtained, and thus result in a lower growth rate. In the case of the pygmy whitefish the size of the food particles does not appear to differ but there is a very distinct difference in the growth rates from lake to lake. The reason for this may lie in the variation in density of food of the appropriate size in the volume of water inhabited by the pygmy whitefish in the different lakes. In the first place, McLeese and MacLure Lakes, with higher TDS and shallower waters, would be expected to produce greater quantities of zooplankton and small bottom organisms than either Tacheeda or Cluculz. Secondly, much of the pygmy whitefish population of Tacheeda and Cluculz is confined to considerable depths where low temperatures and low light intensities must severely limit the production of food organisms and at the same time reduce the efficiency of food conversion. Differences in average size would undoubtedly exist even if the depth distributions of pygmy whitefish in the four lakes were identical but they might not be nearly as great.

Pygmy whitefish are obviously capable of inhabiting shallower water. Why then are they found only in deep water in Tacheeda or Cluculz? The answer may lie in the fact that the young of both mountain and the lake whitefishes have a diet essentially similar to that of the pygmy whitefish -- plankton and other small organisms. It may be that the pygmy, unable to compete for food in the inshore nursery areas of these species, has been forced into deeper, less productive water.

The pygmy whitefish might have reacted to competition and the supposedly decreased food supply by a drastic reduction in numbers rather than by an equally drastic reduction in size of individuals. Dwarfed races of otherwise normal species are often encountered in competitive situations. Evidently dwarfing gives these species some advantage in competition with larger ones. Lindström and Nilsson (1962) suggest that the shorter life span and more rapid population turnover of dwarf fish may result in a greater utilization of the available resources and thus afford them a greater measure of success in competition.

To answer the original question, then, there does appear to be some indication of interactive segregation between the pygmy whitefish and the two other whitefishes which results in distinct differences in depth distribution and growth rate. The evidence is hardly conclusive however, and until the fish are subjected to a greater measure of experimental control, no definite conclusions are possible.

SUMMARY

1) An analysis of meristic variation in twelve populations of pygmy whitefish inhabiting British Columbia and Alaska revealed a high degree of variability both within and between populations.

2) A latitudinal comparison of means of meristic characters for these and five additional populations revealed a tendency, in counts of anal rays and vertebrae, toward an increase in parts in the more southerly populations. The same tendency may be present in counts of pectoral rays and pyloric caeca. Lateral line scale counts seem to vary randomly. The relation between gill raker counts and latitude appears to be V-shaped.

3) Age and growth was determined for four British Columbia lakes using the scale diameter measurement. Other scale dimensions were unusable because of inflections in the scale-body relationship subsequent to the first annulus (antero-lateral ridge and anterior radius) or because the annuli were unclear (scale length).

4) As adults, MacLure pygmy whitefish are largest, followed in order by fish from McLeese, Cluculz and Tacheeda Lakes. Adult size is correlated with the rate of decline of the instantaneous annual growth rate (i).

5) In MacLure Lake pygmy whitefish were not all mature until age IV. In the other three, most fish were mature at age II.

6) Analysis of covariance reveals that the dwarf pygmys of Cluculz and Tacheeda Lakes have significantly larger eyes, larger heads, longer maxillaries, shallower bodies, narrower interorbital width, and longer paired and median fins. Predorsal length does not appear to vary in any predictable manner. The width of the anal base appears to be related to the number of anal rays. Length of the dorsal base is not related to the number of fin elements.

7) The dwarf fish of Cluculz and Tacheeda lakes inhabit much deeper water than those of McLeese and MacLure Lakes.

8) Pygmy whitefish appear to be restricted to a diet of small bottom and planktonic organisms. There was no apparent difference between the diets of fish from the four lakes.

9) There may be a relationship between the absence of other whitefish species and the large size of pygmy whitefish

in McLeese and MacLure Lakes.

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