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THE PYGMY WHITEFISH, *PROSOPIUM COULTERI*, IN WESTERN MONTANA

G. F. Weisel,[1] D. A. Hanzel,[2] and R. L. Newell[3]

ABSTRACT

The pygmy whitefish, *Prosopium coulteri*, is a glacial relict which has been considered to be the most primitive of coregonines. It is relatively abundant in lakes of western Montana and is undoubtedly an important source of food for Dolly Varden and lake trout. Compared to other members of its subfamily, it is characterized by low meristic counts. These counts differ somewhat in populations from Montana, Alaska, and Lake Superior.

Major food items consumed by the pygmy whitefish shift with availability but the main reliance is on cladocera and chironomid larvae and pupae. The annual growth in Flathead Lake, Mont., is greater than that in Lake Superior but below that in some Alaskan lakes. No males were found older than age III and no females beyond age IV. Many of the males mature at age I, a year earlier than most females. The spawning season is in December and January when the fish move into tributary streams. The species spawns in successive years. The fecundity of the Montana fish is similar to that of pygmy whitefish from other areas.

The pygmy whitefish successfully competes with other coregonines in reproduction by spawning at a later date and earlier age, and by having smaller eggs which yield more eggs per unit weight of fish. The small size and early age at maturity are considered adaptations developed for survival in cold and nutrient-poor water during glaciation.

The pygmy whitefish, *Prosopium coulteri*, is considered a glacial relict that survived in deep lakes after the retreat of the Wisconsin glaciation. Until the past 20 years the species was infrequently captured, or recognized when it was. It usually inhabits depths of over 30 ft and, because of its small size, escapes capture by most fishing gear. The present distribution is given as the Columbia, Fraser, Skeena, Yukon, and MacKenzie River systems, and both the Pacific Ocean and Bering Sea drainages of southwest Alaska (Heard and Hartman, 1966). In 1955 the report of this little fish from Lake Superior disclosed a remarkable case of disjunct distribution (Eschmeyer and Bailey, 1955).

Only in recent years has it been recognized how ubiquitous the pygmy whitefish is in western Montana. It was first reported in Montana by Schultz in 1941 from tributaries of Lake McDonald in Glacier National Park. The next report was from Bull Lake, a tributary to the Kootenai River (Weisel and Dillon, 1954). In the past 10 years it has been taken with small-mesh gill nets from Flathead, Ashley, Swan, Seeley, and the Little Bitteroot Lakes—all tributary to the Clark Fork River (Brown, 1971). Careful collecting will undoubtedly show the species to be present in many other glacially formed lakes in western Montana.

Our studies show the pygmy whitefish to be one of the most abundant fishes in Flathead Lake. According to Hanzel's 1968-71 extensive nettings, this species constituted 4.8% of the total catch; it ranked in order only below lake whitefish (*Coregonus clupeaformis*), peamouth (*Mylocheilus caurinus*), kokanee (*Oncorhynchus nerka*), northern squawfish (*Ptychocheilus oregonensis*), Dolly Varden (*Salvelinus malma*), and yellow perch (*Perca flavescens*).

[1] Zoology Department, University of Montana, Missoula, MT 59801.
[2] Montana Fish and Game Department, Kalispell, MT 59901.
[3] Department of Biology, Idaho State University, Pocatello, ID 83201.

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Because of the small size and abundance of the pygmy whitefish, it must be important as a primary carnivore available to species next in the food chain. The only extensive detailed publications on pygmy whitefish, however, are those of Eschmeyer and Bailey (1955) dealing with Lake Superior populations and of Heard and Hartman (1966) and McCart (1970) with Alaskan populations. Our work is concerned with populations from Flathead Lake and Bull Lake in the upper Columbia River drainage but involves comparisons where applicable to the Lake Superior and Alaskan forms. Some comparisons are also made with the mountain whitefish, *Prosopium williamsoni*, a closely related sympatric species.

ASSOCIATED FISHES AND DESCRIPTION OF THE LAKES

Flathead Lake is a large oligotrophic lake covering 126,000 surface acres and reaching a depth of 365 ft. Its major tributaries are the Flathead and Swan Rivers. Its outlet, the Flathead River, joins the Clark Fork River of the Columbia River.

Like many glacial lakes, Flathead Lake is depauperate in native fishes. Indigenous fishes in the lake are cutthroat trout (*Salmo clarki*), Dolly Varden, pygmy whitefish, mountain whitefish, longnose sucker (*Catostomus catostomus*), largescale sucker (*C. macrocheilus*), peamouth, redside shiner (*Richardsonius balteatus*), northern squawfish, and slimy sculpin (*Cottus cognatus*).

Around the turn of the century a number of other species were introduced. The exotic forms presently in the lake are rainbow trout (*Salmo gairdneri*), lake trout (*Salvelinus namaycush*), brook trout (*S. fontinalis*), kokanee, lake whitefish, black bullhead (*Ictalurus melas*), yellow perch, pumpkinseed (*Lepomis gibbosus*), and largemouth bass (*Micropterus salmoides*). Plants of other exotics, including a 1969 plant of coho salmon, *Oncorhynchus kisutch*, were not successful. The northern pike, *Esox lucius*, thrives in Flathead River below the hydroelectric dam at the lake's outlet but is not reported from the lake. Fish species most often taken in the same net settings with pygmy whitefish are lake whitefish, lake trout, and Dolly Varden.

Bull Lake is comparatively small and shallow and is somewhat eutrophic. The total surface is 1,250 acres and the maximum depth is 64 ft. Ross Creek, where the pygmy whitefish were captured during their spawning runs, is the largest tributary.

No thorough studies have been made of the fish species in Bull Lake but, besides pygmy whitefish, it is known to contain rainbow trout, cutthroat trout, brook trout, Dolly Varden, kokanee, mountain whitefish, redside shiner, northern squawfish, peamouth, longnose sucker, largescale sucker, largemouth bass, and a sculpin.

MATERIALS AND METHODS

Pygmy whitefish were collected from Flathead Lake during an investigation on fish populations by the Montana Fish and Game Department. A 35-ft former commercial fishing boat modified to handle specialized fishing gear and provided with a recording sonar was used to set and pull nets from 11 sample areas during 4 seasons from November 1967 through August 1971. Six hundred feet of gill netting ranging from ⅝-inch to 4-inch stretched mesh were laid in 165 settings. Except for spawning populations practically all pygmy whitefish were caught in the ⅝-inch and 1¼-inch mesh portion and were taken within 3 ft of the bottom. The largest collections were taken during the late summer at depths of 60 to 270 ft. Unfortunately, too few pygmy whitefish were taken to interpret an overall distributional pattern.

The Bull Lake collections were taken with seines from spawning aggregations in the lake's inlet during December of 1952, 1955, and 1967.

Counts on scales, gill rakers, and vertebrae followed the methods outlined by Hubbs and Lagler (1964). Gill raker counts included rudimentary rakers and sutures in the hypural complex were regarded as separating vertebrae. Specimens used for vertebral counts were eviscerated, filleted, cleared in KOH, and stained in alizarine red S according to the procedure of Evans (1948).

Standard lengths were measured in millimeters and weights in tenths of grams. To compare our results with the data of other authors who used fork length or total length, it was necessary to use conversion factors. Total length was considered equal to 0.21 plus 1.19 standard length, and the standard length equal to -0.09 plus 0.83 total length. The conversion of fork length to total length used was that given by Heard and Hartman (1966) where fork length times 1.0777 equals total length for specimens shorter than 100 mm and times 1.0845 for the larger specimens.

Scales for age and growth studies were removed from an area above the lateral line just posterior to the dorsal fin. Plastic impressions were made of the scales and projected to an enlargement of 67 times for measurement.

SOME MERISTIC CHARACTERS

Lateral-Line Scales

A striking character of the pygmy whitefish is its large scales. In its northern range the lateral-line scales number 50 to 73, in Lake Superior 54 to 62, in Flathead Lake 52 to 65, and Bull Lake 54 to 63 (Table 1). The mean number of scales varies somewhat among different populations. A low mean of 54.29 is given for fish from Chadburn Lake, Yukon, and a high of 71.57 for low-rakered fish from Lake Aleknagik (McCart, 1970). Pygmy whitefish from Flathead Lake and Bull Lake are intermediate. The closely related mountain whitefish possesses lateral-line scales ranging from 73 to 92 in the Columbia River drainage (Holt, 1960).

TABLE 1.—Frequency distribution of the lateral-line scale counts in pygmy whitefish.

Number of scales	Flathead Lake	Bull Lake
52	3	—
53	4	—
54	3	1
55	5	2
56	12	1
57	14	3
58	14	6
59	15	11
60	9	10
61	6	4
62	4	6
63	6	4
64	1	—
65	3	—
Mean	58.2	59.5

Gill Rakers

The number and length of gill rakers have proved useful in the systematics of coregonines. The range in gill rakers is considerable in pygmy whitefish, from 12 to 21. On the basis of gill raker number and other meristic and morphological data, McCart (1970) distinguished two forms of pygmy whitefish which occur sympatrically in some Alaskan lakes. One form has high raker counts and the other has low raker counts. McCart suggested a western refugium south of the ice sheet for the origin of the Alaskan low gill raker form, a Yukon-Bering Sea refugium for the Alaskan high gill raker form, and a Mississippian refugium for the Lake Superior form.

Pygmy whitefish from Flathead Lake have a range of 14 to 18 gill rakers (mean 15.83); those from Bull Lake range from 15 to 18 (mean 16.28). These means are considerably lower than the 18.28 mean of fish from Lake Superior (Table 2). According to McCart's figures, the Flathead Lake and Bull Lake populations would be classified as high-rakered in comparison with Lake Aleknagik populations,

TABLE 2.—Frequency distribution of gill raker counts in pygmy whitefish.

Locality	Number of gill rakers							
	14	15	16	17	18	19	20	Mean
Lake Superior[1]	—	—	1	6	17	13	3	18.28
Columbia River drainage:								
Lake McDonald[1]	—	2	5	5	3	5	—	17.20
Bull Lake[1]	—	2	6	10	2	1	—	16.71
Flathead Lake	4	15	24	8	3	—	—	15.83
Bull Lake	—	4	13	5	3	—	—	16.28
Alaska:								
Lake Aleknagik:[2]								
High raker			range 14-17					15.28
Low raker			range 12-15					13.46
Naknek Lake:[2]								
High raker			range 16-19					17.33
Low raker			range 13-16					14.54
Chignik Lake:[2]								
High raker			range 17-21					19.21
Low raker			range 13-16					14.16

[1] From Eschmeyer and Bailey (1955).
[2] From McCart (1970).

but intermediate compared to Naknek Lake and Chignik Lake populations. Our counts, as well as those on Lake McDonald fish, do not support McCart's contention that the low-rakered form persisted in the vicinity of the Columbia River Basin during the Pleistocene glaciation.

Vertebrae

As with other meristic characters, the vertebral count of the pygmy whitefish is low for a coregonine. The number of vertebrae is variable however—from 49 to 55. The plasticity of this character is within individual populations as the species exhibits similarity in the mean count of vertebrae throughout its range. The Flathead Lake fish have a mean number of 52.3 and the Bull Lake specimens, a mean of 52.7 (Table 3). Mean vertebral count of the fish from Lake Superior was given as 52.9 by Eschmeyer and Bailey (1955). The lowest mean is 51.5 for Chignik Lake (McCart, 1970).

It appears that most of the variation in the vertebral number is in the caudal rather than precaudal vertebrae. The number of caudal vertebrae ranges from 21 to 26 whereas the precaudals vary from 27 to 31 in Flathead Lake and Bull Lake fish. The number of caudals individually plotted with their respective total number have means that nearly increase by the value of one with each increase in similar value in total number of vertebrae (Table 4).

Although low, the total number of vertebrae of the pygmy whitefish overlaps the lower range of the mountain whitefish. Holt (1960) gave a range of 53 to 61 for the mountain whitefish in the Columbia River drainage. Twenty specimens of the mountain whitefish from Lolo Creek used in our study had caudal vertebrae ranging from 25 to 27, again a slight overlap.

TABLE 3.—Frequency distribution of total number of vertebrae in pygmy whitefish.

No. of vertebrae	Flathead Lake	Bull Lake
50	2	—
51	6	3
52	24	16
53	26	18
54	2	7
55	—	1
Mean	52.3	52.7

TABLE 4.—Relation of number of caudal vertebrae to total number of vertebrae in pygmy whitefish.

Item	Total vertebrae				
	51	52	53	54	55
Caudal vertebrae:					
Range	21-24	21-25	21-25	24-25	26
Mean	21.86	22.82	23.39	24.43	26.00
Number of specimens	7	33	33	7	1

AGE AND GROWTH

Age was determined for 494 pygmy whitefish taken from Flathead Lake during April 1967 through May 1971. Sex was determined on 272 specimens, mostly from mature fish captured in November and December.

Only one fish of age 0 was collected. Fish of this age are so small that they are unlikely to be captured in the collecting gear we used. The percentage of the total fish by age group was: 0, 0.2% ; I, 47.2% ; II, 46.1% ; III, 5.9% ; and IV, 0.6%. Overlap was considerable in the length-frequency distribution between adjacent age groups and between the sexes (Table 5).

Growth rate was calculated by establishing the relationship between the body length and the anterior scale radius. The value of 0.9854, the coefficient of variation r, developed on the 493 measurements, suggests a strong degree of linearity between the body-scale measurements. This linearity differs from the sigmoid body-scale relationship found for pygmy whitefish from Alaskan waters by Heard and Hartman (1966).

The equation fitted from the individual pairs of body and scale measurements was: Total body length = 0.913 anterior scale radius + 61.63. Mean body lengths from each scale radius were plotted against the calculated regression line shown in Figure 1. Total lengths were back calculated by direct proportion (Table 6).

Annual growth of females in Flathead Lake exceeded growth reported for Brooks Lake (Alaska), Lake McDonald (Montana), and Lake

TABLE 5.—Length frequency of age groups of pygmy whitefish from Flathead Lake, 1967-71.

[F, females; M, males.]

Total length	I		II		III		IV		Total	
(mm)	M	F	M	F	M	F	M	F	M	F
84	—	1	—	—	—	—	—	—	—	1
89	1	—	—	—	—	—	—	—	1	—
91	—	—	—	—	—	—	—	—	—	—
94	1	—	—	—	—	—	—	—	1	—
99	1	—	—	—	—	—	—	—	1	—
102	1	—	—	—	—	—	—	—	1	—
104	2	—	1	—	—	—	—	—	3	—
107	4	1	—	—	—	—	—	—	4	1
109	8	3	1	1	—	—	—	—	9	4
112	8	2	—	—	—	—	—	—	8	2
114	31	2	—	3	—	—	—	—	31	5
117	21	3	1	—	—	—	—	—	22	3
119	18	2	5	—	—	—	—	—	23	2
122	10	—	2	1	—	—	—	—	12	1
124	6	1	5	1	—	—	—	—	11	2
127	5	—	7	1	—	—	—	—	12	1
130	—	—	5	—	—	—	—	—	5	—
132	2	—	12	8	—	1	—	—	14	9
135	1	—	4	3	—	—	—	—	5	3
137	—	3	7	6	—	—	—	—	7	9
140	—	—	1	5	1	—	—	—	2	5
142	—	—	2	5	—	1	—	—	2	6
145	—	—	3	7	—	—	—	—	3	7
147	—	—	3	4	—	—	—	—	3	4
150	—	—	1	4	—	1	—	—	1	5
152	—	—	—	4	—	2	—	—	—	6
155	—	—	—	3	—	2	—	—	—	5
157	—	—	—	1	—	1	—	—	—	2
160	—	—	—	1	—	4	—	—	—	5
163	—	—	—	—	—	—	—	2	—	2
170	—	—	—	—	—	—	—	1	—	1
Mean length	116	116	129	140	132	153	—	165	121	138
Total number	120	18	60	58	1	12	—	3	181	91

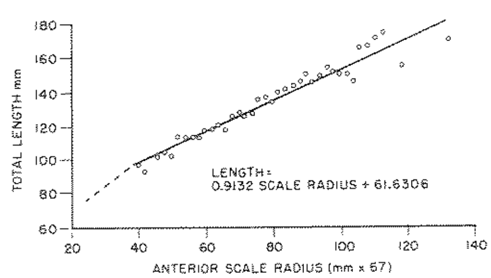

FIGURE 1.—Body length-scale radius relation of pygmy whitefish from Flathead Lake. Solid line is calculated equation; circles represent mean body lengths for given scale radii; dashed line connects estimated intercept at 25 mm length at scale formation.

Superior. Growth was nearly the same in Bull Lake. The initial growth of the Flathead Lake population was exceeded in Wood Lake, Alaska, and after the third year in MacLure Lake, British Columbia, where the fastest growth rate has been reported for the species (Figure 2).

Both Bull Lake and Flathead Lake collections indicate that few males live beyond their third growing year whereas some females reach the fifth growing year. Data from Wood River and the Naknek River systems in Alaska and from Lake Superior also show that females are longer lived. Females in Wood River can attain age VI and those in Lake Superior attain age VII.

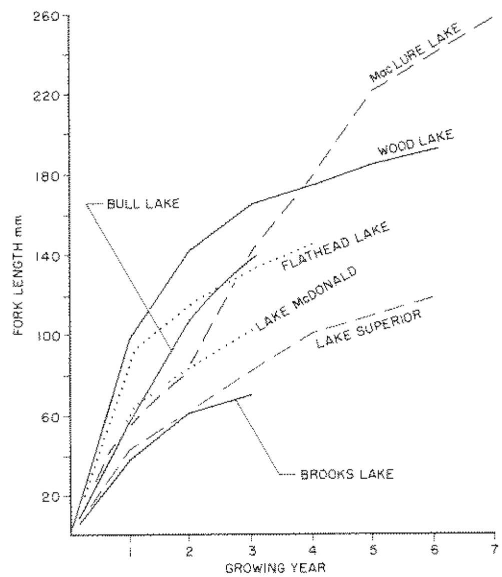

FIGURE 2.—Calculated growth of female pygmy whitefish from Flathead Lake compared with data from Bull Lake and Lake McDonald, Mont., and Lake Superior (Eschmeyer and Bailey, 1955); Wood Lake, Alaska (Rogers, 1964); Brooks Lake, Alaska (Heard and Hartman, 1966); and McLure Lake, British Columbia (McCart, 1963).

FOOD HABITS

The importance of major food items of the pygmy whitefish of Flathead Lake shifts from month to month, undoubtedly according to availability. Chironomid larvae and pupae were the most important items consumed both by

TABLE 6.—Average calculated length and average length at capture of pygmy whitefish, from Flathead Lake, 1967-71.

[F, females; M, males; U, unknown sex.]

Age group	Sex	Number of fish	Average total length at capture (mm)	Calculated length at annulus formation			
				I	II	III	IV
0	U	1	79	—	—	—	—
I	M	120	117	100	—	—	—
	F	18	116	99	—	—	—
	U	95	110	95	—	—	—
II	M	60	128	98	116	—	—
	F	58	140	98	122	—	—
	U	110	134	101	123	—	—
III	M	1	140	100	124	142	—
	F	12	154	100	124	141	—
	U	16	150	101	122	137	—
IV	F	3	168	99	130	145	155
			Average increment				
	M	181	122	99	18	25	—
	F	91	138	98	24	20	13
	U	221	—	98	22	14	—
			Average length				
	M			99	117	142	—
	F			98	122	142	155
	U			98	123	137	—
	Combined			99	121	139	155

TABLE 7.—Percentage frequency of occurrence of food items in stomachs containing food and (in parentheses) percentage estimate of volume for pygmy whitefish from Flathead Lake.[1]

[The two percentage figures are the same or approximate because most stomachs contained only one kind of food.]

Food	May	June	July	Aug.	Sept.	Oct.	Nov.	Average
Cladocera: (including ephippia)	—	—	50 (50)	80 (80)	13 (15)	47 (48)	53 (56)	35
Diptera: Tendipedidae (chironomid larvae and pupae)	67 (67)	89 (95)	33 (37)	20 (20)	69 (71)	44 (45)	10 (8)	47
Trichoptera: (Hydroptilidae and Hydropsychidae)	11 (11)	4 (2)	2 (1)	—	3 (2)	—	—	3
Unknown insect parts	—	4 (2)	6 (4)	—	5 (4)	—	—	2
Fish eggs	—	—	—	—	—	—	6 (6)	1
Detritus and sand	22 (22)	3 (3)	9 (8)	—	10 (8)	9 (7)	31 (30)	12
Empty/full	3/12	0/27	14/68	1/6	5/44	12/44	26/77	61/278

[1] Items appearing in only one or two stomachs included: diatoms, copepods, Podocopa (Ostracoda), Mayfly nymphs (Ephemerotera), midge adults (Tendipedidae), leaf hopper (Cicadellidae), ants (Hymenoptera), terrestrial beattle (Coleoptera), and water mites (Hydracarina). All of these items composed only a small part of stomach contents.

volume and frequency of occurrence; cladocerans were close second (Table 7). No cladocera was consumed during May and June when chironomids were the main food source. Crustaceans became the prime food in July and August, but in September the reliance returned to dipterans. Cladocera apparently became more available in October and November and once more were the important source of food, particularly in November. Other foods were of minor importance during the months when stomachs were collected. The frequent presence of detritus and sand in the guts is evidence that this whitefish feeds at or near the bottom as visually confirmed by Heard and Hartman (1966).

Crustacea identified from the guts of pygmy whitefish from Flathead Lake included an ostracod; the cladocerans *Daphnia thorata, D. rosea, D. longiremis, Bosima longirostris,* and *Leptodora kindtii*; and the copepods *Diaptomus ashlandi, Epischura nevadensis,* and a cyclopoid copepod.

A December collection of spawning pygmy whitefish from Ross Creek demonstrates that these fish feed actively during their spawning period. Fish eggs, laid by fellow spawners, were the most frequently ingested food and made up by far the greatest volume. Chironomids were still taken in numbers, however, along with a few other insects (Table 8).

The feeding habits of this whitefish in other lakes are usually similar to those of fish in Flathead Lake. In Lake Superior, crustacea, mostly ostracods and amphipods, occurred in 95% of the stomachs. Chironomids were taken frequently but made up only 8% of the total volume. Fish eggs, presumably coregonine, occurred in collections of May and January (Eschmeyer and Bailey, 1955). Pygmy whitefish from a tributary of Lake Aleknagik, Alaska, fed on the larvae and pupae of chironomids (Rogers, 1964). In the Naknek River system the relative importance of food items differs between lakes. Chironomids accounted for 88% of the stomach volume in some lakes but only 5% in other waters. Plecopteran nymphs were important as food in some lakes or outlets. Periphyton never accounted for more than 4% of stomach contents. Fish eggs, probably from salmon, were taken in November (Heard and Hartman, 1966). Low-rakered Alaskan forms fed predominantly on bottom fauna and the high-rakered fish were almost exclusively plankton feeders (McCart, 1970).

TABLE 8.—Percentage frequency of occurrence of food items in stomachs containing food. Pygmy whitefish from Ross Creek during spawning run, 12 December 1967. The number of fish eggs eaten ranged from 1 to 21 per fish with an average of 6.

Cladocera	8
Diptera:	
Tendipedidae (chironomid larvae)	38
Ceratopogonidae larvae	3
Ephemeroptera:	
Heptagenia nymph	3
Unknown insect remains	8
Fish eggs	75
Detritus and sand	33
Empty stomachs	9 of 50

REPRODUCTION

Age and Size at Maturity

Collections of pygmy whitefish were made from the inlet of Bull Lake during the spawning runs in December of three different years. Only the last collection (1967) included a large number of fish—280, all but 4 were males. The predominance of males in the three collections may be explained by the earlier arrival of males to the spawning aggregation. None of the gonads examined was spawned out.

In the three combined collections, 50% of the males were in their second growing season (age I), 47% at age II, and only 3% at age III. In the small sample of females, none was age I, 64% were age II, and 36% were age III. Except for one large male with three annuli, the females were consistently larger than the males in each age group (Table 9). The smallest ripe male was 86 mm standard length and the largest was 130 mm; the smallest female was 120 mm and the largest was 139 mm.

In late November and December large numbers of pygmy whitefish move from the deep water of Flathead Lake and congregate at the mouths of the Swan and Flathead Rivers before they enter the river systems presumably to spawn. The males outnumber the females 6.7:1 in these concentrations. Of the age I males,

TABLE 9.—Frequency distribution according to standard length of three age groups of ripe pygmy whitefish taken from Ross Creek in three different years.

Sex and standard length (mm)	2 Dec. 1952		10 Dec. 1955			20 Dec. 1967		
	I	II	I	II	III	I	II	III
Males:								
86- 90	4	—	—	—	—	2	—	—
91- 95	4	—	16	—	—	4	—	—
96-100	2	2	7	—	—	4	1	—
101-105	—	5	1	5	—	—	2	—
106-110	—	4	—	12	—	—	8	—
111-115	—	—	—	2	—	—	—	—
116-120	—	—	—	—	2	—	—	—
126-130	—	—	—	—	—	—	—	1
Females:								
116-120	—	1	—	—	—	—	—	—
121-125	—	—	—	1	—	—	1	—
126-130	—	1	—	2	—	—	—	—
131-135	—	—	—	1	1	—	—	2
135-140	—	—	—	—	—	—	—	1

74.5% were sexually mature. All males age II or older were mature. As in the Bull Lake population, the females mature more slowly than the males. The percentage maturity of the females was 27.8 at age I, 90.2% at age II, and 100% for older fish. Younger breeding age in the males and the larger size of mature females characterize the other widely separated populations (Eschmeyer and Bailey, 1955; Heard and Hartman, 1966).

Female pygmy whitefish obviously spawn in consecutive years. Mature ripe eggs were present in the abdominal cavity while smaller eggs, 1 mm in diameter, were developing in the ovaries of ages II and III females.

Sex Ratio

The predominance of males in Bull Lake collections has been discussed previously. Although variable from sample to sample the sex ratio of all pygmy whitefish taken from Flathead Lake in 1969 was nearly equal (Table 10). When collections for 1967 through 1971 were combined, however, males exceeded females by a ratio of 2:1 (Table 5). The sexes were about equal at age II but many more males were taken at age I.

Fecundity

The fecundity of individual fish from Lake Superior and Alaska varied widely. In Flathead Lake egg counts of 28 females ranged from 156 to 918 and averaged 588. The larger fish tended generally to have the most eggs, but exceptions were frequent (Table 11). Four large spawners from Bull Lake had from 1,027 to 1,136 eggs. In Lake Superior egg counts ranged from 93 to 597 and averaged 362 (Eschmeyer and Bailey, 1955); those from the Naknek River system ranged from 103 to 1,153 (Heard and Hartman, 1966).

Conversion of our lengths to total lengths in inches and comparison with Eschmeyer and Bailey's length-fecundity curve shows that pygmy whitefish from Flathead Lake produce more eggs for their size than do the Lake Superior fish and that those from Bull Lake are even more productive. Fish from Bull Lake with total lengths from 6.0 to 6.5 inches have egg counts slightly more than 1,000 compared with about 650 for the Lake Superior fish. If the length-fecundity curve of Heard and Hartman is projected, the Bull Lake population was about the same as fish from South Bay in the Naknek River system, but the Flathead fish produced fewer eggs. Fish in the 5.4- to 5.7-inch range from Flathead Lake had 560 eggs whereas those from South Bay had about 700 eggs. Heard and Hartman explained the differences in fecundity among populations as adaptations to different environmental conditions that produce higher or lower survival opportunities for the species.

TABLE 10.—Length and weight of pygmy whitefish from Bull Lake and Flathead Lake.

[Ranges in parentheses.]

Locality	Number of fish	Sex	Standard length (mm)	Weight (g)
Ross Creek:				
10 Dec. 1955	45	male	102 (90-120)	15.8 (10.3-25.0)
	5	female	130 (125-135)	39.6 (30.7-44.0)
12 Dec. 1967	53	male	107 (90-130)	20.7 (9.3-27.5)
	17	female	137 (125-160)	36.0 (26.8-55.6)
Flathead Lake:				
May-Nov. 1969	102	male	99 (75-116)	11.8 (4.8-22.8)
	117	female	109 (70-140)	18.0 (3.0-42.6)

TABLE 11.—Production of eggs of pygmy whitefish.

Locality	Number of fish	Average weight (g)	Range in standard length (mm)	Number of eggs	
				Range	Mean
Bull Lake	4	43.5	130-135	1,027-1,136	1,084
Flathead Lake	5	16.7	107-110	414-700	547
	11	20.7	111-120	227-733	558
	10	24.9	122-133	156-918	564

Time and Locality of Spawning

No fully mature pygmy whitefish has been found in Bull Lake in November, but ripe fish were readily collected from Ross Creek, the inlet, on 26 December and 12 January 1952, 10 December 1955, and 20 December 1967. Also, fisherman were observed catching ripe fish from the mouth of Stanley Creek, a tributary at the opposite end of the lake, on 3 January 1952 (Weisel and Dillon, 1954). Although milt and roe were easily stripped, the appearance of the gonads indicated that most of the fish had not spawned. The spawning period in Bull Lake must extend from mid-December well into January. All evidence indicates pygmy whitefish spawn in streams rather than in the lake. As previously stated, mature fish were congregated at the mouths of the two major inlets of Flathead Lake in late November and December.

The species spawns in Alaska apparently between mid-November and mid-December in rivers and at the mouths of rivers during the night. In Lake Superior, Glacier National Park, and British Columbia the fish is believed to spawn in November or December in shallow water.

DISCUSSION

The pygmy whitefish is typified by low meristic counts. In gill raker counts the populations from Flathead and Bull Lakes are intermediate compared to Alaskan populations. This does not support McCart's (1970) contention that the low-rakered form persisted in the Columbia River Basin during Pleistocene glaciation. Vertebral counts range widely even within individual populations. Most of the vertebral variation is in the caudal rather than in the precaudal vertebrae.

The pygmy whitefish is flexible in diet and feeding behavior. Depending on the season and locality, the species may feed primarily on insects and zooplankton or on macrobenthic crustaceans. In any one habitat, however, the diet is either highly selective or restricted compared to many other species of fishes.

The pygmy whitefish must be important in the trophic system of Flathead Lake. They are a small, abundant primary carnivore and consequently must be an important food source for the secondary carnivores such as lake trout and Dolly Varden which frequent the deeper water. Its primary food competitor is undoubtedly the lake whitefish. The lake whitefish feeds extensively on molluscs but also includes chironomids and copepods as main dietary items in Flathead Lake (Brunson and Newman, 1951).

The species is short-lived. In the Montana populations no male was found older than age III and no female beyond age IV. In growth rate and fecundity the Montana populations are similar to those from Alaska and Lake Superior.

The pygmy whitefish exists successfully with sympatric salmonoids in spite of its small size and relatively low egg production. The mountain whitefish in Montana, its closest rival in respect to reproduction, produces an average of 4,400 eggs; the largest pygmy whitefish produces a quarter of this number. However the pygmy whitefish produces more eggs per pound of fish—10,000 eggs for Bull Lake specimens compared with 5,340 for mountain whitefish (Brown, 1952). This production is made possible by the reduced size of the eggs of the pygmy whitefish, which are 2.4 to 2.6 mm in diameter when water hardened compared with

3.1 to 4.2 mm for mountain whitefish. Booke (1970) postulated that the large-egg coregonine species gave rise to small-egg types. He admitted that the small-egg size of the pygmy whitefish does not fit his hypothesis because the species is considered to be the most primitive of the subfamily Coregoninae but that this may be a specialized character; and if the pygmy whitefish had the growth potential of the other species in the genus, it would probably have a larger egg. Also compensating for the low egg number per female, the pygmy whitefish spawns at an earlier age. Most mountain whitefish do not mature until their third or fourth year (Sigler, 1951; Brown, 1952), 1 to 2 years later than female pygmy whitefish and 2 years later than male pygmy whitefish. The early maturation and shorter life span of the male pygmy whitefish ensures greater fecundity and abundance of the species at lower consumption of food.

Evidence suggests strongly that direct competition between the two whitefish species on the spawning grounds is avoided by a difference in spawning time. Booke (1970) noted that large-egg coregonines spawn earlier than those with small eggs. From the information available, it appears that in Montana the large-egg mountain whitefish spawns about a month earlier than the small-egg pygmy whitefish.

The small size and consequential small egg diameter of the pygmy whitefish may be explained by the rigors of the glacial period. The known range of the species is restricted to recently glaciated areas. During the glacial period it probably retreated less than other coregonines from the glacial margins. The small size and early spawning age were very possibly adaptations for survival in cold and nutrient-poor waters.

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