

# Growth and Morphometry of Four British Columbia Populations of Pygmy Whitefish (*Prosopium coulteri*)<sup>1,2</sup>

BY P. McCART

*Fisheries Research Board of Canada  
Biological Station, Nanaimo, B. C.*

## ABSTRACT

A comparison is made of the growth, morphometry, age at maturity, food, and depth distribution of pygmy whitefish (*Prosopium coulteri*) in four British Columbia lakes. In Tacheeda and Cluculz Lakes where the species is of the usual dwarfed variety, the fish exists sympatrically with two other whitefishes, the mountain whitefish (*Prosopium williamsoni*) and the lake whitefish (*Coregonus clupeaformis*). These slow-growing pygmy whitefish differ markedly in morphometry and depth distribution from the "giant" pygmy whitefish of McLeese and Maclure Lakes which live in the absence of other whitefishes. The possibility that differences in the populations might be due to interspecific competition is discussed.

## INTRODUCTION

ESCHMEYER AND BAILEY (1955), in reporting the discovery of a relict population of the pygmy whitefish (*Prosopium coulteri*) in Lake Superior reviewed the meristics, morphology, growth, and life history of the species in considerable detail. However, aside from a few localities in the Columbia River drainage, information concerning the biology of the pygmy whitefish in British Columbia, a large segment of its known range, was unavailable to them. The present study examines the growth, morphometry, and life history of four populations of pygmy whitefish from British Columbia.

## MATERIALS AND METHODS

Measurements of standard length and various body parts were obtained from preserved specimens selected from those available for age and growth studies. No correction was made for possible discrepancies due to the effect of preservatives (initially 40% formalin and then 40% isopropyl alcohol). Measurements 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. With two exceptions, the measurements were made exactly as described in Hubbs and Lagler (1949). The exceptions were:

*Body depth* — measured as the distance from the insertion of the dorsal fin to the anterior of the pelvic fin;

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*Length of eye* — measured as the midline distance from the posterior margin of the eyeball to the anterior fold of the vestigial adipose eyelid as indicated in Fig. 1.

#### AGE AND GROWTH

All fork lengths and scale samples were obtained from preserved fish collected by the author during the summer of 1962 and the fall of 1963. The fish were captured in monofilament gillnets of two kinds: nets approximately 8 ft deep and 50 ft long of size 0.5, 0.75, 1.0, 1.5, 2.0, and 2.5 inch stretch measure and nets 25 ft deep and 50 ft long of 1.5, 2.0, and 2.5 inch mesh. Nets were fished in gangs at known depths for periods of from 4 to 36 hr; generally about 12 hr.

Fork lengths were obtained using a measuring board. Sex and state of maturity were determined at the same time. Several scales were taken from each fish from an area midway between the dorsal fin and the lateral line. These were cleaned by gentle scraping and mounted dry between glass slides. One scale, adjudged most readable, was selected for purposes of aging and back-calculation. Measurements of annuli were made at a magnification of  $\times 43.8$  using a Bausch and Lomb slide projector. A simple nomograph was used in calculating the lengths of fish at the time of annulus formation.

Age and growth determinations were made for a total of 437 pygmy whitefish: 114 from Tacheeda, 155 from Cluculz Lake, 60 from McLeese Lake, and 108 from Maclure Lake. The samples from the first three lakes include virtually all the fish captured during the summer of 1962. With the exception of a few fish in the 10–12-cm length range which were specifically selected by the author, the Maclure Lake sample was chosen at random from a total of about 500 fish netted during 1962.

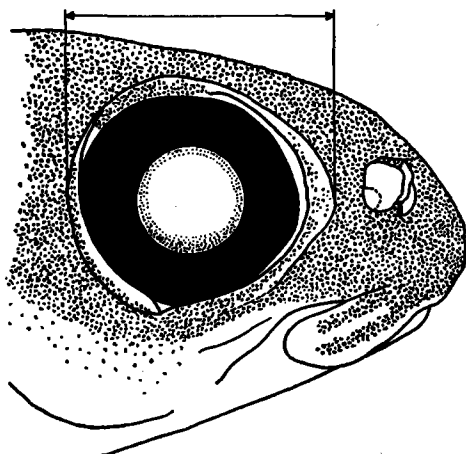


FIG. 1. Method of measuring length of eye.

## HABITAT

Table I presents the available physical, chemical, and biological data for each of the four lakes. None has been the subject of intensive limnological investigation.

TABLE I. Available limnological information and known fish fauna of four British Columbia lakes.

	Tacheeda	Cluculz	McLeese	Maclure
Elevation (ft)	2382	2500	2400	1800
Maximum depth (ft)	195	200	152	73
Mean depth (ft)	57.4	97	53.6	36.4
Total dissolved solids (ppm)	52	118	250	208
Surface area (acres)	1460	6223	841	785
Trout and char				
<i>Salvelinus namaycush</i>	x <sup>a</sup>	x	..	..
<i>S. malma</i>	x	x	..	..
<i>Salmo gairdneri</i>	x	x	x	x
<i>Oncorhynchus nerka</i>	..	x	..	..
Whitefish				
<i>Prosopium coulteri</i>	x	x	x	x
<i>P. williamsoni</i>	x	x	..	..
<i>Coregonus clupeaformis</i>	x	x	..	..
Suckers				
<i>Catostomus macrocheilus</i>	..	x	x	..
<i>C. commersoni</i>	x	x	..	..
<i>C. catostomus</i>	x	x	x	x
Minnows				
<i>Richardsonius balteatus</i>	x	x	x	x
<i>Ptychocheilus oregonensis</i>	x	x	x	x
<i>Mylocheilus caurinus</i>	x	x	x	x
Sculpins				
<i>Cottus asper</i>	x	x	..	x
Burbot				
<i>Lota lota</i>	..	x	..	..

<sup>a</sup>Indicates species present.

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

Northcote and Larkin (1956) have demonstrated a direct relationship between TDS and productivity in British Columbia lakes. If so, we might expect Maclure and McLeese Lakes to be more productive than Tacheeda and Cluculz. Impressions gained in the field and the predominantly salmonid fauna do indicate a greater degree of oligotrophy in the latter pair of lakes.

Figure 2 indicates the location of the four lakes along with other areas in which the pygmy whitefish has been collected in British Columbia.

Eschmeyer and Bailey (1955) suggested that during the late Pleistocene the pygmy whitefish was a common and continuously distributed species along the periphery of the ice sheet. Adapted to such an existence, the species has been able to survive as only a few relict populations inhabiting some of the coldest waters of the United States, western Canada, and Alaska. This view stands in some need of correction. First, the pygmy whitefish is, at least in British Columbia, much more common than formerly supposed and has been taken in five major drainages: the Columbia, Fraser, Skeena, Mackenzie, and Yukon Rivers. Second, the species is not necessarily restricted to cold streams

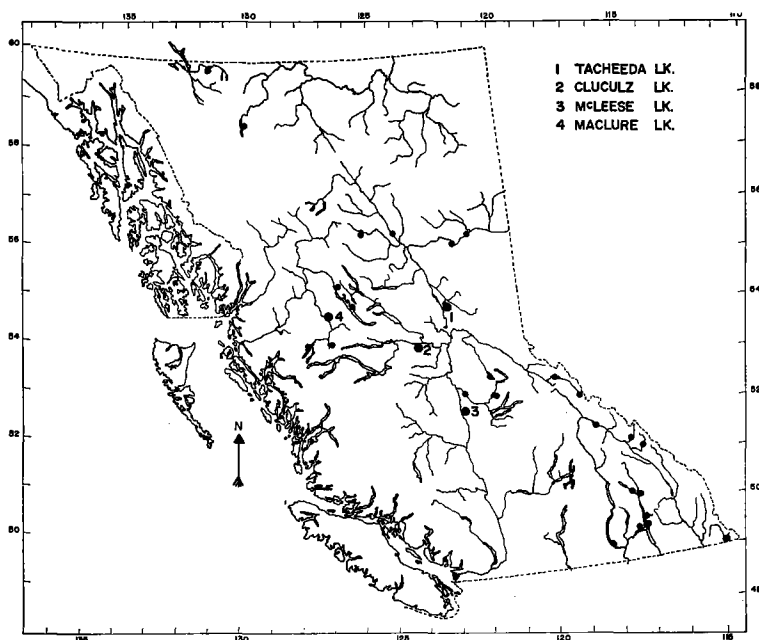


FIG. 2. Map of British Columbia showing the location of the four study lakes and other localities in which the pygmy whitefish has been captured.

and oligotrophic lakes. Its very presence in shallow, eutrophic Maclure Lake disputes this. In this lake, individuals are not only large in size but extremely abundant.

## RESULTS

### AGE AND GROWTH

The length and age distributions reflect the highly selective nature of gillnet sampling (Tables II-V). For example, 47 of the 60 fish (78%) of the McLeese Lake sample are in age group III, and fall within a range of only 4 cm. If there are significant annual fluctuations in growth, calculations based on this sample will have only limited applicability. In the other three samples, at least two or more year-classes are adequately represented.

The only previous attempt to apply the techniques of back-calculation to the pygmy whitefish was that of Eschmeyer and Bailey (1955). They measured scale diameters along the cephalo-caudal axis and calculated *total* lengths from scale measurements by direct proportion. As a preliminary to the present study, the relationship between *fork* length and several scale dimensions was examined. Two of these, the cephalo-caudal and dorso-ventral axes had an approximately linear relationship to fork length but in neither case was the relationship directly proportional. Of the two scale dimensions, the dorso-ventral axis was preferred because of difficulty in identifying annuli along the posterior margin of the scale, especially in older fish.

Because of the length distribution of the samples, reliable body-scale relationships could not be calculated for fish from three lakes, Tacheeda, Cluculz, and McLeese. Instead, back-calculation was carried out using an intercept derived from a sample of 88 fish from Kinbasket Lake. These fish ranged in size from 2.5 to 12.3 cm and were selected to provide a fairly even distribution over the available size range. The Kinbasket Lake population has a typical "pygmy" growth form and the calculated body-scale relation might be generally characteristic. In any case, lengths calculated using the Kinbasket Lake intercept seem to accord fairly well with the measured lengths of same-age fish taken in gillnets. The equation was:

$$L = 1.3241 + .0080 S$$

where L = fork length of fish (cm), and S = dorso-ventral dimension ( $\times 43.8$  in mm).

The lengths of the Maclure Lake sample extended over a wide range and the body-scale relationship of these fish was calculated separately and used in back-calculating the lengths of the sample. The equation used was:

$$L = 0.3888 + 0.0110 S$$

Back-calculation was carried out according to the formula:

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

TABLE II. Length distribution of age groups of *P. couleri* in gill-net samples from Tacheeda Lake.

Length interval (cm)	Age group												Total		
	I		II		III		IV		V		VI		M	F	M + F
	M	F	M	F	M	F	M	F	M	F	M	F			
7.6-8.0	..	..	1	1	..	..	..	..	..	..	..	..	1	1	2
8.1-8.5	2	3	1	..	..	..	..	..	..	..	..	..	3	3	6
8.6-9.0	..	..	2	..	..	..	..	..	..	..	..	..	2	..	2
9.1-9.5	..	..	1	..	..	..	..	..	..	..	..	..	1	..	1
9.6-10.0	..	..	1	1	..	..	..	..	..	..	..	..	1	1	2
10.1-10.5	..	..	..	2	1	2	..	..	..	..	..	..	1	4	5
10.6-11.0	..	..	1	9	1	7	..	1	..	..	..	..	2	17	19
11.1-11.5	..	..	..	2	1	19	..	7	..	..	..	..	1	28	29
11.6-12.0	..	..	..	..	..	15	..	6	..	..	..	..	..	21	21
12.1-12.5	..	..	..	..	..	2	..	15	..	2	..	..	..	19	19
12.6-13.0	..	..	..	..	..	..	..	2	..	4	..	..	..	6	6
13.1-13.5	..	..	..	..	..	..	..	..	..	1	..	..	..	1	1
13.6-14.0	..	..	..	..	..	..	..	..	..	..	..	1	..	1	1
Total number:	2	3	7	15	3	45	0	31	0	7	0	1	12	102	114
Average length:	8.2	8.4	9.0	10.6	10.8	11.4	..	12.0	..	12.6	..	13.6			

TABLE III. Length distribution of age groups of *P. coulteri* in gill-net samples from Cluculz Lake.

Length interval (cm)	Age group												Total		
	I		II		III		IV		V		VI		M	F	M + F
	M	F	M	F	M	F	M	F	M	F	M	F			
8.0-8.5	..	1	..	..	..	..	..	..	..	..	..	..	..	1	1
8.6-9.0	1	..	..	..	..	..	..	..	..	..	..	..	1	..	1
9.1-9.5	1	..	..	..	..	..	..	..	..	..	..	..	1	..	1
9.6-10.0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
10.1-10.5	..	..	..	..	1	..	..	..	..	..	..	..	1	..	1
0.6-11.0	..	..	..	2	2	..	..	..	..	..	..	..	2	2	4
11.1-11.5	..	..	2	..	7	10	2	3	1	..	..	..	12	13	25
11.6-12.0	..	..	..	1	6	17	2	3	1	..	..	..	9	21	30
12.1-12.5	..	..	..	..	4	20	5	15	2	..	..	..	11	35	46
12.6-13.0	..	..	..	..	..	8	1	12	1	1	..	..	2	21	23
13.1-13.5	..	..	..	..	..	1	..	12	..	..	..	..	..	13	13
13.6-14.0	..	..	..	..	..	..	..	2	..	2	..	..	..	4	4
14.1-14.5	..	..	..	..	..	..	..	..	..	1	..	..	..	1	1
14.6-15.0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
15.1-15.5	..	..	..	..	..	..	..	1	..	2	..	1	..	4	4
15.6-16.0	..	..	..	..	..	..	..	..	..	..	..	1	..	1	1
Total number:	2	1	2	3	20	56	10	48	5	6	0	2	39	116	155
Average length:	9.2	8.1	11.3	11.0	11.6	12.1	11.6	12.7	12.2	14.2	..	15.6			

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TABLE IV. Length distribution of age groups of *P. coulteri* in gill-net samples from McLeese Lake.

Length interval (cm)	Age group										Total		
	I		II		III		IV		V		M	F	M + F
	M	F	M	F	M	F	M	F	M	F			
10.0-11.0	..	..	1	3	..	..	..	..	..	..	1	3	4
11.1-12.0	..	..	2	1	..	..	..	..	..	..	2	1	3
12.1-13.0	..	..	..	..	..	..	..	..	..	..	..	..	..
13.1-14.0	..	..	..	..	..	..	..	..	..	..	..	..	..
14.1-15.0	..	..	..	..	5	4	..	..	..	..	5	4	9
15.1-16.0	..	..	..	..	3	19	..	..	..	..	3	19	22
16.1-17.0	..	..	..	..	3	10	..	..	..	..	3	10	13
17.1-18.0	..	..	..	..	..	3	1	..	..	..	1	3	4
18.1-19.0	..	..	..	..	..	..	..	..	..	1	..	1	1
19.1-20.0	..	..	..	..	..	..	..	1	..	3	..	4	4
Total number:	0	0	3	4	11	36	1	1	0	4	15	45	60
Average length:	..	..	11.1	10.9	15.3	15.8	17.8	19.4	..	19.4			



TABLE V. Length distribution of age groups of *P. couleri* in gill-net samples from Maclure Lake.

Length interval (cm)	Age group																		Total		
	I		II		III		IV		V		VI		VII		VIII		IX				
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M + F
10.0-11.0	..	..	12	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	12	9	21
11.1-12.0	..	..	6	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	1	7
12.1-13.0	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	2
13.1-14.0	..	..	4	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	3	7
14.1-15.0	..	..	6	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	1	7
15.1-16.0	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1
16.1-17.0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
17.1-18.0	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	1	1	2
18.1-19.0	..	..	..	..	3	1	2	..	1	..	..	..	..	..	..	..	..	..	6	1	7
19.1-20.0	..	..	..	..	1	4	1	1	..	..	..	..	..	..	..	..	..	..	2	5	7
20.1-21.0	..	..	..	..	..	2	1	..	..	..	1	..	..	..	..	..	..	..	2	2	4
21.1-22.0	..	..	..	..	..	..	7	4	..	..	..	..	..	..	..	..	..	..	7	4	11
22.1-23.0	..	..	..	..	..	..	2	1	..	1	2	..	..	..	..	..	..	..	4	2	6
23.1-24.0	..	..	..	..	..	..	..	3	..	1	1	2	..	..	..	..	..	..	1	6	7
24.1-25.0	..	..	..	..	..	..	..	..	..	5	..	3	..	..	..	..	..	..	..	8	8
25.1-26.0	..	..	..	..	..	..	..	..	..	3	..	4	..	2	..	..	..	..	..	9	9
26.1-27.0	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	1	1
27.1-28.0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	1	1
Total number:	0	0	30	15	4	8	14	9	1	10	4	9	0	3	0	0	0	1	53	55	108
Average 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			

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where  $L_n$  is the length of the fish at the end of the  $n$ th year of life,  $I$  is the intercept of the body-scale relationship,  $L_t$  is the length of fish at capture,  $S_t$  is the diameter of the scale at capture, and  $S_n$  is the diameter of the scale within the  $n$ th annulus. In practice, the calculation was performed using a simple nomograph.

All fish in the 1962 samples showed evidences of new scale growth by the end of May, placing the termination of annulus formation somewhere at the end of April or early in May. Annuli were easily identified except in fishes of advanced age where increments of growth were very small and annuli consequently very close together, and certain fish from McLeese Lake where the annuli tended to be very indistinct, especially early in life. This latter phenomenon may be related to the rapid initial growth of these fish. Any fish scale in which the position of one or more annuli was still questionable after three readings was discarded. The calculated lengths of fish at various ages are given for the four lakes in Tables VI-IX.

In each population, male fish grow at about the same rate as females for the first 2 years of life. Subsequently, there is an increasing disparity in growth, presumably related to the onset of sexual maturity, which differentially affects the sexes. The difference in growth rate is, in some cases, probably even more pronounced than the figures indicate due to the selective effect of gillnet sampling. In Tacheeda Lake, the extreme case, only 12 male fish were taken during the entire summer. There is no reason to believe that the extremely unequal sex ratio in the sample is characteristic of the population, or that the disproportionate number of females is the result of sampling in areas where females are more likely to be found. Probably, most of the males never reach a sufficient size to become available to the gillnets used. Significantly, most of the males were taken during September at a time when they could be approaching their maximum seasonal growth. The sample probably contains only the faster-growing or longer-lived males, and therefore presents a biased picture of male growth rates.

The absence of males from the older age groups in the samples suggests that the slow growth of this sex is coupled with a higher mortality. Because of the poor representation of males in some samples, only the growth of female fish is compared. Figure 3 compares the calculated lengths and annual growth increments of female fish at the end of each year of growth. The figure shows that McLeese Lake pygmy whitefish grow fastest during their first year of growth and are larger than fish from other populations through their third year of life. By the end of their fourth year, however, Maclure Lake fish are larger than those in McLeese and remain so subsequently. Cluculz and Tacheeda pygmy whitefish, whose growth is very like that of Maclure Lake fish during their first and second year, fail to keep pace thereafter.

Growth increments are small after the attainment of maturity and there is considerable overlap in the length distributions of the mature age-groups in three of the samples. The same would probably be true of McLeese Lake fish were the sample larger.

TABLE VI. Calculated fork length (*cm*) at end of each year of life for each age group and average growth for the combined age groups of *P. coulteri* from Tacheeda Lake.

	Age group												Grand average calculated length		Increment of average	
	I		II		III		IV		V		VI					
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Number of fish	2	3	7	15	3	45	0	31	0	7	0	1				
1	5.8	5.8	5.7	6.1	6.4	5.8	..	5.8	..	5.7	..	6.2	5.9	5.8	5.9	5.8
2	..	..	8.0	8.9	8.6	8.5	..	8.5	..	7.9	..	8.4	8.2	8.5	2.3	2.7
3	..	..	..	..	10.0	10.5	..	10.4	..	10.2	..	10.8	10.0	10.5	1.8	2.0
5	..	..	..	..	..	..	..	11.4	..	11.5	..	11.1	..	11.4	..	0.9
5	..	..	..	..	..	..	..	..	..	12.4	..	12.1	..	12.3	..	0.9
6	..	..	..	..	..	..	..	..	..	..	..	13.4	..	13.4	..	1.1

TABLE VII. Calculated fork length (*cm*) at end of each year of life for each age group and average growth for the combined age groups of *P. coulteri* from Cluculz Lake.

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

TABLE VIII. Calculated fork length (*cm*) at end of each year of life for each age group and average growth for the combined age groups of *P. couleri* from McLeese Lake.

		Age group										Grand average calculated length		Increment of average	
		I		II		III		IV		V					
		M	F	M	F	M	F	M	F	M	F	M	F	M	F
Number of fish		0	0	3	4	11	36	1	1	0	4				
Calculated length at end of year	1	..	..	6.5	7.1	7.3	7.0	6.6	6.4	..	6.7	7.1	7.0	7.1	7.0
	2	..	..	9.5	9.5	11.2	10.9	9.7	9.8	..	9.5	10.8	10.6	3.7	3.6
	3	..	..	..	..	14.6	14.8	13.7	15.2	..	13.1	14.5	14.6	3.7	4.0
	4	..	..	..	..	..	..	16.7	17.8	..	16.8	16.7	17.0	2.2	2.4
	5	..	..	..	..	..	..	..	..	..	18.5	..	18.5	..	1.5

TABLE IX. Calculated fork length (*cm*) at end of each year of life for each age group and average growth for the combined age groups of *P. coulteri* from Maclure Lake.

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

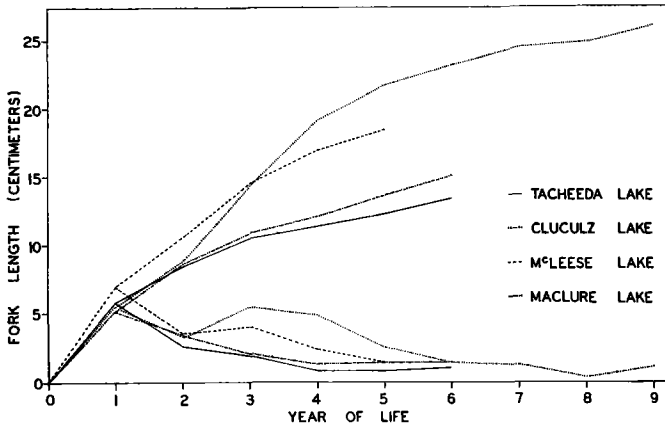


FIG. 3. Calculated lengths and annual growth increments of *P. couleri* from four British Columbia lakes.

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." Table X presents the mean fork length in centimeters and the instantaneous annual growth rate of fish in the four lakes.  $L_t$  and  $L_{t+1}$  are, respectively, the average length of the 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

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

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

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

The average instantaneous annual growth rate is plotted against mean size in Fig. 4. Instantaneous rates for year 0 have not been computed because the initial size of the fish is unknown.

Most fishes attain their highest rate of growth during their first year of life and thereafter the rate declines. In Tacheeda and Cluculz Lakes the decline in growth rate is very rapid at first but seems to become stabilized at low levels as the fish grow. McLeese Lake fish also show a decreasing rate of growth with increasing size but the decline is much less precipitous than in either Tacheeda or Cluculz Lakes. As a consequence, moderately high growth rates

TABLE X. Mean fork length (cm) and instantaneous annual growth rates of female pygmy whitefish in four British Columbia lakes.

Age group	I	II	III	IV	V	VI
<i>Tacheeda</i>						
$L_t$	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	..
<i>Cluculz</i>						
$L_t$	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	..
<i>McLeese</i>						
$L_t$	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	..	..
<i>Maclure</i>						
$L_t$	5.4	8.7	14.3	19.2	21.8	23.3
$L_{t+1}$	8.7	14.3	19.2	21.8	23.3	24.6
Mean size	6.85	11.15	16.60	20.45	22.52	23.94
$i$	.20713	.21582	.12796	.05516	.02890	.02358

are maintained over a wide range of sizes. Growth rates continue to decline, however, and there is no evidence of a low-level stabilization.

The Maclure Lake population is exceptional in that, during part of their second and third years, the instantaneous growth rate is actually increasing and this accelerated growth continues until the fish have reached a length of over 11 cm. It is as a result of this increased rate of growth that Maclure pygmy whitefish overtake and surpass in size, same-age fish from McLeese Lake. In *Salmo gairdneri*, irregularities in the decline of growth rate with length have been attributed to changes in niche which are a function of size, specifically, a change from plankton-feeding to piscivorous habits (Larkin



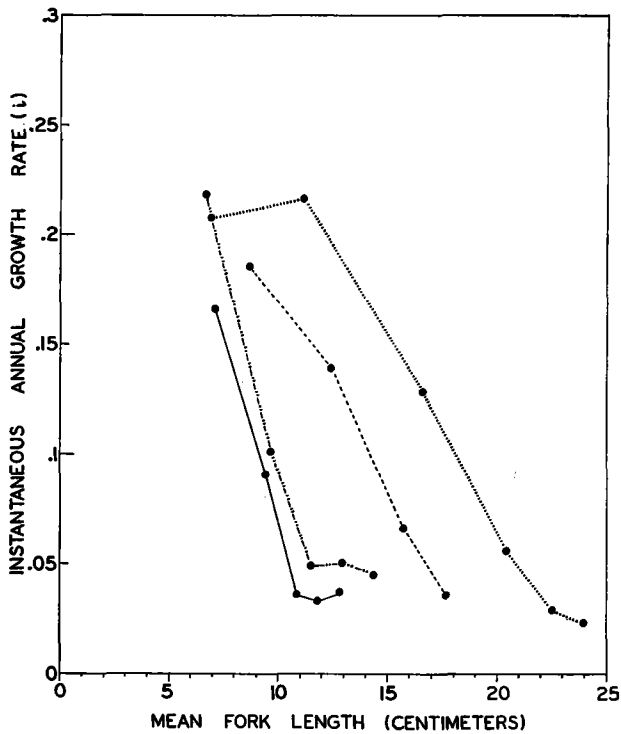


FIG. 4. Size specific, average instantaneous annual growth rate of *P. coulteri* from four British Columbia lakes. Symbols as in Fig. 3.

*et al.*, 1957). Conceivably, the exceptional increase in the instantaneous growth rate of Maclure Lake pygmy whitefish results from the attainment of some size threshold which makes available to them an hitherto unavailable environmental resource. It is not known what this might be.

At lengths above 11 cm the growth rates of Maclure Lake fish go into a moderate decline similar to that of McLeese Lake pygmy whitefish. Again, there is no evidence that growth rates tend to stabilize at low levels.

The size attained by mature fish in Cluculz and Tacheeda Lakes seems to be typical of pygmy whitefish in British Columbia. The pygmy whitefish in McLeese and Maclure Lakes, however, attain sizes beyond anything reported for this species in British Columbia or indeed anywhere else, although fish in Bull Lake, Montana, appear to grow faster during their first 2 years of life (Weisel and Dillon, 1954).

#### AGE AT MATURITY

Table XI presents data concerning the maturity and age of fish in the 1962 collections. Mature fish are those judged ready to spawn in the winter of 1962-63. In most cases, fish were mature by the end of their third summer

TABLE XI. Age at maturity of pygmy whitefish from four British Columbia lakes.

Age group:	Tacheeda				Cluculz				McLeese				Maclure			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
No. males	2	6	3	0	2	2	21	8	0	3	11	1	0	30	4	14
Percentage maturing	0	67	100	-	0	100	100	100	-	100	100	100	-	20	50	100
No. females	3	17	46	31	1	3	56	46	0	4	35	1	0	15	8	9
Percentage maturing	0	100	100	100	0	100	100	96	-	100	100	100	-	0	75	100

(age-group II). Exceptions were Maclure Lake fish of both sexes which were not 100% mature until age-group IV, and Tacheeda Lake males which were not all mature until age III. In all four lakes, age V and older fish of both sexes were 100% mature. In Lake Superior (Eschmeyer and Bailey, 1955) all age-group II males were mature but females matured more slowly and were not 100% mature until age IV, the end of their fifth summer. Weisel and Dillon (1954) found numerous age-I fish spawning in Bull Lake, Montana. These fish have an extremely rapid growth during their first 2 years of life and the early age of maturation may reflect this. Unfortunately, no samples of age-I fish were available from McLeese Lake, another population with rapid initial growth. All available age-II fish from this lake were ripe, and it is quite possible that at least some fish mature at age I.

#### SPAWNING TIME

Eschmeyer and Bailey (1955) fix the spawning period of pygmy whitefish in most localities at some time during November or December. Weisel and Dillon (1954) found pygmy whitefish spawning at the end of December in Bull Lake, Montana. Eschmeyer and Bailey report ripe fish taken in a November 17 collection from Lake MacDonald, Montana. In British Columbia, pygmy whitefish have not yet been observed spawning but indirect evidence points to a similar spawning period. Fish collected as late as September 20, 1962, in the four study lakes were still apparently some time from spawning. Eggs were small in size and tightly bound. Milt could not be expressed from male fish. Nuptial tubercles were not in evidence though these are present on both sexes during spawning (Weisel and Dillon, 1954). Twelve females netted in Kinbasket Lake on November 6, 1963, appeared to be spawned out. Of a collection of 12 males and two females made in the Kinbasket River during the last week of October, 1962, seven males and both females appeared to be spawned out. This lake, a widening in the Columbia River, is fed by cold waters largely of glacial origin and the spawning period here is probably somewhat earlier than in the four study lakes.

In these lakes no ripe fish was taken in the earliest spring collections made during May 1962, although several males from Cluculz Lake still retained their nuptial tubercles. However, three females collected during mid July in Cluculz Lake appeared to be ripe and released large eggs freely when squeezed. One of these was collected in 1962 and the others in 1963. Examination indicated that at least two of these contained hard, compact masses of large eggs in addition to free-running eggs of normal appearance. At the moment, it seems best to regard these as fish which, for some reason, had failed to spawn the previous winter and had retained their burden of eggs.

It is likely that, in McLeese Lake, spawning takes place in the lake. Residents of the area, when questioned, could not recall having seen whitefish in either inlet or outlet streams and were unaware of the presence of whitefish in the lake. Residents of the Cluculz Lake area were also unable to recall

having seen fish of this size spawning in streams but here, due to the size and inaccessibility of suitable streams, they may have been overlooked.

### RELATIVE GROWTH

Marr (1955) emphasized that the use of body dimensions expressed as *per cent* or *per mille* of standard length can lead to confusing and doubtful conclusions, and recommended instead the wider use of regression analysis of the original data as a tool in the interpretation of relative growth. In the present study, a series of 12 measurements was made on fish from the four lakes. The fish measured were selected to provide as even a size distribution as possible consistent with a minimum sample of 60 fish from each lake. Even so, some size groups are considerably over-represented in the sample, especially the middle sizes of female fish from Tacheeda, Cluculz, and McLeese Lakes.

The data were converted to natural logs and a linear regression of size of body part against standard length was carried out for males and females separately, and then for the sexes combined. There were no obvious departures from linearity. The results were compared using covariance techniques to determine first, whether the males and females within populations differed in the size of a particular part, and secondly, whether there were significant differences between populations. Because of the small size and uneven length distribution of the samples, only differences significant at the 1% level were considered to be valid. Complete data are included in an appendix.

Other than head length, which differed significantly between males and females in the McLeese Lake sample, sexual dimorphism was apparent only in the measurements of various fins.

In most instances, the differences between males and females were differences in the adjusted means. Slope differences occurred only in the relations of the height of the dorsal and length of pectoral fins to standard length in the Maclure Lake sample. In every case in which significant sexual differences occurred the measurements of male body parts were greater in relation to standard length than those of females. The greater length of male fins is probably, as Eschmeyer and Bailey suggest, an adaptation to their function in the spawning act. The differences in fin dimensions (and head length in the McLeese sample) may, however, be related in part to the differing growth rate of the sexes.

The lengths of the male and female pectoral and pelvic fins in relation to standard length were significantly different in all four populations. Although the height of the dorsal fin was sexually dimorphic in three samples the length of the dorsal base did not vary significantly between sexes in any of the four lakes. The anal fin varied in both length and base in the Tacheeda and McLeese Lake samples but not in the Cluculz or Maclure samples.

Males were most different from females in McLeese Lake where they differed significantly in six measurements, and least different in Maclure and Cluculz Lakes where they differed in only three.

Graphs relating the common logarithm of various body parts to the common logarithm of standard length have been prepared to illustrate some examples of sexual dimorphism (Fig. 5). Shown are the two instances in which the slopes of the male and female regressions differ significantly: the height of the dorsal fin and the length of the anal fin in the Maclure Lake sample. In both cases the male fin dimension is initially very like that of the female but becomes proportionately larger with growth. The other graphs illustrate differences in the adjusted mean size of body parts, the more usual form of sexual dimorphism.

In comparisons between populations (Fig. 6), data for males and females combined were used wherever there was no demonstrated differences between the sexes. Where there is significant sexual dimorphism in even a single population, female fish only were compared as these were best represented in the samples. In every case, there are significant differences in measurements.

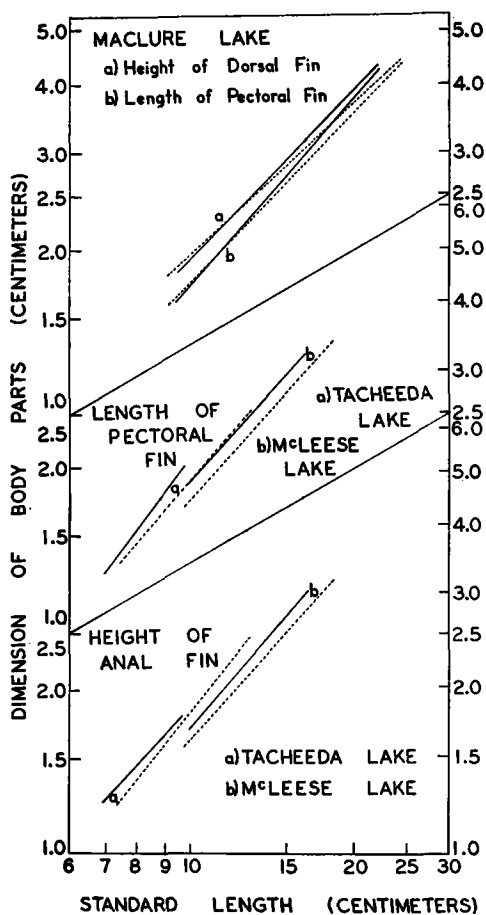


FIG. 5. Some examples of sexually dimorphic growth of body parts in *P. couleri*. Males solid lines, females dotted lines.

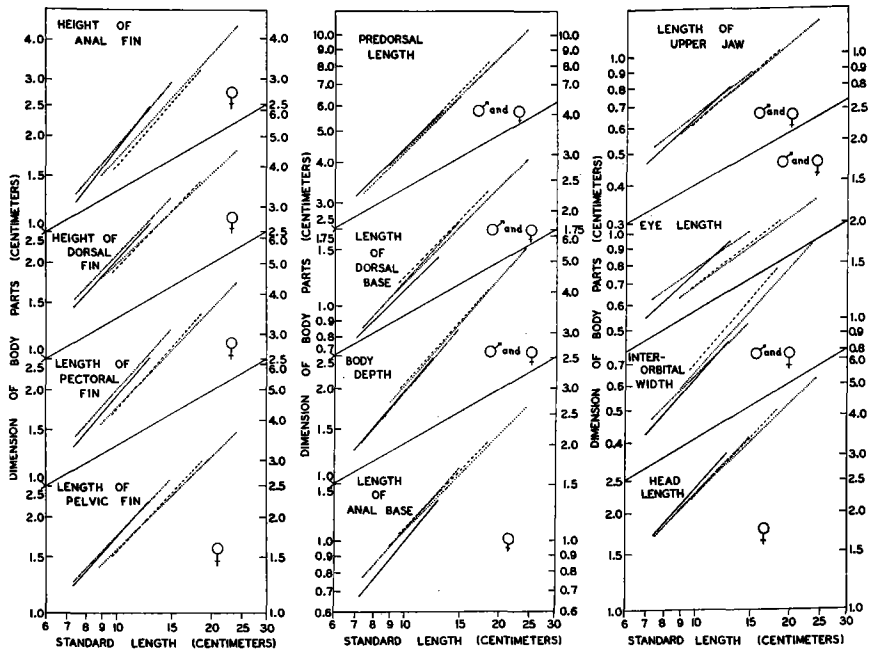


FIG. 6. Relative growth of some body parts in four British Columbia populations of *P. coulteri*. Symbols as in Fig. 3.

The regression lines for the two dwarf populations indicate that they have larger eyes, longer heads, longer maxillaries, shallower bodies, and a narrower interorbital width than the larger fish from Maclure and McLeese Lakes. They also have longer paired and median fins. However, the lengths of the dorsal and anal fin bases and predorsal length do not appear to vary in relation to the growth of the populations.

A relationship between rate of growth and relative size of body parts has been noted in other whitefishes. Svärdson (1950), in a series of transfer experiments involving two species of whitefishes, found that in each case the more slowly growing population of the same species had larger heads, shallower bodies, larger eyes, and long maxillaries. Koelz (1929) showed that slow-growing lake whitefish, *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. Godfrey (MS, 1948), comparing the lake whitefish of Morrison and Babine Lakes, found that the smaller Morrison Lake fish had, with the exception of the anal fin, larger fins and larger eyes.

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.

## DEPTH DISTRIBUTION

The depth distribution of whitefishes in the four lakes is shown in Fig. 7. The figure summarizes data for all bottom gillnet sets made during 1962 as the catch per unit of effort for each depth stratum. The unit of effort, the net-hour, was defined as a single 50-ft long, 8-ft deep, monofilament nylon net fished for a period of 1 hr. Catches in 25-ft nets were not used because these were not consistently employed. The data are given for 20-ft depth intervals except for Maclure Lake where the catches were determined for each 10-ft stratum. The depth distributions of lake whitefish and mountain whitefish, *Prosopium williamsoni*, in Cluculz and Tacheeda have been included.

Figure 7 shows two distinct patterns of depth distribution. In both McLeese and Maclure Lakes, pygmy whitefish extended from a depth of about 15 ft downward to depths of 70 and 50 ft, respectively. Extensive netting in deeper waters failed to produce pygmy whitefish. In the other two lakes, Cluculz and Tacheeda, the upper limit of distribution is about 35 ft and fish are numerous as far down as the limit of netting, 120 ft in Cluculz and 100 ft in Tacheeda Lake.

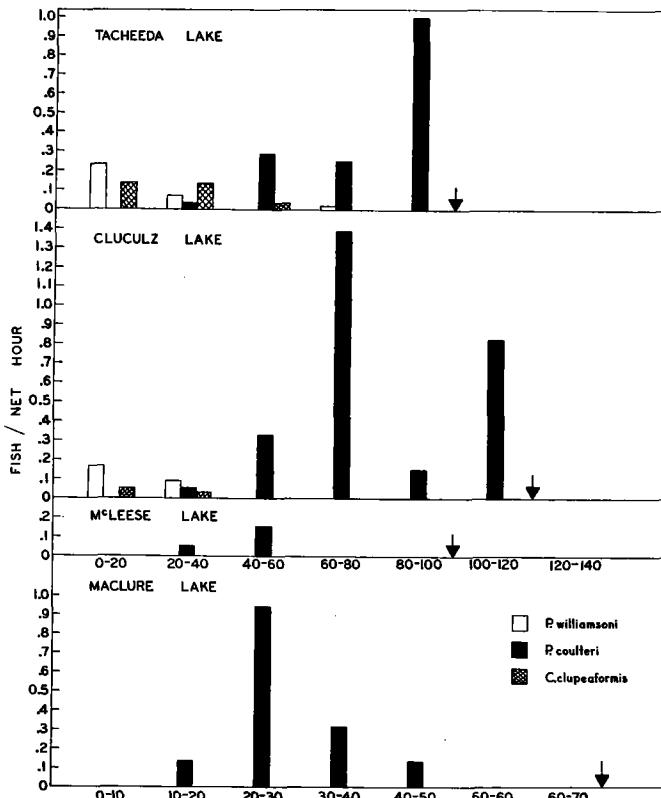


FIG. 7. Depth distribution of whitefishes in four British Columbia lakes. The arrows indicate the lower limit of gill-netting.

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 largely the result of competitive exclusion by the other two whitefish. Both of these, the lake whitefish and the mountain whitefish, are most abundant inshore and their lower limit of distribution almost exactly coincides with the upper limit of pygmy whitefish distribution. The lumping of data partly obscures this. Although all three whitefish often occurred in the same depth stratum, rarely was another species of whitefish found deeper than a pygmy whitefish in a net. Exceptions were a mountain whitefish taken June 20-21 in the 60-80-ft stratum in Tacheeda Lake and four lake whitefish taken in 50 ft of water on July 21 in Tacheeda Lake.

The shallow lower limit of pygmy distribution in Maclure and McLeese Lakes may be due to low oxygen tensions in the bottom waters. Both lakes have high TDS values and seem quite productive. On July 31, 1962, the waters of Maclure Lake from 33 ft to the bottom contained only 2.4 mg/litre 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 ft in Cluculz Lake contained 4.4 mg/litre of oxygen.

There is no evidence of any diurnal vertical or horizontal (inshore-offshore) movements in the pygmy whitefish. There is evidence, however, of an offshore movement into somewhat deeper water during late spring. In shallow Outlet Bay, Cluculz Lake, numerous pygmy whitefish were taken at depths of 25-30 ft during May. Nets set in the same area later in the summer failed to take any pygmy whitefish. Apparently the fish had moved out of Outlet Bay into the deeper waters of the main lake. 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 occurred, the pygmy whitefish was 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 15 and 20 ft where the redbelt shiner (*Richardsonius balteatus*), peamouth chub (*Mylocheilus caurinus*), and squawfish (*Ptychocheilus oregonensis*), were all common but below this depth, nets contained pygmy whitefish almost exclusively.

#### FOOD HABITS

Only limited study has been made of the food of whitefishes in the four lakes. Small numbers of pygmy whitefish stomachs were examined from each lake. In addition, the contents of some mountain and lake whitefish stomachs from Cluculz Lake were recorded. The results are shown in Table XII.

In samples from each of the lakes the diet of the pygmy whitefish was largely restricted to two or three forms. Except for Cluculz Lake, the three most important food items are cladocerans, midge larvae and pupae, and



TABLE XII. Estimated percentage volume of food items in whitefish stomachs.

	Tacheeda		Cluculz		McLeese	Maclure
Lake species:	<i>P. coulteri</i>	<i>P. coulteri</i>	<i>P. williamsoni</i>	<i>C. clupeaformis</i>	<i>P. coulteri</i>	<i>P. coulteri</i>
Stomachs examined	15	15	30	41	10	25
Plant material	..	..	trace	15	..	..
Mollusca						
Gastropoda	..	..	6	11	..	..
Pelecypoda	..	trace	..	trace	..	..
Annelida						
Hirudinea	..	..	9	..	..	..
Crustacea						
Ostracoda	..	trace	..	trace	..	..
Cladocera	45	..	trace	16	7	75
Copepoda	1	..	..	..	trace	trace
Amphipoda	..	trace	8	trace	..	..
Insecta						
Tendipedidae larvae and pupae	44	52	24	7	42	13
Chaoborus	2	8	..	6	46	3
Trichoptera larvae	..	..	20	27	..	..
Unidentifiable	8	40	33	18	5	9

*Chaoborus*. In Cluculz Lake only the latter two are of any importance. In contrast, the diets of the mountain whitefish and lake whitefish from Cluculz Lake were considerably more varied, comprising, respectively, five and six groups of animals present in measurable quantity. This may only reflect the fact that fewer types of prey inhabit the depths frequented by the pygmy whitefish.

Both the mountain and lake whitefishes devoured Tendipedidae larvae and pupae, the most important prey of the pygmy whitefish in Cluculz Lake. In addition some lake whitefish fed on *Chaoborus*, another pygmy whitefish food.

#### DISCUSSION

One of the original objectives of this study was to determine whether the differences in the growth form of the pygmy whitefish which have been described might be related in some way to competition with other whitefish species. No

direct evidence of interspecific competition has been adduced but there are hints that it might have some effect. First, McLeese and Maclure Lakes, where the pygmy whitefish reaches its maximum size, are the only two lakes in British Columbia where, to the author's knowledge, a pygmy whitefish population persists in the absence of either the mountain whitefish or the round whitefish, *P. cylindraceum*, two closely related *Prosopium* species. In many areas (as in Cluculz and Tacheeda Lakes) whitefish of the genus *Coregonus* are also present. Second, the depth distribution of pygmy whitefish in lakes containing other whitefish (Tacheeda and Cluculz) differs from that in lakes in which other whitefish are absent (McLeese and Maclure). Alone, the pygmy whitefish occupies shallower water than it does when coexisting with other whitefish.

These facts suggest that in McLeese and Maclure Lakes the pygmy whitefish fills a different niche from what it does in Tacheeda and Cluculz: in the former a large fish occupying moderate depths in the absence of other whitefish, in the latter an extremely slow-growing fish inhabiting deeper waters not utilized by the other whitefish in the lake.

Are these differences the result of interspecific competition? In the past, seemingly parallel situations have been ascribed to interspecific competition. 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.

On the whitefishes, interspecific competition often severely retards the growth of the one of the competing species or forms (Fenderson, 1964). Svärdson (1949) has shown that the growth of even individual whitefish is highly flexible depending upon the ecological situation with which it is presented. Slow-growing forms of various *Coregonus* species often displayed extreme changes in growth rate when transferred as mature fish to new environments. Svärdson related most of this difference to the presence or absence of competing species. 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.

Unfortunately, most demonstrations of interspecific competition in fishes are "... hampered by the difficulties of ruling out the effects of changes in the environment other than changes in fish fauna ..." (Lindström and Nilsson, 1962). In four lakes as limnologically dissimilar as Tacheeda, Cluculz, McLeese, and Maclure, environmental effects might be considerable and it is therefore not possible definitely to implicate interspecific competition as a reason for the observed differences in the growth and ecology of the pygmy whitefish.

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# APPENDIX

Covariance statistics comparing the relations between standard length and the size of various body parts for male and female pygmy whitefish from four British Columbia populations.

	Body depth	Pre-dorsal length	Length dorsal base	Length anal base	Height dorsal	Height anal	Length pectoral	Length pelvic	Head length	Inter-orbital width	Length orbit	Length upper jaw
<i>Males</i>												
Log <sub>e</sub> Slope	1.079	0.976	0.523	1.366	0.969	1.096	1.292	1.140	0.941	0.925	0.827	0.793
Log <sub>e</sub> Intercept	-1.853	-0.751	-1.170	-3.063	-1.501	-1.914	-2.246	-2.031	-1.306	-2.626	-2.165	-2.240
Correlation coeff.	0.885	0.992	0.620	0.899	0.931	0.924	0.955	0.936	0.923	0.863	0.789	0.779
Log <sub>e</sub> SEE <sup>a</sup>	0.056	0.012	0.065	0.066	0.038	0.045	0.040	0.042	0.039	0.053	0.063	0.063
<i>Females</i>												
Log <sub>e</sub> Slope	1.185	1.008	1.050	1.227	1.078	1.289	1.145	1.123	1.084	1.123	1.000	1.028
Log <sub>e</sub> Intercept	-2.086	-0.834	-2.305	-2.829	-1.769	-2.375	-1.984	-2.049	-1.619	-3.072	-2.591	-2.799
Correlation coeff.	0.972	0.986	0.889	0.935	0.968	0.966	0.965	0.977	0.959	0.930	0.922	0.898
Log <sub>e</sub> SEE	0.040	0.023	0.075	0.064	0.038	0.047	0.043	0.034	0.045	0.062	0.058	0.070
<i>Males and females</i>												
Log <sub>e</sub> Slope	1.163	0.985	0.985	1.141	1.012	1.192	1.080	1.041	1.058	1.066	0.896	0.916
Log <sub>e</sub> Intercept	-2.035	-0.777	-2.153	-2.617	-1.610	-2.141	-1.822	-1.848	-1.557	-2.937	-2.338	-2.529
Correlation coeff.	0.973	0.990	0.899	0.934	0.970	0.966	0.965	0.971	0.968	0.941	0.916	0.898
Log <sub>e</sub> SEE	0.043	0.022	0.075	0.068	0.040	0.049	0.046	0.040	0.043	0.060	0.062	0.070
<i>Covariance analysis — between sexes</i>												
Slope F	0.646	0.260	5.832 <sup>c</sup>	0.516	0.896	1.884	1.348	0.024	1.210	1.200	0.951	1.312 <sup>c</sup>
Adj. mean F	0.119	2.651	0.001	8.077 <sup>b</sup>	5.940 <sup>c</sup>	7.611 <sup>b</sup>	12.358 <sup>b</sup>	17.799 <sup>b</sup>	0.133	0.896	6.218 <sup>c</sup>	4.569

		<i>Males</i>											
<b>Cluculz Lake</b>	Log <sub>e</sub> Slope	1.152	1.053	1.065	1.208	0.982	1.162	1.208	1.158	0.925	1.158	0.647	0.905
	Log <sub>e</sub> Intercept	-2.005	-0.955	-2.278	-2.698	-1.494	-2.053	-2.061	-2.086	-1.298	-3.107	-1.728	-2.468
	Log <sub>e</sub> Correlation coeff.	0.927	0.975	0.877	0.827	0.958	0.908	0.944	0.938	0.959	0.909	0.794	0.846
	Log <sub>e</sub> SEE	0.048	0.025	0.061	0.086	0.031	0.056	0.044	0.045	0.028	0.055	0.052	0.059
		<i>Females</i>											
<b>Cluculz Lake</b>	Log <sub>e</sub> Slope	1.139	0.986	1.100	1.109	1.034	1.136	1.089	1.049	0.988	0.980	0.778	0.791
	Log <sub>e</sub> Intercept	-1.972	-0.802	-2.366	-2.488	-1.647	-2.013	-1.826	-1.874	-1.456	-2.731	-2.064	-2.234
	Correlation coeff.	0.949	0.986	0.925	0.921	0.957	0.957	0.954	0.950	0.961	0.925	0.917	0.861
	Log <sub>e</sub> SEE	0.050	0.022	0.060	0.062	0.042	0.046	0.045	0.046	0.037	0.054	0.045	0.062
		<i>Males and females</i>											
	Log <sub>e</sub> Slope	1.146	1.002	1.083	1.100	0.972	1.109	1.049	1.010	0.959	0.961	0.693	0.771
	Log <sub>e</sub> Intercept	-1.991	-0.839	-2.322	-2.461	-1.488	-1.943	-1.719	-1.768	-1.376	-2.677	-1.850	-2.176
	Correlation coeff.	0.956	0.987	0.930	0.908	0.958	0.953	0.950	0.946	0.967	0.921	0.891	0.866
	Log <sub>e</sub> SEE	0.049	0.023	0.060	0.070	0.040	0.049	0.048	0.048	0.035	0.056	0.049	0.062
		<i>Covariance analysis — between sexes</i>											
		Slope F	0.013	1.466	0.060	0.345	0.328	0.048	1.229	1.011	0.586	1.893	1.334
		Adj. mean F	0.033	0.006	0.108	0.886	7.603 <sup>b</sup>	1.979	9.878 <sup>b</sup>	8.928 <sup>b</sup>	1.065	5.238 <sup>c</sup>	5.873 <sup>c</sup>

(Continued)

APPENDIX — (Concluded)

Covariance statistics comparing the relations between standard length and the size of various body parts for male and female pygmy whitefish from four British Columbia populations.

	Body depth	Pre-dorsal length	Length dorsal base	Length anal base	Height dorsal	Height anal	Length pectoral	Length pelvic	Head length	Inter-orbital width	Length orbit	Length upper jaw
<i>Males</i>												
Log <sub>e</sub> Slope	1.112	1.033	0.977	1.219	0.954	1.170	1.095	1.042	1.011	1.036	0.769	0.918
Log <sub>e</sub> Intercept	-1.840	-0.885	-2.032	-2.730	-1.148	-2.169	-1.906	-1.899	-1.493	-2.748	-2.154	-2.572
Correlation coeff.	0.981	0.997	0.956	0.972	0.974	0.970	0.988	0.979	0.993	0.943	0.956	0.978
Log <sub>e</sub> SEE	0.033	0.012	0.045	0.044	0.034	0.044	0.026	0.032	0.018	0.056	0.036	0.930
<i>Females</i>												
Log <sub>e</sub> Slope	1.114	1.043	1.065	1.048	1.026	1.115	1.121	1.068	1.019	1.199	0.769	0.882
Log <sub>e</sub> Intercept	-1.865	-0.922	-2.264	-2.343	-1.717	-2.089	-2.042	-2.021	-1.538	-3.177	-2.147	-2.512
Correlation coeff.	0.979	0.993	0.963	0.958	0.963	0.964	0.969	0.965	0.984	0.955	0.944	0.900
Log <sub>e</sub> SEE	0.036	0.020	0.047	0.049	0.045	0.048	0.045	0.045	0.029	0.058	0.042	0.067
<i>Males and females</i>												
Log <sub>e</sub> Slope	1.096	1.031	1.034	1.059	0.958	1.077	1.054	1.011	0.997	1.141	0.776	0.864
Log <sub>e</sub> Intercept	-1.811	-0.887	-2.181	-2.336	-1.520	-1.967	-1.842	-1.853	-1.471	-3.023	-2.168	-2.455
Correlation coeff.	0.979	0.994	0.963	0.950	0.954	0.952	0.958	0.958	0.985	0.953	0.952	0.920
Log <sub>e</sub> SEE	0.036	0.018	0.046	0.055	0.048	0.055	0.050	0.048	0.028	0.058	0.040	0.058
<i>Covariance analysis — between sexes</i>												
Slope F	0.001	0.003	1.080	3.848	0.876	0.410	0.131	0.113	0.032	2.410	0.000	0.117
Adj. mean F	4.140	4.106 <sup>a</sup>	0.091	17.150 <sup>b</sup>	20.084 <sup>b</sup>	23.642 <sup>b</sup>	37.822 <sup>b</sup>	23.678 <sup>b</sup>	9.903 <sup>b</sup>	0.206	0.554	4.309 <sup>a</sup>

<i>Males</i>													
<b>Maclure Lake</b>	Log <sub>e</sub> Slope	1.120	1.008	1.027	1.129	1.012	1.142	1.137	1.048	0.940	1.043	0.760	0.815
	Log <sub>e</sub> Intercept	-1.889	-0.842	-2.203	-2.561	-1.676	-2.124	-2.080	-1.968	-1.348	-2.821	-2.149	-2.321
	Correlation coeff.	0.986	0.997	0.978	0.974	0.994	0.994	0.994	0.985	0.995	0.984	0.988	0.974
	Log <sub>e</sub> SEE	0.054	0.023	0.063	0.075	0.033	0.036	0.036	0.052	0.028	0.054	0.033	0.054
<i>Females</i>													
<b>Maclure Lake</b>	Log <sub>e</sub> Slope	1.133	1.016	0.985	1.023	0.935	1.071	1.025	0.965	0.930	1.088	0.724	0.852
	Log <sub>e</sub> Intercept	-1.919	-0.868	-2.106	-2.302	-1.486	-1.949	-1.810	-1.782	-1.332	-2.969	-2.065	-2.443
	Correlation coeff.	0.992	0.998	0.985	0.981	0.996	0.986	0.995	0.996	0.997	0.993	0.977	0.987
	Log <sub>e</sub> SEE	0.050	0.019	0.059	0.068	0.029	0.061	0.034	0.030	0.025	0.043	0.054	0.047
<i>Males and females</i>													
<b>Maclure Lake</b>	Log <sub>e</sub> Slope	1.130	1.012	0.995	1.051	0.956	1.090	1.054	0.983	0.931	1.066	0.734	0.834
	Log <sub>e</sub> Intercept	-1.911	-0.855	-2.126	-2.370	-1.537	-1.987	-1.878	-1.816	-1.329	-2.896	-2.084	-2.383
	Correlation coeff.	0.990	0.998	0.982	0.977	0.994	0.988	0.992	0.989	0.996	0.990	0.981	0.982
	Log <sub>e</sub> SEE	0.051	0.021	0.060	0.073	0.034	0.054	0.042	0.046	0.027	0.049	0.046	0.051
<i>Covariance analysis — between sexes</i>													
<b>Maclure Lake</b>	Slope F	0.081	0.196	0.683	3.109	8.943 <sup>b</sup>	2.949	14.501 <sup>b</sup>	5.754 <sup>c</sup>	0.205	1.238	0.833	0.770
	Adj. mean F	0.071	0.639	1.277	2.469	..	4.725 <sup>c</sup>	..	12.608 <sup>b</sup>	2.655	4.082 <sup>b</sup>	1.224	2.735
<i>Males</i>													
<b>Total</b>	Slope F	0.663	0.626	3.040 <sup>c</sup>	0.640	0.430	0.096	1.177	0.581	0.820	0.531	0.561	0.624
	Adj. mean F	7.076 <sup>b</sup>	13.437 <sup>b</sup>	5.233 <sup>b</sup>	4.335 <sup>b</sup>	27.321 <sup>b</sup>	16.464 <sup>b</sup>	6.235 <sup>b</sup>	25.530 <sup>b</sup>	9.643 <sup>b</sup>	9.962 <sup>b</sup>	37.559 <sup>b</sup>	4.392 <sup>b</sup>
<i>Females</i>													
<b>Total</b>	Slope F	0.447	1.048	1.114	2.869 <sup>c</sup>	4.552 <sup>b</sup>	4.601 <sup>b</sup>	2.962 <sup>c</sup>	5.161 <sup>b</sup>	5.410 <sup>b</sup>	2.325	7.379 <sup>b</sup>	2.402
	Adj. mean F	7.847 <sup>b</sup>	12.607 <sup>b</sup>	16.599 <sup>b</sup>	11.412 <sup>b</sup>	..	..	7.290 <sup>b</sup>	..	..	3.058 <sup>b</sup>	..	7.497 <sup>b</sup>
<i>Males and females</i>													
<b>Total</b>	Slope F	0.609	1.366	0.904	0.849	0.809	1.742	0.146	0.728	6.481 <sup>b</sup>	2.408	5.194 <sup>b</sup>	1.448
	Adj. mean F	15.542 <sup>b</sup>	23.567 <sup>b</sup>	22.434 <sup>b</sup>	14.465	41.466 <sup>b</sup>	46.367 <sup>b</sup>	87.305 <sup>b</sup>	56.112 <sup>b</sup>	..	40.912 <sup>b</sup>	..	8.899 <sup>b</sup>

<sup>a</sup>Standard error of estimate.  
<sup>b</sup>Significant at 1% level.  
<sup>c</sup>Significant at 5% level.

**This article has been cited by:**

1. T. G. Northcote, G. L. Ennis. 1994. Mountain whitefish biology and habitat use in relation to compensation and improvement possibilities. *Reviews in Fisheries Science* **2**:4, 347-371. [[CrossRef](#)]