DISTRIBUTION, FOOD, AND FEEDING OF THE THREESPINE STICKLEBACK, *GASTEROSTEUS ACULEATUS*, IN GREAT CENTRAL LAKE, VANCOUVER ISLAND, WITH COMMENTS ON COMPETITION FOR FOOD WITH JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*

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ABSTRACT

The distribution, relative abundance, and food of the threespine stickleback, *Gasterosteus aculeatus*, was studied in Great Central Lake on Vancouver Island, B.C., in 1970 and 1971 as part of a multidisciplinary study on the production of sockeye salmon, *Oncorhynchus nerka*, following controlled additions of inorganic nutrients (1970-73 inclusive) to an oligotrophic sockeye nursery lake. Stickleback appeared along shore in relatively low numbers prior to mid-April and most were between 30 and 59 mm long. Following spawning in June and July, initially stickleback were smaller, but as fish of the year became more available, both the number and average size of stickleback increased. They were absent in the littoral zone by November, but their presence in the pelagic zone in winter could not be established. Over the diel cycle the larger individuals apparently move offshore during the day. The populations in the 2 yr did not differ greatly in size.

In each of the 2 yr stickleback had a wide but similar diet. They predominantly fed on two cladocerans (*Holopedium gibberum*, *Bosmina coregoni*), two copepods (*Epischura nevadensis*, *Diaptomus oregonensis*), and a cyclopoid copepod (*Cyclops bicuspidatus*). Larvae and pupae of the family Chironomidae were also of some importance. Other food items, but of minor importance, included harpacticoid copepods, insects, pelecypods, ostracods, acarids, Araneida, planaria, Odonata, and fish. Variations in diet in relation to season, size and sexual maturity of stickleback, and time of day were observed. The daily ration for stickleback was estimated to be 6.55% of their body weight in July and 7.80% in October.

Stickleback and juvenile sockeye salmon in the littoral zone exhibited considerable dietary overlap, especially during the late spring and summer. However, since sockeye salmon in this zone are relatively few in number, and stickleback do not inhabit the limnetic zone, serious interspecific competition for food in the lake is probably lacking, especially in years of abundant food supply.

Along the Pacific coast of North America, threespine stickleback, *Gasterosteus aculeatus*, hereafter referred to as stickleback, occur in many coastal lakes, rivers, and streams ranging from western Alaska to lower California (McPhail and Lindsey 1970). In British Columbia and Alaska, large populations have been reported in some nursery lakes of young sockeye salmon, *Oncorhynchus nerka* (Greenbank and Nelson 1959; Ruggles 1965). Separate studies on the food of young sockeye salmon (Ricker 1937; Narver 1970; Barraclough and Robinson 1972) and stickleback (Greenbank and Nelson 1959) in British Columbia and Alaska lakes have generally shown that both species feed mainly on planktonic crustaceans and insects. Rogers (1968) compared the food of both species residing in the same lake in Alaska and, after finding a great similarity in diet, concluded that potential interspecific competition for food exists. Krogius and Krokhin (1956) and Ruggles (1965) studied production of young sockeye salmon in different lakes where the two species were present and observed that sockeye salmon production was inversely related to stickleback abundance.

In 1969, the Pacific Biological Station of the Department of the Environment, Canada, started a multidisciplinary investigation to determine if the production of juvenile sockeye salmon in Great Central Lake on Vancouver Island, B.C., (Figure 1) would be increased by controlled additions of inorganic nutrients. Approximately 100 tons of inorganic nutrients were added from late spring through summer for 4 yr beginning in 1970, usually in 5-ton weekly lots with the ultimate

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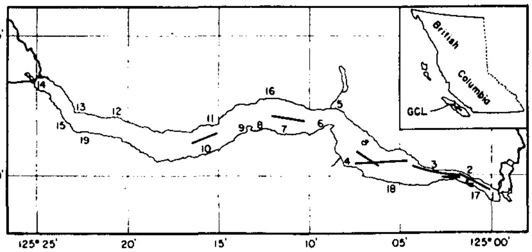

FIGURE 1.–Map of Great Central Lake, British Columbia, showing the location of beach seining (numbers) and mid-water trawling (lines) stations.

purpose of increasing the food resource for young sockeye salmon without significantly altering water quality. Preliminary results for 1970 when compared with 1969 (untreated year), indicate that primary production was increased without substantially changing the nature of the food chain (Parsons et al. 1970; Parsons et al. 1972). Zooplankton standing stock from May through October was approximately 10 times higher (LeBrasseur and Kennedy 1972). Young sockeye salmon generally consumed the important zooplankters in the lake and underyearling sockeye salmon were 30% heavier in weight (Barraclough and Robinson 1972). Considering the results of earlier studies by other investigators on the food of young sockeye salmon and stickleback, and the uncertainty of the response of the stickleback population to lake enrichment, a study on the biology of stickleback with special emphasis on diet and feeding habits was carried out in 1970 and 1971 as part of the overall fertilization experiment in Great Central Lake. This paper reports on the results of studies on distribution, relative abundance, and food and feeding of stickleback, and in addition contains comments on stickleback as a competitor of juvenile sockeye salmon for the food resource in the lake.

DESCRIPTION OF GREAT CENTRAL LAKE

Great Central Lake is an ultra-oligotrophic lake situated in the central part of Vancouver Island, B.C. The lake is approximately 34 km (21 miles) long, varies between 1 and 2.5 km (0.6 and 1.5 miles) in width, and has a surface area of 5,100 hectares. The maximum depth is approximately 250 m (800 feet). The shoreline varies from gentle sloping beaches to rocky, precipitous ledges. The littoral area in comparison to lake perimeter is relatively small and depths of 25 m or more only a few meters from shore are common. Beach cover ranges from small pebbles to rocks and boulders. Water inflow is by two major streams at the west end and several minor streams around the lake, as well as by snow melt in the spring months. The lake is drained at its east end by the Stamp River, which flows approximately 30 km before emptying into the sea at the head of Alberni Inlet. Surface water temperatures in the lake ranged from 4° to 21°C in 1970 and from 4° to 24°C in 1971. Minimal temperatures occur in February; maximal temperatures in late July. In general warm-up is slower in the western end, but once maximum temperatures are reached in July, surface water cools off at approximately the same rate. In some winters, the lake is ice-covered for varying periods of time, more often at the western end.

The fish community consists of at least eight species. Young sockeye salmon are by far the most abundant, followed by stickleback. Other species caught in considerably fewer numbers are juvenile coho salmon, *O. kisutch*; cutthroat trout, *Salmo clarki*; rainbow trout, *S. gairdneri*; Dolly Varden, *Salvelinus malma*; prickly sculpin, *Cottus asper*; pumpkinseed, *Lepomis gibbosus*; and river lamprey, *Lampetra ayresi*.

TAXONOMY

Two morphologically different forms of *G. aculeatus* occur along the Pacific coast of North America: a heavily plated form, *trachurus*, that is usually marine, and a partially plated freshwater form, *leiurus*. McPhail and Lindsey (1970) provided nomenclatural and taxonomic details regarding the *G. aculeatus* complex. Recent studies on isolated freshwater populations indicate considerable geographic variation with the result that their taxonomic status is of considerable uncertainty and interest (Hagen 1967; Narver 1969; Miller and Hubbs 1969; Hagen and McPhail 1970; Hagen and Gilbertson 1972). Hagen and Gilbertson (1972) consider that at least three plate morphs are present in permanent freshwater populations of *Gasterosteus*, namely low plated (3-7), partially plated (8-29), and fully plated (30-35).

The stickleback morph in Great Central Lake was identified from samples collected prior to the spawning season at four stations (3, 5, 13, and 14, see Figure 1) located along the length of the lake. The individual samples contained from 14 to 20 stickleback. The length of the stickleback in the combined samples ranged from 45 to 79 mm. Lateral plates along the left side and caudal keel were counted, using a probe and binocular microscope. Since all individuals in the samples exceeded 30 mm in length, plate formation was considered complete (Hagen and Gilbertson 1972). Analysis of variance revealed no significant difference in plate counts between stations (F = 3.15; df = 3, 66; P>0.05). The mean plate count for the combined samples was 25.17. Considering plate counts, it can be concluded that the stickleback population in Great Central Lake is a freshwater population more representative of the *trachurus* than the *leiurus* form.

DISTRIBUTION AND RELATIVE ABUNDANCE

Methods

Distribution and estimates of relative abundance of stickleback were determined from catches made with a purse seine used as such in mid-lake waters or as a beach seine along the shoreline, in 1970 and 1971. A description of the gear and its operation as a beach seine was provided by Manzer (1971). The net sampled an area between 450 and 550 m^2, or approximately 10 m of shoreline.

The field program in 1970 was carried out over eight surveys between 22 April and 27 November. Some purse seining and sighting were carried out in the early season but most effort was devoted to beach seining along shore. Here 18 different locations representing typical but different shoreline habitats were fished between 0830 and 1730 h (Pacific daylight time). Eleven of these stations were established as key stations. Coverage was more complete between late June and late August when surveys were conducted at 2-wk intervals. The fishing program in 1971 was essentially the same as in 1970. Five secondary stations sampled in 1970 were deleted and one new station was added to provide better coverage of the lake. Seven surveys were carried out between 18 February and 30 November, approximately at monthly intervals beginning in May. Fishing was conducted between 0630 and 1830 h. No fishing was done in September in either 1970 or 1971. The beach seining stations are shown in Figure 1 and grouped by character below, the stations in boldface being key stations.

Description	*Station*
Gentle slope, gravel bottom	**1, 4, 5, 9, 10, 14**
Gentle slope, rocks and boulders	**6, 12,** 15, **16,** 17, 18
Rock slope, sharp dropoff	**2, 3,** 7, 8, **11, 13,** 19

Information on the winter distribution of stickleback was obtained from purse seining operations carried out on 18 February and from mid-water trawling on 23 and 24 March in the pelagic zone, using a mid-water trawl routinely employed to catch age-0 sockeye salmon in the lake (Barraclough and Robinson 1972). Ice cover restricted fishing to the eastern one-half of the lake.

Results

Sighting surveys, purse seining, and beach seining were conducted in the eastern part of the lake in April and June 1970. The purpose of these operations was to determine the distribution of stickleback in proximity to the shoreline. It was considered that the results of these operations would be applicable to the lake as a whole. Stickleback were readily observed in varying numbers close to shore apparently moving at random and feeding in waters from less than 1 foot (0.3 m) to several feet (ca. 2 m) deep. They were rarely seen in offshore waters. This general pattern of distribution was confirmed by purse seine and beach seine catches. Eight "blind" (i.e., uncorroborated by sightings) purse seine sets in the limnetic zone yielded three stickleback. The net was considered effective to a depth of 3-4 m. In contrast, 16 beach seine sets at shore areas ranging from shallow beaches to precipitous slopes yielded stickleback on all but three occasions. As many as 350 stickleback were caught in a single set. Their virtual absence in offshore waters was indicated by the results of townetting for young sockeye salmon in the lake. A total of 480 tows made during 1969-73 in the limnetic zone of the lake at various depths (0-60 m) with trawl nets with mouth openings of approximately 18 m^2 and 4 m^2 yielded 21 stickleback (D.G. Robinson pers. commun.). From these operations it is concluded that stickleback were primarily concentrated close to shore.

Catches of stickleback by beach seining operations are given in Table 1 by survey and location. Catches in each year ranged from zero or a few fish to estimates of 2,500. In 1970, 105 sets were made and 10,727 stickleback were caught. Twenty-one sets failed to catch stickleback. In 1971, 89 sets were made and 10,806 stickleback were caught. Of

TABLE 1.–Beach seine catches of the threespine stickleback in Great Central Lake, 1970 and 1971, by survey and location. Multiple sets shown in parentheses. Estimated catch shown by asterisk.

	1970									1971								
Location	22, 30 Apr.	24, 25 June	8, 9 July	22, 23 July	5, 6 Aug.	19, 20 Aug.	2 Oct.	26, 27 Nov.	Total	18 Feb.	12, 20 May	10, 17 June	9 July	10 Aug.	14 Oct.	30 Nov.	Total
1	74	—	20	—	81	—	—	—	175	—	—	—	—	—	—	—	—
2	—	2(2)	13(2)	459(2)	7(2)	21(2)	63	0(2)	565	—	3	86(2)	12(2)	23	39(2)	0	163
3	—	200*	—	56(2)	95	225	600	3(2)	1,179	0	36	69	24	10	75	8	222
4	1	8(2)	2(3)	384(2)	279	158	300*	0(2)	1,132	0	121(3)	3(2)	145(2)	21	1,000(2)*	8(2)	1,298
5	350	1	—	18	649	2,000*	200*	2	3,220	0	4	26	28	800	293	36	1,187
6	—	—	—	15(2)	—	237	2,000*	0	2,252	0	8(2)	200*	13(2)	500	2,500	—	3,221
7	—	—	—	2	56(2)	—	—	—	58	—	2	16	6	29	—	0	53
8	—	1	—	16	0	2(2)	0	0	19	—	0	—	—	—	—	—	0
9	—	0(2)	—	11	29(2)	15(2)	0(2)	0(2)	55	—	10(2)	3(2)	500	100	27	0	640
10	—	—	—	500(2)	159(2)	300(2)	—	0(2)	959	—	2	134(2)	31	71	77	0	315
11	—	—	—	—	181	124(2)	500*	0	805	—	4(2)	52	296	23	125	1	501
12	—	—	—	1	79(2)	27(2)	—	—	107	—	—	—	—	—	—	—	—
13	—	—	—	—	12	5	—	—	17	—	13	35	400	6	—	—	454
14	—	—	—	0(2)	50	12	—	—	62	—	—	500*	107	8	—	—	615
15	—	—	—	7(2)	21(2)	25	—	—	53	—	—	—	—	—	—	—	—
16	—	—	—	—	—	—	30	2	32	—	13(2)	250	9	9	1,800	0	2,081
17	—	27(2)	—	—	—	—	—	—	27	—	—	—	—	—	—	—	—
18	—	10(2)	—	—	—	—	—	—	10	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	15	34	7	—	—	56
Total	425	249	35	1,469	1,698	3,151	3,693	7	10,727	0	216	1,389	1,605	1,607	5,936	53	10,806
No. sets	3	13	6	19	20	19	10	15	105	4	18	17	16	13	11	10	89
Arith. mean catch	141.7	19.2	5.8	77.3	84.9	165.8	369.3	0.5	102.2	0	12.0	81.7	100.3	123.6	539.6	5.3	121.4
Geom. mean catch	37.41	4.14	3.89	11.07	12.28	21.68	48.53	1.27	9.31	0	1.34	25.24	34.04	33.27	109.20	2.39	12.19

these, 12 sets failed to catch stickleback. Most of the sets which failed to catch stickleback (21 of 33) were made in February and November. Arithmetic and geometric means of the numbers caught in each survey are also provided. The latter are included because of the skewness of the catch data and were obtained from log $(n + 1)$ transformation of the data where n is the stickleback count in each set. This transformation permitted utilization of zero catches in the computations: in all likelihood during the spring to fall months at least one stickleback would have been caught had fishing been repeated.

The distribution and relative abundance of stickleback and size composition of the catches according to small (<30 mm), medium (30-59 mm), and large (60+ mm) stickleback are illustrated in Figure 2. (The size-groups were arbitrarily chosen but in general approximate age-groups: <30 mm = 0 age; 30-59 = 1 yr old; 60+ mm = 2 yr and older.) Gear efficiency was assumed to be reasonably constant, although a few sets were made under conditions of relatively strong wind and current. It was further assumed that after spawning (July and later) stickleback were catchable regardless of size. Abundance levels just prior to spawning may have been higher than catches indicate because of the decreased vulnerability of mature individuals, especially males which repair to nesting areas.

Some differences in survey dates, especially in the early part of the year, and some changes in the sampling sites in the 2 yr prevent a strict time and place comparison of the data. Nevertheless some general conclusions on distribution and relative abundance can be made from Table 1 and Figure 2. Seasonally, stickleback appeared along shore prior to mid-April. Their abundance at this time was low and appeared to vary between locations. Most stickleback in almost all localities ranged in length between 30 and 59 mm. A few larger individuals were caught but none smaller. In both years it was obvious that in all areas stickleback progressively increased in numbers, from July through October, although apparently they were less abundant off rock slopes than on gentle sloping beaches covered by either gravel or boulders. This increase is due to the recruitment of fish of the year as evidenced by the large proportion of fish less than 30 mm in July and August. The average seasonal catch was largest in October and consisted of stickleback measuring between 30 and 59 mm long. Fish belonging to the small and large size groups also were present in considerable numbers, and in some areas small fish predominated (for example, the central part of the north shore). The small or zero catches made in November suggest that stickleback prior to winter had abandoned the shore areas.

Observations on diel size variation in stickleback along the shore were made in conjunction with diel feeding habits, which are described in a later section. Paired samples taken 100 m and 15 min apart were collected at station 1 at 3-h intervals between 0700 and 1900 h in October 1970 and through the 24-h cycle in July 1971. Diel size changes observed during each series are illustrated in Figure 3 using the graphic method developed by Dice and Leraas (Simpson and Roe 1939). At each site and date the size of stickleback decreased from dawn to midday and then increased again by dusk, suggesting that the large fish are less available in the littoral area during the day. This trend is most clearly shown by fish in July at site B. Here, stickleback at midday are significantly smaller than at either dawn or dusk.

Stickleback virtually abandon the shore areas by November, but their presence in numbers in the pelagic zone of the lake during the winter could not be established. Limited purse seining (four sets) in February in the pelagic zone of the eastern part of the lake failed to yield any stickleback. Mid-water trawling in March, along transverse and longitudinal axes of the lake over a lineal distance of 22 km and at depths ranging from 10 to 100 m in the eastern half of the lake, resulted in the capture of one stickleback; ice cover prevented trawling in the western half of the lake. This stickleback measured 37 mm long and could have been caught at some depth down to 50 m. From the results of these fishing operations stickleback apparently either leave the lake or retreat to areas where they cannot be caught for the winter months, becoming available again between February and April.

Reliable estimates of the size of the stickleback population could not be made from the available catch data. Within any survey, catches varied widely between locations. In addition, local variance in the catches is not precisely known, although judging from a few instances when two sets were made in the same location the numbers caught can vary greatly. The catch data are considered more informative for the period beginning in July when coverage was more complete and stickleback availability increased. Assuming that factors contributing to variability in

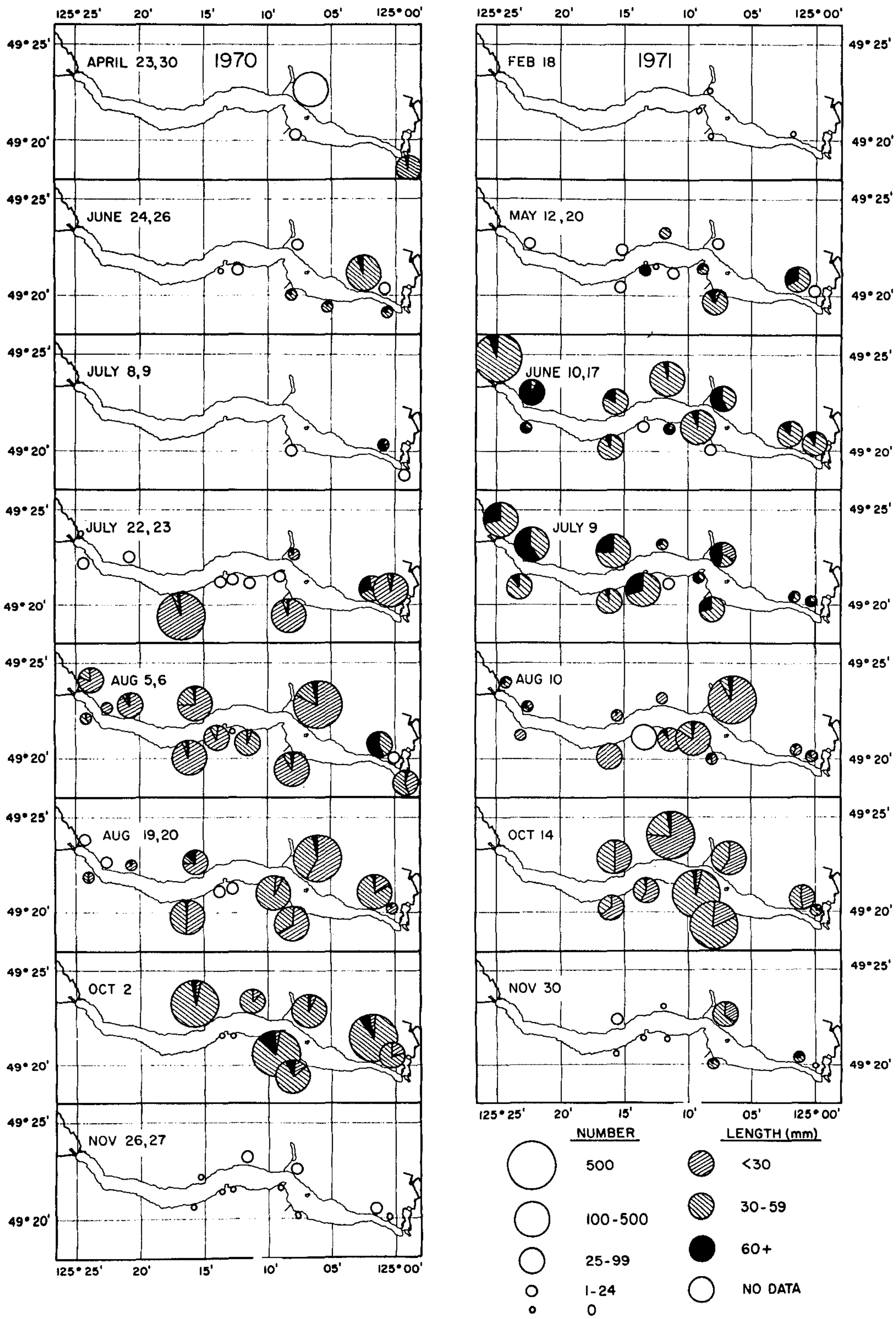

FIGURE 2.–Distribution and size composition of catches of threespine stickleback in Great Central Lake, 1970 and 1971.

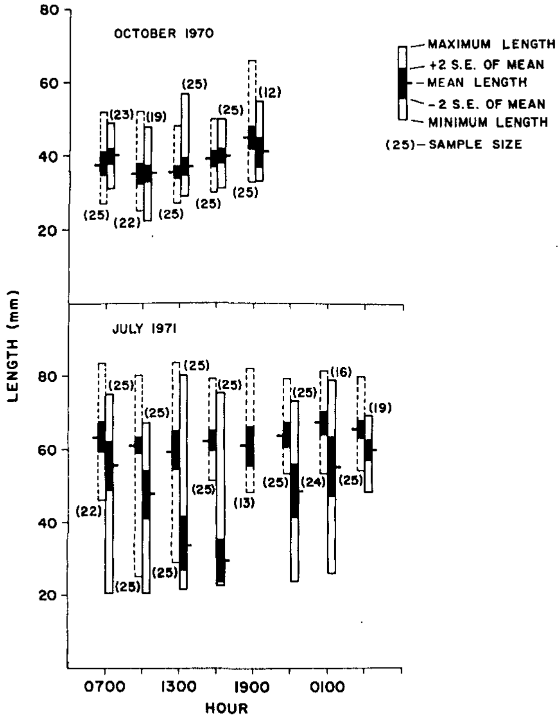

FIGURE 3.—Diel changes in the length of threespine stickleback as indicated by paired catches at station 1, October 1970 and July 1971. Open bars = length range; solid bars = ±2 SE of mean; dash = mean length. Site A = left bar, site B = right bar.

the catches in the 2 yr averaged out, the mean catch for surveys in 1971 was consistently higher than that for the same period in 1970. The difference between yearly mean catches was only 20%, suggesting that the stickleback populations in the 2 yr were approximately similar in size.

Discussion

Seasonal changes in abundance and distribution have been described for several lake populations of threespine stickleback. Greenbank and Nelson (1959), on the basis of beach seine catches, reported that in Bare and Karluk lakes, Alaska, from late May into September stickleback in varying numbers essentially inhabited shallow waters. A few were sighted on the surface of Karluk Lake at a considerable distance from shore, and some were caught by fyke nets at depths of 30 and 80 feet (approximately 9 and 25 m) but not in sets at 126 or 200 feet (approximately 39 and 61 m). Ruggles (1965), while studying juvenile sockeye salmon in Lake Owikeno, B.C., observed that during April to October, stickleback were most abundant in areas suitable for spawning and were taken in two netting operations in midlake surface waters in considerable numbers. Stickleback fry were caught throughout the spring to fall seasons but largest catches were made in the spring. In some years, a secondary increase in abundance occurred in the fall. In Lake Aleknagik, Alaska, Rogers et al. (1963), and Rogers (1968) using beach seines, trawls, and tow nets, observed stickleback in the spring and early summer to inhabit mainly the littoral area. By midsummer, fish of age I and II became pelagic while age 0 and III tended to remain inshore. Observations on stickleback distribution, movement, or numbers during the late fall and winter are lacking for these lakes, presumably because of ice cover. Markovtsev (1972), however, in Lake Dalnee from January through August observed that stickleback are present over winter in the pelagic zone and the population started moving from the pelagic to the littoral zone about May and resumed pelagic residence in the summer.

The seasonal occurrence of threespine stickleback in Great Central Lake is generally similar to those described for other lake populations along the Pacific coast, but their distribution during summer appears to be somewhat different. In other lakes, beginning in midsummer, some stickleback leave the littoral area to inhabit pelagic waters; those in Great Central Lake remain relatively close to or along the shore throughout lake residence. The reason for this apparent difference in distribution patterns is not known although it seems unlikely that it is the result of different fishing gears and methods employed by various investigators. The distribution patterns in the different lakes may be related to lake bathymetry. By comparison with other lakes studied Great Central Lake has relatively little littoral area. Expanses of water exceeding 25 m or more in depth only a few meters from shore are common. This bathymetric feature may provide stickleback with a food supply close to shore thus making it unnecessary for them to move into offshore feeding areas.

The virtual absence of stickleback in the pelagic zone in Great Central Lake does not conflict with the documented onshore-offshore movements of larger individuals during midsummer and fall. Offshore movement during the day and corresponding onshore movements at night were reported for marine threespine stickleback in the

Baltic (Meek 1916). The stimulus for this size-related behavioral difference remains unknown. In Great Central Lake some survival or feeding advantage may accrue to smaller individuals remaining close to shore but the affinity for shore shown by large individuals in July is probably associated with reproduction because virtually all these fish were physically mature or gravid.

FOOD AND FEEDING

Methods

Feeding Relationships

Seasonal and spatial differences in stickleback diet were determined from catches or samples of catches, if large, made during each fishing survey in 1970 and 1971. By coincidence, stomachs from 544 stickleback, or approximately 5% of the total number caught in each year, were examined for content. Stickleback examined in 1970 ranged in length from 15 to 78 mm; in 1971, from 14 to 86 mm. The numbers of fish examined from each station and by survey in the 2 yr are given in Table 2.

Fork length (millimeters), body weight (milligrams, minus the weight of the body cavity parasite, *Schistocephalus*, if present), and stomach content weight (to nearest 0.2 mg) were obtained. Stomach content weight was determined by first weighing the stomach with food and then without. The stomach contents were identified to species when possible, and counted using a binocular microscope. The content weight expressed as a percent of body weight was used as an index of feeding intensity. Gravid females were excluded from the analyses because they appeared to feed less intensively, judging from the occluded stomachs of many individuals. Supplementary information on feeding periodicity was also obtained by subjectively classifying stomachs as either full, three-fourths full, one-half full, one-fourth full, trace of food, or empty, and noting whether the contents were fresh, partially digested, or digested and therefore unidentifiable. The basic data are reported by Manzer (1971, 1972).

Three methods were used to determine the importance of organisms as food:

a. Occurrence–the percent of stickleback feeding on a particular organism.
b. Numerical–mean number of a particular organism per stomach.
c. Points–relative importance of organisms considering size and numbers.

The relative merits of these methods have been discussed by Hynes (1950) and Windell (1968). For the points method, the equivalent units assigned different organisms are given in Table 3. The units for common planktonic crustacea are in the ratio of their wet weight, as determined from zooplankton studies in Great Central Lake (LeBrasseur and Kennedy 1972). Equivalent units for other organisms, including insects, were determined by inspection and assigned the same unit value as other organisms or groups of organisms of similar volume, assuming a common specific gravity. Since individual size of a given organism

TABLE 2.–Numbers of threespine stickleback stomachs examined, by survey and location, 1970 and 1971.

		Location																		
Survey	Date	1	2	3	4	5	6	7	9	10	11	12	13	14	15	16	17	18	19	Total
1970:																				
1	22, 30 Apr.	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15
2	24, 25 June	—	—	23	8	—	—	—	—	—	—	—	—	—	—	—	15	10	—	56
3	8, 9 July	—	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13
4	22, 23 July	—	30	20	10	10	—	—	—	10	—	—	—	—	—	—	—	—	—	80
5	5, 6 Aug.	19	—	15	32	36	—	—	10	25	15	13	12	10	10	—	—	—	—	197
6	19, 20 Aug.	—	13	20	13	22	10	—	—	10	10	10	—	—	10	—	—	—	—	118
7	2 Oct.	—	15	10	10	10	10	—	—	—	10	—	—	—	—	—	—	—	—	65
Total		34	71	88	73	78	20	—	10	45	35	23	12	10	20	—	15	10	—	544
1971:																				
1	12, 20 May	—	—	20	20	3	8	—	10	—	3	—	—	—	—	10	—	—	—	74
2	10, 17 June	—	10	10	—	10	10	10	—	10	10	—	10	10	—	10	—	—	10	110
3	9 July	—	10	10	20	15	6	—	10	10	10	—	10	10	—	9	—	—	10	130
4	10 Aug.	—	9	10	10	12	11	10	—	10	10	—	6	8	—	9	—	—	—	105
5	14 Oct.	—	11	10	10	12	10	—	11	10	10	—	—	—	—	15	—	—	—	99
6	30 Nov.	—	—	8	8	10	—	—	—	—	—	—	—	—	—	—	—	—	—	26
Total		—	40	68	68	62	45	20	31	40	43	—	26	28	—	53	—	—	20	544

TABLE 3.–Equivalent units of important dietaries.

Organism	Bulk units	Organism	Bulk units
Alona	2	Nauplius	0.2
Holopedium	3	Copepodids	1
Bosmina	1	Harpacticoid	1
Daphnia	2	Chironomid larva	5
Epischura	11	Chironomid pupa	50
Diaptomus	2	Egg, zooplankton	1
Cyclops	1	Egg, stickleback	2

was reasonably uniform with time, seasonal adjustment of equivalent units appeared unnecessary. Items which averaged less than one per stomach or less than 1.0% of the bulk were recorded as trace (T) quantities.

Stomachs of large stickleback frequently contained several hundred organisms. In such cases, contents were identified and enumerated from a weighed portion of the total bolus and the resulting counts were then prorated to the total weight to estimate the numbers of organisms consumed. The remaining portion of the bolus was examined for food organisms not represented in the sample. Correlation analysis indicated a very significant positive relationship between actual and estimated counts of major food items ($r = +0.964, P<0.01, n = 15$).

Major features of the stickleback diet were adequately described from examinations of 10 stomachs per sample. In a few cases, smaller numbers were examined to eliminate gaps in time or place. On the basis of two separate tests of association between stomach contents of 10 and 25 fish samples from the same catch, ranked by numbers, Spearman's rank correlation test (Siegel 1956) gave r_s values of $+0.943$ and 1.000. The extent of lake coverage in the 2 yr, especially 1970, differed between surveys. The dietary agreement among stickleback taken at different locations within surveys was examined using Kendall's coefficient of concordance test (Siegel 1956). For each survey, the most common food items at each location were ranked according to mean number in the sample, excluding material rendered unidentifiable through digestion. Corrections were made for items tied in rank and W, the index of divergence of observed from perfect agreement, and related chi-square values were calculated. For eight of the nine surveys tested (four in 1970 and five in 1971) the agreement observed in rankings of dietaries among locations was higher than it would be by chance ($P = 0.05$) (Table 4). Therefore, it seemed reasonable to combine the data for all locations by survey to facilitate detection of possible seasonal changes in diet. From plankton studies conducted in Great Central Lake in 1970, LeBrasseur and Kennedy (1972) stated that "the epilimnion is well mixed, thus assuring a nearly uniform dispersal of planktonic organisms along the lake."

Diet in relation to sexual maturity was determined from combined samples of stickleback caught during the first three surveys (mid-May to early June) in 1971. Mature and immature females were separated on the basis of size, 60 mm being used as the dividing length. Of 54 females 60 mm or larger examined, 4 were immature and 50 were mature. Of the latter group, 28 were ripe. Blue coloration of the iris and red coloration of the pelvic region were used to separate mature from immature males (Craig-Bennett 1931; Greenbank and Nelson 1959). Because female sticklebacks are larger than males of equivalent age (Greenbank and Nelson 1959; van Mullem and van der Vlugt 1964) males larger than 60 mm were considered to be sexually mature. From testes inspection, ripe males were few in number and accordingly no attempt was made to treat functional and nonfunctional males separately. The relative scarcity of ripe males is believed due to their behavior of attending spawning females or nests.

Diel Feeding Rhythm

Diel feeding periodicity and food composition studies were based on paired catches made at station 1 on 1-2 October 1970, and 21-22 July 1971 at two sites (A and B), approximately 100 m apart. In the October series, fishing started at 1300 h 1 October and during the next 24-h period was conducted at 1600, 1900, 2200, 0630, and 1000 h.

TABLE 4.–Summary of results of Kendall coefficient of concordance (W) tests (Siegel 1956) for agreement in diet of threespine stickleback at different sampling locations.

Survey date	Number of locations (k)	Number of food categories (N)	W	Chi-square	P level
1970:					
22-23 July	5	12	0.566	31.13	0.01
5-6 Aug.	11	9	0.383	26.12	0.001
19-20 Aug.	9	12	0.498	49.30	0.001
2 Oct.	6	12	0.581	41.83	0.001
1971:					
12, 20 May	5	9	0.220	8.80	0.70
10, 17 June	10	9	0.317	25.36	0.01
9 July	12	9	0.450	43.20	0.001
10 Aug.	10	6	0.230	11.50	0.05
14 Oct.	9	9	0.629	45.29	0.001

Fishing at 2200 h at each site failed to yield any stickleback, presumably because of inefficient operations under conditions of total darkness. As a consequence further sampling was suspended until 0630 h 2 October. Fishing during the July series began at 0700 h and was repeated at 1000, 1300, 1600, 1900, 2200, 0100, and 0400 h. Gear problems precluded fishing at site B at 1900 h. During each series, the time interval between fishing at the two sites at any time of day was approximately 15 min and for practical purposes can be considered concurrent.

The target sample size for each site and time of day was 25 fish. Except for sampling times already indicated, this number was achieved or closely approximated. The smallest sample contained 12 fish (site B, 1900 h). All fish in the sample were processed in accordance with methods described earlier and 10 fish, selected at random, were examined for stomach contents. A total of 226 stickleback were examined for the October series, 334 for the July series. The sizes of stickleback by sample are illustrated in Figure 3.

Mean feeding intensity indices (food weight/body weight × 100) for paired samples were similar, and data for each series were pooled by time of day.

Daily Ration and Maximum Meal Size

In this study, daily ration is defined as the weight of food consumed over a 24-h period expressed as a percent of body weight. Daily rations were estimated from the diel feeding rhythm curve, using a modification of the method developed by Keast and Welsh (1968). Essentially, differences between maximal and minimal feeding indices during successive periods over a 24-h cycle were determined and these values and the residual content were summed. The method is most applicable to species which completely empty their stomachs between meals.

Maximum individual meal size was determined from regression analysis of stickleback taken during the maximal feeding period in July and which were judged to have "full" stomachs according to the subjective "fullness" scale described earlier.

TABLE 5.—Seasonal change in the diet of threespine stickleback in Great Central Lake, 1970.

Date	22, 30 Apr.			24-25 June			8-9 July			22-23 July			5-6 Aug.			19-20 Aug.			2 Oct.		
No. fish examined	15			56			13			80			197			118			65		
% empty	0			3.6			15.4			13.7			3.6			3.4			0		
Size range (mm)	33-63			36-72			16-70			18-75			15-74			19-76			27-76		
Mean size (mm)	48			49			51			43			33			35			39		
Mean content wt (mg)	34.6			27.4			14.6			25.4			15.3			14.3			17.4		
Organism	1[1]	2[2]	3[3]	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Rotifera	—	—	—	46	15	T	62	91	T	26	47	T	75	52	T	76	67	T	59	56	T
Cladocera:																					
Holopedium	—	—	—	41	39	12	46	37	63	53	95	60	76	115	60	75	141	61	88	129	47
Bosmina	100	2,419	95	73	235	24	77	37	21	60	14	3	65	18	3	79	88	13	98	116	14
Daphnia	—	—	—	11	1	T	8	T	1	—	—	—	T	T	T	2	T	T	2	T	T
Alona	—	—	—	5	T	T	23	2	2	16	1	T	44	2	T	46	4	1	23	1	2
Copepoda:																					
Epischura	40	2	T	55	46	51	31	1	6	45	10	23	63	17	33	36	7	5	29	4	5
Diaptomus	—	—	—	—	—	—	—	—	—	6	1	T	4	T	T	19	9	3	49	98	24
Cyclops	100	88	3	16	T	T	—	—	—	1	T	T	3	T	T	42	4	T	60	38	4
Copepodids	—	—	—	—	—	—	—	—	—	4	T	T	19	6	1	32	27	4	57	20	2
Nauplii	—	—	—	—	—	—	—	—	—	13	1	T	21	10	T	38	32	T	35	9	T
Harpacticoid	—	—	—	9	T	T	—	—	—	14	T	T	4	T	T	22	2	T	19	1	T
Insecta:																					
Chironomid larvae	—	—	—	27	5	2	15	T	T	39	3	3	25	1	T	33	5	4	14	1	T
Chironomid pupae	—	—	—	50	2	10	8	T	T	26	1	10	14	T	T	28	1	7	5	T	T
Other	—	—	—	11	T	T	—	—	—	4	T	T	8	T	T	10	T	T	8	T	T
Eggs - zooplankton	93	18	T	19	4	T	62	10	6	9	T	T	26	1	T	45	8	1	34	8	1
Other:																					
Pelecypoda	—	—	—	11	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda	—	—	—	—	—	—	15	T	T	8	T	T	1	T	T	11	T	T	T	T	T
Acari	—	—	—	—	—	—	—	—	—	3	T	T	3	T	T	5	T	T	5	T	T
Planaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	T	T	T	T	T
Odonata	—	—	—	—	—	—	—	—	—	—	—	—	1	T	T	—	—	—	—	—	—
Fish	—	—	—	—	—	—	8	T	T	5	T	T	3	T	T	—	—	—	—	—	—
Unidentifiable %									25						3			4			1

[1]% stomachs with item.
[2]Mean no. items per stomach examined.
[3]Item = % of total bulk units. T = Trace = < 1 organism or < 1%.

RESULTS

Feeding Relationships

Seasonal Variations in Diet

Data on size and stomach contents of stickleback examined in 1970 and 1971 are summarized by survey in Tables 5 and 6. The predominant features regarding seasonal change in diet are depicted in Figure 4. Observations for 1970, except for August when almost all stations were sampled, are based mainly on samples taken from the eastern part of the lake. Observations for 1971 are based on samples from most of the key sampling stations except in November when fishing was confined to the eastern end of the lake.

Although the numbers of stickleback examined differed by survey, a similar seasonal trend in the proportion of fish with empty stomachs was observed for the 2 yr: low in the spring and early summer, highest in midsummer, and again low in the fall. The mean weight of stomach contents fluctuated in each year but generally was higher in the spring and early summer. The higher mean values in the early part of the year are probably related to fish size. On the average, stickleback were larger in the spring and early summer than in the late summer and fall. The relatively high proportion of fish with empty stomachs in midseason can be explained by feeding behavioral differences associated with sexual maturity.

In each of the 2 yr stickleback had a wide but rather similar diet. They predominately fed on five species of organisms: two cladocerans (*Holopedium gibberum*, *Bosmina coregoni*), two copepods (*Epischura nevadensis*, *Diaptomus oregonensis*), and a cyclopoid copepod (*Cyclops bicuspidatus*). Larvae and pupae of the family Chironomidae were also of some importance. The distinction between zooplankton eggs and fish eggs in 1971 represents a qualitative refinement in analysis of the data, rather than any difference in diet. Other kinds of organisms consumed at various times but of minor importance were harpacticoid copepods, insects, pelecypods, ostracods,

TABLE 6.—Seasonal change in the diet of threespine stickleback in Great Central Lake, 1971.

Date	12, 20 May			10, 17 June			9 July			10 Aug.			14 Oct.			30 Nov.		
No. fish examined		74			110			130			105			99			26	
% empty		2.7			4.5			18.5			19.1			8.1			3.8	
Size range (mm)		29-86			33-82			15-86			14-80			23-77			24-78	
Mean size (mm)		54			54			58			33			38			34	
Mean content wt (mg)		26.1			45.3			28.0			16.5			18.6			13.9	
Organism	1[1]	2[2]	3[3]	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Rotifer	—	—	—	10	1	T	40	15	T	44	27	T	74	35	T	31	12	T
Cladocera:																		
Holopedium	1	T	T	34	14	1	59	47	16	57	22	28	89	163	67	65	20	35
Bosmina	47	10	2	37	2	T	19	T	T	40	10	4	89	85	12	69	43	25
Daphnia	—	—	—	—	—	—	—	—	—	—	—	—	19	1	T	—	—	—
Alona	5	T	T	4	1	T	2	3	T	54	17	14	20	1	T	23	1	1
Copepoda:																		
Epischura	1	7	19	56	286	95	50	55	68	6	6	28	19	1	1	—	—	—
Diaptomus	—	—	—	10	2	T	—	—	—	5	2	2	71	28	8	54	10	12
Cyclops	40	75	19	49	68	2	35	4	T	4	T	T	65	20	3	42	6	3
Copepodids	40	13	3	23	8	T	40	12	1	6	T	T	48	52	7	50	38	22
Nauplii	32	22	T	—	—	—	13	6	T	—	—	—	28	2	T	—	—	—
Harpacticoid	10	1	T	9	13	T	3	T	T	8	T	T	1	T	T	4	T	T
Insecta:																		
Chironomid larvae	19	1	T	6	T	T	9	T	T	11	T	T	1	T	T	4	T	—
Chironomid pupae	23	3	38	11	T	T	7	1	6	2	T	T	—	—	—	—	—	—
Other	12	1	13	9	T	T	16	1	6	5	1	21	3	T	T	4	T	T
Eggs - zooplankton	5	1	T	19	3	T	39	22	2	1	T	T	54	15	2	31	3	2
Fish	1	T	T	3	T	T	4	T	T	1	T	T	—	—	—	—	—	—
Other:																		
Amphipoda	4	T	T	2	T	T	2	T	T	—	—	—	—	—	—	4	T	T
Pelecypoda	8	1	2	3	T	T	T	T	T	—	—	—	—	—	—	—	—	—
Ostracoda	—	—	—	2	T	T	4	T	T	17	1	T	—	—	—	8	T	T
Acari	8	T	T	4	T	T	—	T	T	22	1	2	—	—	—	—	—	—
Araneida	1	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fish	—	—	—	—	—	—	—	—	—	—	—	—	1	T	T	—	—	—
Coleoptera	2	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ceratopogonidae	11	T	T	3	T	T	—	—	—	—	—	—	—	—	—	—	—	—
Isopoda	1	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentifiable %		51			47			38			24			36			34	

[1] % stomachs with item.
[2] Mean no. items per stomach examined.
[3] Item = % of total bulk units. T = Trace = < 1 organism or < 1%.

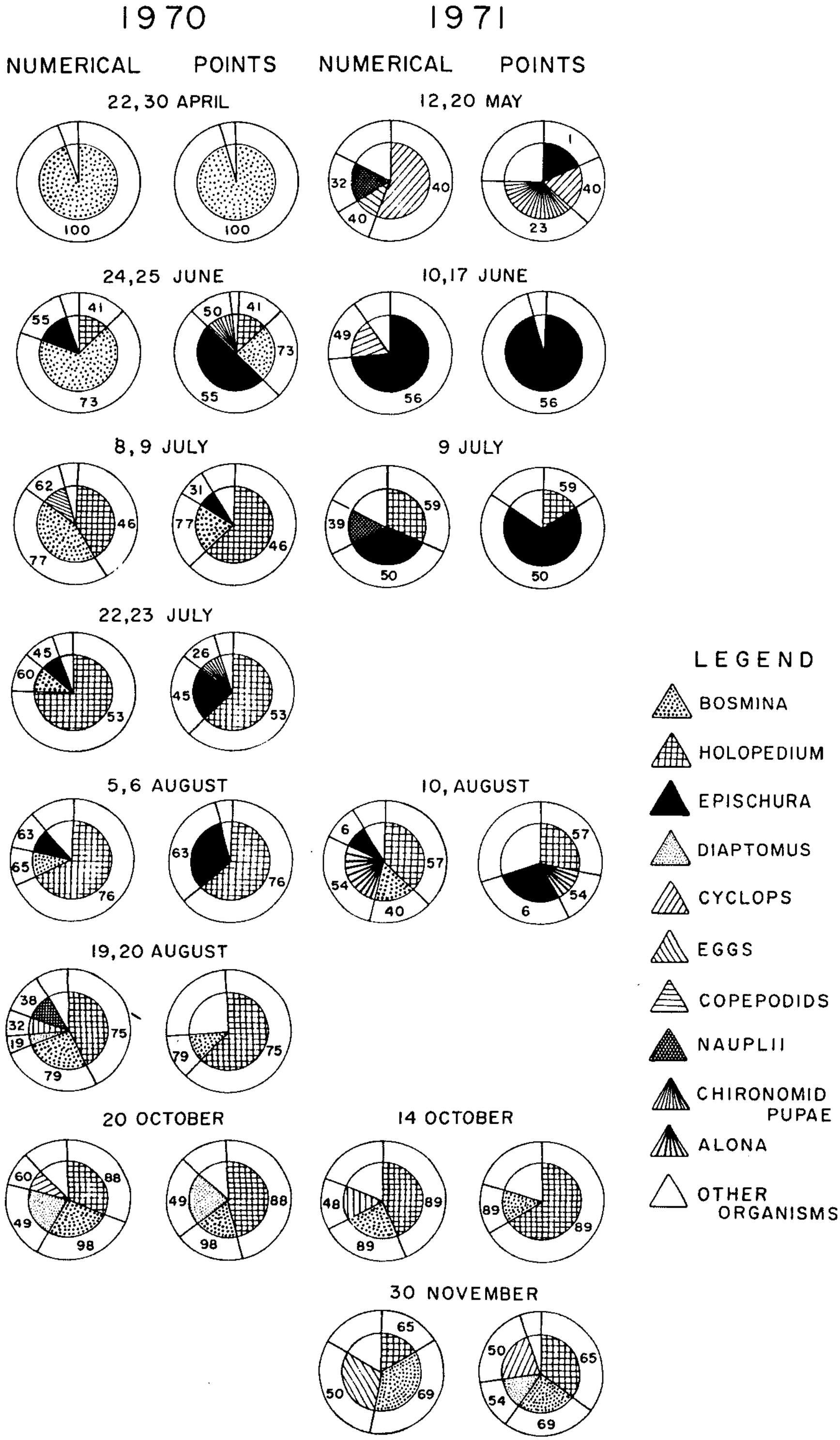

FIGURE 4.—Seasonal change in the predominant food items of threespine stickleback in Great Central Lake, 1970 and 1971. Figures in the periphery of each pie diagram represent the percent of stickleback stomachs containing the particular item.

acarids, Araneida, planaria, Odonata, and fish (cottids).

The different food organisms differed seasonally in their dietary importance. Considering items of major importance, in 1970 in late April, virtually all stickleback stomachs examined contained *Bosmina*, *Cyclops*, and zooplankton eggs, but *Bosmina* was most important, averaging 2,419 individuals per stomach and making up 95% of the bulk. By late June, *Bosmina* was still the dominant food item but had declined somewhat in importance as indicated by an increasing proportion of stickleback feeding on *Epischura* (55%), *Holopedium* (41%), and chironomids, especially pupae. Of these *Epischura* was most important, forming almost 50% of the bulk. Through July and August, *Bosmina* was consumed by a high proportion of stickleback (no less than 60%) but *Holopedium* progressively became the dominant food organism (approximately 60% by bulk). During these two months, the number of stickleback feeding on *Alona*, copepod copepodids and nauplii, and *Diaptomus* increased but none of these items was important quantitatively. In October, *Holopedium* continued to be the dominant food item in terms of bulk, but more stickleback fed on *Bosmina* (98%). *Diaptomus* and *Cyclops* were present in about 50% of the stomachs examined and were of minor importance. Rotifers and eggs were present virtually throughout the study period, the former item occurred rather frequently (26-76%), but were unimportant in terms of bulk. Judging from size, the eggs were from both zooplankton and stickleback. Since stickleback spawn between late June and early August, eggs encountered at other times of the year presumably were zooplankton eggs.

In May 1971, about one-half of the stickleback had *Bosmina*, *Cyclops*, and copepodids in their stomachs. *Cyclops* was most important in terms of numbers per stomach (75) but chironomid pupae, because of relative size of individuals, was important in terms of bulk (38%). By mid-June, more stickleback were feeding on *Epischura* (56%) and *Holopedium* (34%), but *Epischura* was the dominant food organism (95% of total stomach contents). About the same number (49%) of stickleback fed on *Cyclops* as in May, and although the item ranked second in incidence, it accounted for only 2% of the total stomach content. In July, *Epischura* declined in importance but still maintained dominant position among the other food organisms. *Holopedium* continued to increase in importance. This inverse trend in the importance of these two food items was observed into October. In October, *Holopedium* was the dominant food item and *Bosmina* ranked second in bulk and were consumed by as many stickleback as were *Holopedium*. In terms of occurrence, *Diaptomus* (71%), *Cyclops* (65%), copepod copepodids (48%), and zooplankton eggs (54%) were of secondary importance. At the end of November, *Holopedium*, *Bosmina*, and copepod copepodids formed the major part of the diet of stickleback and individually were of about equal importance.

The stickleback diet in 2 yr showed some marked seasonal similarities and differences. *Bosmina* was not as important in the early part of 1971 as in 1970. Another difference is the greater importance of *Epischura* later into 1971 than 1970, and the greater importance of *Holopedium* in July and August in 1970. A feature common to both years is the late season resurgence of *Bosmina* as an important food organism. It is not known for certain whether these differences and similarities represent annual differences in abundance levels of the various kinds of organisms or in sampling dates.

Diet in Relation to Stickleback Size

A total of 205 stickleback taken from the eastern end of the lake on 22 July and 5 August 1970, and ranging in length from 15 to 78 mm were examined for diet differences in relation to size. The stickleback were arbitrarily divided into four size groups: <30 mm, 30-49 mm, 50-69 mm, 70+ mm. Data on diet for the same size group for the 2 days were pooled since samples were obtained in the same general area within a short time interval (Table 7).

A high proportion of the stickleback (75, 65, and 68% respectively) in the <30 mm group consumed *Bosmina*, Rotifera, and *Holopedium*. *Alona*, *Epischura*, and chironomid larvae occurred in about one-half of the stomachs. Of the remaining items consumed only copepod nauplii, chironomid pupae, and zooplankton eggs were of any importance, occurring in 18, 16, and 13% of the stomachs, respectively. Larger stickleback, excluding the 70+ mm group of which only 11 were examined, tended to feed more on *Holopedium*, *Epischura*, chironomid pupae, and zooplankton eggs, and less on Rotifera (except those in the 30-49 mm group), *Bosmina* and *Alona*. Copepod nauplii apparently were not consumed by larger stickleback, but fish

TABLE 7.—Occurrence (percent) of different organisms in the diet of threespine stickleback of four size groups– <30 mm group contained 100 fish; 30-49 mm, 34 fish; 50-69 mm, 60 fish; and 70+ mm, 11 fish. Based on samples taken on 22 July and 5 August 1970.

Organism	Size group (mm) <30	30-49	50-69	70+
Rotifera	65	85	49	9
Cladocera:				
Holopedium	68	88	81	71
Bosmina	75	50	36	28
Alona	46	19	19	—
Copepoda:				
Epischura	50	79	83	57
Diaptomus	3	6	2	—
Cyclops	4	—	—	—
Copepodids	7	—	2	—
Nauplii	18	—	—	—
Harpacticoid	7	10	8	—
Insecta:				
Chironomid larvae	42	22	21	14
Chironomid pupae	16	35	21	—
Other	7	5	7	—
Eggs - zooplankton	13	29	23	28
Other:				
Pelecypoda	—	—	2	—
Ostracoda	6	6	3	—
Acari	2	—	—	—
Araneida	—	3	—	—
Fish	—	—	10	—
Isopoda	—	—	3	14

larvae were, the largest, a cottid, measuring 14 mm. It is reasonably clear that a positive relationship exists between food size and stickleback size. This relationship is also apparent when for each stickleback size-group the different food organisms, especially the common items (namely, *Bosmina*, *Holopedium*, and *Epischura*), are expressed as a percent of the total stomach content for that group (Table 8).

Diet in Relation to Sexual Maturity

Mature males showed a higher incidence of feeding (90%) than did gravid females (61%) (Table 9), the difference being statistically significant. (χ^2 = 13.811, n = 2, P = <0.01).

Nongravid females, gravid females, and mature males fed on a variety of similar kinds of organisms (Table 9) and, except for *Epischura*, none of the items were of great importance as food. Since *Epischura* is the largest planktonic form, its predominance in the diet of large individuals is not unexpected. *Epischura* formed more than 90% of the bulk units and the mean number ingested was very much higher than for any other single item. In contrast to 54% of gravid females which had eaten this item, its occurrence in nongravid females and in males was considerably less, 18 and 16%, respectively. Planktonic crustaceans, insects,

TABLE 8.—Relative importance (percent) of food organisms of different bulk units in the diet of threespine stickleback of four size groups– <30 mm group contained 100 fish; 30-49 mm, 34 fish; 50-69 mm, 60 fish; and 70+ mm, 11 fish. Based on samples taken on 22 July and 5 August 1970.

Bulk units	Size group (mm) <30	30-49	50-69	70+	Item
≤ 1	48	29	26	8	Rotifera, nauplius, *Bosmina*, *Cyclops*, copepodids, harpacticoids, zooplankton eggs
2	3	1	1	3	*Alona*, *Daphnia*, *Diaptomus*, stickleback eggs
3	39	64	67	77	*Holopedium*
5	1	1	1	T	Chironomid larvae
11	8	8	6	12	*Epischura*
≥50	T	T	T	0	Chironomid pupae, fish

TABLE 9.—Stomach contents of nongravid and gravid females and sexually mature male threespine stickleback, Great Central Lake, 12 May-9 July 1971.

	Female						Male		
	Non-gravid			Gravid					
No. examined	22			28			81		
Percent with food	73			61			90		
Organism	1[1]	2[2]	3[3]	1	2	3	1	2	3
Rotifera	9	2	T	—	—	—	10	4	T
Cladocera:									
Holopedium	23	6	1	32	75	7	17	13	1
Bosmina	—	—	—	4	T	T	6	1	T
Alona	5	1	T	—	—	—	2	2	T
Copepoda:									
Epischura	18	141	94	54	268	92	16	230	94
Diaptomus	—	—	—	—	—	—	1	T	T
Cyclops	14	3	T	11	T	T	22	11	T
Harpacticoid	5	T	T	—	—	—	4	T	T
Copepodids	5	2	T	—	—	—	9	1	T
Insecta:									
Chironomidae L	27	4	1	4	T	T	17	1	T
Chironomidae P	18	T	1	11	T	T	15	2	3
Coleoptera	5	T	T	—	—	—	1	T	T
Ceratopogonidae	14	1	2	—	—	—	11	T	T
Other	18	T	T	14	T	T	15	T	T
Araneida	—	—	—	—	—	—	1	T	T
Acari	—	—	—	—	—	—	9	T	T
Ostracoda	5	T	T	—	—	—	5	T	T
Pelecypoda	—	—	—	—	—	—	15	T	T
Isopoda	—	—	—	—	—	—	1	T	T
Amphipoda	5	T	T	4	T	T	7	T	T
Eggs:									
Zooplankton	9	5	T	14	13	T	19	8	T
Stickleback	—	—	—	4	T	T	9	2	T
Detritus	—	—	—	1	—	—	13	—	—

[1]Percentage of stomachs with item.
[2]Mean number of items per stomach examined.
[3]Item = percent of total bulk units. T = Trace = < 1 organism or < 1%.

eggs of zooplankton and stickleback, and other miscellaneous taxonomic groups, some of which are littoral in habitat, made up most of the remainder of the stomach contents. Males ate more benthic and epibenthic forms, as well as detritus (mainly sand and twigs), than did females. Detritus in individual male stomachs made up from 10 to 100% of the contents and was present in 13 stomachs, compared with 1 for females. The ingestion of detritus by males is probably related to its role in nest building and not to feeding behavior per se.

Diel Feeding Rhythm and Variation in Diet

Despite some size differences in stickleback at sites A and B (station 1), feeding intensity indices (food weight/body weight×100) for stickleback caught at a specific sampling time were similar during October and July. Active feeding took place mainly during postdawn and predusk hours, leading to two daily alternating feeding and "nonfeeding" periods (Figure 5). Differences between the mean indices for different times of day in the October and July series were subjected to the Kruskal-Wallis test (Siegel 1956) and found to be significant (October, H = 25.71, 4 df, P = <0.0001; July, H = 28.97, 7 df, P = <0.001). This periodicity in feeding was corroborated by the mean number of organisms present in stomachs at different times of day (Table 10).

The kinds of organisms consumed and their importance at different times of the diel cycle are presented in Table 10 for both the October and July series. Information for October is based on stickleback ranging in mean length from 37 to 44 mm. Stickleback examined in the July series were less uniform in size and ranged in mean length from 49 to 63 mm.

Considering the important food items, the composition of the diet changed through the daily cycle in October and July (Table 10). In October, *Bosmina* and *Holopedium* occurred in a very high percentage of the stomachs examined, regardless of sampling time. In terms of numbers consumed and bulk units, *Holopedium* was the dominant item, especially between 0700 and 1000 h. Between 1300 and 1900 h the relative importance of *Holopedium* was reduced somewhat by the increased consumption of *Bosmina*, *Alona*, *Epischura*, and eggs of zooplankton.

In July, *Holopedium* was the dominant food organism throughout the daily cycle. Although not as important as *Holopedium* in terms of numbers or bulk, eggs of zooplankton were present in a large proportion of the stomachs examined, ranging from 40% (0100 h) to 100% (1000 h), with consumption being greatest in the morning. *Epischura* was present in stomachs at most times of the day, but their contribution to the diet was highest during peak feeding times.

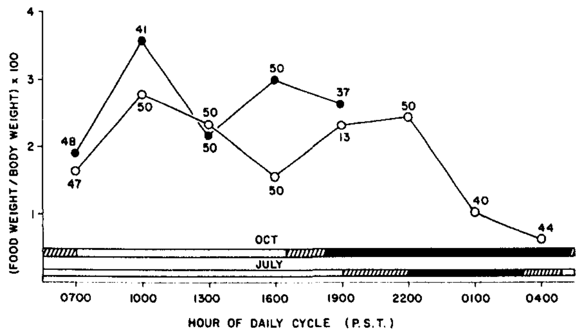

FIGURE 5.—Diel fluctuations in feeding intensity of threespine stickleback in October 1970 (closed circles) and July 1971 (open circles). The number associated with each datum point represents sample size. The horizontal bars indicate periods of daylight and darkness.

Rotifera were present in a large proportion of the stomachs throughout the diel cycle in October and July and were numerous compared to most other items. Their individual small size would tend to depress their importance as a food item.

Daily Ration and Maximal Meal Size

The described diel fluctuations in feeding intensity indicate that in July at least, consumption and evacuation occurred alternately over periods of approximately 6-h duration. On the average, a particle of food required about 6 h to pass through the stomach. Stomachs were least full at 0400 h when the contents amounted to 0.65% of the mean body weight but they were, on the average, never devoid of food, suggesting that feeding was continuous in the population. Freshly ingested organisms were present in some stomachs even during dark hours.

Recognizing two periods of consumption and stomach evacuation each of approximately 6-h duration, and the presence of "residual" content, the daily ratio (DR) in July can be calculated by the formula:

$$DR = R + P_1 + P_2$$

where R = residual content × food particle evacuation time,
P_1 = Major feeding index - residual content,
P_2 = Minor feeding index - residual content.

Substituting actual values indicated in Figure 5, the food consumed by stickleback in July amounted to (0.65 × 24/6) + (2.80 - 0.65) + (2.45 - 0.65) =

TABLE 10.—Occurrence, mean number, and relative importance in bulk units of various organisms consumed by threespine stickleback in Great Central Lake, October 1970 and July 1971. Data for sites A and B combined.

		0700 h			1000 h			1300 h			1600 h			1900 h			2200 h			0100 h			0400 h			Total		
Month	Item	1[1]	2[2]	3[3]	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
October	No. of fish		20			20			20			20			20													
	Mean length (mm)		39.2			37.1			38.8			41.1			43.8													
	Organisms:																											
	Rotifera	75	50	T	75	87	T	60	60	T	75	87	T	80	75	T										73	359	T
	Cladocera:																											
	Alona	—	—	—	45	4	1	—	—	—	30	19	7	20	32	13										19	55	6
	Bosmina	80	6	2	95	17	3	80	38	38	90	31	6	75	20	8										84	112	6
	Daphnia	25	T	T	5	T	T	5	T	T	—	—	—	15	T	T										10	T	T
	Holopedium	70	70	87	90	149	85	80	10	30	60	43	26	75	70	43										75	342	56
	Copepoda:																											
	Copepodids	10	T	T	15	T	T	55	4	4	55	15	3	25	5	1										32	24	1
	Cyclops	5	T	T	55	7	1	5	T	T	—	—	—	10	1	T										15	8	T
	Diaptomus	5	T	T	50	21	8	5	T	T	—	—	—	25	3	1										17	24	2
	Epischura	30	2	9	20	T	T	50	2	22	55	25	55	60	10	23										43	39	23
	Harpacticoid	—	—	—	35	T	T	20	T	T	35	T	T	—	—	—										18	T	T
	Insecta:																											
	Chironomid larvae	—	—	—	10	T	T	20	T	T	5	T	T	5	T	T										8	T	T
	Chironomid pupae	—	—	—	—	—	—	10	T	T	5	T	T	—	—	—										3	T	T
	Ceratopogonidae larvae	—	—	—	5	T	T	—	—	—	5	T	T	—	—	—										2	T	T
	Eggs - Zooplankton	55	3	1	55	3	T	45	2	2	35	2	T	55	42	8										49	52	29
	Other:																											
	Ostracoda	5	T	T	15	T	T	10	T	T	15	T	T	10	T	T										11	T	T
	Oligochaeta	—	—	—	15	T	T	—	—	—	15	T	T	—	—	—										6	T	T
	Turbellaria	—	—	—	10	T	T	5	T	T	—	—	—	—	—	—										3	T	T
	Pelecypoda	—	—	—	—	—	—	5	T	T	—	—	—	—	—	—										1	T	T
	Sum of means		131			348			116			222			258												1,015	
July	No. of fish		20			20			20			20			10			20			20			20				
	Mean length (mm)		58.8			57.2			50.5			49.4			59.8			54.4			59.6			63.1				
	Organisms:																											
	Rotifera	65	20	T	75	48	T	55	120	T	45	92	T	80	152	T	72	208	T	35	19	T	55	43	T	59	702	T
	Cladocera:																											
	Alona	—	—	—	45	56	3	15	T	T	15	T	T	10	T	T	4	13	1	10	3	7	5	16	14	9	88	1
	Bosmina	5	T	—	10	1	T	30	T	T	35	T	T	30	1	T	46	T	T	5	T	T	5	T	T	22	2	T
	Daphnia	—	—	—	10	T	T	—	—	—	10	T	T	—	—	—	—	—	—	—	—	—	—	—	—	T	T	T
	Holopedium	90	471	85	95	825	86	60	182	81	40	148	86	70	396	47	75	496	92	40	22	83	70	56	77	68	2,596	77
	Copepoda:																											
	Nauplii	—	—	—	20	6	T	50	33	1	25	2	T	—	—	—	—	—	—	—	—	—	—	—	—	12	41	T
	Copepodids	—	—	—	15	3	T	30	6	1	10	T	T	10	2	T	—	—	—	—	—	—	—	—	—	8	11	T
	Cyclops	35	6	T	55	17	T	15	T	T	5	T	T	—	—	—	25	1	T	—	—	—	—	—	—	18	24	T
	Diaptomus	5	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	T	T	T
	Epischura	40	18	12	70	20	7	35	9	14	20	4	8	50	113	50	25	2	1	15	T	T	—	—	—	30	166	18
	Harpacticoid	—	—	—	5	T	T	—	—	—	10	T	T	10	T	T	—	—	—	5	T	T	—	—	—	3	T	T
	Insecta:																											
	Chironomid larvae	5	T	T	—	—	—	—	—	—	—	—	—	10	T	T	4	T	T	—	—	—	—	—	—	T	T	T
	Chironomid pupae	15	T	T	—	—	—	—	—	—	5	T	T	—	—	—	—	—	—	—	—	—	10	T	T	3	T	T
	Other	20	T	T	—	—	—	5	T	T	—	—	—	—	—	—	4	T	T	10	T	T	5	T	T	6	T	T
	Eggs:																											
	Zooplankton	95	33	2	100	45	1	65	20	3	45	26	5	8	53	2	72	75	4	40	7	8	65	16	7	70	275	2
	Stickleback	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	T	T	—	—	—	T	T	T
	Other:																											
	Ostracod	5	T	T	5	1	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	T
	Fish	—	—	—	—	—	—	5	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	T	T	T
	Sum of means		548			1,022			370			272			717			795			51			131			3,906	

[1]Percent of stomachs with item. [2]Mean number of organisms per stomach. [3]Item = percent of total bulk units.

6.55% of their body weight. Some digestion would have occurred during consumption so this is a minimal value.

For October, failure to obtain feeding indices between 1900 and 0700 h over the diel cycle precluded similar estimation of the daily ration. However, if the residual content is assumed to be 0.65% of the body weight during periods lacking observations, the daily food consumption can be estimated to be 2.60 + 2.90 + 2.30 = 7.80% of the mean body weight.

Estimates of maximum meal size were obtained by plotting feeding indices for only those fish which were judged to have "full" stomachs during the postdawn feeding period (i.e., the most intensive feeding time of day) against length (Figure 6A). Data for stickleback in July were used because of their wide range in length. Despite considerable individual variation between fish of the same length obviously feeding intensity was inversely related to length (r = -0.788, df = 26, P <0.01). From the regression line fitted by the method of least squares, it can be predicted by extrapolation that, on the average, larval stickleback, which measure approximately 8 mm upon hatching, consume 7.5% of their body weight in a single meal, and that consumption in relation to body weight decreases 0.8% per 10 mm increase in length. As would be expected, large fish in a single meal eat more than do small fish and the relationship is of the positive exponential form (Figure 6B).

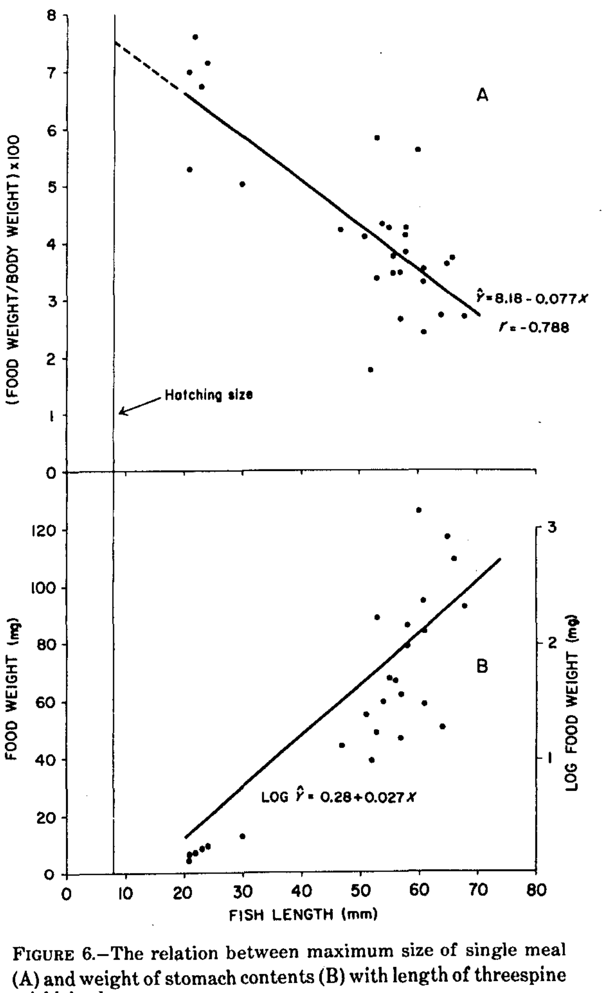

FIGURE 6.—The relation between maximum size of single meal (A) and weight of stomach contents (B) with length of threespine stickleback.

For stickleback in October and July (assuming mean lengths of 40 mm and 60 mm, respectively), the average meal size was approximately 5 and 3.5% of their body weight, respectively. Assuming two feeding periods per day, the daily ration becomes 10 and 7% of body weight. These values are in reasonable agreement with daily ration estimates based on diel fluctuations in stomach contents.

Discussion

During 1970 and 1971, the first 2 yr of a fertilization program attempting to increase sockeye salmon production in Great Central Lake, stickleback were observed to feed on a variety of organisms with planktonic crustaceans (cladocerans and copepods) and insects (chironomid pupae and larvae), to a lesser degree, being the main food organisms. These findings are consistent with observations on food of stickleback in a variety of freshwater habitats made by other investigators (Hartley 1948; Hynes 1950; Greenbank and Nelson 1959; Rogers 1968). From a trophic standpoint, the species is a secondary consumer.

The literature on feeding of fishes in both laboratory and in nature is replete with evidence that consumption is influenced by a multitude of factors. In the present study effort was focussed on examining seasonal and diel changes in feeding habits, possible influencing factors being limited to size and sexual maturity.

The most pronounced feature observed in the feeding of stickleback was the seasonal change in the importance of different kinds of organisms consumed. Although the food resource was not sampled in conjunction with the food studies, some general comments on food availability and selectivity by stickleback in 1970 can be made using results of zooplankton studies by LeBrasseur and Kennedy (1972) (Figure 7). A more precise method of measuring the use of major planktonic forms in relation to availability would have been the employment of Ivlev's (1961) "electivity index," taking into account the comments of O'Brien and Vinyard (1974) regarding distribution of predator and prey. *Bosmina*, *Holopedium*, and *Diaptomus* were consumed approximately in relation to their abundance, although in the early part of the year relative utilization was highest for *Bosmina*. *Cyclops* and *Bosmina* were approximately equally abundant and exhibited somewhat similar seasonal fluctuations but utilization of *Bosmina* was sharply restricted during July and early August whereas *Cyclops* was relatively unutilized throughout the summer. Consumption of *Epischura*, a less abundant form which occurred mainly between May and September, was highest in June during the early part of the "bloom."

The reasons for the apparent differences in the relative utilization of the major food items would appear to differ. The shift from *Epischura*, despite rather uniform abundance, to smaller organisms, mainly *Holopedium* and *Bosmina*, through the season may be due to the decrease in average size of stickleback that occurred in midsummer. *Epischura*, which equals 11 bulk units compared with 3 and 1 for *Holopedium* and *Bosmina*, respectively, may have been too large an item to be consumed by the majority of stickleback present after July. Greenbank and Nelson (1959) and Rogers (1968) observed that feeding habits of *G. aculeatus* in Alaskan lakes changed through the summer and differed between individuals of different size. The disparity in relative utilization of *Bosmina* and *Cyclops*, which were of comparable abundance and individual size, cannot be thus explained. Rather, it would appear that the difference in their dietary importance may be explained by differences in spatial distribution affecting availability: *Cyclops*

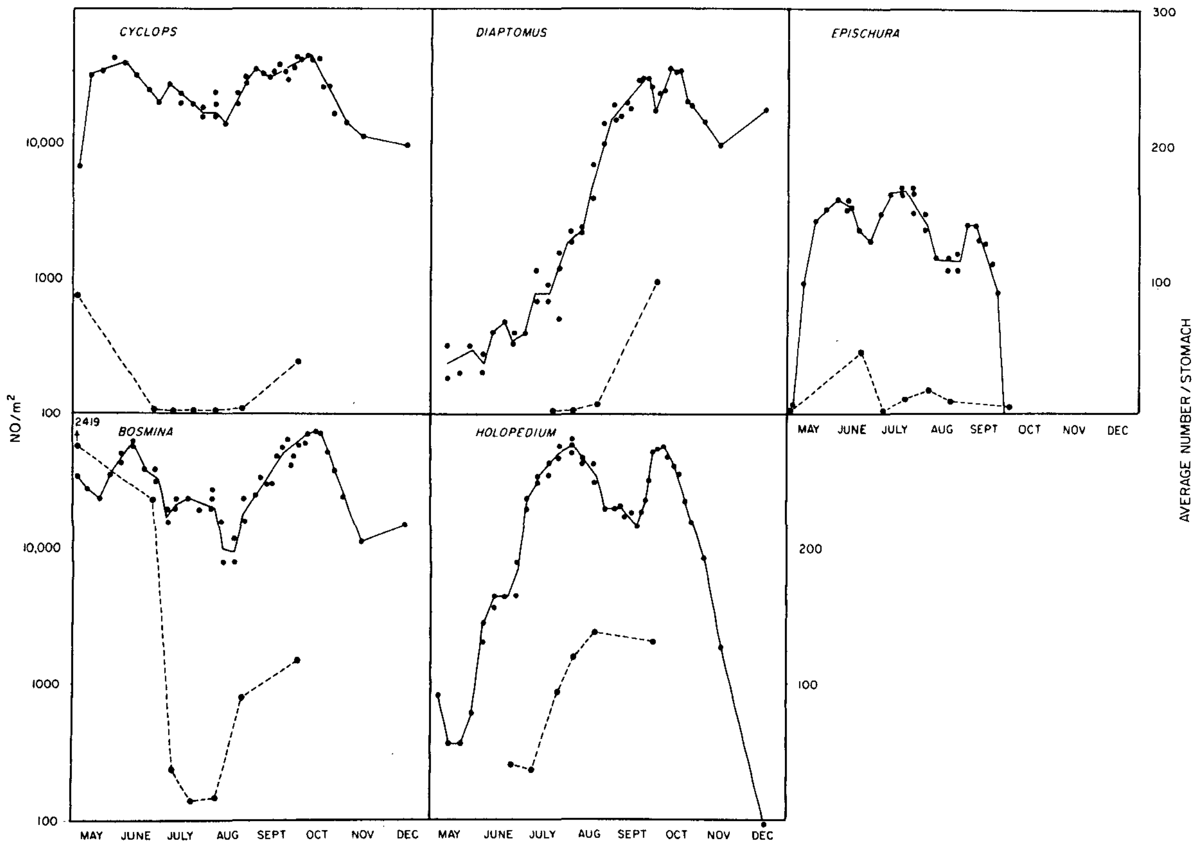

FIGURE 7.–Seasonal change in the biomass (unbroken line) of important prey species for threespine stickleback and the average number present per stomach. Graphs representing biomass were taken from LeBrasseur and Kennedy (1972) and are shown in logarithmic scale.

were hypolimnetic whereas *Bosmina* were mainly epilemnetic (LeBrasseur and Kennedy 1972, Figure 2). If temperature influences their distribution as is suggested by their distribution in relation to the thermocline, one might reasonably infer that *Cyclops* was less available than *Bosmina* to stickleback inhabiting the littoral and nearshore areas where water temperatures generally are highest. Consumption of *Holopedium* increased rapidly as the summer progressed. Consumption of *Diaptomus* increased during August and September. The appearance of these approximately similar sized species in the diet of stickleback paralleled their occurrence in population succession and maximum abundance in the relatively warm surface waters.

The diel feeding rhythm observed during July and October has not been described for *G. aculeatus* in fresh water but the pattern is exemplary of feeding periodicities described for a variety of freshwater and marine fishes. The association of peak feeding with postdawn and predusk periods in summer and late fall when the number of daylight hours differs suggests that feeding is light-dependent.

The literature on meal size and daily ration for *G. aculeatus* is rather scant considering the number of studies on the feeding biology of the species. Krokhin (1957) using the O_2 consumption method estimated that stickleback averaging 4.5 g in summer (August) consumed 5.1% of their body weight daily. Beukema (1968) feeding stickleback (2.5 g mean weight) Tubifex worms concluded that the contents of a well-filled stomach equalled 5.5% of the body weight, and that daily intake amounted to 12% of the body weight. Beukema recognized that the daily ration was rather high for adult fish and suggested that rapid digestibility of the food offered may have been responsible for the rather high food intake value obtained. The mean daily ration estimated in the present study from diel feeding rhythm curves for stickleback in July (mean length = 55 mm, mean weight = 2.4 g) and in October (mean length = 39 mm, mean weight = 0.7 g) was 6.5% and 7.8%, respectively, of their body weight. These estimates are only slightly less than those derived by doubling the maximum meal size of individuals of corresponding length (see Figure 6A), namely 7.8% and 10%. Considering that food intake is influenced by several factors such as size, physiology and behavior of individual, food deprivation, previous meal size, temperature, and prey digestibility (Darnell and Meierotto 1962; Davis and Warren 1968; Keast and Welsh 1968; Swenson and Smith 1973), one may conclude that the mean daily rations determined in this study are in close agreement with those obtained from experimental studies.

FEEDING RELATIONSHIP BETWEEN STICKLEBACK AND JUVENILE SOCKEYE SALMON

Information on competition between stickleback and juvenile sockeye salmon for food must be based on samples of each species from the same catch. Further, it must be assumed that individuals of each species taken together fed in the same area. In 1970, 7 of 105, or 6.6% of the sets yielded both species. Sockeye salmon equalled 5% of the two species combined. In 1971, the two species were caught together in 18 of 89, or 20.2% of the sets, and sockeye salmon equalled 2.2% of the combined catch.

Sockeye salmon and stickleback caught in the littoral zone in October 1970 and May-July 1971 were used in this comparative study (Tables 11 and 12). Only catches containing 5 or more individuals of each species were considered and a maximum number of 10 individuals of each species was examined from any one catch. For convenience, the catches were grouped according to the following time periods: October 1970, May-June 1971, and July 1971.

Stickleback through this period increased in average size as a result of seasonal growth. By contrast, sockeye salmon, although larger, decreased in average size. This decrease in size reflects the emigration from the lake of the larger individuals as smolts in the following spring. The relatively high percentage (20%) of stickleback with empty stomachs in July can be explained by the presence of the gravid females.

In general, stickleback and young sockeye salmon taken together exhibited considerable dietary overlap (Tables 11 and 12). Stomach contents of sockeye salmon were treated and analysed in accordance with methods used for stickleback. The degree of similarity in diet during each period was determined from occurrence data using Spearman's rank correlation coefficient, r_s (Siegel 1956). The r_s value indicates agreement in rank of food items and can range from + 1.0 for complete agreement to -1.0 for total disagreement. The tests were restricted to items which were not rendered unidentifiable through digestion and

TABLE 11.–Stomach contents of threespine stickleback in Great Central Lake, October 1970-July 1971.

Date	October 1970			May-June 1971			July 1971		
No. examined	25			46			56		
Percent empty	0			9			20		
Size range (mm)	27-76			40-86			42-86		
Mean length (mm)	39.5			54.0			59.8		
Food item	Percent of stomachs with item	Average no.[2] per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk
Rotifera	64	17	T[3]	17	2	T	48	10	T
Cladocera:									
Holopedium	100	77	59	39	27	2	63	33	3
Bosmina	100	37	9	46	4	T	14	T	T
Daphnia[1]	4	T	T	—	—	—	—	—	—
Alona	36	1	T	11	3	T	1	T	T
Copepoda:									
Epischura	40	5	14	59	109	40	57	69	22
Diaptomus	16	6	3	22	4	T	—	—	—
Cyclops	60	13	3	59	81	2	32	4	T
Copepodids	56	24	6	41	13	T	41	8	T
Nauplii	8	T	T	—	—	—	12	10	T
Harpacticoid	44	3	T	24	30	1	1	T	T
Insecta:									
Chironomid L	32	2	3	13	1	T	7	T	T
Chironomid P	2	T	T	9	T	T	5	T	T
Other	16	T	T	7	T	T	14	1	1
Mites	4	T	T	4	T	T	—	—	T
Eggs:									
Zooplankton	—	—	—	26	3	T	48	14	T
Fish	—	—	—	1	T	T	1	T	T
Other:									
Amphipoda	—	—	—	—	—	—	4	T	T
Pelecypoda	—	—	—	—	—	—	1	T	T
Ostracoda	—	—	—	7	T	T	1	T	T
Unidentifiable			0.0			52.0			72.0
Total			100.0			100.0			100.0

[1]Mainly *D. pulex*.
[2]Based on stomachs in which condition of contents permitted counts of various dietaries.
[3]T = Trace = < 1% of bulk.

which were present in at least 10% of the stomachs of one or the other foraging species. Infrequent ties in rank were broken in favor of the larger food item.

The r_s values for May-June and July samples were significant at $P = 0.05$ but that for October was not (Table 13). In October *Bosmina*, *Cyclops*, and copepodids were common items in the diet of stickleback compared to the larger *Epischura* and *Holopedium* in the sockeye salmon diet. A possible explanation for the difference between stickleback and sockeye diets in October may be that larger predators feed on larger prey: in October, sockeye salmon on the average measured 74.6 mm, stickleback 39.5 mm.

The observed dietary overlap indicates the existence of potential competition between stickleback and sockeye salmon for food in May-June and July. Accurate assessment of actual competition is contingent not only on information on food and feeding habits of the two foraging species but on other factors, such as their temporal and spatial associations during different life history stages and their abundance and growth in relation to food supply. For this study, data essential for quantitative assessment of competition during different seasons are inadequate or unavailable, although competition in winter is precluded by the apparent absence of stickleback. It is known however that when the two species occur together it is near shore or in the littoral zone, and that relative to stickleback sockeye salmon are few in number: sockeye salmon are almost the exclusive inhabitants of the limnetic zone (D. Robinson, pers. commun.). From the distribution patterns of the two species, it can be inferred that stickleback in Great Central Lake are not serious competitors of sockeye salmon for food despite their similarity in diet. Additionally, during this study the zooplankton abundance had increased substantially as a result of nutrient additions (LeBrasseur and Kennedy 1972) and the growth rate in sockeye salmon was faster than that observed under untreated lake conditions (Barraclough and Robinson 1972). However, in lakes where both species are abundant and overlap extensively in spatial distribution, utilization of a common food resource may affect production of one or both of the foraging species, especially during periods of reduced or limited food supply.

TABLE 12.–Stomach contents of young sockeye salmon in Great Central Lake, October 1970-July 1971.

Date	October 1970			May-June 1971			July 1971		
No. examined	18			40			35		
Percent empty	0			3			3		
Size range (mm)	58-95			28-82			37-75		
Mean length (mm)	74.6			63.0			60.0		
Food item	Percent of stomachs with item	Average no.[2] per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk
Rotifera	11	T[3]	T	—	—	—	24	2	T
Cladocera:									
Holopedium	89	360	22	35	4	T	74	33	8
Bosmina	61	19	T	25	1	T	24	T	T
Daphnia[1]	56	2	T	—	—	—	—	—	—
Alona	6	T	T	—	—	—	—	—	—
Copepoda:									
Epischura	100	234	53	68	52	37	56	32	28
Diaptomus	22	T	T	15	2	T	—	—	—
Cyclops	11	T	T	43	50	3	35	5	T
Copepodids	11	T	T	45	11	T	35	8	T
Nauplii	—	—	—	—	—	—	15	2	T
Harpacticoid	—	—	—	5	T	T	—	—	—
Insecta:									
Chironomid L	—	—	—	3	T	T	—	—	—
Chironomid P	—	—	—	15	T	T	—	—	—
Diptera (pupae & adult)	11	3	3	30	T	T	6	T	T
Araneida	—	—	—	5	—	T	—	—	—
Remains	—	—	—	—	T	T	—	—	—
Other	—	—	—	—	—	—	3	T	T
Eggs - Zooplankton	6	4	T	15	1	T	24	5	T
Unidentifiable			21.0			57.0			62.0
Total			100.0			100.0			100.0

[1]Mainly *D. pulex*.
[2]Based on stomachs in which condition of contents permitted counts of various dietaries.
[3]T = Trace = < 1% of bulk.

TABLE 13.–Similarity in diet of threespine stickleback and young sockeye salmon in the littoral zone, Great Central Lake, October 1970-July 1971. Similarity was measured by Spearman's rank correlation coefficient (r_s). Rotifers are excluded from the calculations.

Time period	No. food items considered	r_s
October 1970	11	−0.068
May-June 1971	12	0.629*
July 1971	8	0.738*

*Significant at $P = 0.05$.

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LITERATURE CITED

BARRACLOUGH, W. E., AND D. G. ROBINSON.
1972. The fertilization of Great Central Lake. III. Effect on juvenile sockeye salmon. Fish. Bull., U.S. 70:37-48.

BUKEMA, J. J.
1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): The influence of hunger and experience. Behaviour 31:1-126.

CRAIG-BENNETT, A.
1931. The reproductive cycle of the three-spined stickleback, *Gasterosteus aculeatus*, Linn. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 219:197-279

DARNELL, R. M., AND R. R. MEIEROTTO.
1962. Determination of feeding chronology in fishes. Trans. Am. Fish. Soc. 91:313-320.

DAVIS, G. E., AND C. E. WARREN.
1968. Estimation of food consumption rates. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 204-225. IBP (Int. Biol. Programme) Handbook No. 3. Blackwell Sci. Publ., Oxf., Engl.

GREENBANK, J., AND P. R. NELSON.
1959. Life history of the threespine stickleback *Gasterosteus aculeatus* Linnaeus in Karluk Lake and Bare Lake, Kodiak Island, Alaska. U.S. Fish Wildl. Serv., Fish. Bull. 59:537-559.

HAGEN, D. W.
1967. Isolating mechanisms in threespine sticklebacks (*Gasterosteus*). J. Fish. Res. Board Can. 24:1637-1692.

HAGEN, D. W., AND L. G. GILBERTSON.
1972. Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific Northwest, America. Evolution 26:32-51.

HAGEN, D. W., AND J. D. MCPHAIL.
1970. The species problem within *Gasterosteus aculeatus* on the Pacific coast of North America. J. Fish. Res. Board Can. 27:147-155.

HARTLEY, P. H. T.
1948. Food and feeding relationships in a community of fresh-water fishes. J. Anim. Ecol. 17:1-14.

HYNES, H. B. N.
1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of

methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

IVLEV, V. S.

1961. Experimental ecology of the feeding of fishes. (Translated from the Russian by Douglas Scott.) Yale Univ. Press, New Haven, 302 p.

KEAST, A. H., AND L. WELSH.

1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25:1133-1144.

KROGIUS, F. V., AND E. M. KROKHIN.

1957. Causes of the fluctuations in abundance of sockeye salmon in Kamchatka. (Tr. Probl. Temat. Soveshch. Zool. Inst. Akad. Nauk SSSR, 1956, 6:144-149.) Fish. Res. Board Can. Transl. Ser. 92, 5 p.

KROKHIN, E. M.

1957. [Determination of the daily food ration of young sockeye and three-spined stickleback by the respiration method.] [In Russ.] Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 44:97-110.

LEBRASSEUR, R. J., AND O. D. KENNEDY.

1972. The fertilization of Great Central Lake. II. Zooplankton standing stock. Fish. Bull., U.S. 70:25-36.

MANZER, J. I.

1971. Data on catch, size and food of the three-spined stickleback in Great Central Lake, British Columbia in 1970. Fish. Res. Board Can. Manuscr. Rep. 1145, 43 p.

1972. Data on catches, size, and food of the three-spined stickleback in Great Central Lake, British Columbia, in 1971. Fish. Res. Board Can. Manuscr. Rep. 1166, 52 p.

MARKOVTSEV, V. G.

1972. Feeding and food relationships of young sockeye and three-spine stickleback in Lake Dalnee. Izv. Tinro 82:227-233.

MCPHAIL, J. D., AND C. C. LINDSEY.

1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Board Can., Bull. 173, 381 p.

MEEK, A.

1916. The migrations of fish. Edward Arnold, Lond., 427 p.

MILLER, R. R., AND C. L. HUBBS.

1969. Systematics of *Gasterosteus aculeatus*, with particular reference to intergradation and introgression along the Pacific Coast of North America: A commentary on a recent contribution. Copeia 1969:52-69.

MULLEM, P. J. VAN, AND J. C. VAN DER VLUGT.

1964. On the age, growth and migration of the anadromous stickleback *Gasterosteus aculeatus* L. investigated in mixed populations. Arch. Néerl. Zool. 16:111-139.

NARVER, D. W.

1969. Phenotypic variation in threespine sticklebacks (*Gasterosteus aculeatus*) of the Chignik River system, Alaska. J. Fish. Res. Board Can. 26:405-412.

1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27:281-316.

O'BRIEN, W. J., AND G. L. VINYARD.

1974. Comment on the use of Ivlev's electivity index with planktivorous fish. J. Fish. Res. Board Can. 31:1427-1429.

PARSONS, T. R., C. D. MCALLISTER, R. J. LEBRASSEUR, AND W. E. BARRACLOUGH.

1972. The use of nutrients in the enrichment of sockeye salmon nursery lakes (a preliminary report). *In* M. Ruivo (editor), Marine pollution and sea life, p. 519-525. Fishing News (Books) Ltd., Surrey and Lond., Engl.

PARSONS, T. R., K. STEPHENS, AND M. TAKAHASHI.

1972. The fertilization of Great Central Lake. I. Effect on primary production. Fish. Bull., U.S. 70:13-23.

RICKER, W. E.

1937. The food and the food supply of sockeye salmon (*Oncorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. J. Biol. Board Can. 3:450-468.

ROGERS, D. E.

1968. A comparison of the food of sockeye salmon fry and threespine sticklebacks in the Wood River lakes. *In* R. L. Burgner (editor), Further studies of Alaska sockeye salmon, p. 1-43. Univ. Wash. Publ. Fish., New Ser. 3.

ROGERS, D. E., M. O. NELSON, J. J. PELLA, AND R. L. BURGNER.

1963. Relative abundance and distribution of fish species in Lake Aleknagik. Res. Fish. Fish. Res. Inst. Univ. Wash. 1962:14-15. (Univ. Wash. Coll. Fish. Contrib. 147.)

RUGGLES, C. P.

1965. Juvenile sockeye studies in Owikeno Lake, British Columbia. Can. Fish Cult. 36:3-21.

SIEGEL, S.

1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Toronto, 312 p.

SIMPSON, G. G., AND A. ROE.

1939. Quantitative zoology. McGraw-Hill Book Co., Inc., N.Y., 414 p.

SWENSON, W. A., AND L. L. SMITH, JR.

1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30:1327-1336.

WINDELL, J. T.

1968. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 197-203. IBP (Int. Biol. Programme) Handbook No. 3. Blackwell Sci. Publ., Oxf., Engl.