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LIFE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* Linnaeus IN KARLUK LAKE AND BARE LAKE KODIAK ISLAND, ALASKA

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CONTENTS

ABSTRACT

The threespine stickleback occurs in large numbers in Karluk Lake, Kodiak Island, Alaska, an important water in studies of red salmon production. The life history of the stickleback in Karluk and Bare Lakes presents many interesting phases. It has few lateral plates, which is characteristic of the fresh-water sticklebacks. It has a lifespan of about two-and-one-quarter years and in that period spawns once, or twice at the most. Structurally, the stickleback is hermaphroditic. It feeds on planktonic invertebrates and insect larvae. A possible interrelationship between stickleback and juvenile red salmon is that both consume the same kinds of food. Both species are preyed on by the Arctic charr.

LIFE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* Linnaeus IN KARLUK LAKE AND BARE LAKE, KODIAK ISLAND, ALASKA

By John Greenbank[1] and Philip R. Nelson, *Fishery Research Biologists*, BUREAU OF COMMERCIAL FISHERIES

Over a period of many years, investigations have been made by the U. S. Fish and Wildlife Service at Karluk Lake and Bare Lake on Kodiak Island, Alaska. These have covered, primarily, the production of red (sockeye) salmon. They have embraced many biological and limnological factors which are related to salmon production, including the presence in these waters of other fishes whose life histories are interrelated with that of the red salmon.

One of these species is the threespine stickleback, *Gasterosteus aculeatus* Linnaeus, which occurs in large numbers in these lakes. As a part of the field studies, stickleback specimens were collected, seine hauls that captured sticklebacks were recorded, stomach samples were analyzed, fish samples for age determination were taken, and numerous observations of habits were made.

Most of the fieldwork on the sticklebacks was done by Nelson, and crews under his supervision. Greenbank has analyzed and evaluated the data. We present this report as a summary of our knowledge of the stickleback in these waters and its relation to red salmon production, and as a contribution to the life history of the species.

C. Y. Conkle, Robert F. Raleigh, C. S. Thompson, Carl E. Abegglen, and others assisted in the collection of specimens and information. The drawings were made by R. J. Kramer; the photograph for figure 13 was taken by Fred Rabe. Information on the Karluk Lake sticklebacks was furnished by C. E. Walker of the Fisheries Research Institute.

HISTORY AND LITERATURE

The threespine stickleback is widespread and easily observed and has been studied by many workers through the centuries. A large number of references exist in the published literature. Many of these, however, consist of little more than notes regarding such things as nest-building behavior.

Leiner (1929, 1930, and 1934) has studied the species intensively. Bertin (1925) published a monograph on sticklebacks. Many of his conclusions have been objected to by later workers, but at least he stimulated research and thought.

M. J. Heuts has made a thorough study of the threespine stickleback in Western Europe and has published (1947, 1947a, and 1949) important papers on variation, physiology, and genetics.

Wunder (1928, 1930) published the results of studies and experiments concerning behavior. The reproduction of the stickleback has been described by Craig-Bennett (1931) and others. Food studies have been made by Markley (1940) and by Hynes (1950). Age and growth of three species of sticklebacks in the British Isles have been worked out by Jones and Hynes (1950).

In North America, few papers have dealt at length with the life history of the stickleback. Cox (1922) reviewed the various species of sticklebacks of the Hudson Bay region; Myers (1930) made a study of races of the threespine stickleback in California and Lower California; and Vrat (1949) reported on the reproduction of the threespine stickleback in California.

DESCRIPTION OF THE WATERS

The southwestern section of Kodiak Island (fig. 1), in which Karluk Lake and Bare Lake lie, is a low plain with numerous mountains rising from it. The coastline is broken by many bays. The drainage pattern is involved. The vegetation is tundralike, composed of grasses, various flowering plants, willows, and alder, with cottonwood and birch trees irregularly distributed along the stream courses.

The area lies in a temperate climate, with much cloudy weather and a mean annual rainfall of about 50 inches. The air temperature ranges

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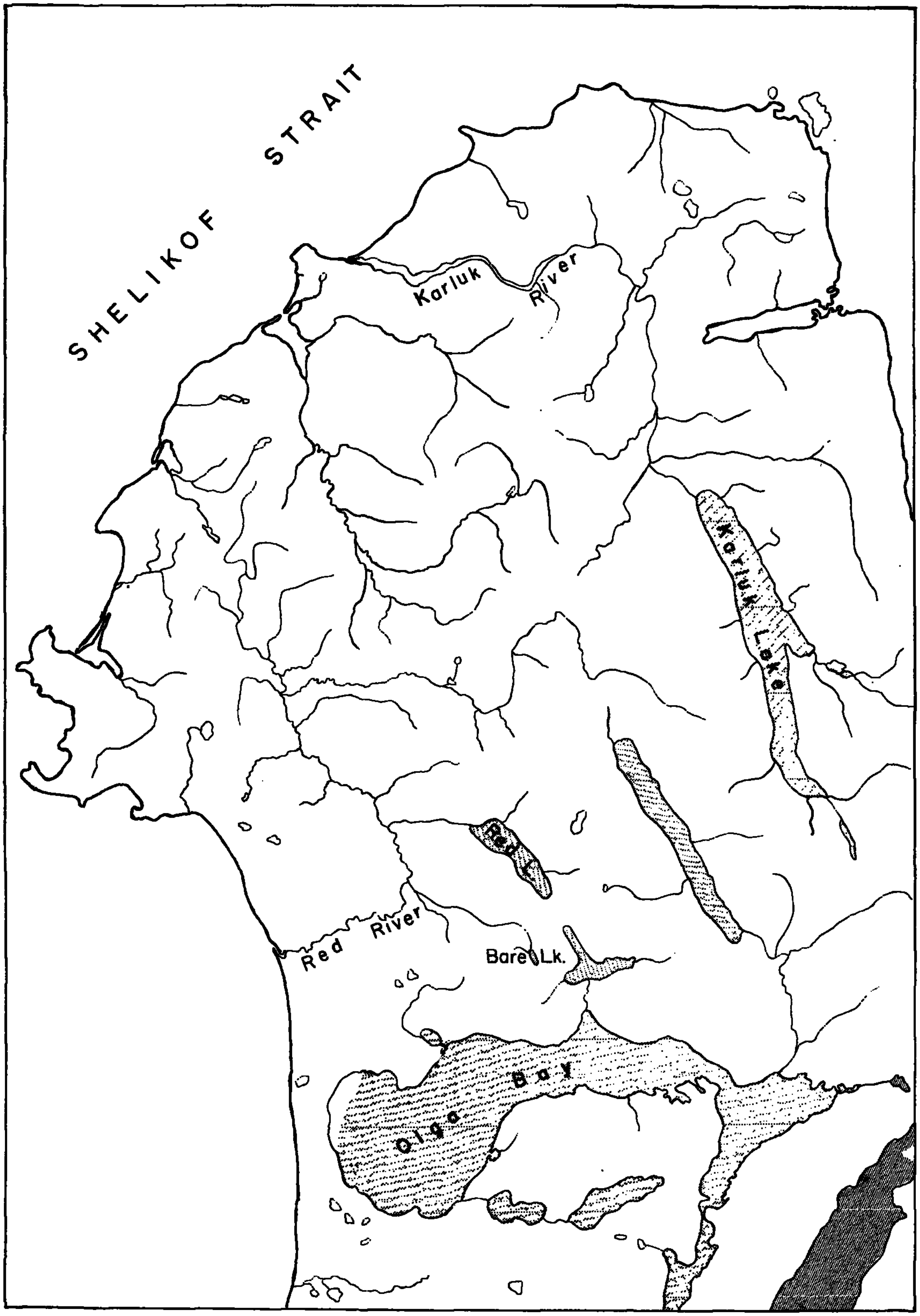

FIGURE 1.—Western Kodiak Island.

from below –18° C. in winter to above 29° C. in summer.

Karluk Lake is drained by Karluk River, which flows some 23 miles and empties into Karluk Lagoon, and thence into the ocean. Several small streams plus the drainage of two small lakes, Thumb and O'Malley, flow into Karluk Lake.

The physical and chemical characteristics of Karluk Lake have been described by Juday et al. (1932). The lake lies at an elevation of 350 feet above sea level. It is 12 miles long; its greatest width is 2 miles, and its area 15 square miles. It has relatively little shoal area, only 10 percent of the total area being less than 30 feet deep. The maximum depth is 410 feet. The beaches are of gravel and rubble, the predominant rock material being shale. The water is clear, has a pH ranging from 7.0 to 8.7, and is low in carbonate and in total dissolved minerals. It contains an abundance of dissolved oxygen at all depths throughout the summer.

Bare Lake is only 15 miles from Karluk Lake but belongs to another drainage. It is drained by a small stream, Bare Creek, that flows into Red River.

Bare Lake is 380 feet above sea level. It is slightly less than 1 mile long; its greatest width is 1,600 feet, and its area about 120 acres. The maximum depth is 25 feet and the mean depth 13 feet. The bottom is gravel and rubble on the shoals and soft mud in the deeper area. The chemical characteristics are similar to those of Karluk Lake.

In both Karluk Lake and Bare Lake, vegetation is sparse. The predominant forms are water moss, *Fontinalis;* quillwort, *Isoëtes;* and water buttercup, *Ranunculus.* There are scattered patches of filamentous algae, and in Karluk Lake there are beds of sparse *Potamogeton.*

Juday et al. (1932) have described the plankton of Karluk Lake, and Nelson and Edmondson (1955) that of Bare Lake. Bottom-dwelling animals are few in numbers of species. Diptera larvae, especially of Chironomidae, are abundant in places, and there are larvae of caddis flies (Trichoptera), mayflies (Ephemeroptera), and other insects. Included also are pea clams (Pelecypoda) and snails (Gastropoda).

The fishes of Bare Lake consist of seven species: red salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), and king salmon (*Oncorhynchus tshawytscha*); rainbow or steelhead trout (*Salmo gairdnerii*), Dolly Varden charr (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), and a fresh-water sculpin (*Cottus aleuticus*).

Karluk Lake has, in addition to these species, arctic charr (*Salvelinus alpinus*) and chum salmon (*Oncorhynchus keta*). Pink salmon (*Oncorhynchus gorbuscha*) spawn in Karluk River and a few enter the lake. Small numbers of the ninespine stickleback (*Pungitius pungitius*) have been seen in Karluk Lake (Charles E. Walker, private communication, 1956).

Karluk Lake has been the site of extensive biological investigations. These date back to 1889, when Tarleton H. Bean made a reconnaissance survey of the lake. Various scientists visited Karluk Lake in the years between 1900 and 1920. Henry O'Malley and Charles H. Gilbert made a survey of the salmon spawning grounds in 1921.

In 1926, a party led by Willis H. Rich conducted a limnological study of the lake including a physical survey (Juday et al., 1932). Studies of the lake, especially of its red salmon runs, have been carried out on a year-to-year basis since then.

A weir for counting adult red salmon ascending the Karluk River was installed near the mouth of the river in 1921. It was moved in 1942 about 13 miles upriver, and moved again in 1945 to its present location just below the outlet of Karluk Lake. The current investigations include counts and estimates of adult salmon entering the lake, of spawning salmon in the tributary streams, and of young salmon leaving the lake to go to the ocean. Studies also are being made of certain aspects of the life history of the red salmon and of the limnology of the lake.

Bare Lake was selected by the Fish and Wildlife Service (Nelson and Edmondson, 1955) for experiments in lake fertilization, because it represents the waters of the area and yet is small enough to be worked on feasibly. Preliminary surveys were conducted in 1949, and each summer, starting with 1950, the lake has been treated with commercial fertilizer. Various limnological observations have been made as a means of assessing the effectiveness of fertilization in increasing lake productivity.

BIOLOGY OF THE STICKLEBACK

Since it was named and described by Linnaeus in 1758, *Gasterosteus aculeatus* has had a long and involved nomenclatural history. Specific and subspecific names have been based in the main on variations in the numbers of bony plates and of fin rays, on length of spines, and on selection of environment.

The threespine stickleback in Karluk and Bare Lakes is of the partially armored form. For present purposes, we shall not assign to it a name designating a subspecies or variety, but shall simply refer it to the species *Gasterosteus aculeatus*.

The ninespine stickleback, *Pungitius pungitius* (Linnaeus), is the only other member of the family which occurs in the waters of the North Pacific area, and it is found only in small numbers in Karluk Lake.

The sticklebacks as a group (family Gasterosteidae) differ considerably in morphology and appearance from even their nearest relatives among the fishes. They are small fish and have as a distinguishing character a number of isolated (free) stout spines in front of the dorsal fin. These spines are short but sharp pointed. At the posterior side of each spine is a small, triangular fin membrane. The dorsal spines can be erected or depressed by the fish and will lock weakly in the erect position. There is one short anal spine, and the pelvic fin consists of one heavy spine and one or two rudimentary rays. There are no scales, but some of the species have bony plates.

Gasterosteus aculeatus, the threespine stickleback, is a moderately slender, streamlined fish. The snout is somewhat pointed. The caudal peduncle is slender, the tail shallowly forked (fork length of fish equals approximately 0.97 times total length). The anal fin originates well back of the dorsal fin (almost even in *Pungitius pungitius*). The species is extremely variable in numbers of lateral bony plates and fin rays. Figure 2 represents an adult threespine stickleback from Karluk Lake.

The color varies with the locality and the type of water. Except for spawning males, dull tones predominate. Generally the upper surfaces are olive, greenish, or brown, the colors becoming lighter on the sides. The ventral surface is light yellow, white, or silver. Dark-brown pigmentation occurs in small indefinite blotches and in a variable pattern of transverse patches along the sides. The fins are pale. The rays of the pectoral fin are outlined by lines of small dots of black pigment. The breeding female in Karluk and Bare Lakes does not assume any bright coloration. The male, in breeding season, from the snout to the back of the pelvic fin, is red to yellowish-salmon colored. The color tones are clear but not bold. Bluish tints may appear along the sides and on the face. Vrat (1949) mentions the iridescent blue-green color in the iris of the eye of the breeding male and indicates that this color is noticeable for a period of many days or weeks. We have found this condition to hold for the Kodiak Island sticklebacks.

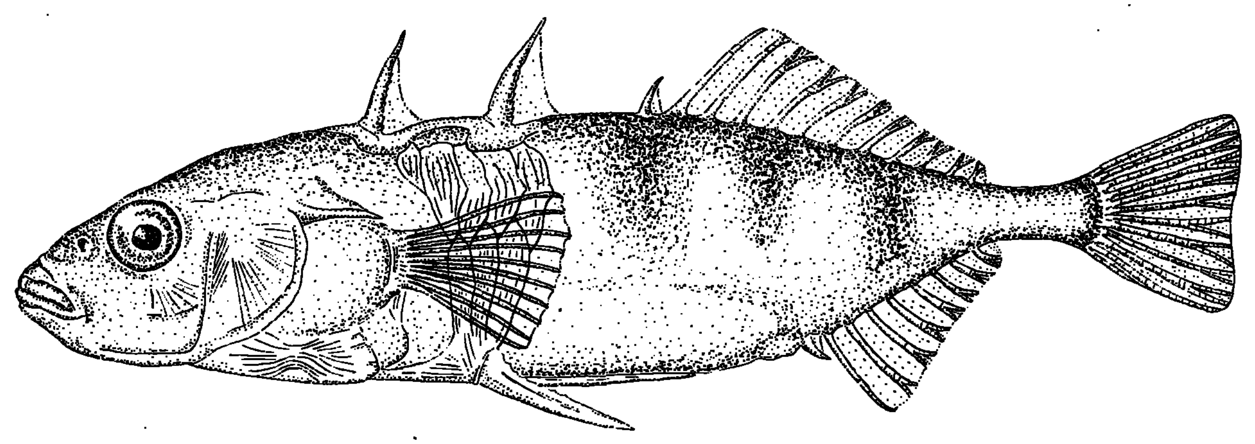

FIGURE 2.—Adult threespine stickleback (*Gasterosteus aculeatus*).

When the female is approaching the time of spawning, the belly becomes distended visibly. In the early part of the year, before the breeding characters are evident, the two sexes look much alike.

Morphological Variation

Throughout its geographical range, the species *Gasterosteus aculeatus* is subject to a large amount of morphological variation. There are minor differences in color and color pattern and in body shape. More pronounced variations occur in numbers of vertebrae, fin rays, and lateral bony plates.

Within the species, the number of lateral plates varies from none to about 35. Most of the long list of specific, subspecific, and racial names which have been used have to do with the degree of armature.

It has long been recognized that populations which are year-round inhabitants of fresh waters have few plates, while those that live in salt water, and enter fresh water only for spawning, are many-plated. Bertin (1925) made an analytical study of populations of threespine stickleback throughout Europe and came to the conclusion that the number of bony plates is directly correlated with the salinity of the environment, and that a continuous gradation occurs from water of high salinity to fresh water.

However, Heuts (1947, 1947a) presents strong evidence that such a clinal gradation does not exist. The European stickleback populations are, instead, of two types, one of which shows a strong mode at about 5 to 7 plates, the other having a mode at around 32 plates. Within a given population, individuals with an intermediate number of plates may occur, but there are no populations which consist only or largely of fish with intermediate plate numbers. Therefore, Heuts concludes that individuals with an intermediate number indicate only a skewed distribution curve of one type or the other and not a genotypical intermediacy.

On the Atlantic coast of North America, both the form with many plates and that with few are present (Bigelow and Schroeder, 1953). As in Europe, the fish with strong armature are to be found in salt water, while the fresh-water populations generally have few plates. The same situation occurs also along the Pacific coast of North America.

The geographic pattern of variability in Alaskan waters has not been worked out thoroughly. Marine collections have been few, and in many fresh waters the species has been recorded without reference to which of the two forms was present. It is likely that there are many bodies of fresh water, particularly those close to the sea, in which both the many-plated and the partially plated forms may occur, at least for part of the year. An instance is Chignik Lake on the south side of the Alaska Peninsula (private communication from Fredrik Thorsteinson of the Fisheries Research Institute, 1956).

There is very little, if any, migration of the Karluk and Bare Lakes sticklebacks to and from the ocean. No substantial numbers of sticklebacks have been observed in movement in Bare Creek or upper Karluk River. There is no evidence of a sea-run stock of sticklebacks in either lake. The number of lateral plates on all specimens examined does not exceed nine.

Plates and fin rays were counted on a total of 200 fish from each of the 2 lakes. The total for each lake was made up of 4 subsamples of 50 fish each, taken in different years (table 1).

Each subsample probably included individuals of at least 2 age groups; therefore, there is considerable overlapping of year classes. However, as there is little if any exchange of stock with outside populations, the genetic makeup of the population of the lake should be about the same from one year to the next.

TABLE 1.—*Subsamples of fish taken in different years from Karluk and Bare Lakes*

Karluk Lake	Subsample *a*	1956
	b	1949
	c	1949
	d	1948
Bare Lake	Subsample *w*	1956
	x	1954
	y	1950
	z	1951

An additional sample consisted of 50 specimens from O'Malley River, a tributary to Karluk Lake. This sample was taken in 1951.

The lateral plates were counted on the left side of the fish under low-power magnification. The point of a scalpel was used to lift the edge of each plate, so that none would be missed in counting. The first (most anterior) plate is small and sometimes hard to find. Fin rays were counted in the dorsal and anal fins and both pectoral fins. In counting the (soft) rays, each element was counted as one ray. The last (most posterior) two elements in the dorsal and anal fins are well separated at the visible base of the fin, not jointed or branched as in some groups of fishes, and hence were counted as separate rays.

Numbers of lateral plates are shown in table 2. The Karluk Lake fish have from 5 to 9 plates, with no specimen having 4. The mean for 200 specimens is 6.55. The fish from Bare Lake have from 4 to 7 plates, no individuals having 8 or 9. The mean for 200 specimens is 5.22.

Between the various pairs of subsamples from Karluk Lake, there are significant differences (for the most widely separated pair, subsamples *c* and *d*, $t=8.0$ and $P<0.001$). The subsamples were captured at different places on a large lake and probably represent separate subpopulations.

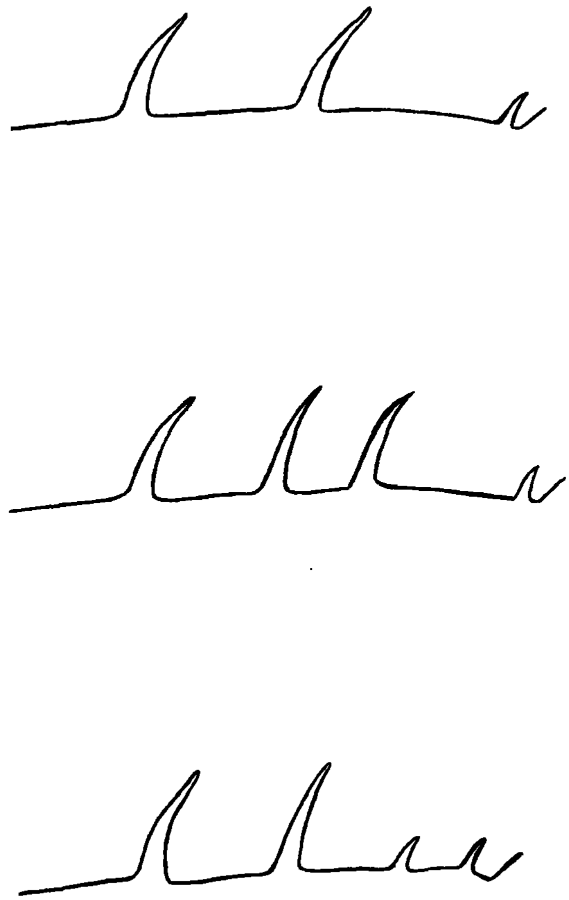

FIGURE 3.—Insertion of dorsal spines. Top, normal position of 3 spines. Center, fourth spine about the same size as, and inserted just posterior to, the second spine. Bottom, fourth spine small and inserted just anterior to third spine.

TABLE 2.—*Number of lateral plates on stickleback from Karluk and Bare Lakes*

Subsample	Number of plates						Mean	σ	σ_M
	4	5	6	7	8	9			
Karluk Lake:									
Subsample *c*	----	1	12	31	6	----	6.84	0.64	0.09
a	----	----	18	26	4	2	6.80	.75	.11
b	----	2	25	15	4	4	6.66	.97	.14
d	----	10	35	5	----	----	5.90	.54	.08
Total	----	13	90	77	14	6	6.55	.84	.06
O'Malley River	----	5	26	14	5	----	6.38	0.80	0.11
Bare Lake:									
Subsample *w*	6	19	21	4	----	----	5.46	.81	.12
x	8	24	18	----	----	----	5.20	.69	.10
y	6	29	14	1	----	----	5.20	.66	.09
z	13	22	15	----	----	----	5.04	.75	.11
Total	33	94	68	5	----	----	5.22	.74	.05

The means for the samples of 200 fish each from the 2 lakes differ by 1.33. The difference is highly significant ($t=16.8$; $P<0.001$).

For the sample from O'Malley River, the mean number of lateral plates lies between the extremes for Karluk Lake.

The number of dorsal spines has a high degree of constancy. Of 400 specimens from the 2 lakes, 391 had 3 spines, only 9 (2.2 percent) had 4 spines, and none had 5 or 2. The fourth spine, when present, may be small and near the last spine, or it may be almost as long as the middle spine and be inserted midway between the last 2 of the 3 normal spines (fig. 3). The fourth spine was not found to occupy a position anterior to the first normal spine or between the first two.

Counts of rays of the dorsal, anal, and pectoral fins are summarized in tables 3–5. In the numbers of dorsal and anal fin rays, there are differences, of varying degrees of significance, between the means of various subsamples from a given lake. These differences, however, definitely are overshadowed by the differences between the means of Karluk Lake and Bare Lake. In each of the latter instances, there is almost one fin ray difference, the mean number for Bare Lake being lower than that for Karluk Lake. The mean for the O'Malley River sample falls between the means for Karluk and Bare Lakes, for dorsal and for anal rays.

TABLE 3.—*Number of dorsal fin rays on sticklebacks from Karluk and Bare Lakes*

Subsample	Number of rays							Mean	σ	σ_M
	8	9	10	11	12	13	14			
Karluk Lake:										
Subsample *c*			3	20	23	3	1	11.58	0.77	0.11
a			3	26	19	2		11.40	.66	.09
d			6	25	16	3		11.32	.76	.11
b			6	29	13	2		11.22	.70	.10
Total			18	100	71	10	1	11.38	.74	.05
O'Malley River		3	11	19	16	1		11.02	0.93	0.13
Bare Lake:										
Subsample *x*		3	27	18	2			10.38	.66	.09
w		6	22	21	1			10.34	.71	.10
y		3	30	16	1			10.30	.61	.09
z	1	2	28	16	3			10.36	.74	.10
Total	1	14	107	71	7			10.34	.68	.05

TABLE 4.—*Number of anal fin rays on sticklebacks from Karluk and Bare Lakes*

Subsample	Number of rays					Mean	σ	σ_M
	6	7	8	9	10			
Karluk Lake:								
Subsample *c*		3	26	19	2	8.40	0.66	0.09
a	1	5	27	15	2	8.24	.76	.11
b		4	34	11	1	8.18	.59	.08
d		9	32	9		8.00	.60	.08
Total	1	21	119	54	5	8.20	.67	.05
O'Malley River	1	5	33	11		8.08	0.63	0.09
Bare Lake:								
Subsample *z*	2	25	20	3		7.48	.67	.09
w	2	25	22	1		7.44	.61	.09
x	3	31	16			7.26	.56	.08
y	3	34	12	1		7.22	.57	.08
Total	10	115	70	5		7.35	.62	.04

TABLE 5.—*Number of pectoral fin rays on sticklebacks from Karluk and Bare Lakes*

Location	Number of rays			Mean
	9	10	11	
Karluk Lake	12	374	14	10.00
Bare Lake	6	378	16	10.02

The ranges of the counts differ also. For dorsal rays (table 3), the fish in Karluk Lake range from 10 to 14 with no individuals having 8 or 9. The Bare Lake counts range from 8 to 12, and no individuals have 13 or 14. For anal rays (table 4), the ranges are 6 to 10, and 6 to 9, for Karluk Lake and Bare Lake, respectively.

Heuts (1949) shows, for *Gasterosteus aculeatus* in Europe, a negative correlation between the number of dorsal and anal rays and the water temperature during development of the embryo. The water temperatures at the time of embryological development, in Karluk and Bare Lakes, are not known with any degree of accuracy.

For the sample from both lakes, there is a significant positive correlation between the number of dorsal rays and the number of anal rays in an individual fish. The figures for Karluk Lake are $r=0.46$, $P<0.005$; for Bare Lake, $r=0.22$, $P<0.005$.

The number of pectoral fin rays is remarkably constant (table 5). Of 800 fins counted (both fins of each of 400 fish), only 48 (6.0 percent) had more or fewer than 10 rays. The data are too few to yield information on correlation between numbers in the left and right pectoral fins.

Numbers

Almost every published account of the threespine stickleback in any location describes it in such terms as abundant, plentiful, or numerous. Low egg counts per female, and the fact that it spawns only once or, at the most, twice during its life, are balanced by a high rate of survival of young and the adaptability of the species to various physical conditions and types of food.

No quantitative estimates of stickleback populations have been made for Karluk and Bare Lakes. During three summers, a considerable number of fish marked by fin clipping were released in Bare Lake, but recoveries were inadequate to produce a reliable estimate of population numbers. Nelson and Edmondson (1955) state that the stickleback is the most abundant fish species in Bare Lake, and it may be so in Karluk Lake. Morton,[2] on the basis of fyke net catches, believed the stickleback outnumbered by far the juvenile red and coho salmon in the littoral zone in Karluk Lake.

Over almost any shoal of either lake, on almost any day in summer, sticklebacks may be seen in widely varying numbers. Usually they are more or less evenly distributed over a considerable area and are not in tightly packed clumps or streams. A single haul with a 70-foot beach seine, sweeping some 200 square yards, often catches from 300 to 1,500 sticklebacks. Large concentrations have been observed at the mouths of tributaries

[2] The ecology of two Alaskan charrs as shown by their parasites. By William Markham Morton. Master's thesis, University of Washington, Seattle. Typewritten, 31 pp., 1942.

to Karluk Lake, presumably fish in spawning migration.

The degree of fluctuation of numbers from year to year is not known. Certain beach locations in Bare Lake were seined several times each summer in the years 1951–55. The catches varied widely, from less than 50 to more than 4,000 (table 6). No attempt has been made to make a statistical analysis of the variance or to arrive at a measure of its significance; since many external factors, such as light and wave action, are involved. Assuming that these factors averaged out to some extent, there is indication that a population peak was reached in 1953.

The proportionate strength of the different year classes cannot be estimated, since seine hauls may not constitute random samples of the population.

TABLE 6.—*Seine hauls, southwest corner Bare Lake, and catch of sticklebacks per haul*

Date	Catch [1]	Average for year
1951		
July 8	1,000	500
July 22	350	
Aug. 25	400	
Sept. 12	150	
1952		
June 25	1,000	300
July 8	100	
July 29	50	
Sept. 11	50	
1953		
May 23	150	1,300
June 8	1,700	
June 27	4,300	
July 24	1,400	
Aug. 12	250	
Aug. 26	150	
1954		
May 23	850	450
June 7	950	
June 24	300	
June 26	800	
July 12	650	
July 26	50	
July 29	([2])	
Aug. 7	----------	
Aug. 10	700	
Aug. 17	----------	
Aug. 27	250	
Sept. 28	250	
1955		
May 23	1,300	500
June 7	400	
June 24	600	
July 12	700	
July 18	250	
July 30	----------	
Aug. 10	----------	
Aug. 17	100	
Aug. 27	150	
Sept. 6	1,300	
1956		
May 30	250	300
June 20	500	
July 10	400	
July 23	250	
Aug. 4	200	
Aug. 28	150	

[1] Figures rounded to nearest 50.
[2] Dash indicates fewer than 25.

Habitat

Essentially, the stickleback in Bare and Karluk Lakes is an inhabitant of the shallow waters. A few fish, but no large numbers, have been observed on the surface of Karluk Lake at a considerable distance from the shore. Morton caught 12 sticklebacks in one set of a fyke net at a depth of 80 feet in Karluk Lake, but did not take any sticklebacks in a set at 200 feet. Similarly, C. E. Walker (private communication) reports having taken sticklebacks in Karluk Lake in a fyke net set at a depth of 30 feet but not in a net set at 126 feet.

Presumably, food is more readily obtainable along the shoals; although plankton animals, which comprise a substantial part of the stickleback diet, are plentiful in at least the upper layers of the water in the center of the lake. It is probable, also, that conditions of light, temperature, and shelter are not as suitable to the stickleback in the lower levels as in the surface water. Bigelow and Schroeder (1953, p. 309) state that *Gasterosteus aculeatus* in the North Atlantic Ocean often is picked up far from land, but nearly always on the surface, usually in patches of weeds.

There is little aquatic vegetation on the shoals of Karluk and Bare Lakes. Often, when disturbed, the sticklebacks dart to the bottom to hide among rocks and moss. Much of the time they stay in open water and depend for protection on their appearance and behavior. Weeds, where present, furnish feeding opportunity in the way of insect larvae and small Crustacea and Mollusca attached to the plants.

Age, Size, and Growth

In the published literature to date, the most comprehensive work on age determination in sticklebacks, which has come to our attention, is that of Jones and Hynes (1950). These authors determined age by means of the otoliths and drew up growth-rate tables and curves for three species of sticklebacks from the Birket River in England.

We have examined otoliths of about 250 sticklebacks from Bare Lake and Karluk Lake. Also, we have drawn up length-frequency histograms for about 65 samples as described below. The information obtained by the two methods is in good agreement and provides a reasonably reliable estimate of age and growth.

In preparing and examining the stickleback otoliths, we have followed essentially the technique used by Jones and Hynes. Only fresh fish,

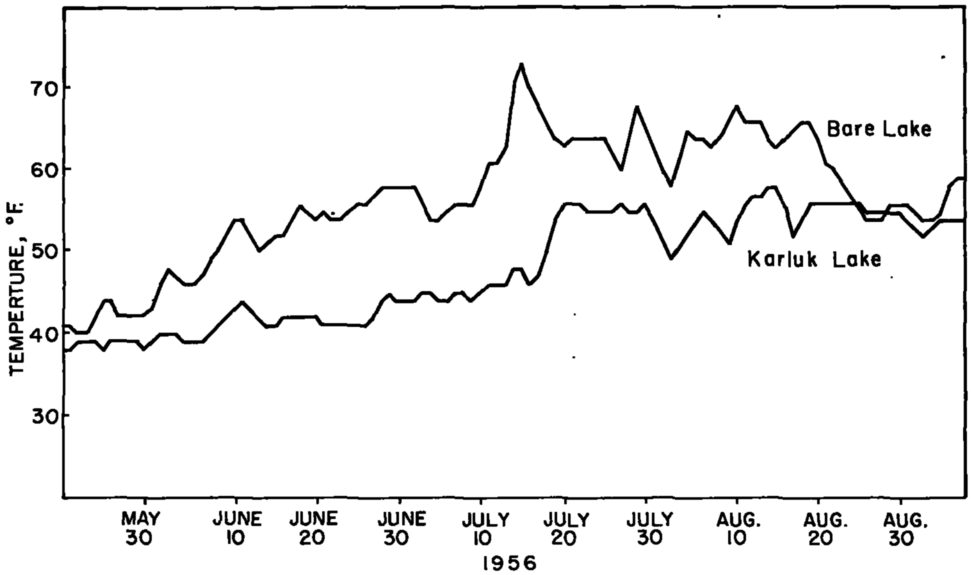

FIGURE 4.—Water temperatures, surface, summer of 1956. Upper curve, Bare Lake. Lower curve, Karluk Lake. Curves smoothed slightly.

or those preserved in alcohol, can be used, as formalin destroys the otoliths in only a few weeks.

The standard length in millimeters, and the sex and state of maturity are recorded for each fish. Then, working under a low-power microscope, the top of the skull is sliced off, and the otoliths are extracted by sharp-pointed forceps. Only the sagitta, the largest of the three otoliths to be found in each side of the skull, is used. Both sagittae from one fish are treated and mounted together.

The otoliths (sagittae) are placed in 65 percent alcohol, where they are cleaned of bits of tissue. Then they are put into pure creosote for from 5 to 15 minutes for clearing. Finally, they are mounted in Canada balsam or some other clear mounting fluid. They are read under a magnification of about 40 diameters, using a strong light reflected from the surface of the otolith, with a black mat background.

For a description of the appearance of the otolith and an interpretation of its markings, we quote Jones and Hynes.

The sagitta first appears when the fish is about 6 mm. long, i. e., a few days after its emergence from the nest; the otolith is then a small body either uniformly transparent or more or less opaque. By the end of June the center is usually completely formed. Otoliths in this state or in an earlier state of development were designated S—. During June or early July the first transparent (S) ring appears, followed by the opaque zone (+) which is visible in some fish in July and in all by September. At first the opaque zone is narrow, but it rapidly increases in width during the summer. From September until the following June the otoliths of all fish in their first year read S+, i. e., they consist of center, one transparent ring and an opaque zone. Thereafter the S ring becomes evident in July, not June or July as in young fish: This may be due to the fact that it is not so easy to see the S ring on the edge of the larger otoliths. The opaque zone (+) begins to be visible in August or September, and is present in all fish by October.

This delineation appears to hold true for the Kodiak Island sticklebacks with minor variations. In the otoliths from the Bare Lake and Karluk Lake fish, the transparent rings apparently form during a rather short period in June and early July. In about early August, the material which gives cloudiness starts to be deposited, Seemingly (although it is difficult to be certain), this material accumulates to some extent in the outer portion of the previously clear zone, as well as in a newly formed zone. Thus the result is that the apparent clear bands are narrower than the cloudy bands.

At any rate, in age determination each opaque ring (outside of the centrum and first transparent ring) is read as one winter (although the opaque band actually starts to form in late summer or early fall). For example, the otolith of a fish

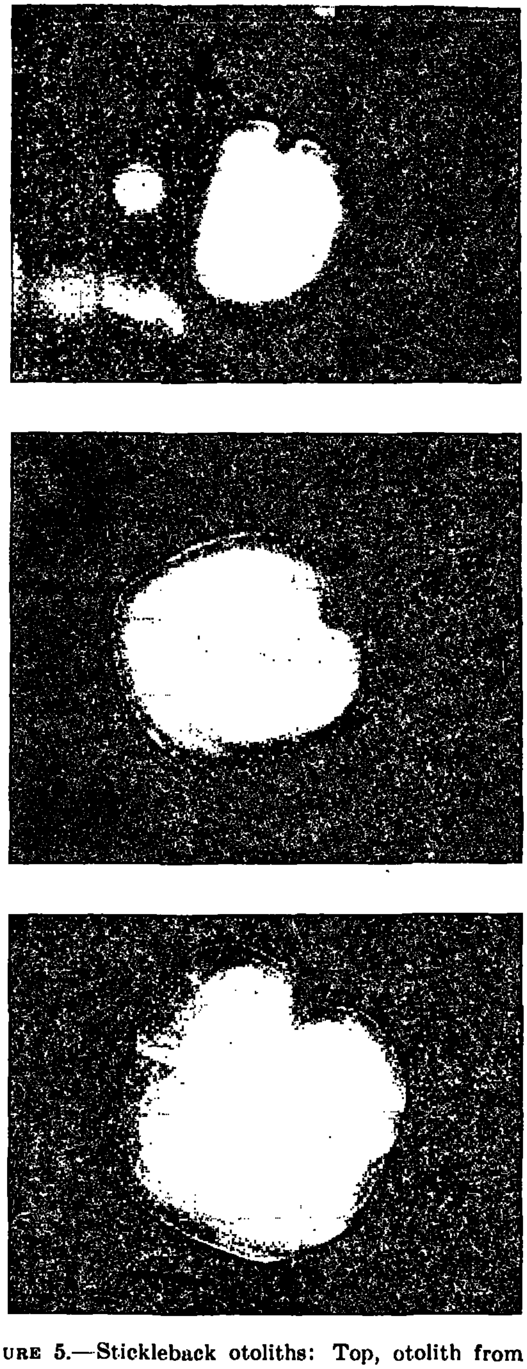

FIGURE 5.—Stickleback otoliths: Top, otolith from fish age 2–3 months; Middle, otolith from 1-year-old fish; Bottom, otolith from 2-year-old fish.

1 year old, taken in June, would show in order: centrum, first transparent ring, first opaque ring, and, at the outer edge, the beginning of the second transparent ring. The same fish, if captured in September of the same year, would have two transparent rings, and the second opaque ring would be forming at the edge. Shown in figure 5 are photographs of otoliths taken from fish of a few months, 1 year, and 2 years of age.

As mentioned by Jones and Hynes, the times of formation of the light and dark rings in the otolith are not the same for all species of fish. In certain fishes, such as *Clupea harengus*, the transparent ring appears to be formed in winter and the opaque ring in the summer, the reverse of *Gasterosteus*.

Our samples for length-frequency determination were taken by seining, which is probably more nearly nonselective as to size than any other method available to us. However, it may be that a completely random sample of the population cannot be obtained, since the sticklebacks may sort and distribute themselves by size to some extent. It is believed though that size selectivity in the sampling is more or less smoothed out by the large number of samplings.

Samples in Bare Lake were taken at intervals of 1 to 2 weeks during the summers (approximately June 1 to September 1) of 1950–56, inclusive, and in Karluk Lake during the summers of 1948 and 1949. In Bare Lake almost all of the sampling was done in one area, the beach at the southwest corner of the lake. In Karluk Lake most of the samples were taken around or near Camp Island on the east side of the lake.

Each sample consisted of from 100 to 400 fish. Standard length of each fish was measured in millimeters. A length-frequency histogram was drawn for each sample expressed in percentage of the total number of fish in the sample. For the Bare Lake samples, the lengths were grouped in 2-mm. intervals; for the samples from Karluk Lake, in 3-mm. intervals. The histograms showing the sequence of samples from Bare Lake for one summer (1954) are presented in figure 6. In figure 7 the sequence for Karluk Lake in the summer of 1949 is shown.

Standard lengths may be converted to fork lengths or total lengths (all of these terms are well defined in recent literature) by use of the following factors: F. L./S. L.=1.17, and T. L./S. L.=1.21.

Jones and Hynes (op. cit.) give a summary of the information regarding age and size of the threespine stickleback. Various authors have

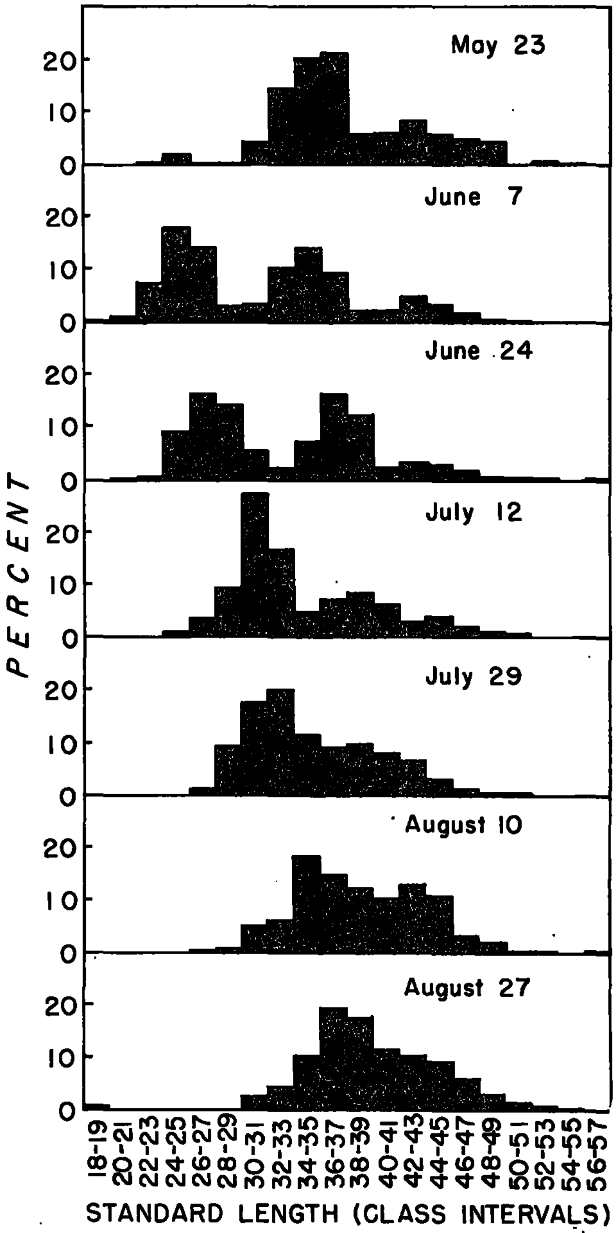

FIGURE 6.—Length-frequency histograms, sticklebacks from Bare Lake, 1954. Each diagram represents a sampling of 100–400 fish on a given date. Vertical ordinate, percent of total sample. Horizontal ordinate, standard length group.

placed the lifespan of the species at from 1 to 4 years. Some have said that the fish breeds only once, others that it may breed in each of 2 or 3 successive years. No doubt there is considerable variation, which is due to differences in race or strain or to environmental differences.

In the Birket River sticklebacks (*Gasterosteus aculeatus*), Jones and Hynes found the maximum lifespan to be 3 years plus. The fish at the end of the first summer of life (i. e., when a few months old) averaged about 24 mm., standard length. At the end of the second summer, the average was about 34 mm., and at the end of the third summer about 40 mm. Most of the growth occurred during the summer. Maximum size achieved was about 65 mm.

Assuming that our interpretation of the otoliths is correct, the sticklebacks in Karluk and Bare Lakes have a lifespan of about two and one-fourth years. Most of the 2-year-old fish die shortly after spawning, as indicated by the successively smaller numbers of large fish in the samples as the summer progresses. A very few otoliths appeared to show an extra winter ring. It may be that an occasional fish survives the third winter.

In the samples from Bare Lake in the summer of 1954 (fig. 6), at the time of the first sampling on May 23, very few young-of-the-year fish were present. The frequency mode at about 35 mm. apparently represented 1-year-old fish, the 2-year-old fish being much fewer and showing a broad frequency mode at about 45 mm.

In the next sample, taken on June 7, the small fish predominate, with a mode at about 25 mm. The fish of the other two size groups (age classes) have fallen off in comparative numbers. Successive samples throughout the remainder of the summer show: (1) a fairly rapid increase in size of the fish of the year; (2) a somewhat slower but steady growth of the 1-year-old and 2-year-old fish; and (3) a reduction in numbers of the older fish, especially of the 2-year-old group, probably caused by their death and disappearance from the population.

The same picture holds good for the summers of 1951 and 1953, with certain variations, probably caused in part by differences in spawning dates and hence in the growth achieved in the first summer. In the 1953 samples the 1-year-old group appeared in weak numbers throughout the summer, possibly indicating poor survival through the preceding winter.

In Karluk Lake in 1949 (fig. 7), the first sample of the summer was taken on June 23. The young-of-the-year group was almost or entirely

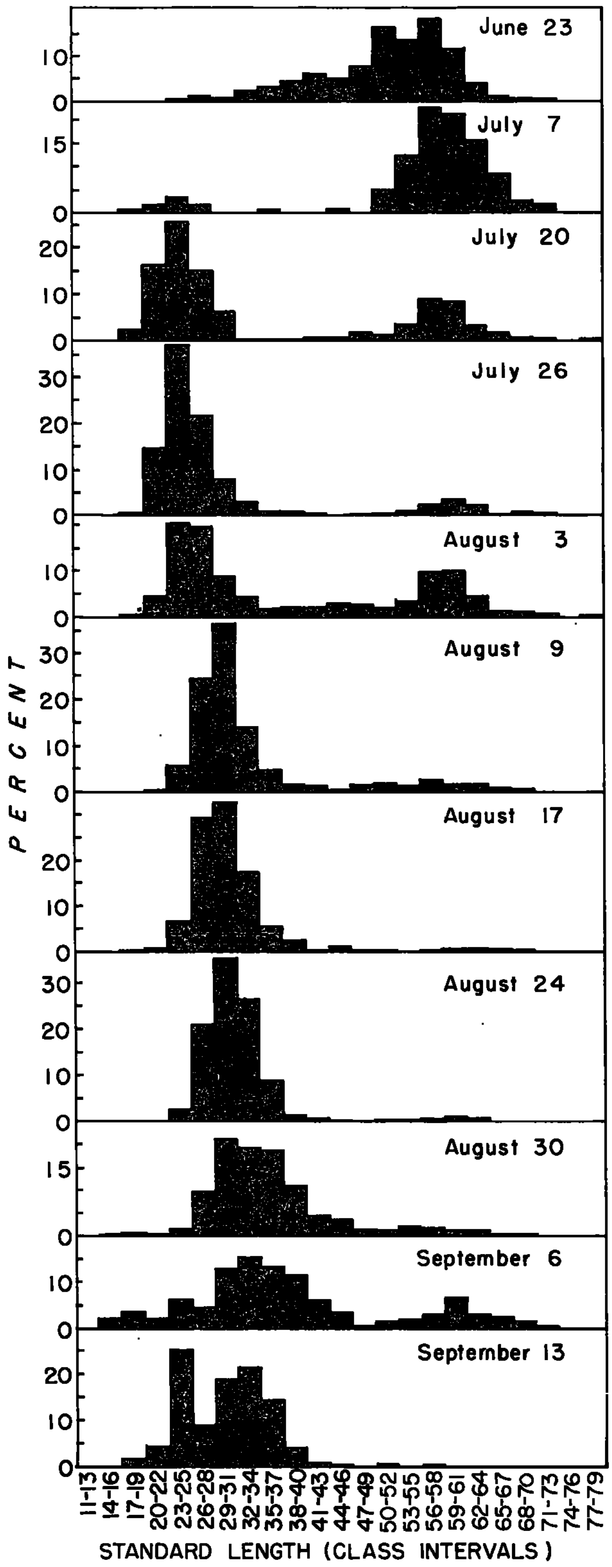

FIGURE 7.—Length-frequency histograms, sticklebacks from Karluk Lake, 1949. Arrangement as in figure 6.

absent. It is thus indicated that the sticklebacks probably spawn later in Karluk Lake than in Bare Lake, presumably because the water warms up later in Karluk Lake. The next sample, taken on July 7, contained a few small fish, and by July 20, the young fish predominated in numbers. From that date through the remainder of the summer, the young-of-the-year were the group with by far the largest numbers in the samples. The older fish steadily dwindled in numbers, except for a showing such as that on September 6, possibly occasioned by nonrandom sampling. Apparently, as in Bare Lake in 1953, the Karluk Lake stickleback population in the summer of 1949 was weak in 1-year-old fish; although, because of overlapping in size, some of the apparent modes may have been composed of fish from two age groups.

The Karluk Lake samples for September 6 and September 13, 1949, show an apparent bimodality for the young-of-the-year group, probably caused by the appearance of a late hatched brood.

The figures in table 7 represent peaks (apparent modes) in the length-frequency histograms for the sampling dates for Bare Lake. Each vertical column thus portrays the growth of a certain year class (fish hatched in the summer of a certain year), assuming that the peaks represent the average length of the fish of a particular age group at a given time.

These data are plotted in figure 8 as points on growth curves. Each curve in this figure represents the growth of the fish of a given year class. The early growth, in the first few weeks after hatching, cannot be shown, as the fish were not available in the areas sampled. Spawning no doubt takes place at different times in different years, and the young fish thus get a slower or faster start and achieve a different average length at the end of the first summer. Thus in 1954 the hatching probably was early, and the first summer's growth was greater than in most other years. Carrying over this increased growth, the fish of this year class were somewhat larger than normal at the start of the next summer.

The growth curves for the year classes of 1951, 1952, and 1953 fall close together (fig. 8). A curve representing the average or composite for these 3-year classes is redrawn in figure 9. Superimposed on it are symbols, each of which repre-

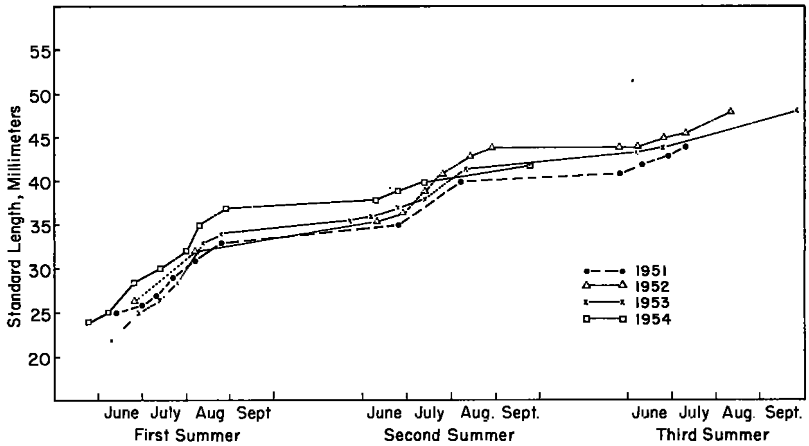

FIGURE 8.—Growth of Bare Lake sticklebacks. Each curve represents a year class. Points on curves derived from modes of length-frequency histograms.

sents a fish whose age was determined by otolith reading.

In these symbols, the sexes are separated for the fish in their third summer (2 years old). The females attain a somewhat larger size than the males.

The fact that the curve, which presumably indicates average sizes, does not pass through the median of the lengths indicated by the otolith readings may be due to an unconscious tendency on the part of the technician to select usually the larger fish in a given size-group for otolith samples.

In a similar diagram for the Karluk Lake sticklebacks (fig. 10), the symbols represent mean lengths of fish of length-frequency modes (for samples through the summers of 1948 and 1949), and the curve indicates the regression line as drawn by visual inspection. The vertical bars show the ranges of lengths of fish the ages of which were determined by otolith reading. Samples for otolith determinations were available only for dates in mid-July (1956).

As shown in figures 8–10, the Karluk Lake and Bare Lake sticklebacks do most of their growing from June 1 to September 1 and make comparatively little growth through the fall, winter, and spring.

The sticklebacks in Bare Lake average from 32 to 35 mm. in standard length at the end of

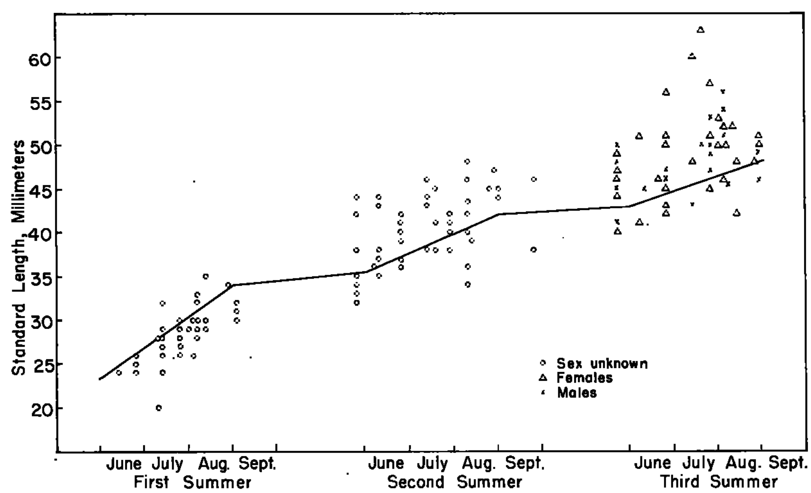

FIGURE 9.—Growth of Bare Lake sticklebacks. Curve is composite of growth of 3-year classes (from figure 8). Scattered points represent ages and lengths of individual fish determined by otolith reading.

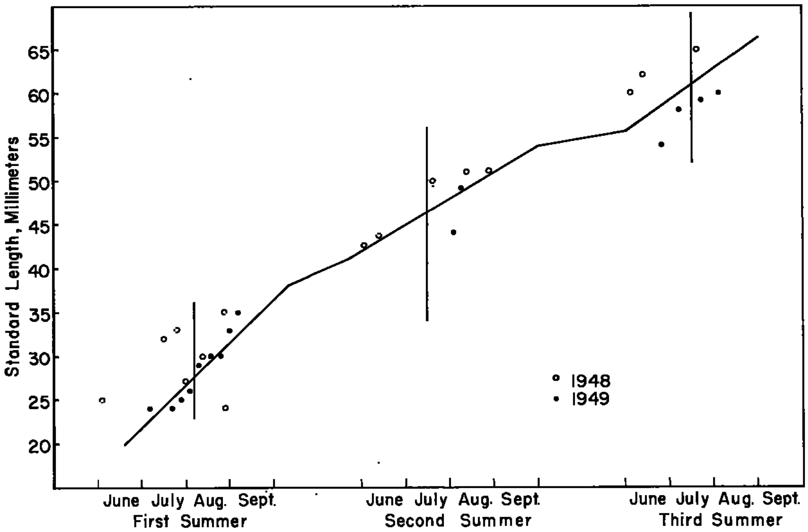

FIGURE 10.—Growth of Karluk Lake sticklebacks. Scattered points, modes from length-frequency histograms, 1948 and 1949. Curve drawn by inspection. Vertical bars, range of lengths from otolith readings.

TABLE 7.—*Bare Lake, average standard length of sticklebacks on various dates*

[Each entry in table represents a peak [mode] on length-frequency diagram of a sample taken on that date]

Sampling date		Year class					
Year	Date	1954	1953	1952	1951	1950	1949
1951	June 13	--------	--------	--------	24	34	40
	June 29	--------	--------	--------	25	35	41
	July 8	--------	--------	--------	27	36	41
	July 22	--------	--------	--------	30	39	44
	Aug. 7	--------	--------	--------	31	39	--------
	Aug. 25	--------	--------	--------	33	41	--------
	Sept. 12	--------	--------	--------	--------	42	--------
1952	June 25	--------	--------	26	35	41	--------
	Aug. 6	--------	--------	32	40	45	--------
1953	May 23	--------	--------	--------	42	--------	--------
	June 8	--------	22	35	41	--------	--------
	June 27	--------	25	36	43	--------	--------
	July 11	--------	28	39	44	--------	--------
	July 24	--------	29	41	--------	--------	--------
	Aug. 12	--------	34	43	--------	--------	--------
	Aug. 26	--------	34	44	--------	--------	--------
1954	May 23	24	35	42	--------	--------	--------
	June 7	25	35	43	--------	--------	--------
	June 24	27	36	43	--------	--------	--------
	July 12	30	38	45	--------	--------	--------
	July 29	32	--------	--------	--------	--------	--------
	Aug. 10	35	43	48	--------	--------	--------
	Aug. 27	37	--------	--------	--------	--------	--------
1955	June 7	38	44	--------	--------	--------	--------
	June 24	39	45	--------	--------	--------	--------
	July 12	40	44	--------	--------	--------	--------
	July 18	40	--------	--------	--------	--------	--------
	Sept. 25	42	48	--------	--------	--------	--------

the first summer, depending somewhat on the date of hatching. At the end of the second summer (about 16 months after hatching), the average length is about 42 to 44 mm. At the start of the third summer, the average is about the same, and at the end of August of that summer, the few fish of that age group still alive are from 45 to 60 mm. long. The largest individual stickleback measured from Bare Lake was 69 mm. standard length (3.3 inches total length).

In Karluk Lake growth in the early part of the first summer is somewhat less than in Bare Lake because of later hatching. However, the growth thereafter is faster in Karluk Lake, and the maximum size achieved is greater. At the end of the first summer, the average standard length of the Karluk Lake fish is about 32 mm. At the end of the second summer it is about 50 mm. At the end of August in the third summer, the average for the fish of that age group still alive is about 60 to 65 mm. The maximum size recorded for Karluk Lake is 78 mm. standard length (3.8 inches total length).

The growth rate of the Karluk Lake and Bare Lake sticklebacks is greater than that of those in Birket River (Jones and Hynes, 1950), but the latter attain about the same maximum size, since they live 1 year longer. Sticklebacks of various populations from salt and fresh waters in western Europe (Heuts 1947a) ran up to 70 mm. standard length in maximum size.

Reproduction

The stickleback in Karluk and Bare Lakes spawns at the age of 1 or 2 years. It is strongly indicated that those fish of either sex which spawn at the age of 2 years die within a few weeks after spawning. In the late summer many spawned sticklebacks are found along the shores of the lakes or at the outlets. These fish are either dead or in a weak, emaciated condition.

The proportion of sticklebacks that spawn at age 1 year is not known with certainty. Judging from egg development in females (ages obtained by reading otoliths of 1-year-olds), fewer than one-half spawn at 1-year-old. Moreover, it is not known whether a stickleback that spawns at 1 year dies, or lives another year without spawning again, or spawns again the next year.

Bertin (1925) believed that the life cycle of the stickleback in Europe is accomplished in 1 year (in other words, that the fish spawn at the age of 1 year), and that the fish die after breeding. He stated, however, that in some localities the fish may live longer. Leiner (1934) wrote that *Gasterosteus aculeatus* breeds at least 2 or 3 times during its life. Jones and Hynes (1950) found the sticklebacks in England to live 3 years and to show gonad maturation from the first year, but did not indicate how many times the fish spawns during its life.

The sexually mature sticklebacks are structurally hermaphroditic. Schneider (1904) reported an instance of hermaphroditism in *Gasterosteus* in which one of the paired gonads contained both ovarian and testicular tissue. C. W. Huver in 1955 discovered that the sticklebacks at Bare Lake and Karluk Lake have gonads of both sexes present in the same fish, and Greenbank in 1956 examined a large number of mature specimens and found all of them to show this condition. In the ripe male (fig. 11), the testes are enlarged to occupy at least one-third of the abdominal cavity. Between the testes and the other organs, there is a thin septum. Against the ventral side of this septum lie the paired ovaries. These are 8 to 12 mm. long. They contain no cells which can be identified under low-power magnification as ova. No staining or sectioning has been done.

The oviduct is Y-shaped and apparently enters the cloaca separately from the vas deferens. The cloaca is simple and is continuous with the hind gut. There is a single external opening.

Just anterior to the cloaca and ventral or slightly lateral to the posterior portion of the gut, there is a pear-shaped, thin-walled sac some 8 to 12 mm. long. This sac, as spawning time approaches, becomes filled with a clear, viscous fluid, presumably the material which is used to cement the nest.

The ovaries of the ripe female (fig. 12) occupy a large proportion of the abdominal space. There is a septum as in the male. The testes are not prominent but definitely are discernible as ribbonlike structures and readily distinguishable from the darker streak of the kidney. No cytological examination of the testes has been made. The vas deferens and the oviduct apparently enter the cloaca separately as in the male.

A female stickleback, 70 mm. standard length, captured in Karluk Lake on July 25, 1956, had ovaries well distended with eggs. Among the eggs were several which were well eyed (fig. 13). While it may be possible that sperm cells had entered the cloaca from the water outside and had made their way up the oviduct, there is the possibility that the spermatozoa were derived from testicular material in the same fish.

Aside from the change in coloring in the male discussed earlier, and a visible swelling of the ripe female, secondary sex characters attendant on maturity are lacking.

There is little agreement in the literature about the time of spawning of *Gasterosteus aculeatus* or external factors with which it may be related. Roule (1945) states that the stickleback spawns in the latter part of spring or the first part of summer. Carl (1953) says that the spawning period is prolonged from the first week in April to the first week in September. In the estuaries and streams tributary to the Gulf of Main (Bigelow and Schroeder, 1953), the fish is said to spawn probably in May to June.

Eechhoudt (1947) was able to induce a considerable degree of sexual development in the stickleback by exposure to artificial light. Apparently this development did not reach the point of actual spawning.

We do not have information to fix the spawning date of the sticklebacks in Karluk and Bare Lakes with any degree of precision. In Karluk Lake in 1948 stickleback eggs were recovered from a stickleback stomach on June 7. On the other hand, females still carrying ripe eggs were taken from Karluk Lake as late in the summer

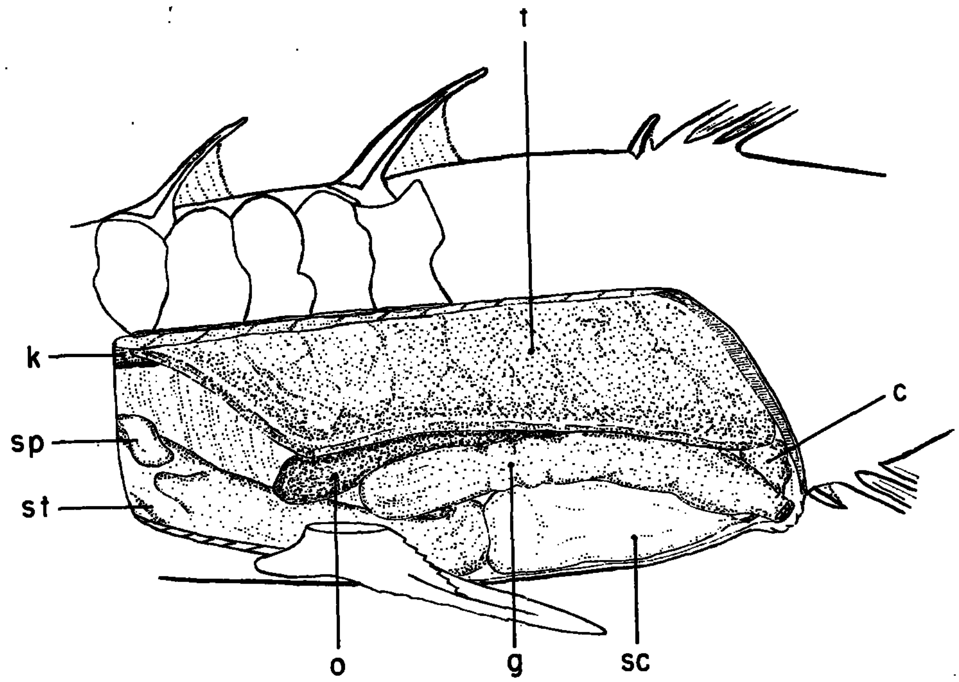

FIGURE 11.—Internal anatomy of normal, sexually mature, male stickleback showing presence of ovaries. c=cloaca; g=gut; k=kidney; o=ovary; sc=sac; sp=spleen; st=stomach; t=testis.

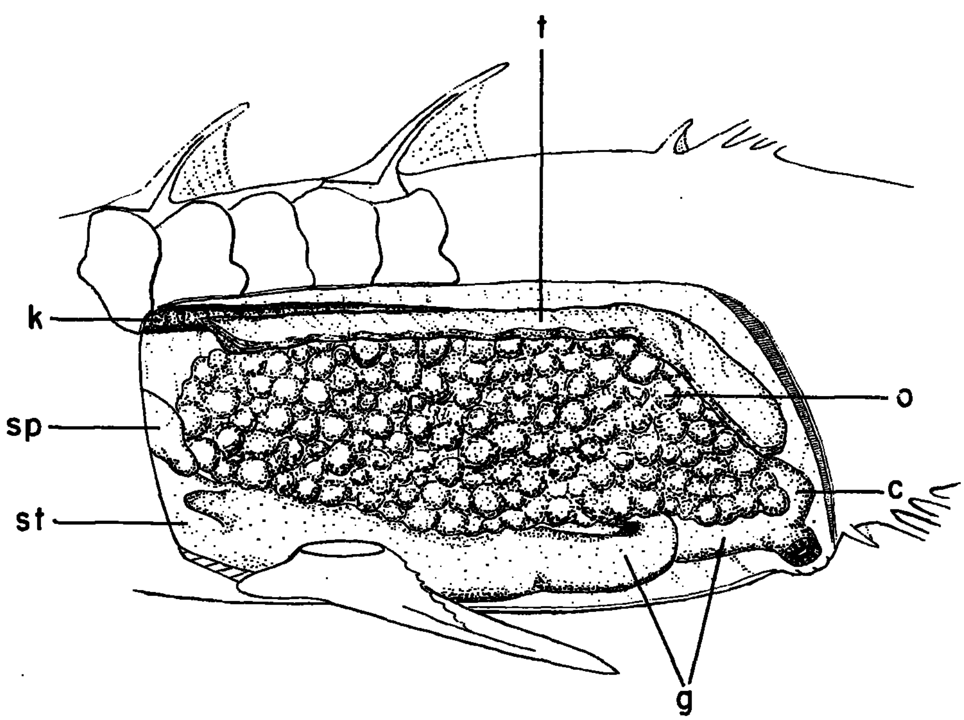

FIGURE 12.—Internal anatomy of normal, ripe, female stickleback showing presence of testes. c=cloaca; g=gut; k=kidney; o=ovary; sp=spleen; st=stomach; t=testis.

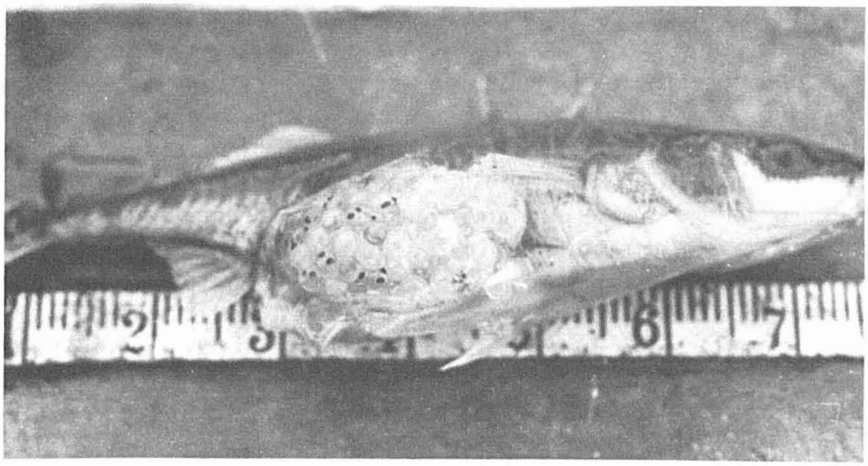

FIGURE 13.—Dissection of female stickleback with eyed eggs in ovary.

[of 1949] as August 3. Morton[3] found stickleback eggs in the stomachs of charrs taken in Karluk Lake in June, July, and August, but not in those taken in April, May, and September.

A collection of sticklebacks, made along the shore of Karluk Lake on July 15, 1956, had a few spawned-out females, but most of the females were ripe with eggs. Observations on July 25 showed many females still to be carrying eggs. But a collection made on August 6 had no fish with ripe eggs, all the large females having spawned.

In Bare Lake we have taken ripe females as early as May 23 [1954] and as late as July 29 [1952]. Specimens less than 20 mm. standard length were captured on June 7, 1954. Judging from the size of the young-of-the-year in June and July (fig. 6), many of the sticklebacks in Bare Lake presumably spawn in May.

A collection from Bare Lake on July 23, 1956, had a few fish still gravid with eggs, but most of the mature fish were spent. On August 1 all the larger fish in a collection were spawned out. A nest with eyed eggs in it was found on August 4, and on August 15 a young stickleback was taken.

These scanty data indicate that perhaps the stickleback spawns earlier in Bare Lake than in Karluk Lake. Such should not be the case if light (length of day) were the sole factor controlling spawning date. Bare Lake, being small and shallow, warms faster in the early summer and maintains a higher surface water temperature through the summer than does Karluk Lake (fig. 4). It is suggested that water temperature may influence the time of spawning.

Spawning takes place in Bare Lake in shoal water around the shores of the lake. In Karluk Lake, too, many sticklebacks utilize the lake shore for spawning. Congregations of possibly hundreds of thousands of sticklebacks have been noted by C. E. Walker at the lower ends of Lower Thumb and O'Malley Rivers, the two principal tributaries of Karluk Lake, from early May until June 1950. Walker states (private communication) that the fish ascended these streams to Thumb and O'Malley Lakes, where they spawned.

The literature contains many references to the nest-building habits of the stickleback. In some waters the male constructs an elaborate nest of small sticks, twigs, or pieces of vegetation held together by a sticky substance presumably secreted by the kidney (Wunder 1930; and others). However, Vrat (1949) reports that the sticklebacks which he studied in California did not use leaves or twigs in their nests. These nests took the form of a hole in the sand, excavated by the male and shaped by strokes of his head.

The nests in Karluk and Bare Lakes are well hidden and camouflaged. The very few that we have been able to discover did not contain sticks or plant material but appeared to be made mostly

[3] Food studies of the Dolly Varden (*Salvelinus malma*) and arctic charr (*Salvelinus alpinus*) at Karluk, Alaska, from 1939 through 1941. By William Markham Morton. (In preparation.)

of sand grains. We have not observed the male in the process of nest-building.

As stated in the literature the male, having constructed the nest, induces one or more females to enter it and lay eggs which he immediately fertilizes. He then maintains a guard over the eggs and newly hatched young, and perhaps provides aeration by his swimming or fanning movements.

In Karluk Lake many stickleback eggs have been found more or less scattered through aquatic vegetation. Possibly these eggs were deposited free, without construction of nests.

At Bare Lake, in 1955, C. W. Huver stripped eggs from female sticklebacks, fertilized them with macerated testes from mature males, and succeeded in hatching them in a bowl floated in a tub. At a water temperature varying from 9° to 16° C., the eggs were eyed in 9 days and started hatching at 14 days.

The embryological development of the threespine stickleback has been studied by Vrat (1949), who published a series of drawings of various stages. The development follows a pattern typical in teleost fishes.

Physiology and Behavior

The literature, at least in North America, contains little information regarding physiological responses, tolerances, and adaptations of the three-spine stickleback. It is believed to be a hardy fish in many respects. For instance, it is known to survive over winter in shallow lakes in northern temperate and subarctic zones, where the chemical conditions become severe. Dissolved oxygen sinks to a trace, and dissolved carbon dioxide and other gases build up considerable tensions. The mechanism for survival is not known; presumably it combines a greatly reduced metabolic rate with the ability to extract oxygen at low pressure.

The threespine stickleback has been used, particularly in Europe, as an aquarium fish. Possibly it would be a satisfactory subject for tank and jar experiments on physiological responses and adaptations. However, Cope et al. (1949) state that "Sticklebacks could not stand holding in the live jars, and mortalities were high at 24 hours." These authors used *Gasterosteus aculeatus* for some experiments in tolerance to certain insecticides. They found the stickleback to be more tolerant to emulsions of DDT, benzene hexachloride, chlorinated camphene, and chlordan than were salmonid fishes (the criterion of tolerance being the amount of agitation after 15-minute test periods). However, in certain tests with acetone solutions of pyrethins they noted that the sticklebacks "were rendered helpless within the time of treatment, while only a few salmonids were so affected." They suggest that selective poisoning might possibly be used in control of sticklebacks. Jones (1935, 1938, 1939, 1947) has made extensive use of *Gasterosteus aculeatus* as a test fish, particularly in determining the toxicity of various metals to fish.

The sticklebacks in Karluk and Bare Lakes apparently suffer a heavy mortality after spawning. The physiology of this post-spawning mortality is not known. Feeding apparently continues until the time of spawning but perhaps ceases with spawning. The dead, spawned-out fish picked up along shores are extremely emaciated.

Except for spawned-out fish, nutrition is satisfactory. All individuals are in reasonably plump condition throughout the summer. Nothing is known concerning diseases in the Karluk and Bare Lake sticklebacks.

These fish harbor various parasites. One of these is the ligualid cestode, *Schistocephalus*, the plerocercoids of which lie in the abdominal cavity of the fish. Crustacea are the host of the initial larval stage, and fish-eating birds, such as mergansers, of the adult tapeworm. At least 20 percent of the adult sticklebacks are infested. These cestode larvae reach 20 mm. or more in length, and one larva can fill all the available space in the fish and cause a visible distension of the abdomen. A few of the infested fish have from 2 to 8 of the worms each.

Morton (1942) states that the stickleback in Karluk Lake carries in its intestines the larva of a proteocephalid cestode, presumably *Proteocephalus arcticus* Cooper. The adult worm is found in the intestine of the lake charr, *Salvelinus alpinus*, which feeds on the stickleback.

Also reported by Morton, a larval cestode of the Dyphyllobothriid type, provisionally called *Dibothrium fasteni*, is found in the stickleback as well as in the lake charr and in young red salmon. It occurs either free or in a cyst on the viscera. Presumably it is the worm, the adult form of which has been reported from bears and mergansers as *Diphyllobothrium*.

A nematode, identified by Morton [4] as *Dacnitis laevis* Zschokke and Heitz, is fairly common in the stomach and intestine of the stickleback, usually occurring in small numbers. This worm is found in both species of charr (*Salvelinus alpinus* and *S. malma*). Morton reports also an acanthocephalan worm, *Neoechinorhynchus rutili* (Müller), in the Karluk Lake stickleback and states that Meyer (1932) has found this worm in sticklebacks (*Gasterosteus*) in Europe.

A parasitic copepod, identified by Wilbur M. Tidd as *Ergasilus cotti* Kellicott, is found on the Karluk Lake sticklebacks. A large proportion of the fish carry from 1 to 5 of these copepods each, attached to the skin at the base of the pelvic or dorsal fins or more often in the gill chamber and gills.

Bigelow and Schroeder (1953) state that the stickleback "is a proverbially pugnacious fish, using its spines with good effect as weapons of offense and defense, even on fishes much larger than itself." We have not observed any demonstration of this pugnacity in the sticklebacks in Karluk and Bare Lakes. As will be discussed under food habits, the stickleback in these waters is not known to feed on other fishes large or small. It is preyed upon by the arctic charr, but the act of capturing a stickleback by a charr has not been observed. We may surmise that the act takes so little time that the stickleback has no opportunity for defensive action. Juvenile red salmon have been found with sticklebacks in their mouths or stomachs, but the act of capture has not been observed.

According to our observation, the stickleback depends to a large extent for protection on a sort of camouflage. In clear, calm water, over a shoal, it will lie at the surface, perfectly motionless for many minutes at a time. In such a position, it resembles a floating stick or twig.

It is possible that the male stickleback makes effective use of his spines in chasing females into the nest and in guarding the nest after the eggs are laid.

[4] See footnote 2, p. 543.

Food Habits

Norman (1936), Jordan (1905), and others have remarked on the voracity of *Gasterosteus aculeatus* and stated that it is strongly predaceous on the eggs and young of other fishes. However, Markley (1940) found the sticklebacks of Sacramento River (sample taken in October) to be feeding mainly on insects and other invertebrates, especially amphipods. Carl (1953) examined a small number of stickleback stomachs from Cowichan Lake, British Columbia, and found zooplankton (Cladocera, copepods, amphipods) and insect larvae to be the chief items in the diet. Bigelow and Schroeder (1953) list as food for the threespine stickleback in the Gulf of Maine copepods, isopods, small shrimp, young squid, diatoms, small fish fry, and fish eggs. It is evident that the stickleback will eat a wide variety of (animal) foods depending on what is available.

Stomach examinations of sticklebacks in Karluk and Bare Lakes are summarized in tables 8–10. The larvae and pupae of chironomid flies (Diptera) were found, often in considerable numbers, in a large percentage of the stomachs. Other insects, such as caddis-fly larvae and damselfly and stonefly nymphs, occurred irregularly.

Also of importance were copepods, of the genera *Diaptomus* and *Cyclops;* and Cladocera, of the genera *Daphnia* and *Bosmina*. Stomachs were examined that contained well over 200 invertebrate plankters of 1 one more of these 4 genera.

TABLE 8.—*Contents of stickleback stomachs, Bare Lake, 1951*

[Numbers in parentheses are range of number of organisms per stomach]

Food	Date					
	June 13	June 29	July 8	Aug. 7	Sept. 12	Totals
Number of stomachs containing food	15	14	17	17	16	79
Number of stomachs containing—						
Chironomids	14 (4-124)	9 (5-88)	11 (1-11)	9 (1-104)	2 (2-3)	45
Other insects	7	8	5	13	5	38
Copepods	14 (7-63)	10 (2-36)	16 (1-16)	10 (1-108)	16 (7-242)	66
Cladocera	2 (1-2)	3 (1-5)	15 (1-112)	9 (2-218)	13 (11-229)	42
Ostracods	3 (1-2)	3 (1-2)	5 (1-11)	1 (1)	6 (1-121)	18
Rotifers	1 (1)	--------	9 (2-15)	--------	--------	10
Clams	1 (9)	1 (1)	--------	1 (5)	3 (1-7)	6
Stickleback eggs	4 (1-3)	2 (1-11)	--------	--------	--------	6

TABLE 9.—*Contents of stickleback stomachs, Karluk Lake*

[Numbers in parentheses are range of number of organisms per stomach]

Food	Date							
	June 4, 1948	June 7, 1948	June 13, 1948	July 25, 1948	July 7, 1949	Aug. 9, 1949	Sept. 13, 1949	Totals
Number of stomachs containing food	11	23	50	15	68	25	25	217
Number of stomachs containing—								
Chironomids	7 (4-14)	10	9		31	2	3	62
Other insects	1				4			5
Copepods	10 (11-20)	23	22	9 (1-71)	59 (1-276)	24	25	172
Cladocera	3	20		13 (1-182)	31	23	25	115
Ostracods	3 (1)	2	2	5 (1-22)	9 (1-134)	1	1	23
Rotifers	2	13	24		1	1		41
Clams					2			2
Stickleback eggs		1		5 (1-38)	23 (5-58)	1		30

TABLE 10.—*Contents of stickleback stomachs from fish of three size groups, Karluk Lake, July 7, 1949*

Food	Standard length of fish, mm.		
	31-45	46-60	61-75
Number of stomachs containing food	21	23	24
Number of stomachs containing—			
Chironomids	11	10	10
Other insects		1	3
Copepods	20	19	20
Cladocera	14	14	3
Ostraeods	1	2	6
Rotifers		1	
Clams		2	
Stickleback eggs		3	20

Ostracods and rotifers were present. Several stomachs contained pea clams, sometimes in large enough numbers to constitute considerable bulk. Other food items, encountered only occasionally, included snails, leaches, planarians, and water mites. Vegetation or phytoplankton, in identifiable form, was never or scarcely ever present.

Several stomachs contained fish eggs, easily identifiable as stickleback eggs. No other fish material was found.

Some changes in the feeding habits throughout the summer may be noticed (tables 8 and 9). Chironomids were fewer in the stomachs in the latter part of the season. Various plankton invertebrate species fluctuated in numbers in the stickleback diet, probably in relation to fluctuations of numbers of these species present in the water.

There are also differences in the food selected by fish of various size groups (table 10). Fewer of the large fish were feeding on Cladocera, more of them on ostracods. Stickleback eggs were found in only the larger fish. Possibly the eggs are too large to be swallowed by the small fish. Or perhaps the larger fish were in a nesting area and thus had ready access to eggs.

Role as Prey

Several species of fish present in Karluk and Bare Lakes may be predators on the stickleback. The arctic charr (*Salvelinus alpinus*), which does not occur in Bare Lake, is a year-round resident in Karluk Lake in substantial numbers. According to Morton [5] and DeLacy [6], this charr feeds on sticklebacks and stickleback eggs, especially in the months of June and July. In the study of the food habits of the arctic charr, in the Wood River drainage in western Alaska, it was found that the charr consumed large numbers of sticklebacks, particularly when young red salmon were not readily available.

The Dolly Varden charr (*Salvelinus malma*) is said by Morton not to utilize sticklebacks in Karluk Lake. Of 60 stomachs of Dolly Varden taken in Bare Lake in the period June–August 1956, only 3 contained stickleback. It is likely that sticklebacks are eaten to some extent by the fingerling coho salmon and the rainbow trout, especially during the winter, when food items such as insects are not available in large numbers. Baxter (1956) found the stickleback to be an important item in the diet of the rainbow trout in a lake near Anchorage, Alaska. Also, the

[5] See footnote 2, p. 543.

[6] Contributions to the life histories of two Alaskan charrs, *Salvelinus malma* (*Walbaum*) and Salvelinus alpinus (Linnaeus). By Allan Clark DeLacy. Doctoral thesis, University of Washington, Seattle. (Typewritten) 114 pp., 1941.

sculpin *Cottus aleuticus* may eat stickleback eggs and small sticklebacks.

Sticklebacks are eaten by several kinds of birds including probably mergansers (Munro and Clemens, 1937), gulls, loons, and kingfishers. The quantitative relationships are not known. Of some significance to the overall ecology of the lake may be the fact that the stickleback carries one or more species of internal parasites which are transmitted to other fish or to birds.

The stickleback has been used to some extent in northwestern Europe in the production of fish oil and meal, and in Russia and possibly in northwestern Alaska for human food. It has been reported that sticklebacks on Kodiak Island sometimes are used for dog food, and are consumed by humans on occasion. For these uses the fish are stored in frozen blocks.

Relation to Red Salmon

Aside from such intangible things as dual occupation of and competition for space, the relation between the stickleback and the production of young red salmon involves four possible major factors: the predation of the stickleback on the salmon, food competition between the stickleback and the young salmon, the use of stickleback fry or eggs as food for the salmon, and the role of the stickleback in the diet of charr and other predators on the salmon.

Predatory habits of the stickleback have been mentioned by various authors. Kincaid (1919) makes the (unsupported) statement: "The damage done by the stickleback is out of proportion to his size, as he is able to kill the fry of larger fish, notably the salmon, for which reason the stickleback is known locally as the Salmon Killer." We have no evidence of sticklebacks in Karluk and Bare Lakes feeding on red salmon eggs or fry. We have not examined any stickleback stomachs taken in the spring while the salmon fry were very small. Rounsefell (1958), states that: "there seems to be little evidence that they [sticklebacks] are actual predators (on young salmon)." Rounsefell cites White (1930) who performed experiments on the consumption of brook trout (*Salvelinus fontinalis*) fry by large trout of the same species and by adult threespine sticklebacks. The results of White's experiments showed the stickleback to be an almost negligible factor in the loss of trout fry. Rounsefell comments, "Salmon fry are much larger than the fry of the brook trout, so that there would seem to be even less chance of any destruction."

The feeding habits of the young red salmon in Karluk Lake are not fully known. It is probable that the fry eat insects and plankton animals, but the larger juveniles may eat a few small fish. Therefore, although there may be some points of difference, the food habits of the small red salmon and the sticklebacks are similar in large measure. Both fishes eat insect larvae (mainly chironomids) and plankton crustaceans. The diet is suited to the fare. Whether and to what extent the consumption of part of the available food supply by the stickleback has an adverse effect on red salmon production is not a matter easy to assess.

As we have suggested above, small sticklebacks may be an item in the food supply of the salmon fingerlings, especially the larger smolts. However, data for making a quantitative estimate of the effect on salmon production are lacking.

Certain predators, in particular the arctic charr, have been shown to utilize sticklebacks for food. This use of sticklebacks may in some measure relieve predation on the young red salmon and possibly be a favorable factor in the production of salmon smolts. However, relationships between predators and prey are complex and not understood fully. A reduction in numbers of sticklebacks present in Karluk Lake might mean that more salmon would be eaten by the charrs. Or it might mean only that the charr population would decline, because the total food supply had decreased, and thus the number of salmon smolts eaten by chars might remain substantially the same.

SUMMARY

The threespine stickleback, *Gasterosteus aculeatus*, is found in large numbers in Karluk Lake and Bare Lake in southwestern Kodiak Island, Alaska. Its presence may have a relation to the production of red salmon (*Oncorhynchus nerka*) in these waters.

This species of stickleback has a wide distribution in the subarctic and temperate zones of the northern hemisphere. It has had a history

of much confusion in classification and nomenclature, largely because of wide variations in morphological characters from one locality or one type of environment to another. The stickleback in Karluk and Bare Lakes is of the partially naked (few lateral plates) form, which is characteristic of populations that reside permanently in fresh water. Counts of lateral plates and fin rays show the populations of the two lakes to be discrete.

Estimates of numbers of fish in the stickleback populations are difficult to make. Sticklebacks appear to be more numerous in Karluk and Bare Lakes than any other species. There is evidence of considerable fluctuation in numbers from year to year.

The sticklebacks are often to be found in large numbers along the shoals and have been observed on the surface in the center of the lake and in small numbers in deep water. Apparently there is little or no movement to and from the ocean, but spawning runs ascend the two main tributaries of Karluk Lake to Thumb and O'Malley Lakes.

The species is at least moderately hardy and resistant to adverse conditions. It carries several species of parasites in these waters, notably the pleroceroid of a cestode (*Schistocephalus*) which has a plankton crustacean (Cladocera) as its initial host and a bird as the final host.

The sexually mature fish have both male and female gonads. The male has paired ovaries and the female a mass of testicular tissue. A large female from Karluk Lake had several eyed eggs in the ovary.

Spawning takes place in early summer. In some years a part of the spawning occurs as late as August. In these waters the male does not use plant material to any great extent in constructing the nest (as has often been reported in the literature), but makes a nest of sand cemented together with a secretion from within his body and more or less buried in sand and gravel in shoal water. Sticklebacks may spawn also in weed beds, with little or no nest construction.

The lifespan is about two and one-fourth years. A standard length of 60 to 65 mm. is attained in Bare Lake and up to 80 mm. in Karluk Lake. Spawning may occur only once during life or at most twice. At least part of the fish die within a few weeks after spawning.

The principal foods for the stickleback in both lakes are midge fly (Chironomid) larvae, and plankton crustacea (Copepods, Cladocera, Ostracoda). Minor items include other insects, water mites, rotifers, small clams, snails, leeches, and stickleback eggs. Stomachs examined at various times during the summer did not contain eggs or fry of fish other than sticklebacks. The period covered by these examinations included the spawning time of the red salmon, but not the time of emergence of red salmon fry.

The stickleback is a component of the food of the arctic charr, which is a predator also on young red salmon. Birds, rainbow trout, and possibly large juvenile coho salmon eat sticklebacks. Small sticklebacks may be used to a small extent as food by the larger juvenile red salmon.

The principal means by which the stickleback in Karluk and Bare Lakes may influence red salmon production include competition with young salmon for food and by reducing predator pressure on red salmon by furnishing food to the charr. Quantitative information is insufficient to assess accurately the benefit or harm to salmon production caused by the stickleback population.

LITERATURE CITED

BAXTER, RAE.
1956. Effectiveness of gill nets and sport fish tackle in sampling fish populations. Quart. Progress Report, Federal Aid in Fish Restoration; U. S. Fish and Wildlife Service and Alaska Game Commission, June 30, 1956. 149 pp., mimeographed.

BERTIN, LEÓN.
1925. Recherches bionomiques, biométriques et systématiques sur les épinoches. Ann. Inst. Océanogr. Monaco, vol. 2, pp. 1–208.

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U. S. Fish and Wildlife Service, vol. 74, Fishery Bulletin 53, pp. 1–577.

CARL, G. CLIFFORD.
1953. Limnobiology of Cowichan Lake, British Columbia. Jour. Fish. Res. Bd. Canada, vol. 9, pp. 417–449.

COPE, OLIVER B., CLAUDE M. GJULLIN, and ALF STORM.
1949. Effects of some insecticides on trout and salmon in Alaska, with reference to blackfly control. Trans. Amer. Fish. Soc., vol. 77, pp. 160–177.

COX, PHILIP.
1922. Results of the Hudson Bay expedition, 1920. II. The Gasterosteidae of Hudson Bay. Contrib. to Can. Biol., 1921, No. 10, pp. 149–153.

CRAIG-BENNETT, M. A.
1931. The reproductive cycle of the three-spined stickleback, *Gasterosteus aculeatus*, Linn. Philos. Trans. Royal Soc. London, series B, vol. 219, pp. 197–279.

EECHHOUDT, JEAN-P. VANDEN.
1947. Recherches sur l'influence de la lumiére sur le cycle de l'épinoche (*Gasterosteus aculeatus*). Ann. Soc. Roy. Zool. Belgique, vol. 77, pp. 83–89.

HEUTS, M. J.
1947. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. Evolution, vol. I, pp. 89–102.
1947a. The phenotypical variability of *Gasterosteus aculeatus* (L). populations in Belgium. Verhand. Akad. Wetensch. van Belgie, vol. 9, No. 25, pp. 1–63.
1949. Racial divergence in fin ray variation patterns in *Gasterosteus aculeatus*. Jour. Genetics, vol. 49, pp. 183–191.

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. Jour. An. Ecol., vol. 19, pp. 36–58.

JONES, J. R. E.
1935. The toxic action of heavy metal salts on the three-spined stickleback (*Gasterosteus aculeatus*). Jour. Exp. Biol., vol. 12, pp. 165–173.
1938. The relative toxicity of salts of lead, zinc, and copper to the stickleback (*Gasterosteus aculeatus* L.) and the effect of calcium on the toxicity of lead and zinc salts. Jour. Exp. Biol., vol. 15, pp. 394–407.
1939. The relation between the electrolytic solution pressures of the metals and their toxicity to the stickleback (*Gasterosteus aculeatus* L.). Jour. Exp. Biol., vol. 16, pp. 425–437.
1947. The oxygen consumption of *Gasterosteus aculeatus* L. in toxic solutions. Jour. Exp. Biol., vol. 23, pp. 298–311.

JONES, J. W., and H. B. N. HYNES.
1950. The age and growth of *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Spinachia vulgaris*, as shown by their otoliths. Jour. An. Ecol., vol. 19, pp. 59–73.

JORDAN, DAVID STARR.
1905. A guide to the study of fishes. New York, Henry Holt & Co., 2 vols.

JUDAY, C., WILLIS H. RICH, and G. I. KEMMERER.
1932. Limnological studies of Karluk Lake, Alaska, 1926–1930. Bull. Bur. Fish., Bulletin 12 (vol. 42), pp. 407–436.

KINCAID, TREVOR.
1919. An annotated list of Puget Sound fishes. Wash. State Dept. Fish., pp. 1–51.

LEINER, M.
1929. Ökologische Studien an *Gasterosteus aculeatus*. Zeitschr. Wiss. Biob. A. Morphol. u. Ökol. Tierre., vol. 14, pp. 360–399.
1930. Forsetzung der ökologischen Studien an *Gasterosteus aculeatus*. Z. morph. Ökol. Tiere., vol. 16, pp. 499–540.
1934. Die drei europaischen Stichlinge (*Gasterosteus aculeatus* L., *Gasterosteus pungitius* L. und *Gasterosteus spinachia* L.) und ihre Kreuzungsprodukte. Z. Morph. Ökol. Tiere., Vol. 28, pp. 107–154.

MARKLEY, MERLE H.
1940. Notes on the food habits and parasites of the stickleback *Gasterosteus aculeatus* Linn. in the Sacramento River, California. Copeia, 1940 (No. 4), pp. 223–225.

MEYER, A.
1932. Acanthocephala. Bronn's Klassen u Ordnung Tier-Reichs. Vermes Askhelminthen. Vol. 4 (Abt. II, Buch 2, Lief 1), pp. 1–332.

MYERS, GEORGE S.
1930. The killifish of San Ignacio and the Sticklebacks of San Ramon, Lower California, Proc. Calif. Acad. Sci., vol. 19, pp. 95–104.

MUNRO, J. A., and W. A. CLEMENS.
1937. The American merganser in British Columbia and its relation to the fish population. Biol. Bd. Canada, Bulletin 55, pp. 1–50.

NELSON, PHILIP R., and W. T. EDMONDSON.
1955. Limnological effects of fertilizing Bare Lake, Alaska. U. S. Fish and Wildlife Service, Fishery Bulletin 102 (vol. 56), pp. 415–436.

NORMAN, J. R.
1936. A history of fishes. 2d ed. London, Benn. 463 pp.

ROULE, LOUIS.
1945. Les poissons et le monde vivant des eaux. Paris, Librairie Delagrave. 10 vols.

ROUNSEFELL, GEORGE A.
1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U. S. Fish and Wildlife Service, Fishery Bulletin 130 (vol. 58), pp. 83–169.

SCHNEIDER, G.
1904. Ueber einen Fall von Hermaphroditismus bei *Gasterosteus aculeatus*. Helsingfors Medd. Soc. Faun. et Fl. Fenn., vol. 30, pp. 7–8.

VRAT, V.
1949. Reproductive behaviour and development of the three-spined stickleback (*Gasterosteus aculeatus*) of California. Copeia, 1949, pp. 252–260.

WHITE, H. C.
1930. Trout fry planting experiments in Forbes Brook, Prince Edward Island, in 1928. Contrib. Can. Biol. and Fish., vol. 5, pp. 203–211.

WUNDER, W.
1928. Experimentelle Unterschungen an Stichlingen (Kämpfe, Nestbau, Laichen, Brutpflege). Zool. Anz. (Suppl.) 3 (Verh. Deutsch. Zool. Ges. 32), pp. 115–127.
1930. Experimentelle Untersuchgen am drei-stachligen Stichling (*Gasterosteus aculeatus* L.) während der Lachzeit. Z. Morph. Ökol. Tiere., vol. 16, pp. 453–498.

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