PYGMY WHITEFISH *PROSOPIUM COULTERI* IN THE NAKNEK RIVER SYSTEM OF SOUTHWEST ALASKA

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ABSTRACT

The pygmy whitefish is widely distributed throughout the lakes of the Naknek River system in southwest Alaska. It is a small abundant species in some lakes of the system and may occupy a more prominent place in the population dynamics of fishes in the Naknek system than in other geographic areas where it has been studied. Specimens were collected with a variety of sampling gear including gill nets, tow nets, otter trawls, and seines. Pygmy whitefish occurred in all benthic habitats from shallow littoral depths to bathybenthic areas. Seasonally in certain age groups and in certain areas they occurred in limnetic areas of lakes and in streams. In the Naknek system, 18 species, including the young of commercially valuable sockeye salmon and the closely related round whitefish, were ecological associates of pygmy whitefish.

Two populations, one in South Bay of Naknek Lake and the other in Brooks Lake, were studied in detail. The oldest and largest pygmy whitefish collected was an age V 163-mm. female from South Bay. An age III 83-mm. female was the oldest and longest specimen from Brooks Lake. Length frequency distributions from other lakes were intermediate between these extremes. Growth rates were back calculated from polynomial body length–scale length equations for Brooks Lake and South Bay populations.

Dipteran insects were the principal foods eaten by pygmy whitefish in South Bay. Crustacean plankton dominated their diet in Brooks Lake. In other areas insects and zooplankton were about equal in importance. Growth and insect consumption were correlated positively.

Spawning occurs in November and December, apparently only at night. South Bay fish spawn in lower Brooks River. Eggs in ripe females from South Bay averaged 2.4 mm. in diameter, and the ovaries were 16.5 percent of the body weight. The fork length-fecundity relation of Naknek system pygmy whitefish has the equation

$$\text{Log } E = -2.9552 + 2.7513 \text{ Log } L$$

Both sexes mature earlier in Brooks Lake than in South Bay.

Slow growth, low fecundity, and short life characterize pygmy whitefish in Brooks Lake. These factors are compensated for in part by early maturity and probably by a low mortality from fertilized egg to maturity. The wide range of pygmy whitefish populations in the Naknek system probably reflects adaptive responses of a highly plastic species to the wide variety of environmental characteristics found in different lakes of the system.

Pygmy whitefish, *Prosopium coulteri* (Eigenmann and Eigenmann), are widely distributed throughout lakes of the Naknek River system in southwest Alaska (fig. 1). These lakes, which are important fresh-water rearing areas for juvenile sockeye salmon, *Oncorhynchus nerka* (Walbaum), are studied by the Bureau of Commercial Fisheries to determine factors limiting fresh-water production of this highly important commercial species. These studies embrace a variety of limnological and biological research, including interspecific relations of fishes associated with juvenile salmon.

Pygmy whitefish are apparently the most abundant species in some lakes of the Naknek system, and it is possible that they may compete directly

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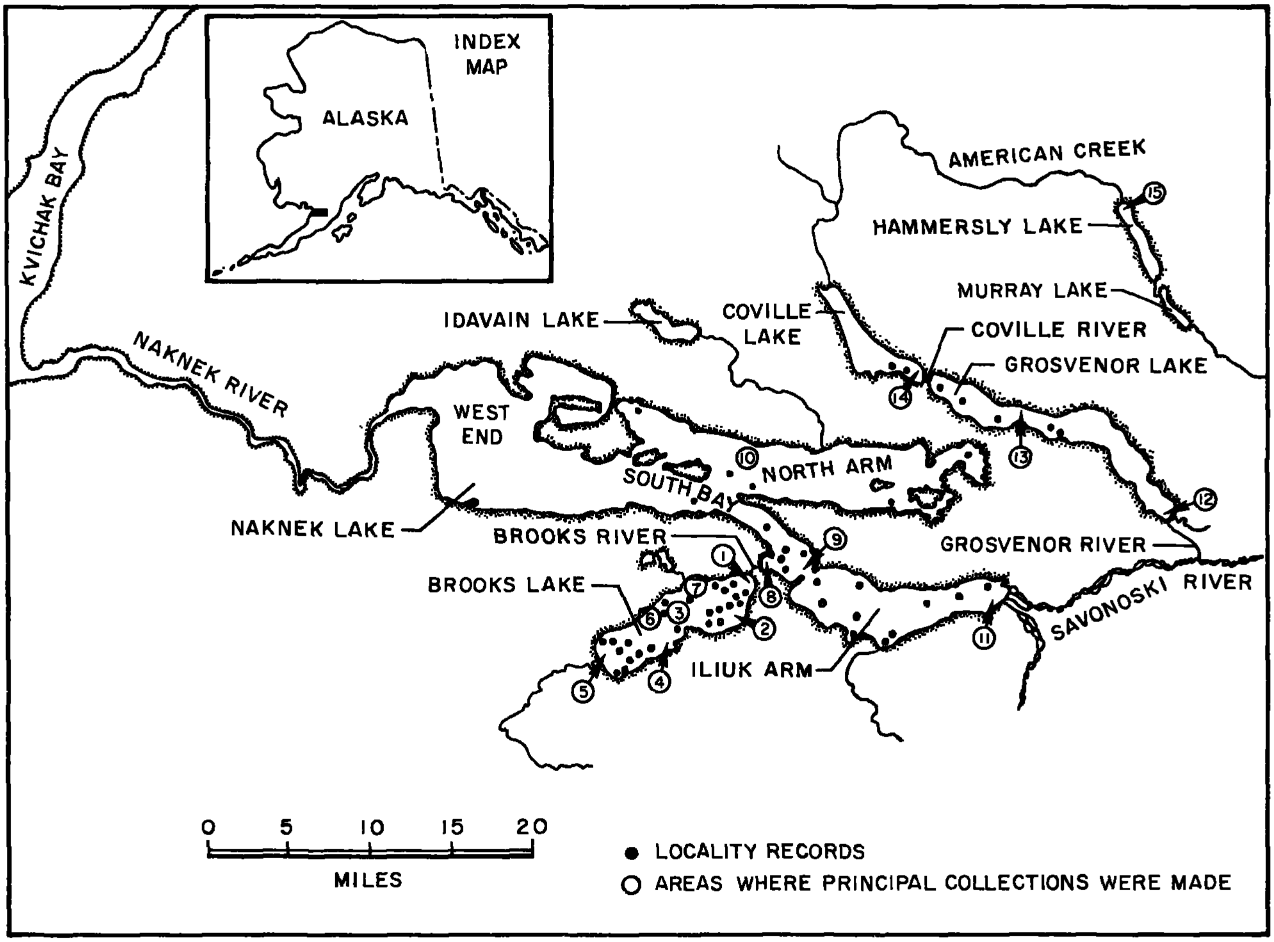

FIGURE 1.—Naknek River system of southwest Alaska, showing areas where pygmy whitefish were collected. Dots represent locality records; circled numbers are locations where 10 or more pygmy whitefish were collected in a specific sampling effort.

or indirectly with juvenile sockeye salmon for food or space. Other fishes, for instance the threespine stickleback (*Gasterosteus aculeatus*), have also been characterized as actual or potential competitors with juvenile sockeye salmon (Krogius and Krokhin, 1948; Greenbank and Nelson, 1959; and Burgner, 1960). Pygmy whitefish may also act as a buffer between salmon predators and young salmon.

There is relatively little literature concerning pygmy whitefish, and specific studies on the biology of this species are few. They were discovered in British Columbia in 1892 and were first collected in Alaskan waters in 1912 (Kendall, 1917). Although locality and life history data accumulated for several years (Snyder, 1917; Kendall, 1921; Schultz, 1941; and Wynne-Edwards, 1947 and 1952), published material was based on few specimens. Meyers (1932) reported on 21 specimens from Chignik River on the Alaska Peninsula, and Weisel and Dillon (1954) reported on 23 pygmy whitefish from western Montana. Eschmeyer and Bailey (1955) collected 1,623 pygmy whitefish from Lake Superior during a 2-year study and reported the discovery of a relatively large population in the lake and described its morphology and life history. Comparisons were made with previous collections from the Pacific slope. McCart (1963) has recently studied the growth and morphology of pygmy whitefish from several British Columbia lakes.

Pygmy whitefish were first collected in the Naknek River system at Brooks Lake in 1957, and observations in Brooks Lake have continued since then.[1] Beginning in 1961 and continuing through 1963, observations were extended throughout the Naknek system. More than 10,000 specimens have been collected by various methods since 1961.

The present study was undertaken to investigate the distribution, age and growth, food habits, reproduction, and general life history of pygmy whitefish in the Naknek system. Emphasis was placed on determining the relation of pygmy whitefish biology to that of other fishes in the system, particularly the sockeye salmon.

STUDY AREA

The Naknek River system, much of which lies within Katmai National Monument, consists of seven interconnecting lakes: Hammersly, Murray, Coville, Grosvenor, Brooks, Idavain, and Naknek. These lakes drain into the northeast side of Bristol Bay through the Naknek River (fig. 1). All are glacial in origin, dating from Wisconsin times (Muller, 1952; and Karlstrom, 1957). Naknek Lake comprises three major basins and a shallow outwash plain. The basins, Iliuk Arm, North Arm, and South Bay, and the outwash plain, West End, will be referred to hereafter without reference to Naknek Lake. The maximum depths are not known for Murray, Idavain, or Hammersly Lakes. The other lakes vary between a maximum depth of 53 m. in Coville Lake and 173 m. in Iliuk Arm.

The lakes and basins of the Naknek system include a broad range of environmental types. Most of them are oligotrophic and usually have ice cover from December through early May. Iliuk Arm frequently does not freeze over completely, probably because of its depth and excessive turbidity, which is due to glacial melt water and volcanic ash. In Iliuk Arm, Secchi disk visibility is generally less than 0.5 m., while in the other basins and lakes it ranges between 3 and 12 m. A horizontal turbidity gradient occurs in South Bay, increasing in intensity toward Iliuk Arm. Thermal gradients commonly exist, although classical thermoclines develop only occasionally and are unstable. The waters are slightly alkaline, and oxygen levels remain at or near saturation at all depths measured throughout the year. The basic limnology of lakes in the Naknek River system is described in detail elsewhere.[2]

MATERIALS AND METHODS

Most pygmy whitefish were collected in the Naknek system with small otter trawls, tow nets, beach seines, and small-meshed gill nets. A few specimens were collected with fyke nets and floating lake traps and by divers using hand nets. These same methods were used to sample juvenile sockeye salmon in various stages of their freshwater life. Heard (1962) described the small-meshed gill nets, and the three other principal types of gear are described below. All mesh sizes are given in stretch measure.

The otter trawls were Gulf Coast shrimp try-trawls about 6 m. long, 2.6 m. wide, and 0.6 m. deep. The cotton webbing varied from 50.8-mm. mesh in the front section to 25.4-mm. in the cod section, with a 13-mm. mesh cod liner. The footrope was weighted with a 19-mm. mesh chain, and the otter doors were 30.5 by 45.7 cm. Except for use of a tow cable guide ring on the transom, our use of these trawls behind an outboard skiff was basically the same as described by Baldwin (1961).

Trawl drags varied in time, in length of drag, and in depth. Generally they were between 8 and 15 minutes long and covered from 325 to 1,000 m. The trawls were fished effectively for pygmy whitefish to depths of 79 m.

The tow nets were 3.1 m. in diameter and 6.9 m. long, and they were used generally at night in limnetic (offshore or open water) portions of the lakes. They were towed behind two outboard skiffs with the top of the net at the surface or 3.1 m. deep. A standard tow was 492 m. Mesh sizes of nylon webbing varied from 38 mm. at the net opening to 3 mm. in the cod end. Burgner (1960) describes the construction and general use of this net. A 1-m. tow net such as that described by Johnson (1956) was used to collect one sample of pygmy whitefish in Brooks Lake.

Three types of beach seines were used. The two principal types, which were set in a semicircular pattern from shore with an outboard skiff, were 3.1 m. deep and 32.8 or 42.6 m. long. The 32.8-m. seine consisted solely of 3 mm. webbing, and the

[1] The annual field reports of the research operations at Brooks Lake (1957–62) are on file at the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska.

[2] Hartman, Wilbur L., and Robert L. Burgner. The limnology of sockeye salmon nursery lakes in southwest Alaska. The manuscript is filed in the U.S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska.

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42.6-m. seine consisted of a center section (9.8 m. long) of 6-mm. webbing and two end sections (16.4 m. long) of 12-mm. webbing. The third type was 1 m. deep with 3-mm. webbing and was either 3.1 or 6.1 long.

Most collections of pygmy whitefish were preserved and processed for various biological data; specimens from the other collections were discarded after the catch was recorded. Fork lengths were measured in millimeters and weights in tenths of grams. Most collections were preserved in 10-percent formalin for at least 48 hours before processing. The conversion factor of 0.977 to account for shrinkage was applied to length data on one group of fresh specimens. All lengths given are preserved lengths or equivalents. Because Eschmeyer and Bailey (1955) presented their pygmy whitefish data in total lengths, we determined factors for converting fork lengths to total lengths. Fork length times 1.0777 equals total length for specimens shorter than 100 mm., and fork length times 1.0845 equals total length for specimens longer than 100 mm.

Biological information determined from individual specimens included age and growth determinations, stomach content analyses, and reproductive data. Age and growth were analyzed from scale samples and length frequencies. Stomach content analyses were made either on all of the specimens or on random samples from different collections. The occurrence of food items was determined for individual fish, while volumetric analyses were made by combining food items from all fish in a specific collection. Sex ratios and age and length at maturity were determined for random samples or for all fish in different collections. Egg content was determined for 85 females by total count.

DISTRIBUTION AND ABUNDANCE OF PYGMY WHITEFISH

Pygmy whitefish have the greatest discontinuous range of any fresh-water fish in North America according to Eschmeyer and Bailey (1955). In addition to its occurrence in Lake Superior of the Atlantic slope, this species has been recorded from the Columbia River drainage in Washington, Montana, and British Columbia (Schultz, 1936; Weisel and Dillon, 1954) and from the Fraser, Skeena, Yukon, and Mackenzie River systems of the Pacific and Arctic slopes (Carl, Clemens, and Lindsey, 1959). It also occurs in both Pacific and Bering Sea drainages of southwest Alaska, having been reported from the Nushagak (Snyder, 1917), Chignik (Kendall, 1917), Naknek (Merrell, 1964), and Kvichak (personal communication, Ole A. Mathisen and O. E. Kerns) River systems. Pygmy whitefish probably occur in other Bristol Bay river systems on the Alaska Peninsula, such as the Ugashik and Egegik, where large lakes appear to provide suitable habitat.

Eschmeyer and Bailey (1955) concluded that the present disjunct populations of pygmy whitefish are all referable to the same species and most likely represent relicts of a continuously distributed species in late Pleistocene that survived in deep lakes after the retreat of Wisconsin glaciation. McCart (1963) compared meristic and morphological variation in pygmy whitefish from British Columbia with those from other areas and found the species to be highly variable both within and between populations.

The sizes attained by pygmy whitefish in different geographic areas varied, most likely because of differences in growth rates related to different environments. The maximum size reported from Lake Superior was 149 mm. Carl, Clemens, and Lindsey (1959) reported a population of "giant" pygmy whitefish in Maclure Lake, British Columbia. McCart (1963) found pygmy whitefish in this lake as large as 262 mm. The maximum sizes in the Naknek system varied considerably between lakes, ranging from 84 mm. in Brooks Lake to 163 mm. in South Bay (fig. 2).

NAKNEK SYSTEM

Pygmy whitefish are widely distributed throughout the Naknek system and were collected in every major water area in the system except Idavain and Murray Lakes and West End (table 1). No attempt was made to collect them in Idavain Lake, and only one small-meshed gill-net set, which was unproductive, was made in Murray Lake. Pygmy whitefish may have been collected in 1962 from the West End in tow nets, but the discarded specimens were recorded on field data sheets only as "whitefish." It is likely that they do occur in these three major areas, however.

The abundance of pygmy whitefish varied throughout the system. The distribution is best

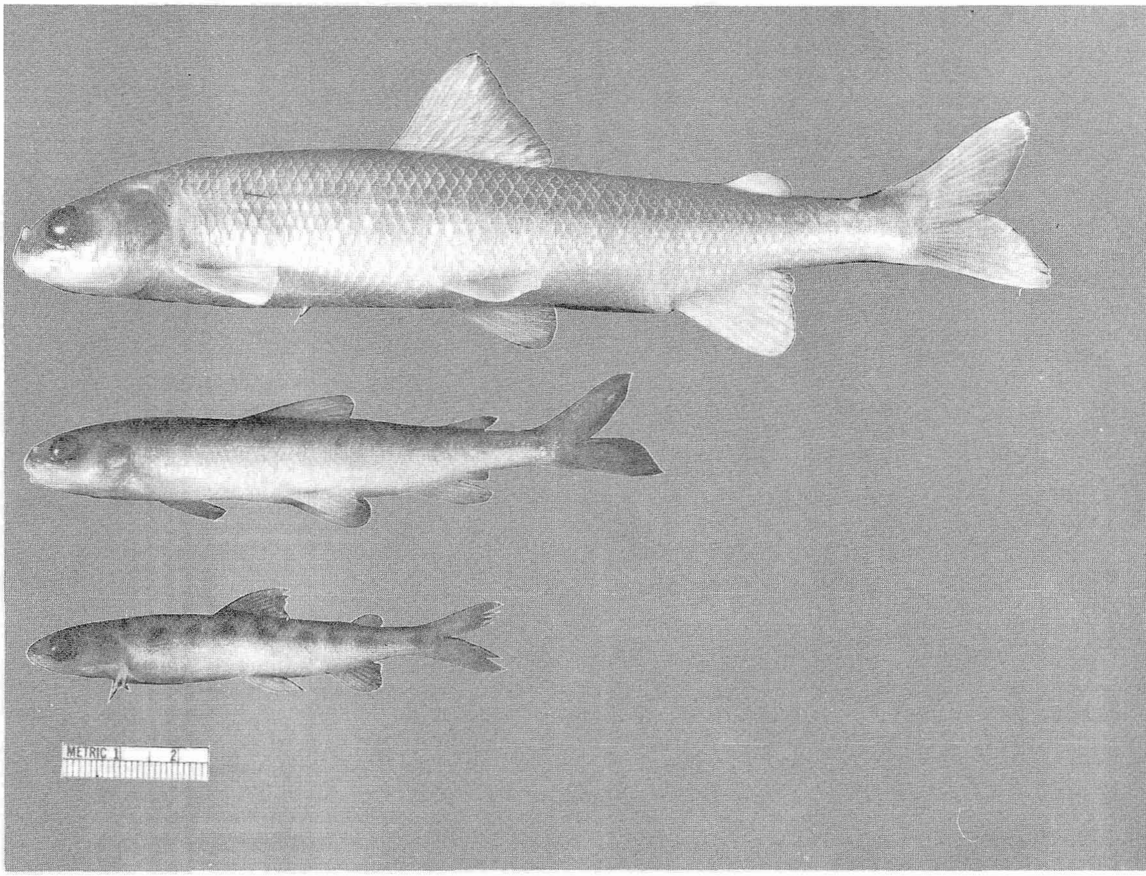

FIGURE 2.—Pygmy whitefish from the Naknek system. From top to bottom: 5-year-old mature female, 163 mm. long, collected November 9, 1962, in South Bay; 2-year-old immature female, 98 mm. long, collected November 9, 1962, in South Bay; 3-year-old mature female, 76 mm. long, collected November 7, 1962, from Brooks Lake.

known in Brooks Lake where the greatest sampling effort was expended. Pygmy whitefish were collected in all sections of Brooks Lake, and two areas of heavy abundance were found at opposite ends of the lake (areas 1 and 5 (fig. 1)). They also occurred throughout South Bay and Iliuk Arm. A concentration of this fish apparently occurs in the semiprotected bay of South Bay near the mouth of Brooks River and in the upper end of Iliuk Arm. The known distribution of pygmy whitefish in North Arm is spotty, but it is believed to be widely distributed in this basin. In 1962 and 1963, small whitefish were not specifically identified on field collection sheets of seine records from that basin. We suspect that at least some of these were pygmy whitefish. In Grosvenor Lake, pygmy whitefish were collected in most areas of the lake; but, in Coville Lake, they were collected only from the east end of the lake. The one Hammersly Lake collection was made near the lake outlet.

The most widely used sampling gear throughout the system was tow nets, which was used in open-water limnetic areas, primarily to sample juvenile sockeye salmon. Otter trawls, gill nets, and seines, which were more effective than tow nets in sampling pygmy whitefish, were used to different degrees in different areas (table 1). The unknown vulnerability of pygmy whitefish to different types of gear and the unequal use of each type in various lakes and basins should be kept in mind when considering relative abundance.

On the basis of the number of specimens obtained in other geographic areas by previous collectors, populations of pygmy whitefish may occupy a more dominant role in the overall fish population structure in parts of the Naknek system than in other areas. In the Lake Superior study, the greatest single collection of pygmy

TABLE 1.—*Sampling efforts*[1] *with otter trawls, tow nets, small-meshed gill nets, and beach seines in Naknek system and percent of samples yielding pygmy whitefish, 1961–63*

Sampling area and year	Otter trawl		Tow net		Gill net[2]		Seine	
	Sampling efforts	Samples with pygmy whitefish	Sampling efforts	Samples with pygmy whitefish	Sampling efforts	Samples with pygmy whitefish	Sampling efforts	Samples with pygmy whitefish
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Brooks Lake:								
1961	79	33	108	31	----	----	3	33
1962	60	43	154	8	2	100	28	36
1963	4	75	40	8	9	78	4	75
Coville Lake:								
1961	----	----	60	0	----	----	5	[3] 0
1962	15	0	41	2	1	100	37	[3] 24
1963	5	0	47	2	3	0	----	----
Grosvenor Lake:								
1961	----	----	101	3	----	----	7	[3] 0
1962	21	10	53	4	----	----	26	[3] 12
1963	1	100	20	5	----	----	----	----
Naknek Lake:								
South Bay:								
1961	1	100	57	4	----	----	6	33
1962	8	75	61	10	3	100	47	68
1963	2	100	39	3	6	100	6	83
Iliuk Arm:								
1961	2	0	49	2	2	100	4	50
1962	----	----	72	6	----	----	12	58
1963	----	----	36	6	2	50	2	100
North Arm:								
1961	----	----	32	0	3	100	8	0
1962	----	----	94	1	3	100	24	[3] 0
1963	----	----	12	0	1	100	5	0
West End:								
1961	5	0	21	0	----	----	----	----
1962	----	----	52	[3] 0	----	----	5	0
1963	----	----	44	0	----	----	----	----
Hammersly Lake:								
1962	----	----	----	----	1	100	----	----
Murray Lake:								
1962	----	----	----	----	1	0	----	----
Brooks River:								
1963	4	100	----	----	----	----	2	100

[1] A sampling effort equals one trawl haul, tow net haul, gill net lift, or individual seine haul.
[2] Includes only those gill net sets with mesh sizes 1-inch stretch measure or smaller.
[3] Not including sampling efforts containing unidentified small whitefishes which may have included pygmy whitefish.

whitefish was 171 specimens taken in an otter trawl in Siskiwit Bay (Eschmeyer and Bailey, 1955). Our largest single collection was 1,701 specimens taken in a beach seine haul on August 14, 1962, in Brooks Lake (table 2). The largest Lake Superior collection had about 80 percent age 0+ fish, while the largest Brooks Lake collection had 100 percent age 0+ fish. Our second largest collection was made July 10, 1962, by a trawl drag in Brooks Lake that yielded 1,567 age I+ and age II+ fish. A beach-seine haul in South Bay on August 4, 1962, yielded 964 specimens (table 2). Of these, 962 were age I+ and older. All of the 1961–63 collections of pygmy whitefish from the Naknek system in which 10 or more specimens were caught in a sampling effort are listed by date, area, gear, depth, and number of specimens in table 2.

ECOLOGICAL AND SEASONAL DISTRIBUTION

Pygmy whitefish occupy a wide variety of ecological habitats in the Naknek system. They were caught not only in benthic habitats, ranging from a depth of 168 m. (in Iliuk Arm and North Arm) to littoral areas less than 1 m. deep, but also in limnetic areas at or near the surface over deep water and in several streams.

The capture of pygmy whitefish in littoral areas with seines and trawls and in limnetic areas with tow nets was somewhat unexpected. In Lake Superior, Eschmeyer and Bailey (1955) caught pygmy whitefish only in benthic areas below 10 fathoms. Except for six specimens caught in gill nets, all Lake Superior pygmy whitefish were caught in otter trawls.

Most littoral catches of pygmy whitefish in the Naknek system were made at the northeast end of Brooks Lake and in a semiprotected bay in South Bay (areas 1 and 8, fig. 1). Part of this littoral area in Brooks Lake consisted of a shallow sandy shelf 1 to 2 m. deep that extended 300 to 500 m. into the lake. This shelf is subject to heavy wave action and is barren of vegetation except for small patches of *Ranunculus* sp. Large schools of age 0+ pygmy whitefish were observed by biologists

TABLE 2.—*Collections of pygmy whitefish from the Naknek system in which 10 or more specimens were caught per sampling effort*[1] *by area, gear, depth, and number of specimens, 1961–63*

Sampling area and date	Numbered area[2]	Type of gear	Depth	Total specimens caught
			Meters	*Number*
Brooks Lake:				
July 17, 1961	1	Otter trawl	8	290
July 18, 1961	7	do	12	11
July 20, 1961	1	do	2	89
July 21, 1961	2	do	3	32
Aug. 7, 1961	4	do	5	150
Aug. 8, 1961	5	do	5	308
Aug. 8, 1961	5	do	8	344
Aug. 10, 1961	5	do	15	12
Aug. 10, 1961	5	do	32	10
Aug. 11, 1961	1	Tow net (3.1 m.)	0–3.1	16
Aug. 11, 1961	2	do	0–3.1	321
Sept. 1, 1961	1	do	0–3.1	10
Sept. 14, 1961	1	Otter trawl	5	96
Sept. 26, 1961	6	Tow net (3.1 m.)	3.1–6.1	10
June 29, 1962	1	Otter trawl	4	70
June 29, 1962	1	do	10	425
July 10, 1962	1	do	8	1,567
July 11, 1962	5	do	2	88
July 22, 1962	1	do	8	18
July 22, 1962	1	do	8	46
July 23, 1962	1	Tow net (1-m.)	0–1	168
July 26, 1962	7	Otter trawl	5	40
July 27, 1962	2	do	3	69
Aug. 10, 1962	4	Seine	2	24
Aug. 10, 1962	5	do	2	88
Aug. 10, 1962	5	do	2	15
Aug. 10, 1962	5	do	2	36
Aug. 14, 1962	1	do	1	1,701
Sept. 14, 1962	1	Otter trawl	8	15
Nov. 7, 1962	1	do	8	306
Nov. 8, 1962	1	Gill net	12	67
Nov. 8, 1962	2	do	3	11
July 2, 1963	1	Hand net	1	17
July 8, 1963	1	Seine	1	65
July 16, 1963	1	do	1	17
July 22, 1963	3	Gill net	66	14
July 22, 1963	3	Otter trawl	65	10
July 26, 1963	3	Gill net	78	10
Aug. 7, 1963	1	Seine	1	18
Aug. 9, 1963	3	Gill net	78	18
Aug. 20, 1963	3	do	[3] 75	11
Dec. 16, 1963	1	do	12	29
South Bay:				
July 15, 1962	8	Seine	2	46
July 22, 1962	9	do	3	36
South Bay—Con.				
July 23, 1962	9	Seine	3	16
July 23, 1962	9	do	3	25
July 23, 1962	9	do	3	16
July 23, 1962	9	do	3	53
July 23, 1962	9	do	3	10
Aug. 4, 1962	8	do	2	542
Aug. 4, 1962	8	do	2	16
Aug. 4, 1962	8	do	2	22
Aug. 4, 1962	8	do	2	345
Aug. 4, 1962	8	do	2	11
Aug. 4, 1962	8	do	2	964
Aug. 24, 1962	8	do	2	96
Sept. 26, 1962	8	do	2	148
Nov. 9, 1962	8	do	2	124
Nov. 10, 1962	8	Gill net	8	116
Apr. 16, 1963	8	do	7	20
May 30, 1963	8	do	8	12
June 14, 1963	8	Seine	1	12
July 11, 1963	8	do	1	144
Oct. 29, 1963	8	Gill net	8	33
Nov. 5, 1963	8	do	8	56
Dec. 12, 1963	8	do	3	81
Brooks River:				
July 27, 1963	8	Seine	1	458
Aug. 24, 1963	8	Otter trawl	1	178
Aug. 24, 1963	8	do	1	18
Aug. 25, 1963	8	do	1	200
Aug. 25, 1963	8	do	1	150
Iliuk Arm:				
July 9, 1963	11	Seine	3	12
July 27, 1963	11	do	3	27
North Arm:				
July 22, 1962	10	Gill net	169	10
Aug. 9, 1962	10	do	169	21
Coville Lake:				
June 7, 1962	14	Seine	2	12
June 7, 1962	14	do	2	10
June 9, 1962	14	do	2	10
July 12, 1962	14	do	2	12
Grosvenor Lake:				
June 30, 1962	12	do	2	48
Aug. 5, 1962	13	Otter trawl	8	54
Aug. 19, 1963	12	do	7	96
Hammersly Lake:				
Aug. 20, 1962	15	Gill net	20	12

[1] A sampling effort is an individual trawl haul, tow net haul, beach seine haul, or gill net lift.
[2] See figure 1.
[3] Gill net was buoyed so that it was fishing horizontally 3 m. off the bottom in water 78 m. deep.

skin diving along this shelf during June, July, and August, 1962 and 1963. These fish were routinely caught with seines or hand nets. On July 23, 1962, 168 age 0+ pygmy whitefish were caught on the edge of this shelf in a 1-m. tow net (table 2). This particular catch was made in an area where Arctic Terns (*Sterna paradisaea*) were feeding on small fishes near the surface, presumably pygmy whitefish. Littoral collections in South Bay were made during April, May, June, July, August, September, October, November, and December in either 1962 or 1963 (table 2). Pygmy whitefish apparently remain in the littoral area of this bay throughout most of the year. No sampling was attempted during late winter or early spring.

In addition to the above areas, substantial numbers of pygmy whitefish were also caught in littoral areas in the narrows between South Bay and Iliuk Arm, at the upper end of Iliuk Arm, and near the outlets of Grosvenor and Coville Lakes (areas 9, 11, 12, and 14, fig. 1).

Pygmy whitefish in the Naknek system apparently are associated with the benthic zone at all lake depths. Benthic collections have been made from all depths in Brooks Lake with seines, trawls, or gill nets and from shallow shoreline and the deepest areas of North Arm and Iliuk Arm with seines and gill nets. This distribution differs from the bathybenthic distribution found in Lake Superior (Eschmeyer and Bailey, 1955) and the intermediate benthic distribution found in four British Columbia lakes (McCart, 1963). In each of these studies, pygmy whitefish were sampled primarily with one collecting gear—trawls in Lake Superior and gill nets in British Columbia.

Although pygmy whitefish are generally associated with the benthic zone, concentrations of them were typically spotty. A series of 11 consecutive seine hauls made along a 600-m. stretch of beach in South Bay on August 4, 1962 (table 3), shows that catches are variable and suggests that pygmy whitefish are frequently grouped in large schools. Approximately 80 percent of the pygmy whitefish collected throughout the Naknek system came from specific sampling efforts that yielded 100 or more specimens.

TABLE 3.—*Age 0+ and older pygmy whitefish caught in 11 consecutive seine hauls in South Bay, August 4, 1962*

Seine haul number	Fish per haul	
	Age 0+	Age I+ and older
	Number	*Number*
1	0	542
2	1	0
3	1	3
4	2	3
5	12	4
6	20	2
7	0	0
8	0	0
9	4	341
10	7	3
11	2	962

Underwater observations on the schooling and feeding behavior in lower Brooks River indicated that pygmy whitefish are frequently grouped in schools of several thousand fish. Fishes in these schools were evenly spread out over several meters of stream bottom. Individuals fed independently of other fish, and the undisturbed school of fish would slowly move from one area to another. When disturbed by an observer or predator, schools of pygmy whitefish in Brooks River became tightly grouped.

The distribution of age 0+ pygmy whitefish, particularly in Brooks Lake, changes in late summer. Many of these young whitefish remain in littoral areas on the sandy shelf along the northeast shoreline of Brooks Lake throughout much of the summer, but by mid-August they begin disappearing. They are scarce in this area in September. During the same period, limnetic catches of pygmy whitefish in tow nets increase. Age 0+ sockeye salmon in Wood River Lakes behave similarly (Burgner, 1960). Naknek system age 0+ sockeye salmon also show this behavior, although it is not as pronounced. The reasons for this fall change in distribution of young pygmy whitefish are not known. The autumn lake turnover, changes in diet attendant with shifts in food supplies, or other limnological changes may be involved. During the fall, weather on the Alaska Peninsula is characterized by severe storms with gale winds. The resultant heavy wave action may tend to disperse young pygmy whitefish from littoral areas.

About 95 percent of the pygmy whitefish caught with tow nets in all lakes and basins were age 0+ fish. In 1961 tow nets were used in Brooks Lake from mid-August throughout September, while otter trawls were used primarily from mid-July to mid-August. A comparison of length frequencies of pygmy whitefish caught in limnetic areas with tow nets with those caught in benthic areas with trawls during these periods indicates (fig. 3)

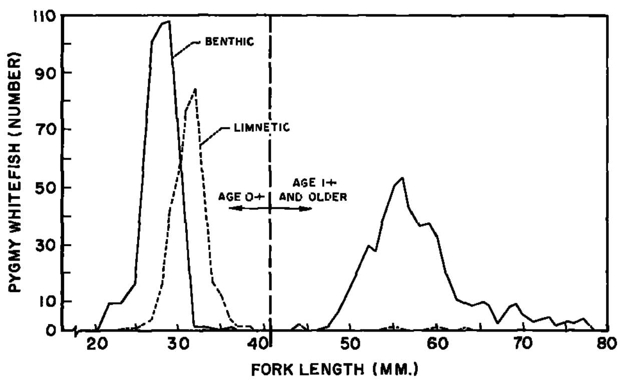

FIGURE 3.—Comparison of length frequencies of pygmy whitefish caught from mid-July to mid-August in benthic areas with otter trawls with those caught from mid-August through September in limnetic areas with 3.1-m.-diameter tow nets. Brooks Lake, 1961.

that while both age 0+ and older fish were caught in the benthic zone, most of those caught in the limnetic zone were age 0+. Differences in the selectivity of the two gears could have affected these catches; however, we do not feel trawls were selectively collecting older, larger pygmy whitefish since comparative catches of other fishes suggest that larger specimens are usually caught in tow nets. Our interpretation of these data is that fewer age 1+ and older pygmy whitefish were present in limnetic areas than in benthic areas. Differences in length frequencies of age 0+ fish shown in figure 3 are due to sampling periods and not to differences in size of fish caught in separate ecological areas or with different sampling gear. In 1962 and 1963 when tow nets were used in Brooks Lake throughout July and August, no pygmy whitefish were caught in limnetic areas until late August. Some age 0+ fish may have been present in limnetic areas before this time, although they probably would have been too small to capture in the available gear. Few tow net hauls were made in September, except in Brooks Lake in 1961.

Although no permanent stream populations of pygmy whitefish are known to exist in the Naknek system, large numbers seasonally occupy the lower 100 to 400 m. of Brooks River. These fish are part of the South Bay population (area 8, fig. 1) and do not go above a rapids area below Brooks River falls. They occupy lower Brooks River from late June to early September for feeding and from mid-November to mid-December for spawning. Feeding pygmy whitefish in Brooks River characteristically occupy neither the fastest moving nor the slowest moving water, but seem to prefer a moderate current adjacent to a faster one.

A few pygmy whitefish have been collected or observed in other streams in the system. With the possible exception of an annual downstream drift of spent fish in midwinter, these collections apparently represent only sporadic downstream movements of fish from Brooks, Coville, and Grosvenor Lakes. Underwater surveys of upper Brooks River from May through November and of Coville River from May through August revealed that pygmy whitefish did not occupy these streams during this period.

ASSOCIATED FISHES

Nineteen species of fishes were collected with pygmy whitefish in various parts of the system. The percent frequency occurrence of these species (table 4) provides a basis for discussing associated species. Throughout the system the cottids *Cottus aleuticus* Gilbert and *C. cognatus* Richardson were the most frequent associates, occurring in 55 percent of all sampling efforts that yielded pygmy whitefish (table 4). Juvenile sockeye salmon were the second most frequent associates, occuring in 42 percent of the samples. Next in frequency of association with pygmy whitefish were ninespine sticklebacks, threespine sticklebacks, round whitefish, and least cisco (table 4). The greatest number of sympatric associates in a specific area was 17 species in South Bay.

Certain fishes in the Naknek system were not caught with pygmy whitefish in all lake areas. Least cisco, humpback whitefish, pond smelt, and longnose sucker, were collected widely in other parts of the system but not in Brooks Lake. Alaska blackfish, abundant in Brooks Lake, were not collected in South Bay or Iliuk Arm. Differences in sampling gear and effort may account for species not being caught in certain areas.

The two most common associates of pygmy whitefish in Lake Superior were cottids and ninespine sticklebacks (Eschmeyer and Bailey, 1955). Round whitefish, which were never collected in association with pygmy whitefish in Lake Superior, occurred in 17 percent of the Naknek system samples yielding pygmy whitefish. These whitefishes were collected together in six of eight major lakes, basins, or streams (table 4). This apparent difference in association between pygmy whitefish and its closest relative in Lake Superior

TABLE 4.—*Percent frequency occurrence of associated fishes in sampling efforts*[1] *that yielded pygmy whitefish*

Species	Brooks Lake	South Bay	Iliuk Arm	North Arm	Coville Lake	Grosvenor Lake	Hammersly Lake	Brooks River	All areas combined
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Cottid, *Cottus* spp	60	53	38	63	67	42	100	17	55
Sockeye salmon, *Oncorhynchus nerka*[2]	35	41	71	25	67	58		33	42
Ninespine stickleback, *Pungitius pungitius*	39	36	10	62	25				33
Threespine stickleback, *Gasterosteus aculeatus*	29	24	38	38	92	17			31
Round whitefish, *Prosopium cylindraceum*	7	29	29	50		8		67	17
Least cisco, *Coregonus sardinella*		20	52	38				33	12
Alaska blackfish, *Dallia pectoralis*	18								9
Pond smelt, *Hypomesus olidus*		15	38		8				8
Arctic lamprey, *Lampetra japonica*	10	2							6
Lake trout, *Salvelinus namaycush*	1	3	14	38	8			100	4
Arctic grayling, *Thymallus arcticus*	2	11						17	4
Humpback whitefish, *Coregonus pidschian*		3	10	50					3
Coho salmon, *Oncorhynchus kisutch*[2]	3	3		13				17	3
Arctic char, *Salvelinus, alpinus*		5	5	25			100		3
Rainbow trout, *Salmo gairdneri*	2	3						100	2
Dolly Varden, *Salvelinus malma*		9							2
Longnose sucker, *Catostomus catostomus*		3	14	13					2
Northern pike, *Esox lucius*			14						1
Burbot, *Lota lota*		2							T

[1] Sampling efforts of all gears were combined for each area, then for all areas; see table 1 for total sampling effort by gear and area.
[2] Juveniles only.

and the Naknek system may be related to the use of only trawls in Lake Superior and several gears in the Naknek system. In the present study few round whitefish were captured in trawls. McCart (1963), using gill nets, found little or no association between pygmy whitefish and mountain whitefish *Prosopium williamsoni* (Girard) or lake whitefish *Coregonus clupeaformis* (Mitchill) in Cluculz and Tacheeda lakes, British Columbia.

AGE AND GROWTH

BODY-SCALE RELATION

The relation between body length and the anterior scale radius (mm. multiplied by 80) was determined for 456 pygmy whitefish from Brooks Lake and 500 from South Bay. Data from both lakes indicate this relation is highly sigmoid. Rounsefell and Everhart (1953, p. 324) suggest that problems of curvilinearity can be solved by omitting the earliest years and back calculating only those ages that do not deviate appreciably from linearity. The persistence of a curvilinear body-scale relation in the older age groups of Naknek system pygmy whitefish prevented any linear treatment of older fish. Also, these fish are relatively short lived, reaching a maximum age of 3 years in Brooks Lake and 5 years in South Bay. Age was determined from scale annuli, which, excluding scales from a few older fish, were not difficult to locate.

Fourth degree polynomial equations were found, excluding highly spurious intercepts, to fit fairly closely the empirical data for the body-scale relations of Brooks Lake and South Bay pygmy whitefish. These equations were calculated from individual pairs of body-scale observations. Mean body lengths for each scale radius are plotted against the calculated relations for both areas (figs. 4 and 5). Body length at scale formation is apparently between 22 and 27 mm. as determined by: (1) staining small fish for the first evidence of scale development and (2) calculating the intercept for collections of age 0+ fish after scale development. Separate equations were necessary for the Brooks Lake and South Bay collections because of strikingly different growth rates in the

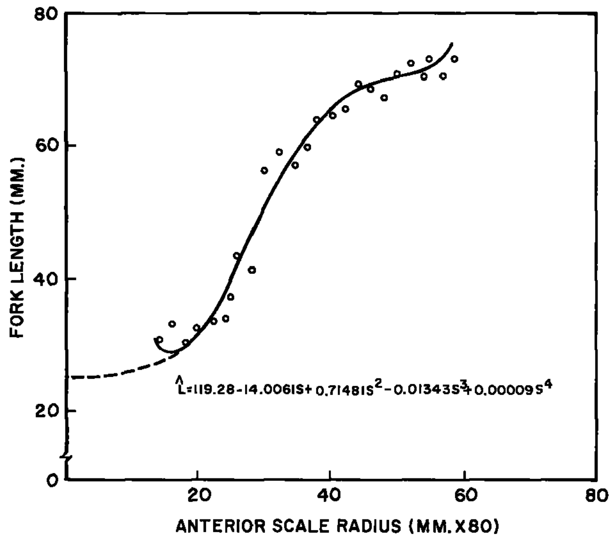

FIGURE 4.—Body length-scale radius relation of pygmy whitefish in Brooks Lake. Solid line is calculated equation; points represent mean body lengths for given scale radii; dashed line connects estimated intercept of 25 mm. with the logical portion of calculated curve.

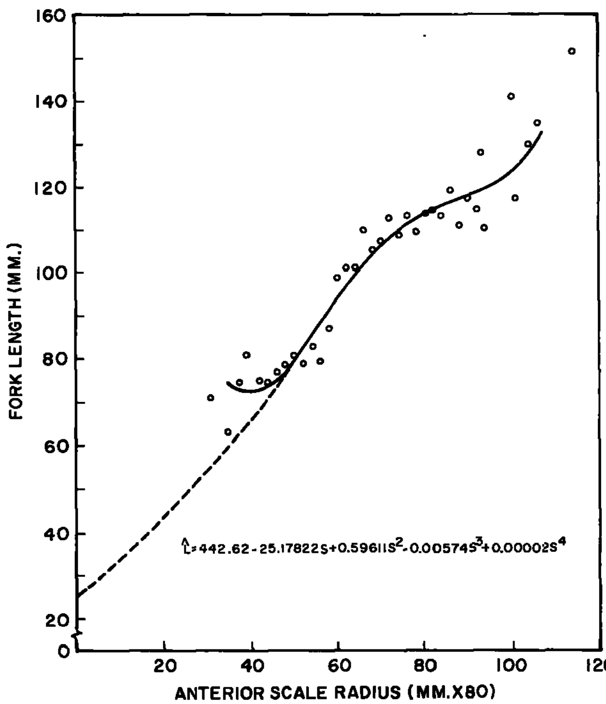

FIGURE 5.—Body length-scale radius relation of pygmy whitefish in South Bay. Solid line is calculated equation; points represent mean body lengths for given scale radii; dashed line connects estimated intercept of 25 mm. with the logical portion of calculated curve.

two populations.[3] Growth rates were back calculated from these quartic equations.

CALCULATED GROWTH

Fork lengths attained at each year of life and the annual increments were calculated by sex for 330 pygmy whitefish from Brooks Lake (table 5) and 779 from South Bay (table 6). A comparison of these growth rates reveals that pygmy whitefish grew considerably faster in South Bay than in Brooks Lake. The largest pygmy whitefish collected from Brooks Lake was an 84-mm. mature female that had just completed its third growing season. Two slightly older (III+) but smaller, slower growing females were collected from Brooks Lake. In South Bay the largest and oldest pygmy whitefish was a 163-mm. age V mature female.

During their first year of life, males in Brooks Lake grew slightly faster than females. In subsequent years in Brooks Lake and in all years in Naknek Lake, females consistently grew at a faster rate than males (tables 5 and 6). Males in Lake Superior grew slightly faster than females during the first year, grew at about the same rate as females during the second year, and grew slower than females during later years. Male pygmy whitefish in Lake McDonald, Mont., grew faster in their first year but slower than females in subsequent years, while females in Bull Lake, Mont., grew faster in all years (Eschmeyer and Bailey, 1955). With minor variations, these growth patterns are similar to those reported by McCart (1963) for pygmy whitefish in MacLure, McLeese, Cluculz, and Tacheeda Lakes, British Columbia. Males grew at about the same rate as females for the first 2 years, after which females consistently grew faster than males.

[3] Additional study is needed to understand fully the curvilinear body–scale relation of these whitefish. Few specimens have been collected from South Bay as small as the age I and II fish from Brooks Lake with usable scales. Obviously the calculated curve for South Bay fish below 75 mm. is not biologically valid. With adequate data the lower portion of the South Bay curve could approach the Brooks Lake curve for the same size fish, in which case a single equation might express the body–scale relation for both populations. The problem is aggravated by the ease with which small pygmy whitefish lose their relatively large scales. Also, South Bay fish grow as large in 1 year as Brooks Lake fish do in 2 years, and it is not known what effect different growth rates between populations or between year classes within the same population have on body–scale relation curvilinearity.

TABLE 5.—*Average fork length at time of capture and calculated length at end of each year of life for pygmy whitefish collected in Brooks Lake during summer and fall 1962*

Age group	Sex	Fish in sample	Fork length at capture	Calculated fork length at end of year of life		
				1	2	3
		Number	*Mm.*	*Mm.*	*Mm.*	*Mm.*
I	Male	80	57.2	42.4		
	Female	70	57.2	42.4		
II	Male	32	63.9	41.0	61.3	
	Female	134	69.6	41.7	65.2	
III	Male	2	70.5	41.9	66.1	68.9
	Female	12	74.5	35.6	64.2	71.3
Grand average	Male			42.0	61.6	68.9
	Female			41.6	65.1	71.3
Average increment	Male			42.0	19.6	7.3
	Female			41.6	23.5	6.2
Number of fish	Male	114		114	34	2
	Female	216		216	146	12

TABLE 6.—*Average fork length at time of capture and calculated length at end of each year of life for pygmy whitefish collected in South Bay during summer and fall 1962*

Age group	Sex	Fish in sample	Fork length at capture	Calculated fork length at end of year of life				
				1	2	3	4	5
		No.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
I	Male	161	77.0	61.5				
	Female	175	76.2	60.6				
II	Male	214	108.6	62.8	100.7			
	Female	181	112.4	64.7	103.3			
III	Male	14	117.6	65.0	98.9	114.1		
	Female	16	127.1	64.1	99.6	116.2		
IV	Male	4	132.5	64.0	103.3	116.6	119.9	
	Female	12	138.2	64.2	103.8	118.0	129.1	
V	Male	0						
	Female	2	155.0	59.0	82.4	117.5	125.7	135.8
Grand average.	Male			62.4	100.6	114.6	119.9	
	Female			62.8	102.8	117.0	128.6	135.8
Average increment.	Male			62.4	38.2	14.0	5.3	
	Female			62.8	40.0	14.2	11.6	7.2
Number of fish.	Male	393		393	232	18	4	
	Female	386		386	211	30	14	2

The annual growth of female pygmy whitefish from Lake Superior (Keweenaw and Siskiwit Bays), Mich., and Bull Lake and Lake McDonald, Mont., when compared with growth of females from Brooks Lake and South Bay (fig. 6), revealed that the slow growth in Brooks Lake was similar to that in Lake Superior, while growth in South Bay was intermediate between growth in Bull Lake and Lake McDonald. Comparisons of annual growth rates of female pygmy whitefish from the Naknek system with those from MacLure, McLeese, Cluculz, and Tacheeda Lakes (McCart, 1963) indicate (fig. 6) that growth in South Bay was intermediate between growth in McLeese and Cluculz Lakes, while growth in Brooks Lake was slower than in any of the British Columbia lakes. The length attained by pygmy white-

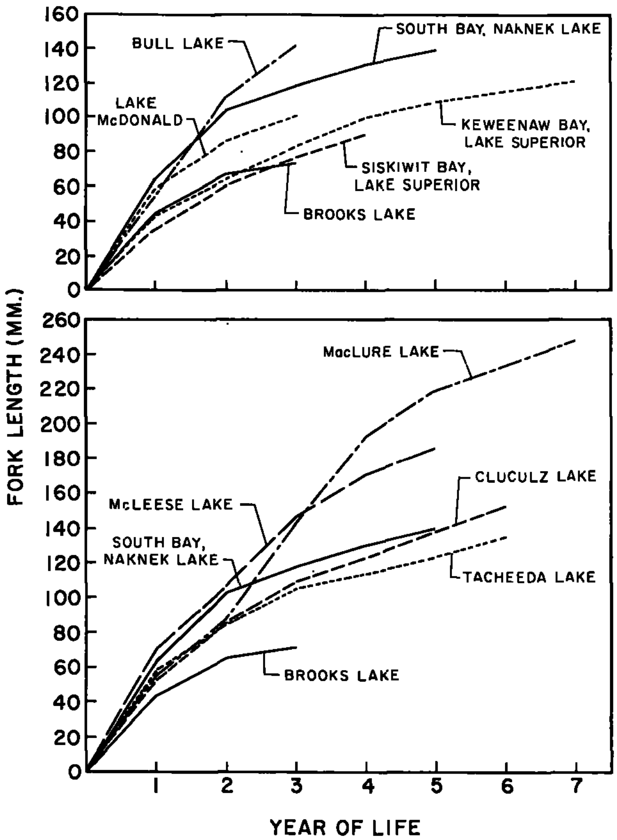

FIGURE 6.—Calculated growth of female pygmy whitefish from Brooks Lake and South Bay, Naknek River system, compared with data from Lake Superior, Mich., and Lake McDonald and Bull Lake, Mont., (Eschmeyer and Bailey, 1955) and MacLure, McLeese, Cluculz, and Tacheeda Lakes, British Columbia (McCart, 1963). Data from Eschmeyer and Bailey were converted from total to fork length.

fish in MacLure Lake is by far the greatest known for this species.

EMPIRICAL GROWTH

Although the average annual growth was not calculated for all lakes in the Naknek system, length frequency distributions of collections from six areas (table 7) provide a basis for growth comparison. The broad range of length frequencies suggests differences in growth rates that reflect the ecological differences in various lakes and basins in the system. The oldest pygmy whitefish collected from Grosvenor Lake, Hammersly Lake, and North Arm were age III+ females 95, 96, and 100 mm.[4] long, suggesting growth rates intermediate between those from Brooks Lake and South Bay. In Iliuk Arm the length of the largest pygmy whitefish, a 132-mm. age IV+ female, is comparable with the average calculated length of the same age fish in South Bay.

The striking difference in growth of pygmy whitefish in Brooks Lake and South Bay is apparent during the first summer. The earliest collections of age 0+ pygmy whitefish were made there in late June and early July. In early July, age 0+ pygmy whitefish were about equal in length in the two areas, averaging between 20 and 23 mm. long. By late August, however, age 0+ pygmy whitefish from South Bay were almost 10 mm. longer than fish from Brooks Lake (fig. 7). Based on the average calculated growth rates, South Bay pygmy whitefish are about 20 mm. longer than Brooks Lake fish at the end of the first growing season (fig. 6). There was little difference in the lengths of age 0+ fish taken in mid-July from Brooks River, North Arm, South Bay, and Brooks Lake. A sample of age 0+ pygmy whitefish from Grosvenor Lake in mid-August indicated an average length similar to that in Brooks Lake in mid-August.

An interesting comparison of the first year growth of pygmy whitefish with that of its close relative, round whitefish (fig. 8), indicates that age 0+ samples of both species collected in the same seine haul from Brooks Lake on August 10, 1962, had no overlap in lengths and round whitefish were considerably larger.

FOOD HABITS

Stomach contents were examined from 62 age 0+ and 396 age I+ and older pygmy whitefish. The age 0+ fish were from South Bay and Brooks and Grosvenor Lakes, while the older fish were from Brooks, Grosvenor, and Hammersly Lakes, South Bay, North Arm, Iliuk Arm, and Brooks River. These fish were collected with seines, otter trawls, and gill nets.

DIET OF AGE I+ AND OLDER FISH

Insects and zooplankton were the two principal groups of food in the diet of age I+ and older pygmy whitefish in the Naknek system (table 8). The relative importance of these two foods varied greatly between lakes. Dipteran insects dominated

[4] Two larger females, 102 and 115 mm. long were collected in North Arm with gill nets on Aug. 9, 1962. Both specimens were mutilated, however, and no scales were available for aging.

the South Bay and Iliuk Arm samples, while crustacean zooplankton dominated samples from Brooks Lake. Stomach samples from Brooks River fish contained predominantly insects, while samples from North Arm and Hammersly and Grosvenor Lakes fish contained about equal amounts of insects and zooplankton.

Larvae, pupae, and adult dipteran and plecopteran nymphs were the main insects eaten by Naknek system pygmy whitefish. Dipteran larvae and pupae (chiefly Chironomidae) accounted for 68, 50, 33, and 88 percent of the food volume from the four South Bay collections (table 8). Forty-seven percent of the volume of stomachs examined from Iliuk Arm consisted of dipteran adults. In all other samples, adult insects accounted for 5 percent or less of the volume. Plecopteran nymphs were the second most important insects eaten, accounting for 32 percent of the volume from a South Bay sample and 40 percent from a Brooks River sample. Five additional orders of insects were occasionally eaten by pygmy whitefish, but these never accounted for more than 5 percent of the volume of any sample.

The principal crustacean foods eaten were the cladocerans *Daphnia*, *Bosmina*, and *Holopedium* and the copepods *Cyclops* and *Diaptomus* (table 8). The crustacean percentage of total volume varied from a trace (South Bay, August 24, 1962) to 100 percent (Brooks Lake, November 7, 1962). Ostracods and amphipods, which were the principal foods eaten by pygmy whitefish in Lake Superior (Eschmeyer and Bailey, 1955), were minor items in the diet of Naknek system fish, occurring in only 8 of 13 samples and never accounting for more than 6 percent of the sample volume.

TABLE 7.—*Length frequencies of pygmy whitefish age I+ and older collected from various areas in the Naknek system, 1961–63*

[M represents males; F, females; C, sexes combined]

Fork length in mm.	Brooks Lake								Grosvenor Lake				Hammersly Lake		
	Aug. 7, 1961		Sept. 14, 1961		June 29, 1962		July 10, 1962	Total	Aug. 5, 1962		Aug. 19, 1963	Total	Aug. 20, 1963		Total
	M	F	M	F	M	F	C		M	F	C		M	F	
26–28															
29–31															
32–34															
35–37															
38–40							1	1							
41–43							6	6							
44–46					9		23	32		1		1			
47–49	4	1	1		28	15	67	116		2		2			
50–52	9	9		2	68	64	254	406	2	4	1	7			
53–55	22	14	3	2	44	49	361	495	3	10	1	14			
56–58	15	14	6	4	5	3	276	323	1	5	7	13			
59–61	8	9	3	6	14	4	79	123	1	3	12	16			
62–64	1	7	3	5	14	11	111	152		2	10	12	1		1
65–67	1	5	1	4	8	13	114	146		3	3	6		1	1
68–70		3		3		8	102	116		3	6	9	1		1
71–73		3		2		6	97	108		2	10	12	2	2	4
74–76		1				1	54	56		10	9	19		2	2
77–79						1	18	19			4	4			
80–82							4	4		1	3	4		1	1
83–85											3	3		1	1
86–88											2	2			
89–91										1	2	3			
92–94											1	1			
95–97											1	1		1	1
98–100															
101–103															
104–106															
107–109															
110–112															
113–115															
116–118															
119–121															
122–124															
125–127															
128–130															
131–133															
134–136															
137–139															
140–142															
143–145															
146–148															
149–151															
152–154															

TABLE 7.—*Length frequencies of pygmy whitefish age I+ and older collected from various areas in the Naknek system, 1961–63*—Continued

Fork Length in mm.	North Arm			Iliuk Arm					South Bay				
	July 21–Aug. 9, 1962		Total	Aug. 2, 1962		July 9, 1963	July 27, 1963	Total	July 22, 1962		Aug. 4, 1962		Total
	M	F		M	F	C	C		M	F	M	F	
26–28													
29–31													
32–34													
35–37													
38–40													
41–43													
44–46													
47–49													
50–52										1			1
53–55					1	1		2					
56–58						1		1					
59–61						4		4		1			1
62–64						5		5		1	2	7	10
65–67				1		4		5	1	4	12	13	30
68–70						5		5	6	3	23	56	88
71–73							3	3	13	14	95	107	229
74–76						2	1	3	11	12	174	244	441
77–79	3		3				2	2	14	8	193	229	444
80–82							2	2	2	6	124	145	277
83–85		3	3								52	45	97
86–88		4	4								10	9	19
89–91		7	7								2	1	3
92–94		5	5										
95–97		6	6			1		1				3	3
98–100		3	3		1			1			6	3	9
101–103		1	1		1		1	2	1	1	17	7	26
104–106									5		49	10	64
107–109						1	1	2	4	5	44	23	76
110–112									14	5	40	37	96
113–115		1	1				1	1	8	6	19	41	74
116–118									7	3	9	26	45
119–121						1		1	6	5	4	13	28
122–124					1			1	1	2	2	6	11
125–127										1	1	4	6
128–130						1	1	2	2	1	2	2	7
131–133						1	1	2	2	3		2	7
134–136										1		2	3
137–139										1		1	2
140–142										1		1	2
143–145													
146–148												2	2
149–151												2	2
152–154													

Other invertebrates found in the diet were pelecypods, nematodes, and arachnids (table 8). Only pelecypods, which accounted for from 5 to 13 percent in samples from North Arm and Brooks and Grosvenor Lakes, were of more than minor importance.

Periphyton (diatoms and other algae), which were present in one Brooks Lake sample and two Brooks River samples, never accounted for more than 4 percent by volume of any sample (table 8).

Fish eggs occurred in both of the Brooks River samples and in the November South Bay samples, amounting to 3, 14, and 38 percent of the volume of food (table 8). Although the eggs were partially digested in some stomachs and could not be identified, they all appeared to be salmon eggs. Large numbers of adult sockeye salmon spawn in Brooks River during the summer and early fall. Even after spawning is completed in the fall there is a frequent drift of dislodged eggs out of Brooks River into South Bay. Kendall (1921) found salmonid eggs in stomachs of pygmy whitefish collected from Lake Aleknagik in August, and Eschmeyer and Bailey (1955) found whitefish eggs in stomachs of pygmy whitefish collected from Lake Superior in January. Eschmeyer and Bailey speculate that fish eggs, when available, may be an important item in the diet of the pygmy whitefish.

Sand grains accounted for 29 percent of the volume in the Grosvenor Lake sample and represented from 6 to 10 percent of the volume in four additional samples (table 8). Only two samples, both from Brooks Lake and containing principally zooplankton, were entirely devoid of sand grains. Occasionally fish were found with more than 100 sand grains in their stomachs. Eschmeyer and Bailey (1955) found sand grains in 9 percent of the Lake Superior fish examined.

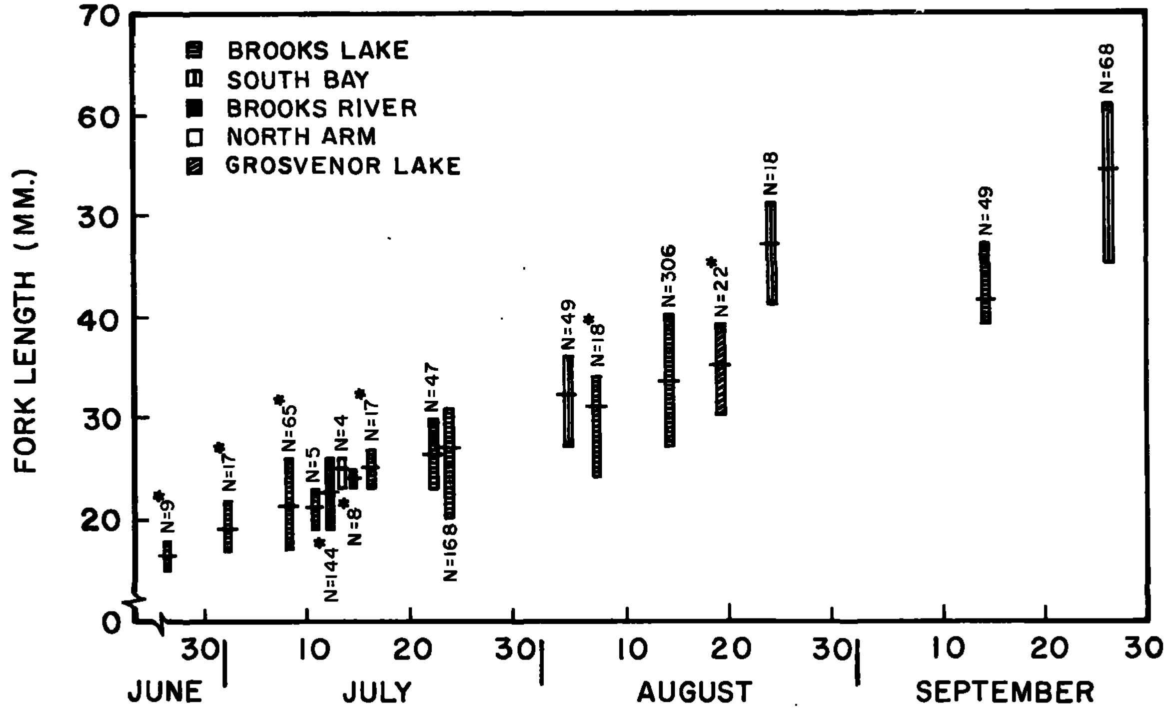

FIGURE 7.—Length frequencies of age 0+ pygmy whitefish collected in 1962 and 1963. Vertical bar represents length range; horizontal line represents mean length of each collection. Asterisk indicates collection was made in 1963.

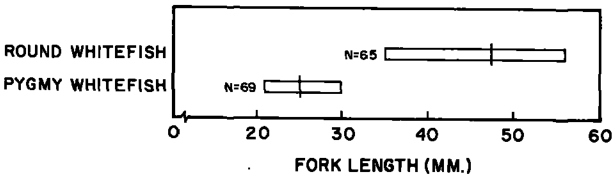

FIGURE 8.—Range and mean length of age 0+ round whitefish and pygmy whitefish caught in the same seine haul in Brooks Lake, August 10, 1962. Horizontal bar shows range; vertical bar indicates mean length of samples.

Plant debris such as small twigs, bits of wood, grass, seeds, and spruce needles occurred in nine samples and accounted for 14 percent of the volume in both samples from Brooks River (table 8). The relatively high occurrence of these items in Brooks River probably represents drift items.

The significance of fish scales in six samples (table 8) is not understood. All undigested scales that could be identified were from pygmy whitefish. No fish remains other than scales were found in any stomachs. Our observations suggest that pygmy whitefish might readily ingest any small bright object either in the current or from the stream or lake bottom.

Underwater observations of pygmy whitefish feeding in lower Brooks River showed that they frequently picked up mouthfuls of material off the bottom and passed fine silt, sand grains, and bits of debris posteriorly through their gill openings. They did not feed along the bottom in a suckerlike manner, but made short distinct jabs or darts, apparently at specific food items, such as insect larvae, when picking up mouthfuls of bottom material. Sand grains and other bits of debris are undoubtedly passed into the alimentary tract during such feeding behavior. Not all pygmy whitefish feeding activity in Brooks River was associated with the bottom. Frequently individual fish would rise off the bottom, as much as 35 to 50 cm. in water 1 m. deep and would pick specific items out of the passing current. With the diet of pygmy whitefish being primarily zooplankton and insects in various parts of the Naknek system and macrobenthic crustaceans in Lake Superior (Eschmeyer and Bailey, 1955), it is obvious that the species has a flexible diet and feeding behavior.

TABLE 8.—*Percentage of total volume*[1] *of different food items in stomachs and (in parentheses) percent frequency occurrence*[2] *for 13 samples of age I+ and older pygmy whitefish taken with seines, gill nets, and otter trawls from various parts of the Naknek system*

[T represents Trace]

Food item	South Bay				Brooks River		Iliuk Arm	North Arm	Grosvenor Lake	Hammersly Lake	Brooks Lake		
	Aug. 4, 1962, Seine	Aug. 24, 1962, Seine	Nov. 9 1962, Seine	Apr. 16, 1963, Gill net	July 28, 1963, Seine	Aug. 24–25, 1963, Trawl	July 9, 1963, Seine	July 22–Aug. 9, 1962, Gill net	Aug. 19, 1963, Trawl	Aug. 17–20, 1962, Gill net	July 10, 1962, Trawl	Nov. 7, 1962, Trawl	July 22–26, 1962, Trawl
Insects:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Dipteran:													
Larvae	49 (67)	9 (70)	33 (50)	87 (100)	9 (83)	14 (95)	7 (59)	34 (78)	28 (90)	28 (75)	T (25)	-	15 (57)
Pupae	19 (43)	41 (97)	-	1 (5)	9 (70)	24 (80)	16 (70)	-	5 (30)	34 (88)	1 (18)	-	T (5)
Adults	T (6)	-	-	-	1 (3)	5 (40)	47 (85)	-	-	-	-	-	4 (24)
Plecopteran:													
Nymphs	9 (13)	32 (73)	-	-	40 (73)	8 (43)	6 (44)	-	-	-	-	-	-
Tricopteran:													
Larvae	2 (11)	-	-	-	-	T (10)	-	-	T (5)	-	-	-	-
Other insects[3]	T (2)	-	-	-	-	1 (13)	5 (30)	-	-	-	-	-	-
Crustaceans:													
Cladocerans[4]	4 (15)	T (10)	8 (40)	2 (21)	9 (37)	4 (40)	16 (81)	16 (67)	20 (85)	9 (38)	69 (100)	70 (100)	26 (76)
Copepods[5]	1 (7)	T (3)	4 (10)	2 (21)	7 (23)	5 (43)	2 (30)	27 (89)	14 (65)	27 (62)	29 (95)	30 (94)	44 (100)
Ostracods	T (2)	-	-	6 (26)	-	-	-	3 (17)	T (5)	1 (38)	1 (34)	-	T (5)
Amphipods	-	-	-	-	-	-	T (4)	-	-	-	-	-	-
Other invertebrates:													
Pelecypods[6]	-	-	-	-	-	-	-	13 (28)	5 (10)	-	-	-	6 (5)
Nematodes	-	1 (10)	-	T (11)	T (10)	1 (32)	T (4)	5 (39)	-	T (25)	-	-	1 (38)
Arachnids	-	1 (17)	-	-	-	T (3)	-	-	-	-	T (2)	-	-
Miscellaneous:													
Periphyton[7]	-	-	-	-	T (10)	4 (35)	-	-	-	-	-	-	4 (10)
Fish eggs	-	-	38 (30)	-	3 (13)	14 (22)	-	-	-	-	-	-	-
Sand grains	10 (67)	1 (27)	9 (80)	1 (26)	6 (87)	6 (82)	T (11)	1 (17)	29 (90)	1 (25)	-	-	T (10)
Plant debris[8]	2 (17)	1 (20)	8 (30)	1 (21)	14 (60)	14 (70)	T (18)	T (6)	-	-	-	-	T (5)
Fish scales	3 (22)	15 (40)	T (10)	-	1 (30)	1 (27)	T (22)	-	-	-	-	-	-
Number of stomachs examined	60	30	20	20	30	63	27	20	21	9	44	31	21
Percent empty stomachs	10	0	50	5	0	5	0	10	5	11	0	0	0
Length range	68–130	72–113	100–134	80–111	97–136	81–144	56–130	76–100	52–97	68–80	53–80	55–77	55–77
Mean volume of contents[2] (in ml.) per stomach	0.11	0.23	0.13	0.09	0.27	0.46	0.39	0.10	0.18	0.12	0.18	0.17	0.06

[1] Based on aggregate contents of all stomachs in each sample.
[2] Based only on stomachs containing food.
[3] Tricopteran adults, coleopteran adults and larvae, hemipteran, hymenopteran, and collembolan adults.
[4] *Daphnia longiremis, D. rosea, Bosmina coregoni, Holopedium gibberum.*
[5] *Cyclops strenuus* and *Diaptomus gracilis.*
[6] *Pisidium.*
[7] Diatoms and filamentous algae.
[8] Small sticks, bits of wood, seeds, and leaves.

DIET OF AGE 0+ FISH

Crustacean zooplankton was the major food in two samples of age 0+ fish—one from South Bay, July 11, 1963, and one from Brooks Lake, August 14, 1962. Insects and zooplankton were about equal in volume in the September 26, 1962, South Bay and August 19, 1963, Grosvenor Lake samples (fig. 9). It appears that in those areas where insects are heavily utilized by older pygmy whitefish, the diet shift of fish from zooplankton to insects occurs late during the first summer of life. Eschmeyer and Bailey (1955) found copepods to be the dominant food of age 0+ pygmy whitefish from Lake Superior in September.

DIEL VARIATIONS IN DIET

The sample of age I+ and older fish from Brooks River on August 24–25, 1963 (table 8), was collected from the same riffle area at four adjacent 6-hour intervals to determine diel differences in quantity and quality of foods eaten. No significant difference in the composition of diet items was found throughout the 24-hour period; however, the average volume of food material per stomach was three times as great at midday as at midnight (fig. 10). The most intense feeding period during this 24-hour period apparently was during daylight hours and not during darkness.

COMPARISONS OF GROWTH AND DIET

By comparing the dramatically different growth rates and sizes that pygmy whitefish attain in the Naknek system (figs. 2 and 6) with the differences in diet, a strong positive correlation between size of fish and utilization of insects becomes apparent. An analysis was made by first grouping all contents from each sample into three categories (insects, zooplankton, and other), then grouping the samples according to the relative importance of insects and zooplankton. Three rather distinct groups of samples resulted: one with heavy, one with moderate, and one with almost no insect utilization. These grouped samples compared with the largest known pygmy whitefish from the same grouped areas (fig. 11) illustrate the correlation between insect utilization and size. Maximum size is not the only index, because the general ranges of length frequencies from different parts of the system (table 7) fall into the same groupings. If this correlation is biologically valid, it raises a question as to why Brooks Lake pygmy whitefish do not eat insects. Merrell (1964) has shown that other Brooks Lake fishes utilize insects, which indicates their general availability. No comparative data are available, however, on differences in insect populations in the Naknek system.

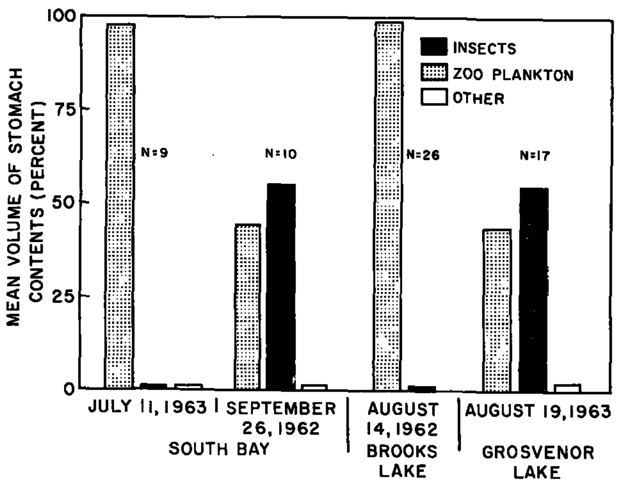

FIGURE 9.—Percent of total volume of stomach contents of age 0+ pygmy whitefish by major food categories.

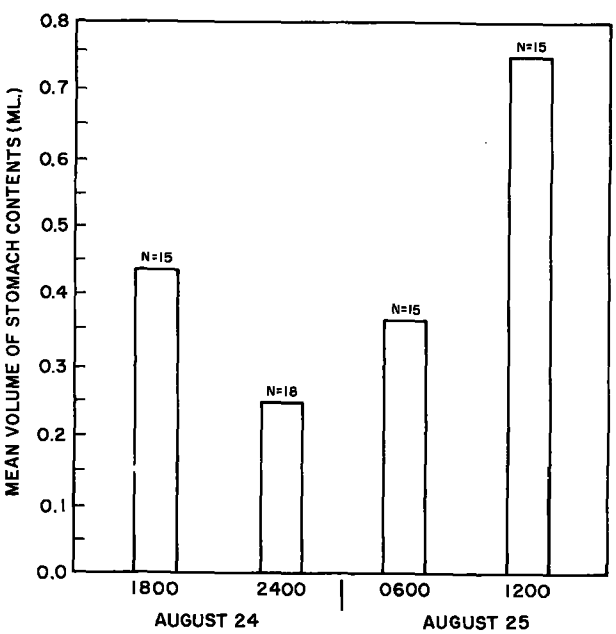

FIGURE 10.—Variation by time of day in mean volumes of stomach contents of 63 pygmy whitefish caught at 6-hour intervals from the same area in Brooks River, August 24 and 25, 1963.

Preference for, access to, or utilization of specific foods may not directly account for differences in growth rates of pygmy whitefish populations in Brooks Lake and South Bay-Iliuk Arm. Basic differences in ecological characteristics of the areas such as morphometry, limnology, productivity,

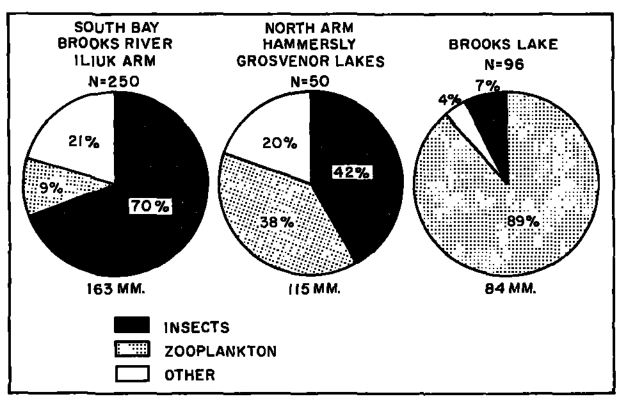

FIGURE 11.—Relative importance of insects, zooplankton. and other foods in diet of pygmy whitefish from three areas of Naknek system. Data based on percent of sample volumes shown in table 8. Number beneath each figure represents largest pygmy whitefish collected from the grouped area.

species combinations of fishes, and food organisms are interwoven in a complex of relations that result in distinctly different environments. Differences in growth rates, longevity, and food habits of pygmy whitefish in the Naknek system probably reflect adaptive responses to these overall environmental differences and not simply the availability or use of certain food items.

The differences we found in *Prosopium coulteri* populations in Brooks Lake and South Bay-Iliuk Arm parallel the differences in *Coregonus peled* (Gmelin) populations in the Swedish lakes Vjomsjon and Uddjaur-Storavan (Lindstrom and Nilsson, 1962). In Sweden, *C. peled* was a slow-growing plankton feeder in Lake Vjomsjon and a fast-growing insect feeder in Lakes Uddjaur-Storavan. As previously discussed, *P. coulteri* is a slow-growing plankton feeder in Brooks Lake and a fast-growing insect feeder in South Bay-Iliuk Arm. Lake Vjomsjon had fewer associated whitefish species, proportionately less littoral area, and probably lower productivity than Lakes Uddjaur-Storavan. In the Naknek system, Brooks Lake has fewer associated whitefish species, less littoral area, and lower productivity than South Bay-Iliuk Arm. The observed plasticity of the genus *Prosopium* in response to environmental differences in the Naknek system is similar to that widely recognized in coregonid and leucichthid whitefishes (Walters, 1955; Svardson, 1957; and others). The variability in meristics and morphology found in pygmy whitefish by McCart (1963) also emphasizes this plasticity in *Prosopium*.

REPRODUCTION

Data on pygmy whitefish reproduction were collected from various areas as follows: sex ratio and age and size at maturity—South Bay and Brooks Lake; fecundity—South Bay, Brooks Lake, and North Arm; and seasonal maturation and spawning behavior—South Bay and Brooks River.

SEX RATIOS

Only a few large samples from Brooks Lake and South Bay were processed for sex ratios, but they revealed nearly equal ratios (table 9). The largest specimens were almost always females (table 7), a phenomenon undoubtedly due to the greater longevity and the faster growth rate of females. These larger females, however, constituted a numerically minor segment of the population. Eschmeyer and Bailey (1955) and McCart (1963) also found females to be the oldest and largest fish in their collections.

TABLE 9.—*Sex ratios of pygmy whitefish, Brooks Lake and South Bay, collected during the summers 1961–62*

Location and date	Number of fish	Sex ratio females to males
Brooks Lake:		
Aug. 7, 1961	127	1:0.92
June 29, 1962	365	1:1.08
South Bay:		
July 23, 1962	182	1:1.13
Aug. 24, 1962	1,907	1:0.82

AGE AND SIZE AT MATURITY

The degree of maturity in age groups I and II varied between lake populations and between sexes within a single population (table 10). In Brooks Lake 10 percent of the females and 36 percent of the males reached sexual maturity during their second growing season (age I+). In South Bay no females and only 2 percent of the males matured as age I+ fish. In both lakes more than 95 percent of the age II+ fish and all of the older fish were mature.

TABLE 10.—*Age at maturity of pygmy whitefish collected during the summer and fall from Brooks Lake and South Bay, 1961–62*

Age	Brooks Lake				South Bay			
	Males		Females		Males		Females	
	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
I+	67	36	58	10	160	2	175	0
II+	28	96	96	97	214	99	181	97
III+	2	100	11	100	14	100	16	100
IV+					4	100	12	100
V+							2	100

In Brooks Lake and South Bay, only a slight tendency exists for males to mature at a smaller size than females. In contrast, Eschmeyer and Bailey (1955) found 100 percent of the males mature at sizes smaller than the smallest mature females. Because of the great differences in growth rates in the Naknek system, there is no overlap in the size at maturity between Brooks Lake and South Bay pygmy whitefish (table 11).

TABLE 11.—*Size at maturity of pygmy whitefish collected during the summer and fall from Brooks Lake and South Bay, 1961–62*

Length groups	Brooks Lake				South Bay			
	Males		Females		Males		Females	
	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature
Mm.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
44–46	10	0						
47–49	35	0	16	0				
50–52	81	0	72	0			1	0
53–55	73	8	71	0				
56–58	28	29	29	3				
59–61	25	76	19	21			1	0
62–64	18	94	24	71	2	0	8	0
65–67	13	100	26	96	13	0	17	0
68–70	3	100	22	100	29	0	59	0
71–73	3	100	36	100	105	0	121	0
74–76			20	100	185	0	256	0
77–79			4	100	207	0	237	0
80–82			2	100	126	2	151	0
83–85					42	5	45	2
86–88					10	20	9	11
89–91					1	0		
92–94								
95–97							3	67
98–100					6	100	2	100
101–103					18	94	8	100
104–106					54	100	10	100
107–109					48	98	28	90
110–112					54	100	42	98
113–115					27	100	47	98
116–118					15	100	29	100
119–121					10	100	18	100
122–124					3	100	8	100
125–127					1	100	5	100
128–130					4	100	3	100
131–133					2	100	6	100
134–136					2	100	5	100
137–139							4	100
140–142							3	100
143–145								
146–148							5	100
161–163							1	100

FECUNDITY

The total number of maturing eggs in pygmy whitefish ovaries were counted for 59 fish from South Bay, 19 from Brooks Lake, and 7 from North Arm. The number of eggs ranged from 103 to 1,153 per female. Body length-fecundity equations computed for each sample showed some difference between areas. However, a single equation was determined (fig. 12) by grouping all 85 females, because there was no overlap in the size range of females between samples.

The salient features of these fecundity data are (1) that a broad range of fecundities exists in different parts of the system and (2) that pygmy whitefish from the Naknek system are considerably more fecund than the same size fish from Lake Superior. We transformed the total length-fecundity relation given by Eschmeyer and Bailey (1955) into a fork length-fecundity relation for comparison with our data. A 120-mm. female

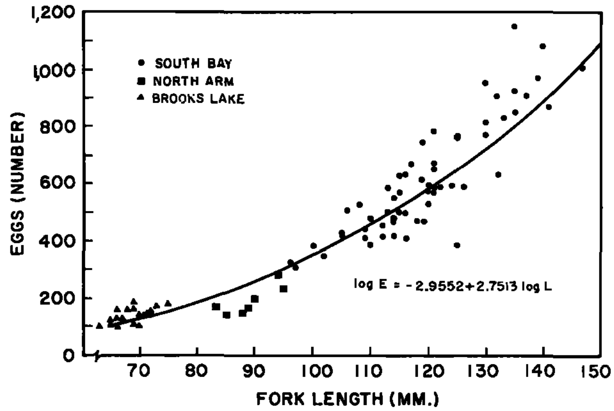

FIGURE 12.—Length-fecundity relation of pygmy whitefish from three areas of Naknek system. Equation derived by combining data from the three areas.

from Lake Superior (130 mm. total length) averaged about 440 eggs, while the same size female from the Naknek system averaged about 580 eggs. These differences in fecundity could be adaptive responses of the various populations to different environmental conditions that produce higher or lower survival opportunities for the species (Svardson, 1949; Nikolsky, 1963).

SPAWNING SEASON AND BEHAVIOR

Egg size in maturing females from South Bay in 1962 increased markedly between late summer and the fall spawning period. Egg diameters that averaged 1.1 mm. in early August increased to 2.4 mm. in ripe females in early November, while ovary weight increased from 3.5 to 16.5 percent of the total body weight (fig. 13). Egg size and ovary weight relative to body weight in near ripe fish from Lake Superior (Eschmeyer and Bailey, 1955) were 2.0 mm. and 15 percent.

Spawning of pygmy whitefish in Brooks Lake and South Bay in 1962 and 1963 apparently occurred between mid-November and mid-December. Mature, ripe males and females from South Bay were collected near the mouth of Brooks River on November 7 and 9, 1962. The water temperature in South Bay on November 9, 1962, was 3.9° C. Both eggs and sperm could easily be extruded by exerting slight pressure on the abdomen, and females as well as males were tuberculate over much of the body. The ventral fins of both sexes were orange. Pygmy whitefish from Brooks Lake on November 7, 1962, were not quite

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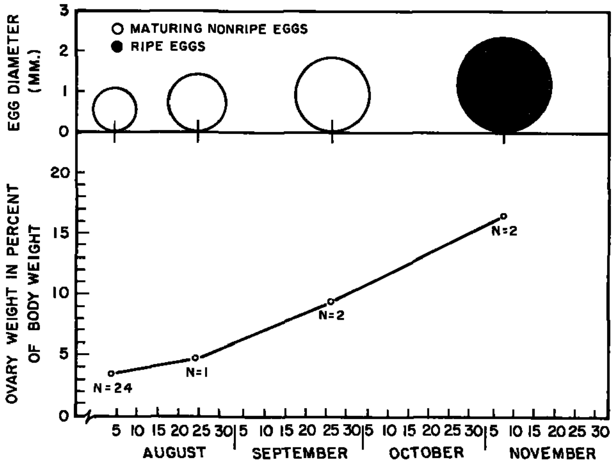

FIGURE 13.—Seasonal maturation of pygmy whitefish collected from South Bay, 1962. Average egg diameter based on minimum of 10 eggs per female. N equals number of females examined.

as ripe as those from South Bay. Although mature fish taken in South Bay on October 29 and November 5, 1963, were not quite ripe, three specimens taken from Brooks River on the night of November 6 apparently were, because sex products could be readily extruded from them.

The spawning period in the Naknek system agrees with most other spawning information on pygmy whitefish. The time of spawning in Lake Superior (Eschmeyer and Bailey, 1955), Glacier National Park, Mont. (Schultz, 1941), and four British Columbia lakes (McCart, 1963) was believed to be in November or December. The November–December spawing in the Naknek system compares closely with the supposed time of spawning in Lake Superior and Glacier National Park, Mont. (Eschmeyer and Bailey, 1955; and Schultz, 1941). Weisel and Dillon (1954) collected sexually mature and spent pygmy whitefish from Bull Lake between December 26 and January 12. Kendall (1917 and 1921) reported on six pygmy whitefish collected from the Chignik River system, Alaska, about November 1, 1912. These fish (Kendall, 1921) were "mature individuals ready to spawn," which agrees with the other known spawning times of this species.

Exceptions to the late fall and winter spawning of pygmy whitefish have been noted. Kendall (1921) reported that some pygmy whitefish collected on July 20, 1909, and August 2, 1912, from the outlet of Lake Aleknagik were in breeding condition. Apparently the collector of one of these samples reported that pygmy whitefish were passing out of Lake Aleknagik in large numbers, and Kendall interpreted this as a spawning run. We question the validity of this interpretation and doubt that a spawning migration was occurring as early as July 20 or August 2, although individual specimens might have seemed ready to spawn. McCart (1963) found a physiologically atypical female in Cluculz Lake, British Columbia, on July 15, 1962, which appeared to be ripe. We examined pygmy whitefish collected on July 13, 1963, from Wood River just below the outlet of Lake Aleknagik by Dr. R. L. Burgner of the Fisheries Research Institute, University of Washington, and found the condition of the gonads to be 3 or 4 months from full maturity. Two of the Wood River females had average egg diameters of 1.0 mm., and the ovaries made up only 2.7 percent of the body weight (fig. 13). Burgner (personal communication) reports that large numbers of pygmy whitefish can be seen throughout much of the summer in Wood River below Lake Aleknagik. These observations and Kendall's (1921) comments on fish passing out of the lake could represent the seasonal feeding movements of a lake population similar to that observed during the summer in South Bay and lower Brooks River. Pygmy whitefish may spawn below Lake Aleknagik, but probably later than Kendall believed.

Although specific details of spawning behavior were not observed, we determined that pygmy whitefish (in Brooks River at least) spawn only at night, as do mountain whitefish in Montana (Brown, 1952). Routine underwater surveys in early November in 1962 and 1963 revealed no pygmy whitefish in Brooks River during daylight hours, although large numbers of ripe or nearly ripe fish were known to be in South Bay off the river mouth. On a dive just after dusk on November 5, 1963, divers using underwater hand lamps observed that a few large pygmy whitefish had moved into lower Brooks River from South Bay. Between 20 and 25 pygmy whitefish were observed in the same area the following night about 3 hours after darkness. These fish probably represented the beginning of the spawning run in 1963.

South Bay fish probably remain in the lake in the vicinity of Brooks River until they reach full maturity, when they move into the river at night to spawn. Periodic observations along the streambank at night with a lantern in late November and early December in 1963 continued to reveal the presence of pygmy whitefish in the stream. Unseasonably cold temperature, however, caused ice conditions that precluded intensive observations. About 100 fish were seen just at the mouth of Brooks River during a night dive on December 16, 1963. Most of these fish were individually scattered over the stream bottom, although one congregation of 8 to 10 fish may have represented a spawning group. These particular fish darted wildly about upon encountering the underwater spotlight. The water temperature in Brooks River on December 16 was 0.3° C. All adult pygmy whitefish taken in gill nets under ice in South Bay near the river mouth on December 12 and 18 were spent.

DISCUSSION

In the Naknek River system pygmy whitefish apparently reach their greatest density in Brooks Lake where they may be the most abundant species in the lake. These conclusions are based on the combined numbers of each species caught in all sampling gears from 1961 to 1963. In Brooks Lake, South Bay, and Iliuk Arm, pygmy whitefish are commonly associated with juvenile sockeye salmon. This relation merits consideration because of the commercial value of the Naknek River system sockeye salmon.

Although the association of two species predetermines some sort of interspecific relation, in fishes it is usually difficult to determine the exact nature of this relation. Larkin (1956), who considered competition in a concise limited sense, points out that competition itself is difficult to separate from other complex interrelations between fish species. Rogers (1961), after carefully considering the diets of young-of-the-year sockeye salmon and three age groups of threespine sticklebacks collected from similar ecological areas of Wood River Lakes, could only conclude that "potential food competition exists." Greenbank and Nelson (1959), in studying the threespine stickleback in Karluk Lake, conclude that "Quantitative information is insufficient to assess accurately the benefit or harm to salmon production caused by the stickleback population." Johnannes and Larkin (1961) could demonstrate severe competition between redside shiners (*Richardsonius balteatus*) and rainbow trout for amphipods in Paul Lake, British Columbia, only because of long-term data that included preshiner amphipod densities along with feeding habits and growth rates of the trout.

In the present study it is impossible on the basis of existing data to demonstrate direct interspecific competition in any form between pygmy whitefish and juvenile sockeye salmon or other whitefishes. It is possible, however, that the combined effects of interspecific and intraspecific relations of these species may influence the growth and general well-being of each in various parts of the Naknek system. Although McCart (1963) could not demonstrate direct competition between pygmy whitefish and other whitefishes, he found indications of interactive segregation between whitefishes which resulted in differences in depth distribution and growth rates. He also noted that the large MacLure and McLeese Lake pygmy whitefish were the only ones in British Columbia that did not coexist with another species of the genus *Prosopium*. In the present study the largest pygmy whitefish were found in South Bay and Iliuk Arm where three other whitefishes occur (round and humpback whitefish and least cisco), while the smallest pygmy whitefish were found in Brooks Lake where round whitefish is the only other whitefish. Although growth rates of pygmy whitefish in the Naknek system are correlated with different diets, McCart (1963) found no differences in diets of this fish in four lakes where growth was quite different.

Both pygmy whitefish and juvenile sockeye salmon feed heavily on zooplankton in Brooks Lake, although Merrell (1964) points out that during late spring and early summer, insects may be the most important item in the diet of Brooks Lake sockeye salmon (age I+ and older). Even though differences in the production of sockeye salmon smolts in Brooks Lake have varied from 60,000 to 360,000 during recent years, there has been little difference in the mean size of age I+ smolts. This suggests that densities of young salmon, together with other environmental influences such as potentially competitive dense populations of pygmy whitefish, have not altered the basic growth rate of sockeye salmon in Brooks Lake.

Interspecific association of juvenile sockeye salmon and pygmy whitefish in South Bay and Iliuk

Arm is complicated by several factors. First, a greater number of other associated species occur in these areas than in Brooks Lake. Second, in addition to serving as primary rearing areas for salmon produced in adjacent spawning areas such as Brooks River and Margot Creek (a tributary of Iliuk Arm), both South Bay and Iliuk Arm, of necessity, serve as migration lanes for salmon produced in upsystem areas. This point is further complicated by interlake movement whereby some juvenile sockeye salmon begin their nursery lake existence in upstream lakes (i.e. Coville and Brooks), then migrate into downstream nursery areas (i.e. Iliuk Arm and South Bay) to complete their first year of life.[5] Thus, the juvenile sockeye salmon populations in South Bay and Iliuk Arm are frequently undergoing dramatic changes in density apart from normal fluctuations in the local population. Although pygmy whitefish feed primarily on insects in South Bay and Iliuk Arm, the diet of young sockeye salmon in these areas is not known. It may be that no possible food competition exists between these species in South Bay and Iliuk Arm.

The reasons for the marked differences in the biology of pygmy whitefish populations in Brooks Lake and South Bay are poorly understood. Pygmy whitefish in Brooks Lake grow slower, mature earlier, and live shorter lives than those in South Bay or Iliuk Arm. Consequently, spawning females are younger, significantly smaller, and less fecund in Brooks Lake. Yet, the species is extremely successful in Brooks Lake, as evidenced by abundance. Factors contributing to this success undoubtedly deal with lower mortalities from fertilized egg to maturity. Because of early maturity, short life span, and small size, pygmy whitefish in Brooks Lake fit the concept of a "dwarfed or small form" discussed by Svardson (1957), Alm (1959), and Fenderson (1964). As pointed out by Alm, a "dwarfed form" with short life and early maturity is distinct from a slow-growing "normal form" which has greater longevity and matures at an older age but still at a small size. Dwarfism may provide a species with advantages in survival and competition (Lindstrom and Nilsson, 1962; McCart, 1963; and Fenderson, 1964).

On the basis of recent data from Lake Aleknagik and Chignik Lake, Peter J. McCart (personal communication) believes that two distinct sub-populations of pygmy whitefish may occur sympatrically in these lakes. One form, which is generally larger, is a river-oriented insect feeder with low gill raker counts and is apparently confined to shallow water. The other form is a lake-oriented plankton feeder with high gill raker counts and inhabits deep water. These criteria, in part, apply to some of the differences found in populations in the Naknek system. This is particularly true with the insect feeders in South Bay where the population is strongly oriented to Brooks River and the relatively shallow waters of South Bay. In other parts of the system, however, differences in ecological distribution represent exceptions to this general scheme. In Iliuk Arm, large fast-growing insect feeders occur from shallow beaches to maximum depths of 168 m., whereas in Brooks Lake, slow-growing insect feeders occur from the shallow to the deepest depths. Although we have not studied meristic variation of populations of pygmy whitefish in the Naknek system in detail, the insect feeders in South Bay and Brooks River have lower gill raker counts than the plankton feeders in Brooks Lake. Eschmeyer and Bailey (1954, p. 174) point out that gill rakers from pygmy whitefish in rivers, or lakes dominated by rivers, tend to be fewer in number and shorter in length than those from lacustrine environments. Whether differences found in populations of pygmy whitefish in the Naknek system represent genetically distinct subpopulations or the adaptive responses of the species in utilizing the many environments present in the system cannot be determined without additional study.

Differences in diet in various parts of the system have been discussed and correlated with growth rates. Actually, growth rates are correlated not only with the degree of insect utilization but also with the rate of phytoplankton productivity in various areas. Primary productivity is relatively high in South Bay and Iliuk Arm, low in Brooks Lake, and intermediate in North Arm and Grosvenor Lake.[6] A notable exception to correlating growth rates of pygmy whitefish with primary

[5] Summary report of studies on the optimum escapement of sockeye salmon in southwestern Alaska, 1961–62. Prepared by the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and Fisheries Research Institute, University of Washington, Seattle. (Manuscript on file at the BCF Laboratory.)

[6] See footnote 2 on p. 557.

productivity is that Coville Lake, which has the shallowest mean depth, the highest water temperatures, and the highest primary productivity in the system, apparently has only a small population of intermediate size pygmy whitefish; however, Coville Lake may have denser populations of other species (i.e. pond smelt, humpback whitefish, and juvenile sockeye salmon) than other parts of the system.

Until comparative data are available on the relative abundance of various food groups and the diets of associated fishes in different areas, it is impossible to determine the role of food availability or preference for specific foods in evaluating differences in the biology of pygmy whitefish in the Naknek system. Rather than simple differences in diet, growth, or ecological distribution, we feel the dramatic differences found in pygmy whitefish populations in the Naknek system probably reflect widely varying adaptive responses of a highly plastic species to the complex of environmental differences found throughout the system.

SUMMARY

The pygmy whitefish has the greatest discontinuous distribution of any fresh-water fish in North America, occurring in the Atlantic, Pacific, and Arctic Ocean drainages. It is widely distributed and locally abundant in lakes of the Naknek River System in southwest Alaska.

More than 10,000 pygmy whitefish were collected from the Naknek system with seines, otter trawls, tow nets, and gill nets from 1961 to 1963. This species seems to have a prominent role in the dynamics of some Naknek system fish populations.

In the Naknek system, pygmy whitefish occur in all benthic areas from shallow littoral depths to the deepest areas available. Seasonally, in certain age groups and in certain areas, they occur in limnetic waters of lakes and in streams.

Nineteen species, including the closely related round whitefish, occurred in catches with pygmy whitefish in various parts of the Naknek system.

Polynomial equations were used to express the curvilinear relation between body length and anterior scale radius. Body length at scale formation is about 25 mm.

The oldest and largest fish from the two areas studied most intensively was an age V 163-mm. female from South Bay and an age III 84-mm. female from Brooks Lake. Length frequency distributions from other areas were intermediate between these extremes. Calculated and observed growth indicated that growth was much greater in South Bay than in Brooks Lake. Both sexes in Brooks Lake showed a tendency to mature at an earlier age than in South Bay.

Dipteran insects were the principal foods eaten by pygmy whitefish in South Bay. Crustacean plankton dominated their diet in Brooks Lake. In other areas insect and zooplankton foods were about equal in importance. In areas where insects were important in the diet of older fish, the shift from zooplankton to insect foods in age 0+ fish began during the first summer of life. A positive correlation between growth and insect utilization was found.

The fork length–fecundity relation of Naknek system pygmy whitefish is expressed by the equation

$$\text{Log } E = -2.9552 + 2.7513 \log L.$$

where E equals number of eggs per female and L equals fork length of the fish. Fecundity in Naknek system fish exceeds that in Lake Superior fish.

Spawning occurs in November and December. South Bay fish move into Brooks River for spawning only at night. Eggs in ripe fish from South Bay averaged 2.4 mm. in diameter, and the ovaries were 16.5 percent of the body weight.

Potential interspecific competition exists between pygmy whitefish and juvenile sockeye salmon, particularly in Brooks Lake where foods are similar and the whitefish are numerous.

Slow growth, low fecundity, and short life characterize Brooks Lake pygmy whitefish. These factors must be compensated for by lower mortality from fertilized egg to maturity than in the South Bay population, which is characterized by fast growth, higher fecundity, and longer life.

The wide range in growth rate, fecundity, longevity, and diet of populations of pygmy whitefish in the Naknek system is probably due to the adaptive responses of a highly plastic species to the variety of environmental characteristics, such as water quality and clarity, drainage geology, phytoplankton productivity, lake morphometry, fish species, and food organism associations found in different parts of the system.

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