456

ECOLOGICAL STUDIES OF SOCKEYE SALMON AND RELATED LIMNOLOGICAL AND CLIMATOLOGICAL INVESTIGATIONS, BROOKS LAKE, ALASKA, 1957

by Theodore R. Merrell, Jr.

SPECIAL SCIENTIFIC REPORT—FISHERIES No. 456

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

UNITED STATES DEPARTMENT OF THE INTERIOR
Stewart L. Udall, *Secretary*
James K. Carr, *Under Secretary*
Frank P. Briggs, *Assistant Secretary for Fish and Wildlife*
FISH AND WILDLIFE SERVICE, Clarence F. Pautzke, *Commissioner*
BUREAU OF COMMERCIAL FISHERIES, Donald L. McKernan, *Director*

ECOLOGICAL STUDIES OF SOCKEYE SALMON AND RELATED LIMNOLOGICAL AND CLIMATOLOGICAL INVESTIGATIONS, BROOKS LAKE, ALASKA, 1957

by

Theodore R. Merrell, Jr.

United States Fish and Wildlife Service
Special Scientific Report--Fisheries No. 456

Washington, D.C.

JUL 1964

CONTENTS

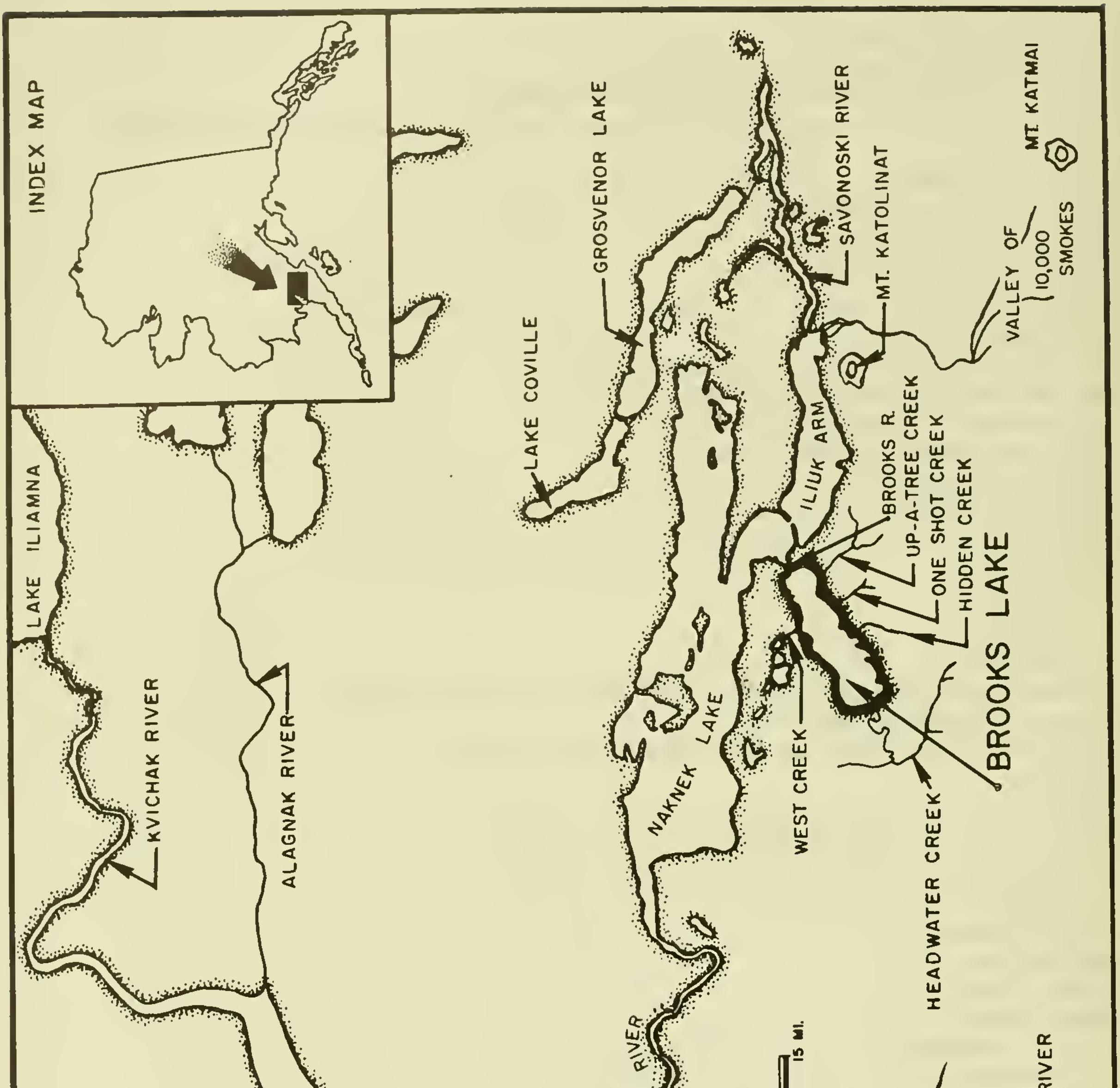

Figure 1.--Brooks Lake, Alaska.

ECOLOGICAL STUDIES OF SOCKEYE SALMON AND RELATED LIMNOLOGICAL AND CLIMATOLOGICAL INVESTIGATIONS, BROOKS LAKE, ALASKA, 1957

by

Theodore R. Merrell, Jr.
Fishery Research Biologist
Bureau of Commercial Fisheries Biological Laboratory
U.S. Fish and Wildlife Service
Auke Bay, Alaska

ABSTRACT

Ecological studies on the fresh-water phases of the life history of sockeye salmon and studies on related limnology and climatology were made at Brooks Lake, Alaska, in 1957.

Data are presented and interpreted on adult sockeye salmon spawning distribution and behavior, age, sex, length, fecundity, and bear predation; on juvenile sockeye salmon ages, food, growth, migration from the lake, relative abundance, and distribution in the lake; and on climatological and limnological factors that may influence sockeye salmon behavior and abundance.

INTRODUCTION

Brooks Lake is located on the Alaska Peninsula 45 miles east of Bristol Bay (fig. 1). It is about 11 miles long and 2 to 4 miles wide, and flows into Naknek Lake via Brooks River. All five species of North American salmon utilize the lake or its tributaries for spawning, but the sockeye salmon, *Oncorhynchus nerka* (Walbaum), is the most abundant. A significant portion of the commercially valuable Bristol Bay sockeye salmon run is produced in Brooks Lake and its outlet stream, Brooks River.

The purpose of the research program at Brooks Lake is to determine the factors that influence abundance and survival of sockeye salmon during their fresh-water life. Knowledge of these factors would assist management of the fishery for maximum production.

Except for 1943, data on adult sockeye salmon have been obtained since 1940 at a weir at the outlet of the lake where the Bureau of Commercial Fisheries maintains a Biological Field Station (fig. 2). In addition to the studies at the weir, since 1947 investigations have been made of juvenile sockeye salmon and of limnology and climatology.

This paper reports the results of investigations at the Brooks Lake Field Station in 1957, when an expanded program of basic research on sockeye salmon was begun. The discussion is in four parts: I, adult sockeye salmon; II, seaward migration of juvenile sockeye salmon; III, lake residence of juvenile sockeye salmon; and IV, limnology and its relation to sockeye salmon.

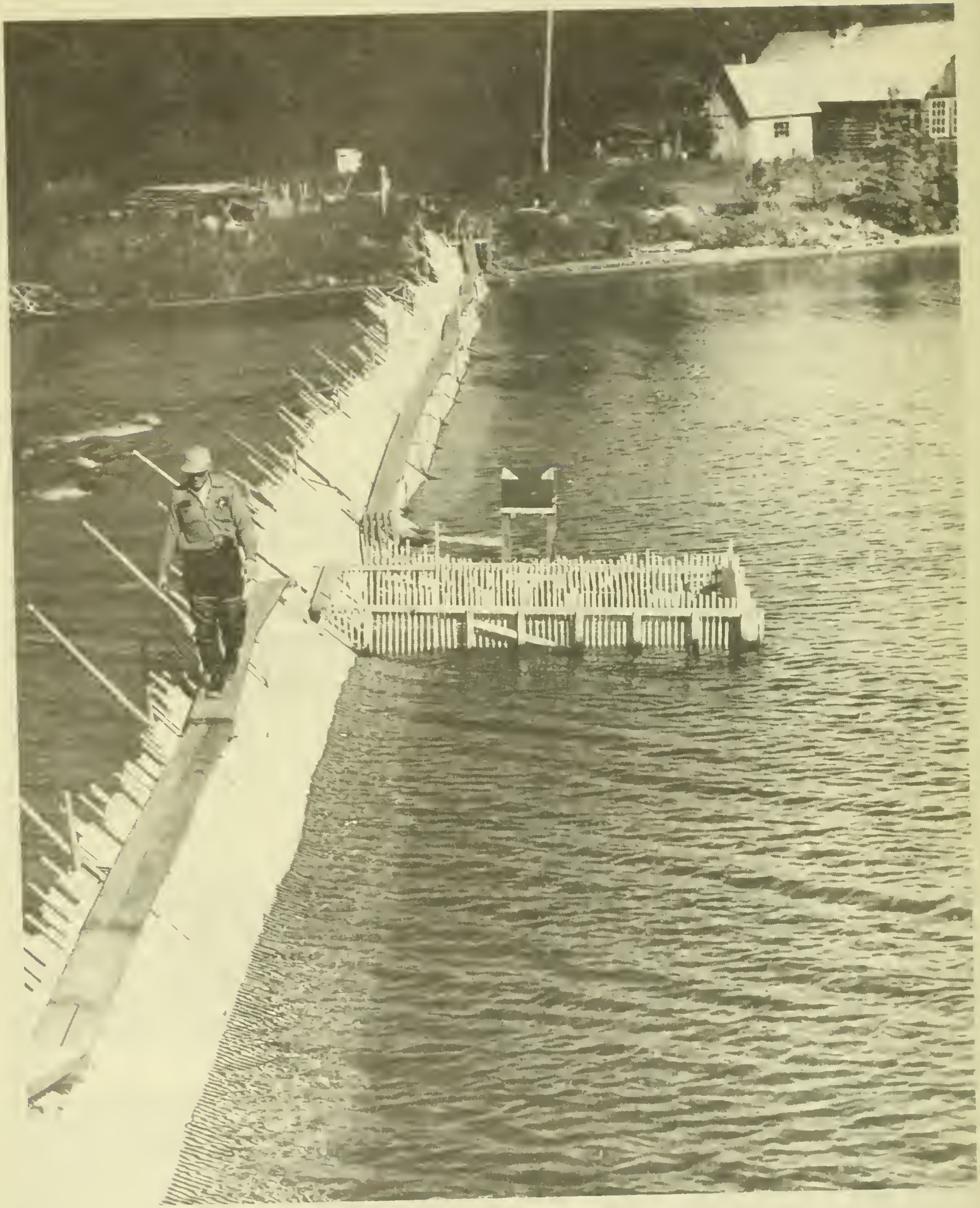

Figure 2.--Bureau of Commercial Fisheries Biological Field Station and weir, Brooks Lake, Alaska.

PART I. ADULT SOCKEYE SALMON

The objectives of the investigations of adult sockeye salmon were to (1) estimate numbers of spawners; (2) determine age and length composition, sex ratio, and fecundity of the spawning population; (3) relate the distribution of adults on the spawning grounds to time of passage and abundance at the weir; (4) determine success of spawning; (5) determine rate of disappearance of carcasses after spawning (6) determine effects of bear predation; (7) observe spawning behavior; (8) evaluate mass movements of sockeye salmon into small tributaries from the lake; and (9) evaluate the importance of lake beach spawning on sockeye salmon production of the lake.

NUMBERS OF SPAWNERS

The counting weir was installed June 18 and was operated until October 5. It had no fixed openings; 10 to 20 pickets were removed at any point where fish congregated below the weir, and fish were counted as they passed through the gap. Multiple-unit hand tallies were used to record both upstream and downstream migrants. Early in the season counters sat on planks suspended from bipods supporting the weir, but since their presence disturbed the fish, the counters changed and stood in the stream several feet from the downstream side of the opening in the weir. To assure good visibility, observers always wore polarizing sun glasses.

The first migrants appeared at the weir on June 25 when 30 were counted (fig. 3). Upstream migration was characterized by one major peak within which were three minor peaks. So that fish from the different peaks could be recognized on the spawning grounds, some from each peak were tagged with Petersen disk tags with distinctive color combinations. One combination was used from June 25 to July 14, a second from July 14 to 19, and a third from July 19 to the end of the migration.

On July 10 a small school of adults was observed for the first time at the upstream side of the weir, and as the season progressed the school grew larger. Occasionally it moved out of the area for several hours or would be

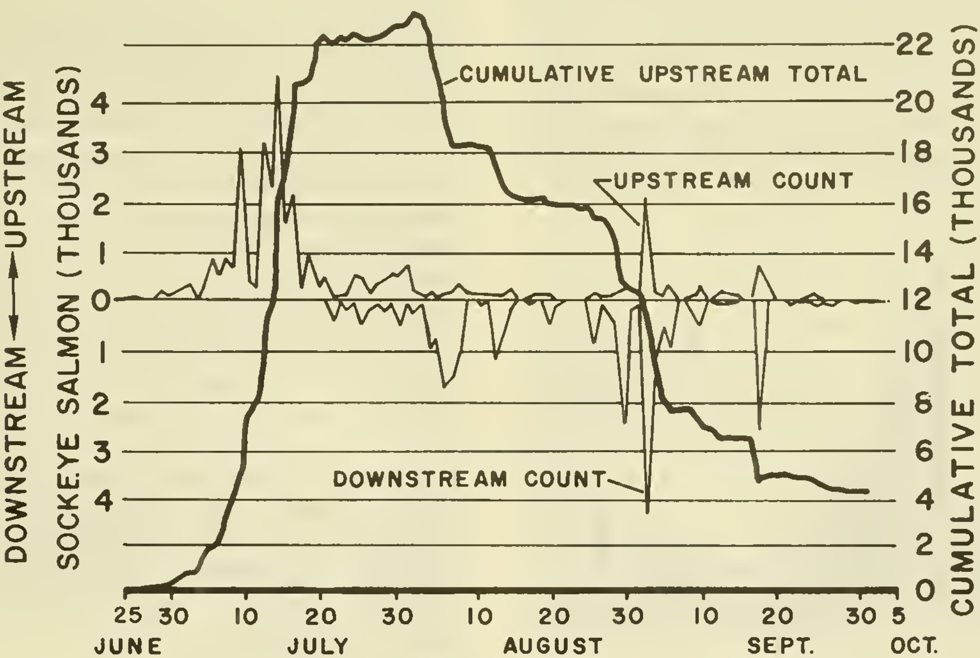

Figure 3.--Daily and cumulative totals of migrating adult sockeye salmon at Brooks Lake weir in 1957.

reduced in size for a period of days, but the wandering fish would eventually return to the weir area at the lake outlet. Although this upstream school was usually quiet and sedentary, sometimes it would rove actively back and forth across the face of the weir. At these times major downstream migrations through the counting openings in the weir were made. These mass behavior displays could not be related to any obvious physical feature of the environment, and further study is needed to explain them.

Eventually 86 percent (27,183 fish) of the total upstream count were counted back downstream into Brooks River, where they ultimately spawned (figs. 3 and 4), leaving only 4,414 spawners in the lake system. Because no provision had been made for estimating downstream migration of spawners from Brooks Lake into Brooks River between 1940 and 1955, the annual counts for these years are not indicative of the true numbers of spawners in Brooks Lake and its tributaries. Therefore, caution must be used in comparing the annual counts shown in figure 4.

Counts of sockeye salmon migrating upstream through the weir should have provided a reliable measure of the number entering the lake, but during the tagging program, it was discovered that many sockeye salmon, as well as other fish, were not counted because of the following reasons: (1) Small sockeye salmon, trout, and pink salmon would sometimes squeeze between the pickets; (2) schools of

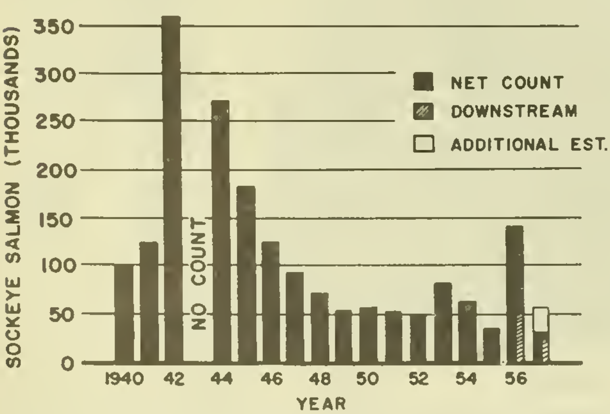

Figure 4.--Annual counts of sockeye salmon at Brooks Lake weir, 1940-57.

sockeye salmon would occasionally be disturbed below the weir and would hit the pickets with great force, pushing themselves through by spreading the pickets; (3) late in the season bears would occasionally molest the weir and dislodge pickets; and (4) the weir had a structural defect. Methods of estimating the uncounted salmon are discussed in the section on the distribution of spawners, p. 9. Since the weir was constructed the same in 1957 as in previous years, unknown and uncounted numbers of salmon probably entered the lake before 1957.

The downstream migration through the weir in 1957 (fig. 3) is assumed to be accurate because fish moving downstream passed only through the openings that were purposely provided for counting and did not attempt to force their way through the pickets.

In addition to the sockeye, other salmon passing through the weir in 1957 included 18 king, 7 chum, 461 coho, and 1 pink.

AGE AND LENGTH COMPOSITION, SEX RATIO, AND FECUNDITY

During the main migration period (June 28 to September 10) 704 adult sockeye salmon were captured in a 6- by 8-foot trap located on the upstream face of the weir 40 feet from the west end (fig. 2). These fish made up a sample to determine age and length composition, sex ratio, and fecundity of the total run. Fish were dipped out of the trap individually with a long-handled net. After they were tagged and the necessary data were recorded, they were immediately released above the weir, excepting those killed to determine fecundity. The trap entrance was usually opened early in the morning and was left open until 2 percent of the previous day's count of adult migrants had entered. It was then closed, the fish tagged and processed, and counting through the weir begun. The trap was checked frequently and the entrance closed before overcrowding occurred. Samples were taken every day there was an upstream migration.

To determine age a scale was taken from the left side of each sample fish about halfway between the dorsal and adipose fins and three rows up from the lateral line. The scale was placed sculptured side up on a numbered spot on a strip of gummed tape. The numbers on the tape corresponded to numbers on waterproof record sheets. Scales were not collected after August 13 when scale resorption became pronounced. Plastic impressions were later made of the scales, using the method described by Clutter and Whitesel (1956). Ages were interpreted by viewing the impressions on a scale projector.

Most of the fish sampled (97.2 percent) were in three age categories: 5_2, 27 percent; 5_3, 8.1 percent; and 6_3, 62.1 percent. The first numeral denotes the total age of the fish and the subscript the number of years in fresh water, including the brood year as 1 year. For instance, a 6_3 fish would have spent two growing seasons in fresh water and three in the sea. Its scales would have five annuli, two formed during its fresh-water life and three during its ocean life.

Snout-fork and mideye-fork lengths were taken to the nearest one-half cm. by placing the fish in a cradle on which metric tapes for each type of length were mounted. Snout-fork length was determined by placing the fish in the cradle and measuring the distance from the snout to the fork of the tail. Mideye-fork length was taken by zeroing the tape at a reference point about 10 cm. from the anterior end of the cradle, sliding the fish backwards until its eye was opposite the zero point, and recording the distance on the tape at the fork of the tail. Mideye-fork lengths are generally preferred in salmon length analyses because of the rapid growth of the snouts of salmon as the fish approach maturity, particularly the males.

Mideye-fork lengths of females ranged from 39 to 62 cm., with a mean of 55.4; and of males, from 29 to 66 cm., with a mean of 55.9 (fig. 5). Length distributions of sexes were different: females were considerably more uniform in size and were more closely grouped around the mode than males. Both sexes were made up two size groups, reflecting an ocean life of either 2 or 3 years.

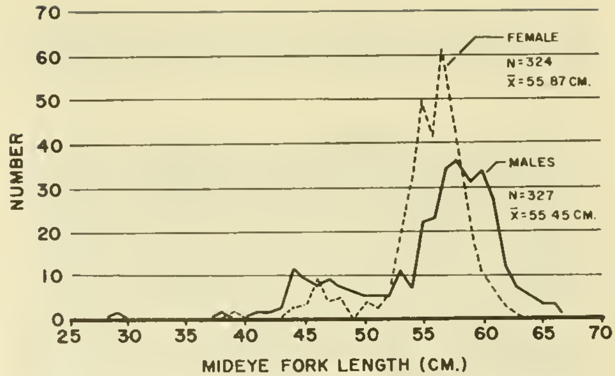

Figure 5.--Mideye-fork lengths of adult sockeye salmon sampled at Brooks Lake weir in 1957.

Sex was determined by external characters. Accurate determination was difficult early in the season but became easier as fish matured. The sex ratio indicated by samples from the trap was 1:1 (328 males and 324 females). The ratio did not change significantly through the season.

Potential egg deposition was calculated from counts of eggs from females selected from the range of sizes in the run (table 1). Initially, females were taken from the trap at the weir; later those that died in gill net sampling were also used. To insure a full complement of eggs, females whose ovaries were sexually mature were not used. The ovaries were hardened in 10 percent formalin for 48 hours. At first one ovary per female was preserved; the total volume by water displacement was measured; and the three samples from that ovary were counted and their volume measured by displacement. The ratio of number of eggs to volume in the small samples was then applied to the entire ovary and doubled to estimate total number of eggs in both ovaries. It soon became apparent that this method produced erratic results, and an actual count of all eggs in one ovary from each fish was begun. The procedure was again modified when a difference was noted between the numbers of eggs in the right and left ovaries--a difference not always closely related to the size of the ovary--and all eggs in both ovaries were subsequently counted. Thirty-eight were counted in this manner to provide an accurate basis for calculating total egg deposition. These 38 are not included in table 1.

The calculated number of eggs per female ranged from 3,044 to 5,060, with an average of 4,115 (table 1 and fig. 6). This is considerably greater than the average of 3,700 for Karluk Lake (Gilbert and Rich, 1927) and the averages for most British Columbia races (Rounsefell, 1957), but lower than the average of 4,500 for Cultus Lake (Foerster, 1936). The regression line in figure 6 was fitted by least squares. Fecundities for fish in each length group were read from this regression, and the potential egg deposition of the run was then calculated (table 1). Since the sex ratio was 1:1, it was necessary only to divide the total number of fish by two to obtain the number of females in the lake. An estimated 14,500 female sockeye salmon in Brooks Lake and its tributaries deposited a theoretical total of 57 million eggs (table 1).

TABLE 1.--Potential egg deposition of sockeye salmon in Brooks Lake and its tributaries. Calculated from fecundity data from range of sizes in the run, June 25 to Sept. 10, 1957

Size range (mideye-fork length)	Fish sampled		Calculated eggs	Calculated females in run	Potential egg deposition
Cm.	*Number*	*Percent*	*Number*	*Number*	*Number*
39	1	0.3	2,300	43.5	100,050
40	0				
41	0				
42	0				
43	0				
44	2	.6	2,740	87.0	238,380
45	3	.9	2,850	130.5	384,750
46	9	2.8	2,950	406.0	1,197,700
47	4	1.2	3,050	174.0	530,700
48	5	1.5	3,160	217.5	687,300
49	0				
50	3	.9	3,350	130.5	437,175
51	2	.6	3,460	87.0	301,020
52	7	2.2	3,565	319.0	1,372,350
53	20	6.2	3,665	899.0	3,294,835
54	33	10.2	3,765	1,479.0	5,568,435
55	50	15.4	3,865	2,233.0	8,630,545
56	41	12.7	3,965	1,841.5	7,301,548
57	61	18.8	4,070	2,726.0	11,094,820
58	43	13.3	4,170	1,928.5	8,041,845
59	22	6.8	4,270	986.0	4,215,150
60	10	3.1	4,380	449.5	1,968,810
61	6	1.9	4,490	275.5	1,236,995
62	2	.6	4,595	87.0	399,765
Total	324	100.0		14,500.0	57,002,173

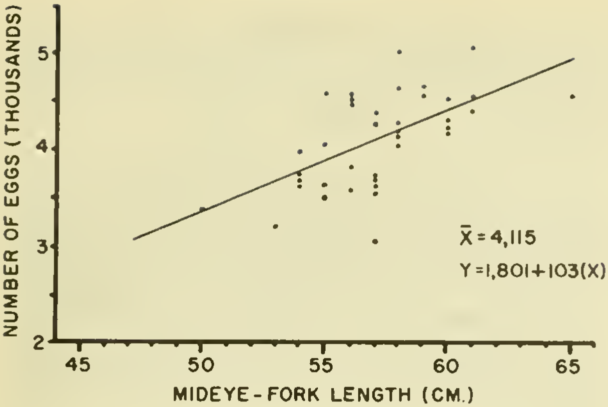

Figure 6.--Relation between numbers of eggs and mideye-fork lengths of 38 sockeye salmon sampled at Brooks Lake, 1957.

RELATION OF DISTRIBUTION ON THE SPAWNING GROUNDS TO TIME OF PASSAGE AND ABUNDANCE AT THE WEIR

To follow their distribution on the spawning grounds, adult salmon were marked daily at the weir with Petersen tags near the insertion of the dorsal fin. Three color combinations were used (red-white, red-yellow, and green-green) to distinguish fish from the early, middle, and late portion of the run (table 2). Only vigorous fish were tagged. No dead tagged fish were observed in the clear water on the lake after being released, indicating that tagging mortality was nil.

To provide equal representation throughout the run, each day we intended to tag 2 percent of the previous day's total number of adult migrants. Through an oversight, however, slightly more than 2 percent were tagged. For each tagged fish observed migrating downstream and later observed migrating back up through the weir, untagged fish should have been accounted for, either by downstream count or deduction from the day's total.

The net number of each color combination remaining in the lake after deducting those which migrated out of the lake indicated that the early run was primarily fish destined for Brooks Lake tributaries and the late run was fish destined for Brooks River. The middle run was a mixture of both (table 2).

Spawning surveys on foot were begun July 26 on Up-a-tree Creek and ended September 28 on Brooks River. Surveys were made at weekly intervals during the spawning period on each stream. Two men made the surveys. One recorded data and carried a rifle for protection from brown bears; the other examined the fish

TABLE 2.--Number of salmon tagged and tags sighted at the weir from early, middle, and late portions of Brooks Lake sockeye salmon run, 1957

Color combination and dates used	Fish tagged	Fish down through weir	Fish back up through weir	Tags remaining in lake
	Number	*Number*	*Number*	*Number*
Red-white				
June 28 to July 13	152	4	2	150
Red-yellow				
July 14-18	250	[1] 153	35	132
Green-green				
July 19 to Sept. 10	176	[1] 146	[2] 25	55
Total	578	[1] 303	[2] 62	337

[1] Includes two tag scars, one assumed red-yellow and one green-green.
[2] Includes one tag scar, assumed green-green.

carcasses. On surveys in brushy areas, whistles were blown every few minutes to alert the bears; if they heard our approach the bears usually avoided us. Polaroid glasses were used to insure maximum and comparable visibility for all surveys. In addition to surveys on foot, three surveys were made from the air. Table 3 summarizes the sightings made on surveys. Of the aerial surveys, only the one on Headwater Creek was used to estimate numbers of fish.

Although tagging 2 percent of the fish passing the weir should have resulted in a 1:50 ratio of tagged to untagged fish in the population above the weir, the number of tagged fish in samples was always less than expected. Five possible explanations for this discrepancy are:

1. Tagged fish suffered a heavier mortality than untagged fish. This can be dismissed because there was no evidence of tagged fish dying before spawning.

2. Tagged fish behaved differently from untagged fish, resulting in biased samples. This is not likely since there was never any evidence of high concentrations of tagged fish in locations where schools were visible. A tagging experiment on Hidden Creek in 1949 further substantiated this conclusion (Eicher, 1951).

3. Calculations for each day's tagging were incorrectly made. On the basis of the observed count, this was not a factor. Each day's tagging, based on the previous day's

TABLE 3.--Summary of sockeye salmon sighted and fin clipped by observers on stream and aerial surveys, Brooks Lake system, July 26 to September 28, 1957

Location and number of surveys	Live fish	Dead fin-clipped fish	Clips subsequently recovered	Total tags recovered from dead fish	Total tags seen on live fish
	Number	*Number*	*Number*	*Number*	*Number*
Up-a-tree Creek					
5	518	79	0	0	6
One Shot Creek					
4	559	119	6	1	7
Hidden Creek					
4	923	93	0	2	15
Headwater Creek					
5	[1] 4,500	1,044	0	17	55
West Creek					
1	0	0	0	0	0
Brooks Lake beach					
3	357	0	0	0	0
Total	6,857	1,335	6	20	83
Brooks River					
3	0	2,043	35	10	0
Grand total	6,857	3,378	41	30	83

[1] Aerial survey estimate.

count, was rechecked, and no significant discrepancies were found. For the early period 161 fish should have been tagged, whereas 152 were actually tagged; for the middle period 257 should have been tagged, whereas 250 were tagged; and for the late period 214 should have been tagged, whereas 176 were tagged. Thus, 632 fish should have been tagged, whereas 578 were actually tagged. Since 62 tagged fish were observed returning upstream after dropping down through the weir, these were deducted from the theoretical 632 total, leaving 570 as the theoretical number which should have been tagged, compared with 578 actually tagged.

4. Many tags were lost before surveying This was unlikely because scars were easily seen on the highly colored mature sockeye salmon, and only a few scars were observed in samples.

5. Many fish passed through the weir without being observed. This did happen, but the reason for it could not be explained.[1]

It was necessary then to estimate the number of spawners actually present, since the recorded count of 4,414 is incomplete. The weir tagging and tag sighting data given in tables 2 and 3 formed a basis for the estimate.

The tag recovery phase of the program was disappointing because bears removed both tagged and untagged fish and because fish passed through the weir undetected, thereby adding untagged uncounted fish which reduced the expected tagged to untagged ratio. The original plan was to sample only dead fish for tags, since determining tagged to untagged ratios from live fish is not as reliable as from dead fish (Schaefer, 1951). In the Brooks system, however, ratios determined from live counts are preferred because bears mutilate dead and dying fish, sometimes making it impossible to determine if a fish has been tagged. Twenty tags were actually recovered (exclusive of Brooks River), but only 18 were usable for a population estimate (table 3). In addition, samples totaling 2,000 live fish, 21 of which were tagged, were also used to determine tag ratios.

The best estimate of the number of fish actually present in the spawning population above the weir, based on spawning ground recoveries of live and dead fish, was 28,818 (rounded to 29,000 in future discussions). This estimate was calculated from the ratio of tags found on the spawning grounds (39) to fish sampled (3,335) and the known number of tags in the lake (337)(tables 2 and 3).

$$\frac{39}{3{,}335} = \frac{337}{\underline{n}} \qquad \underline{n} = 28{,}818$$

Independently supporting this estimate is the fact that approximately 12,600 live and dead spawners were observed on all surveys. Since only a fraction of the fish actually present are observed, the total of 29,000 estimated by tag ratios seems reasonable.

One additional fact should be mentioned. Population estimates based on tag ratios almost always result in estimates that are much too high. Experiments on the Skeena River, which were very similar to those at Brooks Lake in 1957, resulted in estimates almost double the number of sockeye salmon actually present (Brett, 1952). Our estimate at Brooks Lake may also be high.

SUCCESS OF SPAWNING

Three hundred and thirty males and 367 females from Up-a-tree, One Shot, Hidden, and Headwater Creeks were cut open and their gonads examined. The fish were recorded as "spawned," "partly spawned," or "unspawned." Spawned was defined as fewer than 25 eggs remaining or 90 percent of the testes evacuated; unspawned, as 90 percent or more of eggs or testes remaining; and partly spawned, as any intermediate stage. Spawning success was high: only 20 females and 23 males were upspawned or partly spawned.

[1] A defect in the sampling trap was discovered and corrected in 1958.

RATE OF DISAPPEARANCE OF CARCASSES AFTER SPAWNING

Carcasses of fish found on each survey were distinctively marked by amputating one or more of the fins and were replaced where they were found. Any fin-clipped fish found on a survey was recorded. Despite the fact that surveys were made at 7-day intervals and 3,378 carcasses were marked, only 41, or 1 percent, were subsequently found, indicating a rapid disappearance (table 3). On the smaller tributaries scavengers seemed to be responsible, while on Brooks River the fast current caused carcasses to be washed downstream into deep water. The successive survey counts of dead fish on a given stream may therefore be regarded as additive for minimum total enumeration purposes.

EFFECTS OF BEAR PREDATION

Bears were numerous and fed actively on salmon in all tributaries of Brooks Lake during the early and peak spawning periods. Toward the end of spawning in each stream, despite an abundance of salmon, bears moved to berry fields on high ground away from the stream valleys. This seasonal shift in diet from salmon to berries has been described at Karluk Lake on Kodiak Island by Clark (1957). Our program in 1957 was not originally planned to study bear predation, but some knowledge was gained.

From the evidence of fresh signs of bears (feces, footprints, clawmarks) and of partially eaten salmon carcasses, bear activity in order of prevalence by stream was as follows: Hidden Creek, Up-a-tree Creek, One Shot Creek, Headwater Creek, and Brooks River.

Bears could be heard from the streamside field station on Brooks River almost every night during September as they fought with each other and pursued salmon near the weir. This was a temporary situation, however, resulting from the concentration of fish and the presence of the weir, which prevented fish from escaping easily. Under natural conditions bears probably have little effect on sockeye salmon in large streams such as Headwater Creek and Brooks River.

Hidden Creek, the most heavily frequented by bears, was carefully surveyed on September 3 to evaluate the effect bears had on spawning. The creek, about 10 feet wide and flowing about 10 cubic feet per second, is similar in size and terrain to Up-a-tree and One Shot Creeks. The creek was surveyed upstream to beyond the limit of spawning. Most of the banks were covered with brush and high grass, but every 10 or 15 feet the vegetation was flattened, indicating "feeding tables" where bears had fed on salmon. It could not be determined if these were the result of fishing by many bears or of great activity by a few. Fresh bear feces was abundant and contained both berries and salmon bones.

Most of the carcasses mutilated by bears had deep tooth marks, or the posterior section of the body was missing (fig. 7). On the Hidden Creek survey, several live spent salmon were seen with large bite marks on the median and posterior portions of the body. Spawning success was recorded whenever it was possible. The appearance of the gonads in the anterior portion of the body usually provided clues to whether fish had spawned successfully.

Of 290 dead sockeye salmon found on the Hidden Creek survey, 188 were females and 102 males. Bears had mutilated 247, of which 10 females and 9 males were unspawned, and 3 females and 13 males were partly spawned. The remaining 212 fish were completely spawned. Spawning was apparently at or slightly past its peak, since more carcasses (489) were found on this survey than on any preceding or succeeding survey. Although this was only a single sample from one stream. I believe it is a measure of maximum bear damage on the Brooks system. The spawning population in Hidden Creek was more heavily affected by bears than the populations in the other tributaries, as shown by comparative general observations of bear predation during stream surveys.

I conclude that even under conditions of intense bear activity on a small stream where salmon are abundant and vulnerable, bears catch mostly spawned out fish and have little effect on ultimate production.

Figure 7.--Bear-mutilated sockeye salmon found alive on survey of Hidden Creek in 1957.

SPAWNING BEHAVIOR

An important objective of the 1957 program was to learn some basic facts about sockeye salmon spawning behavior in the Brooks system. On Brooks River, 400 yards below the lake, observations were made daily from August 16 through October 7 (except for 6 days) from a portable 20-foot high aluminum scaffold. The tower overlooked a gravel riffle used extensively for spawning. A grid system (fig. 8) was constructed over the area to facilitate location of redds and to orient spawning observations by reference points. The area was 75 feet wide (the width of the river) and 285 feet long and was portioned into 15-foot squares. The portioning was accomplished by driving aluminum weir pickets at 15-foot intervals on each bank of the river and tying lines between them; then small colored cloth strips were tied to the lines at 15-foot intervals, dividing each row into five sections. Rows were assigned numbers, and the five sections within the rows were also numbered. Each of the five sections was visually segregated into an imaginary quadrat. An abbreviated code was used to indicate a desired point: For example, R_6S_2B referred to row 6, section 2, the upper right quadrat.

Sections 12 through 15 of the grid (fig. 8) were used to test the hypothesis that stream bottoms with loose gravel are used more by spawning fish than stream bottoms with compact gravel. Alternate $7\frac{1}{2}$-foot-wide strips of gravel in rows 12 through 15 were loosened with a hand shovel before the onset of spawning. The positions of redds within this area on 3 different days were as follows:

Date	Number of redds in loose gravel	Number of redds in undisturbed gravel
August 24	11	13
August 28	13	21
September 11	39	37
Total	63	71

I had noticed during surveys of streams in Oregon that salmon seemed to choose spawning areas where the gravel was

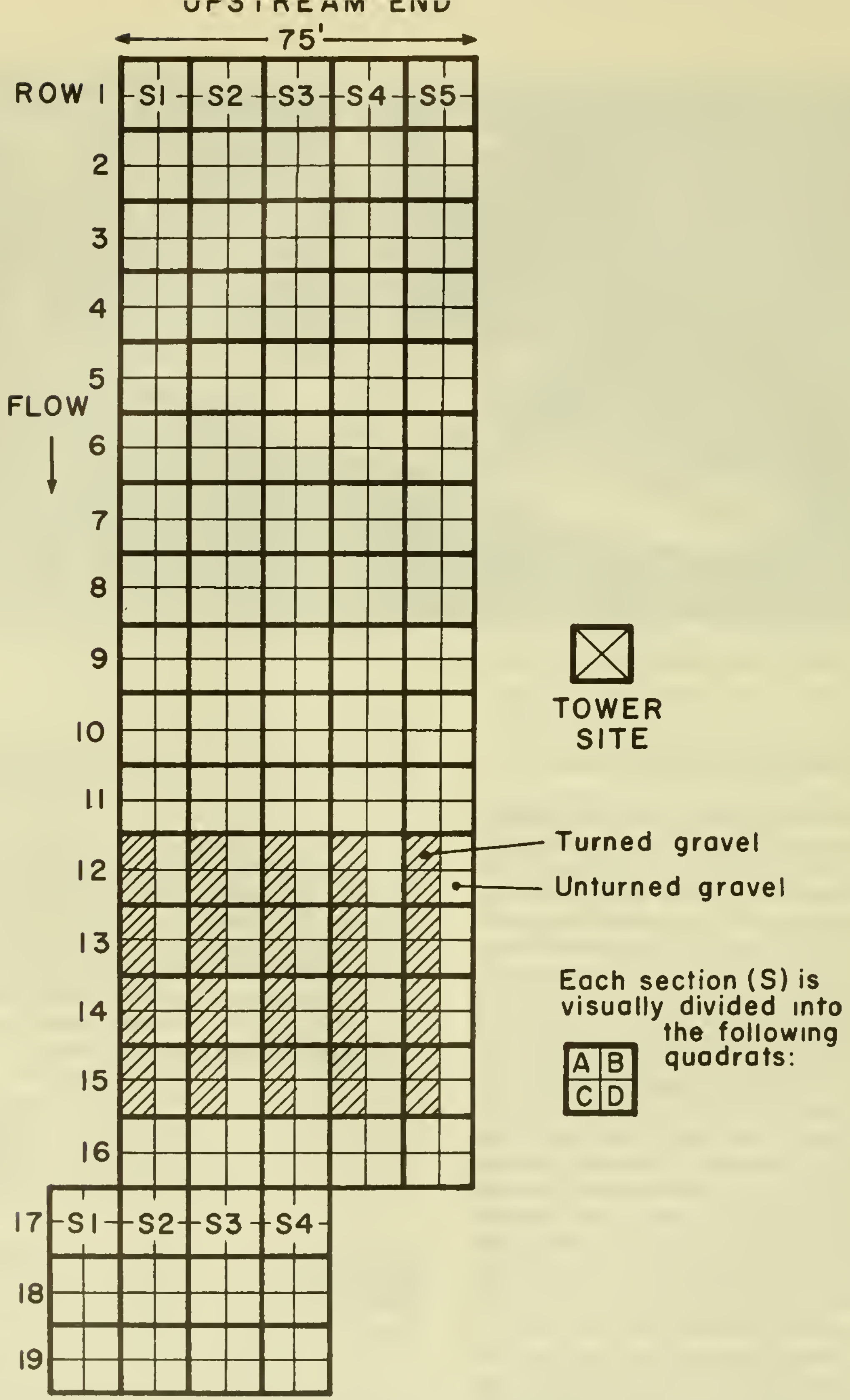

Figure 8.--Grid map of spawning area in Brooks River where sockeye salmon were observed from a tower in 1957.

loosened by gravel removal operation, bulldozing in streambeds, or fording by vehicles. At Brooks Lake, however, the preference for such areas was small. Perhaps under conditions of severe gravel compaction and sparse spawning populations, it would be greater.

To ensure consistent methods and comparable results throughout an observation period, personnel followed the procedures outlined below.

1. To avoid disturbing fish en route to the tower from the field station, the observer crossed the stream at least 100 yards above the study area and then walked on the bank until reaching the tower.

2. To preclude recording behavior that might be influenced by the observer as he climbed the tower, 5 minutes elapsed before observations were recorded.

3. Observations were made of one row at a time for 5-minute periods and were confined to rows 7, 8, 9, and 10 after August 31. These limitations were adopted when it became apparent that a single observer could effectively observe only a limited area where visibility was best.

4. Sex ratios on all redds were noted at the start of each day's observations.

5. Records of individual fish behavior by sex were usually confined to defense activity over redds with a 1:1 sex ratio.

6. A code was devised to simplify and expedite observations and recording. The code was based on three categories of activity that were encountered most frequently as follows:

Male or female activity	One male	Two males	Three males	One female
a	1	2	3	4
b	1	2	3	4
c	1	2	3	4

where a = one chasing or defense activity by a male; b = one chasing or defense activity by a female; and c = one chasing or defense activity by a male and female. Thus, b-4 would signify that a female over a redd chased another female from the redd area.

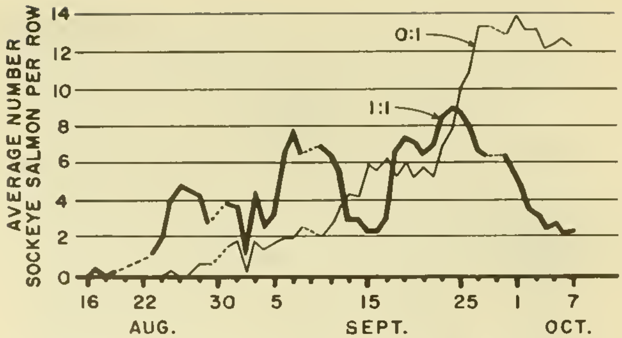

Figure 9.--Daily spawning activity of sockeye salmon, as indicated by sex ratios in Brooks River observation area, August 16 to October 7, 1957. Three peaks indicate periods of maximum spawning activity. Progressive increase of 0:1 sex ratio signifies more completed spawning, with females guarding redds after death of males.

Sex ratios of 1:1 and 0:1[2] were most common during the spawning period and were maintained vigorously by both sexes until the male died (fig. 9). Male and female defense activities (defined as overt actions against other fish) for redds with a 1:1 sex ratio were observed 2,333 times (table 4). Males were almost twice as aggressive as females in defending the redd against intruders (62 percent for males and 38 percent for females). On only 1 day, September 2, were females more active than males, and this day was characterized by a severe wind and rainstorm, which resulted in abnormal stream conditions.

In the area under observation, three separate and distinct waves of sockeye salmon spawned. The first wave reached a peak of activity August 26; the second, September 7 to 9; and the third, September 24. The last wave was the largest and lasted longer than the first two (fig. 9).

The irregular breaking up of 1:1 sex ratios toward the end of the initial wave (fig. 9) was probably due to the occurrence of a severe offshore wind and rainstorm on September 2, which lowered the lake level at the outlet. Concomitant with the decreased flow caused

[2]Males are designated first in all sex ratios in this paper.

TABLE 4.--Observations of activity of spawning sockeye salmon from counting towers on Brooke River, just below outlet of Brooks Lake, August 16 to October 7, 1957

Date	Rows observed	Rows with sex ratios[1] of--		Average 1:1 per row	Average 0:1 per row	Defense activities of pairs			
		1:1	0:1			Males	Females	Male activity	Female activity
August	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Number*	*Number*	*Number*	*Number*
16	4	0	0	0	0	0	0	0	0
17	4	1	0	0.25	0	0	0	0	0
18	4	0	0	0	0	0	0	0	0
19	4	1	0	0.25	0	1	0	0	0
20	0								
21	0								
22	0								
23	5	6	0	1.20	0	21	3	88	12
24	5	10	0	2.00	0	26	19	58	42
25	6	24	1	4.00	0.16	43	23	65	35
26	6	29	0	4.83	0	72	39	65	35
27	6	28	0	4.66	0	27	19	58	42
28	6	27	4	4.49	0.66	20	20	50	50
29	6	17	4	2.83	0.66	36	24	60	40
30	0								
31	4	16	6	4.00	1.50	49	24	66	34
Sept.									
1	5	19	9	3.80	1.80	31	19	62	38
2	4	5	1	1.25	0.25	8	12	40	60
3	4	18	9	4.50	1.80	59	27	69	31
4	4	11	6	2.75	1.50	62	40	61	39
5	4	13	7	3.25	1.75	44	29	60	40
6	3	20	6	6.66	2.00	35	24	59	41
7	3	23	6	7.66	2.00	90	65	58	42
8	4	26	10	6.50	2.50	93	54	63	37
9	0								
10	4	28	8	7.00	2.00	60	25	71	29
11	4	26	11	6.50	2.75	83	56	60	40
12	4	22	15	5.50	3.75	77	62	56	44
13	4	12	18	3.00	4.50	69	45	61	39
14	3	9	13	3.00	4.33	59	38	61	39
15	4	10	24	2.50	6.00	39	23	63	37
16	4	10	23	2.50	5.60	13	6	68	32
17	4	12	25	3.00	6.25	41	22	65	35
18	4	27	19	6.75	4.75	13	6	68	32
19	4	30	24	7.50	6.00	76	35	68	32
20	4	29	19	7.25	4.75	0	0	0	0
21	4	26	23	6.50	5.75	47	25	65	35
22	4	28	22	7.00	5.50	0	0	0	0
23	4	34	28	8.50	7.00	47	25	65	35
24	4	36	31	9.00	7.75	28	17	62	38
25	4	35	41	8.75	10.25	0	0	0	0
26	3	24	33	8.00	11.00	0	0	0	0
27	4	27	54	6.75	13.50	17	13	57	43
28	4	26	54	6.50	13.50	24	20	55	45
29	0								
30	4	26	52	6.50	13.00	0	0	0	0
October									
1	4	21	56	5.25	14.00	18	12	60	40
2	4	15	53	3.75	13.25	20	14	59	41
3	4	13	53	3.25	13.25	0	0	0	0
4	4	10	47	2.50	11.75	0	0	0	0
5	4	11	50	2.75	12.50	0	0	0	0
6	4	9	51	2.25	12.75	0	0	0	0
7	4	9	50	2.25	12.50	0	0	0	0
Total						1,448	885	62	38

1/ Ratios express male in first figure, female in second.

by the drop in lake level was a 10° F. decrease in stream temperature at the outlet of the lake. These factors apparently temporarily upset the normal behavior of the spawning salmon. No relationship could be demonstrated between spawning peaks and daily water level, flow, or temperature.

As the season progressed, the number of spawned females unaccompanied by males increased consistently, reaching a peak by October 1, 7 days after the final spawning peak. This phenomenon was a reflection of the longer life of females after completion of spawning. Females continued to guard the redd aggressively after completing spawning and until they died.

The upstream counts of sockeye salmon at the weir (fig. 3) indicate a trimodal pattern similar to that indicated by spawning activity in the observation area (fig. 9). Tagging data, however, show that the first wave in weir counts included very few Brooks River fish. Most Brooks River fish that subsequently returned downstream through the weir were from the second and third waves of upstream weir counts. I conclude that migration into Brooks Lake, as indicated by weir counts, was not closely related to the spawning waves in Brooks River, but a definite relationship was detected between migration downstream from the lake at the weir and the spawning waves. The August 26 spawning wave was preceded by a peak downstream movement on August 6; the September 7 wave by the September 3 peak; and the September 24 wave by the September 18 peak. Neither the period of precedence nor the comparative magnitude are consistent, but this relationship between downstream migration from the lake and peaks of spawning in Brooks River (and results of tagging at the weir) prove that many of the sockeye salmon included in the counts at Brooks weir are from the Brooks River stock.

From the 1957 data I hypothesize two possible kinds of causative factors responsible for this wave pattern of mass spawning: The time of spawning is governed by an endogenous factor somehow related to the time spent in fresh water or by an exogenous environmental factor that induces sockeye salmon to spawn during successive periods. If the first hypothesis is true, fish must migrate from the ocean in waves timed similarly to spawning waves. In 1957 we had no means of verifying this. If the second hypothesis is true, we should be able to recognize the influencing factors by careful study and observation. In 1957 none of the exogenous environmental factors measured appeared to influence spawning, with the possible exception of competition for spawning space.

The behavior of individual sockeye salmon in the observation area was found to follow certain well-defined patterns closely associated with the three spawning waves. The sequence of behavior through a spawning was generally as follows:

1. Groups of 10 to 50 sockeye salmon, predominantly males, moved upstream from deep pools onto spawning riffles. The most distinctive behavior pattern noted was what we termed a "sidling bluff." This started when two males about the same size moved toward each other until they were side by side. They then swam diagonally across the stream, eye-to-eye. When one bank was reached, they quickly reversed positions and sidled back to the other bank where the process was repeated. After several trips back and forth, one of the males began to give ground. The bluffing was ended with the victor crowding the loser until the loser fled downstream to escape. No biting or other violence was evident during the sidling bluff nor were females ever involved.

2. A pair of fish would establish a redd in a location not strongly defended by another female. When many fish were present, a female was often chased from place to place before finding an undefended site.

3. Small males (jack salmon) actively tried to establish themselves with a female during the redd site-seeking stage. They were never observed succeeding, always being forced away by a larger male.

4. Large females were most sought by the males, resulting in the largest and most powerful males spawning with the largest

females, and the smaller males spawning with the smaller females.

5. Jack salmon constantly attempted to infiltrate an established redd but were driven away by both males and females, usually by the males. As a wave of spawning waned, jack salmon finally gained brief access to redd territories.

6. The male often took an active part in digging the redd but dug more sporadically than the female.

7. Males chased mostly males and females mostly females. This phenomenon would tend to make full use of a spawning stock with an unbalanced sex ratio. For instance, if there were a surplus of females, a male would be able to spawn with many females without interference, as demonstrated in controlled experiments at Wood River Lakes by Mathisen (1955). Of 134 females chased from an established redd with a 1:1 sex ratio, only 16 were chased by males.

8. As a spawning wave waned, the number of lone females increased rapidly (0:1 sex ratio), and males, which died first, disappeared (fig. 9). Lone females on completed redds were very intolerant of digging by new females. The instant a fresh newcomer started a digging movement, all spawned-out females in the vicinity converged in a concerted attack. Perhaps this behavior is a protective instinct to prevent disturbing existing redds.

9. At the peak of spawning and for a day or two after, dead and dying spent males were observed floating through the spawning area. The floating carcasses were almost never females. Spawning fish paid no attention to these carcasses even when they entered a defended redd area.

An attempt was made to follow the behavior of individual fish that had distinctive markings or tags. Only four such fish (all females) could be positively identified through a complete spawning sequence. The chronology of their actions during spawning is shown in table 5. For these four fish, the spawning period averaged slightly longer than the post-spawning period, and the whole spawning process, from redd selection to death, averaged about a week (7.75 days).

If this life span of about a week holds true for the entire spawning population, each of the three spawning waves may be the result of progressive buildups of numbers of spawners. Recruitment over a period of several

TABLE 5.--Observations of four spawning female sockeye salmon, Brooks River, September 11-25, 1957

Identifying mark	Date of first observation	Time with male	Time alone	Date of last observation
		Days	*Days*	
Tag, green-green	Sept. 11	6	3	Sept. 19
Net scar across top of head	Sept. 12	4	2	Sept. 17
Tag, red-white	Sept. 22	3	2	Sept. 26
Tag, red-yellow	Sept. 25	5	6	Oct. 5
Average		4.5	3.25	

days until maximum density for that wave has been reached would explain the shape of the curve comprising each of the 2-week-long peaks (fig. 9).

MASS MOVEMENTS OF SPAWNING SOCKEYE SALMON FROM BROOKS LAKE

Since mass movements of salmon from Brooks Lake to One Shot Creek and back to the lake had been reported in previous years, we set up a 10-foot tower near the mouth of the creek to observe upstream and downstream migrations. The first small school of salmon was seen July 24. The school gradually increased in size and between August 16 and 20 milled about the mouth of One Shot Creek. On August 21 the school entered the stream and migrated upstream to spawn.

A diurnal movement of salmon in and out of Hidden Creek was observed on August 6. During the afternoon of August 5, a large school was in the lake off the mouth of the creek. On the morning of the 6th the school was still there, and no fish were in the creek. At 1 p.m. several hundred ascended the creek for 500 yards, but at 2 p.m. they all turned suddenly and descended to the lake. Their return to the lake coincided with the appearance of two bears in the stream 400 yards above the mouth. By 4 p.m. only a few fish remained in Hidden Creek, and these were near the mouth. Apparently the appearance of the bears caused a mass evacuation of the stream and return to the relative safety of the lake.

LAKE BEACH SPAWNING

Sockeye salmon are known to spawn on suitable beaches in many areas, and spawning has been reported along the beach of Brooks Lake between the outlet and Up-a-tree Creek (Richard Straty, personal communication). From mid-July until mid-September, we surveyed the gravelly beaches in shallow water around the Brooks Lake shoreline from boats. On September 14 during an aerial reconnaissance of the lake shoreline, we saw several hundred sockeye salmon spawning in shallow water along a mile of beach north of the mouth of Up-a-tree Creek. The same area was surveyed by boat on 3 days with the following results:

Date	Number of adults	Number of redds
September 15	357	146
September 22	278	Not counted
October 4	59	136

Since the fish and redds were clearly visible in the shallow water, the maximum count may be regarded as a close approximation of the total numbers of beach spawners. Beach spawning was a minor factor in Brooks Lake production in 1957.

PART II. JUVENILE SOCKEYE SALMON SEAWARD MIGRATION

In the spring juvenile sockeye salmon[3] migrate to the sea from their lake nursery area where they have spent the previous 1 or 2 years. This migration provides an opportunity to evaluate survival from the parent run and to study characteristics of the seaward migration.

Five aspects of the seaward migration of juvenile sockeye salmon were investigated at Brooks Lake in 1957: (1) Age and length composition of seaward migrants; (2) seasonal length-weight relationship of juvenile migrants by age groups; (3) characteristics of daily and seasonal migration by age group of sockeye salmon and of other species migrating out of the lake; (4) migration of juveniles upstream

[3] I define juvenile salmon as any young salmon, in the life history stage between hatching and migration to the sea. Fry are salmon in their first year of life, including the period between hatching and the first winter. Yearlings are salmon in their second year of life, including the period between the first and second winters. Two-year-olds are salmon in their third year of life, between the second and third winters.

from Brooks River into Brooks Lake; and (5) migratory behavior of juveniles.

AGE AND LENGTH OF SEAWARD MIGRANTS

To assess relative abundance, samples of juveniles were captured with fyke nets during the downstream migration. No attempt was made to estimate total migration. Three nets were fished nightly at the lake outlet during periods of heavy migration, one near each shore and one in midriver (figs. 10 and 11). Usually the nets were fished for only an hour a night, but five 24-hour and five all-night samples were also taken. After June 11 when the migration tapered off, only one net (no. 1, fig. 10) was fished, and the sampling schedule was changed from every night to every third night or less.

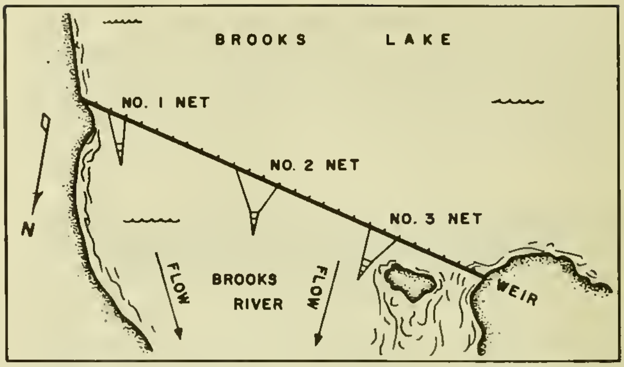

Figure 10.--Locations of fyke nets at Brooks Lake outlet, 1957.

Only portions of each nightly catch were usually processed: from May 21 to 31 (except for all-night samples) about 20 fish per net; from June 1 to 11, 5 fish per net; and from June 17 to October 1, 20 fish per net excepting the June 1-11 period, on nights when the total catch per net was less than 20 fish, the entire catch was processed.

Figure 11.--Fyke nets and method of collecting juvenile sockeye salmon at Brooks Lake outlet, 1957.

Randomness of samples was assured by successively separating a net's catch of live juveniles in a washtub into equal parts with a mesh panel and releasing half of the fish each time until the desired number remained.

Ages of 807 fish were read in the field from scales dry-mounted between two microscope slides. An additional 2,287 fish were aged on the basis of estimated length alone, as described later. Annuli criteria were established by examination and by methods described by Clutter and Whitesel (1956). Each scale was read once after which 49 scales were selected at random and read a second time without reference to the first reading. Agreement between first and second readings was 100 percent. Although reading scales from samples collected at the end of the summer was complicated by early formation of an annulus in September, close agreement was attained in independent readings by two readers. Fork lengths were measured to the nearest millimeter.

A close relationship was found between age and length of the migrants sampled from May 21 to June 10, the main migration period (fig. 12). The migrants fell into two age-length groups: yearlings, which average 83 mm. (range 61 to 96 mm.) and 2-year-olds, which averaged 109 mm. (range 90 to 125 mm.). Since overlap in lengths of the two age groups was almost nonexistent, it was possible to age migrants reliably by their size. There was apparently some digit bias in measuring 2-year-olds, but this did not significantly affect the analysis.

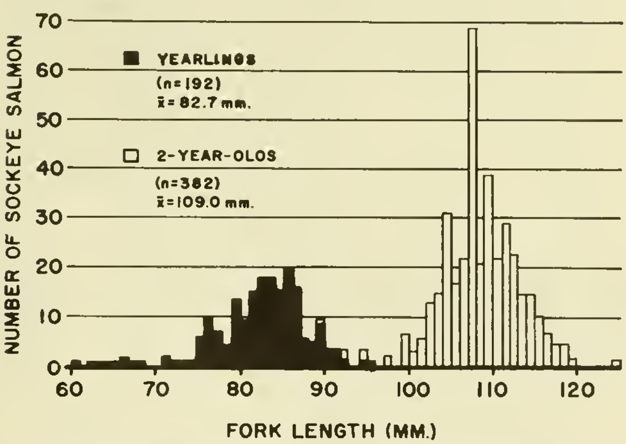

Figure 12.--Relationship between age and length of sockeye salmon migrants sampled at Brooks Lake outlet, May 21 to June 10, 1957.

The mean lengths of migrants from Brooks Lake were compared with those of migrants from other sockeye salmon lakes reported in the literature. Lengths of given age groups from the different lakes varied widely. Average lengths of seaward migrants at Karluk Lake from 1925 to 1936 were invariably much greater than those of migrants at Brooks Lake in 1957 (Barnaby, 1944: table 27). Likewise, migrants at Lake Dalnee, Kamchatka, from 1935 to 1943 were much larger than the 1- and 2-year age groups at Brooks Lake (Krogius and Krokhin, 1948: table 14). Two-year-olds from Brooks Lake, however, were about the same average length as those from Lake Blizhnee, Kamchatka; and both 1- and 2-year-olds at Brooks Lake were larger than migrants at Kurile Lake, Kamchatka (Krogius and Krokhin, 1948). Such size differences might be used as a measure of productivity of different nursery lakes as more comparative data become available.

After mid-June the proportion of 2-year-olds migrating from Brooks Lake dwindled rapidly, leaving only yearling migrants. Fry migrants predominated in September. The overall seasonal age composition was 2 percent fry, 42 percent yearlings, and 56 percent 2-year-olds (table 6). Since the mesh size of the fyke nets was too coarse to retain fry in the spring, the true percentage was probably somewhat higher than indicated. Migration of some fry was observed in the latter part of May and early June and again in September.

Table 6 shows the daily catch and percent of the total of each age class captured in each of the three nets. The numbers and ages for each net were compared for the period May 27 through June 11 (the peak of the migration) when all three nets were fished simultaneously. Although daily catches and age compositions varied considerably, the overall age compositions for each net were in close agreement. Age compositions of the catches of the three nets were similar, indicating that samples from one net site were representative of the populations sampled at the other two sites. The catches were inversely proportional to the amount of water strained--the largest net (no. 2) in the fastest, deepest water caught the fewest fish. Based on our observations, an explanation of this phenomenon might be that the

TABLE 6.--Number and percent of total daily catch of sockeye salmon migrants in each net by age, Brooks Lake, May 20 - October 1, 1957

[Fish of unknown age excluded]

Date	Net 1						Net 2				Net 3						Total					
	Age			Age			Age		Age		Age			Age			Age			Age		
	0	1	2	0	1	2	1	2	1	2	0	1	2	0	1	2	0	1	2	0	1	2
	Number			*Percent*			*Number*		*Percent*		*Number*			*Percent*			*Number*			*Percent*		
May																						
20-21							39	40	49	51	0						0	39	40	0	49	51
21	0	5	7		42	58	10	10	50	50							0	15	17	0	47	53
22	0	17	2		89	11	0	0									0	17	2	0	89	11
23	0	14	6		70	30											0	14	6	0	70	30
24-25																						
25																						
26																						
27	0	3	4		43	57	1	10	9	91	0	2	12	0	14	86	0	6	26	0	19	81
28	0	5	17		23	77	0	21	0	100	0	0	17	0	0	100	0	5	55	0	8	92
29	0	1	18		5	95	1	25	4	96	0						0	2	43	0	4	96
30-31	2	0	20	9	0	91	0	9	0	100	1	7	14	4	32	64	3	7	43	6	13	81
31-June 1	0	311	231		57	43	86	94	48	52	0	114	220	0	34	66	0	511	545	0	48	52
June																						
1	0	25	8		76	24	11	13	46	54	1	38	22	2	62	36	1	74	43	1	63	36
2	1	18	51				3	12	20	80	0	23	37	0	38	62	1	44	100	0	30	70
3	0	3	8		27	73	8	9	47	53	0	22	37	0	37	63	0	33	54	0	38	62
4	0	8	11		42	58	0	2	0	100	5	6	9	25	30	45	5	14	22	12	34	54
5	0	36	51		41	59	3	4	43	57	0	45	117	0	28	72	0	84	172	0	33	67
6	0	54	123		31	69	10	24	29	71	1	44	47	1	48	51	1	108	194	0	36	64
7	0	23	18		56	44	0	2	0	100	0	43	123	0	26	74	0	66	143	0	32	68
8	0	20	65		24	76	4	5	44	56	0	15	11	0	58	42	0	39	81	0	32	68
9	0	7	45		13	87	3	2	60	40	0	11	3	0	79	21	0	21	50	0	30	70
10-11	0	20	49		29	71	0	1	0	100	0	13	21	0	38	62	0	33	71	0	32	68
11	0	2	1		67	33					0	5	1	0	83	17	0	7	2	0	78	22
17-18	0	41	2		95	5											0	41	2	0	95	5
20	0	8	6		57	43											0	8	6	0	57	43
28-29	0	23	1		96	1											0	23	1	0	96	4
July																						
3	0	11	0		100	0											0	11	0	0	100	0
6	0	4	0		100	0											0	4	0	0	100	0
9																						
15-16	2	9	0														2	9	0	18	82	0
18-19																						
22	0	4	0	0	100	0											0	4	0	0	100	0
22-23	0	12	0	0	100	0											0	12	0	0	100	0
25-26	2	19	0	10	90	0											2	19	0	10	90	0
29	0	20	0	0	100	0											0	20	0	0	100	0
August																						
6																						
16																						
30	1	0	0	100	0	0											1	0	0	100	0	0
September																						
2	1	1	0	50	50	0											1	1	0	50	50	0
5	2	0	0	67	0	33											2	0	1	67	0	33
14	17	1	0	94	6	0											17	1	0	94	6	0
18	23	0	0	100	0	0											23	0	0	100	0	0
21	0	0	0														0	0	0			
25	18	1	0	95	5	0											18	1	0	95	5	0
28	2	0	0	100	0	0											2	0	0	100	0	0
October																						
1	3	0	0	100	0	0											3	0	0	100	0	0
Total, May 27-June 11	3	536	720	0	43	57	130	233	36	64	8	388	691	0	36	64	11	1054	1644	0	39	61
Grand total	74	726	745	5	47	48	179	283	39	61	8	388	691	0	36	64	82	1293	1719	2	42	56
Mean		34	45				9	16			.5	26	46									

migrants followed the lake shores on each side of the outlet stream, thereby being concentrated along the stream-banks where the smaller shore nets were located.

From June 1 to 11, to determine if small samples from each net's total nightly catch would yield representative age data, ages of approximately five fish from each net's catch per night were compared with ages of the total catch of each net (table 7). The random method of sample selection described previously was used.

Differences in age between small samples and total catches on individual days were quite large; however, age composition from the small samples was identical with the overall age composition from the entire catch for the period from May 27 to June 11 (table 6), and was only 3 percent different from the total sample of the period June 1-11 (table 7). Small samples were therefore adequate for determining age composition for the season but not for individual days.

LENGTH-WEIGHT RELATIONSHIP

All migrants processed from the fyke net catches were weighed to the nearest 0.5 g. on a triple-beam balance. The average weight by age was computed for each day's sample, and weight-gain curves were plotted by inspection (fig. 13). Each age class was treated separately since there were three separate size groups with little overlap, and combined mean weights would be meaningless. The apparent leveling off of weight after June is not proved by these data because samples taken after June represent small numbers of fish. A rapid weight increase was noted through June for yearlings of the 1955 brood, indicating an adequate supply of food. Average weights for the season were 11.46 g. for 2-year-olds, 8.80 g. for 1-year-olds, and 4.14 g. for fry. In comparison with migrants from Canadian and Russian lakes, the yearlings were somewhat heavier than those of Cultus Lake in 1927 and 1928, but were lighter than the average for yearlings from Kamchatka lakes (Krogius and Krokhin, 1948).

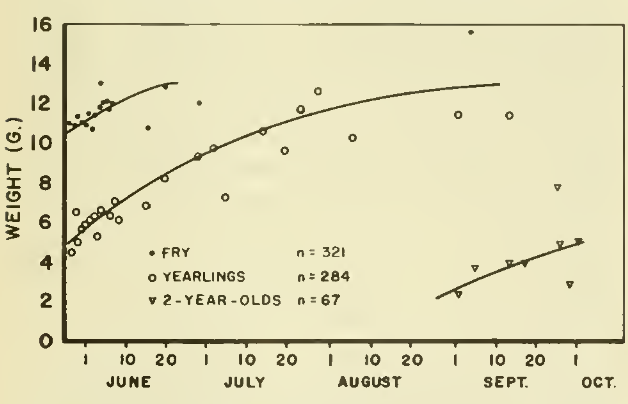

Figure 13.--Mean daily weights in 1957 of Brooks Lake migrants.

Almost all 2-year-olds of the 1954 brood migrated from the lake by the middle of June and during the short spring period gained weight rapidly. Active feeding evidently continues at least until the time of migration from the lake.

DAILY AND SEASONAL MIGRATION PATTERNS

Although the nets were fished for five 24-hour and five all-night periods to determine the diurnal characteristics of the migration, only the catches from May 30 to June 1 were large enough to warrant study.

Only newly hatched fry made any appreciable daytime migration, and these could not be effectively sampled with our coarse-mesh nets. Personnel working near the outlet daily observed only insignificant numbers of yearlings or 2-year-olds during the day. A few yearlings and 2-year-olds were captured during the day in the five 24-hour sets.

Catches on the nights of May 30-31 and May 31 to June 1 (at the peak of the seasonal migration) indicated that most fish left the lake in the darkest hours of the night (fig. 14). All three nets showed similar catch patterns except that catches of net 2 in midstream peaked slightly later than those from nets 1 and 3.

TABLE 7.--Comparison of small samples of fish of ages 1 and 2 years with total samples, caught in three fyke nets, Brooks Lake, June 1-11, 1957

[S=sample catch; A=additional catch not weighed, measured, or aged from scales.] [In number of fish.]

Date and item	Net 1		Net 2		Net 3		Total sample		Percent total sample	
	Age 1	Age 2	Age 1	Age 2	Age 1	Age 2	Age 1	Age 2	Age 1	Age 2
June										
1 S............	5	1	1	4	2	3	8	8	50	50
A............	20	7	10	9	36	19	66	35	65	35
Total............	25	8	11	13	38	22	74	43	63	37
2 S............	1	4	2	3	2	4	5	11	31	69
A............	17	47	1	9	21	33	39	89	30	70
Total............	18	51	3	12	23	37	44	100	31	69
3 S............	1	4	2	3	0	6	3	13	19	81
A............	2	4	6	6	22	31	30	41	42	58
Total............	3	8	8	9	22	37	33	54	38	62
4 S............	1	4	0	2	3	3	4	9	33	66
A............	7	7	0	0	3	6	10	13	43	57
Total............	8	11	0	2	6	9	14	22	39	61
5 S............	10	10	3	4	6	13	19	27	41	59
A............	26	41	0	0	39	104	65	145	31	69
Total............	36	51	3	4	45	117	84	172	33	67
6 S............	0	5	4	7	6	2	10	14	42	58
A............	54	118	6	17	38	45	98	180	35	65
Total............	54	123	10	24	44	47	108	194	36	64
7 S............	4	4	0	2	3	4	7	10	41	59
A............	19	14	0	0	40	119	59	133	31	69
Total............	23	18	0	2	43	123	66	143	32	68
8 S............	1	4	4	5	3	2	8	11	42	58
A............	19	61	0	0	12	9	31	70	31	69
Total............	20	65	4	5	15	11	39	81	33	67
9 S............	1	4	3	2	11	3	15	9	63	37
A............	6	41	0	0	0	0	17	45	27	73
Total............	7	45	3	2	11	3	32	54	37	63
10 S............	0	6	0	1	0	6	0	13	0	100
A............	20	43	0	0	13	15	33	58	36	64
Total............	20	49	0	1	13	21	33	71	32	68
11 S										
A............	2	1	0	0	5	1	7	2	78	22
Total............	2	1	0	0	5	1	7	2	78	22
S............	24	46	19	33	36	46	79	125	39	61
A............	192	384	23	41	229	382	455	811	36	64
Grand total............	216	430	42	74	265	428	534	936	36	64

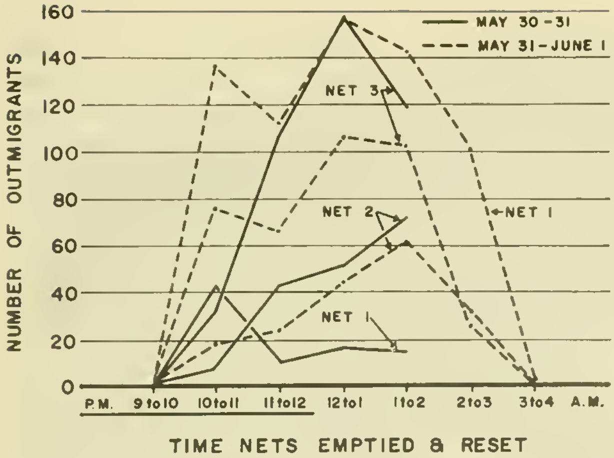

Figure 14.--Migration of sockeye salmon juveniles for two nights in 1957, Brooks Lake outlet.

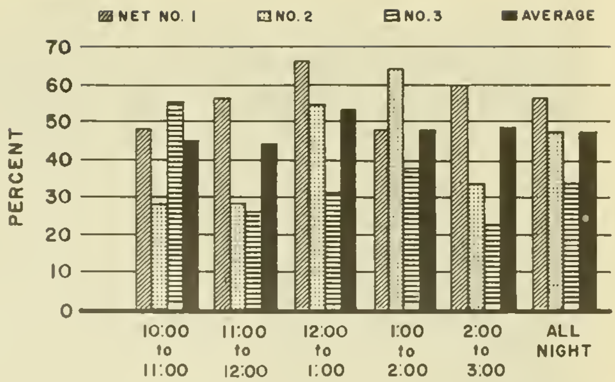

Figure 15.--Hourly catch of yearling sockeye salmon caught in each net expressed as a percentage of each net's total hourly catch, Brooks Lake outlet, night of May 31 to June 1, 1957.

On the basis of these night-long samples, the 1-hour period from 10 to 11 p.m. was selected for subsequent sampling. Later in the summer when darkness fell earlier, sampling was moved first from 9 to 10 p.m. and then 8 to 9 p.m. This early schedule avoided conflict with brown bears that fished for spawning adult salmon at the net sites below the weir later in the night during September.

On the night of May 30-31, the wing leads of net 1 were removed at 11 p.m. to see what effect this reduction in efficiency would have on the catch. The effect was immediate and drastic--although the catch of net 1 was usually the highest, it dropped to the lowest for the remainder of the night. This great reduction in catch was brought about by reducing the effective width of the net from 6.5 to 3 feet.

To detect relative differences in the proportions of yearlings and 2-year-olds caught by each of the three nets, the hourly catch of yearlings on the night of May 31 to June 1 was plotted as a percentage of the combined catch of yearlings and 2-year-olds for each net (fig. 15). For example, in net 2 from 10 to 11 p.m., 28 percent of that hour's catch consisted of yearlings and 72 percent of 2-year-olds. No major differences were apparent. The percentage of yearlings showed a slight increase during the middle of the night, but the range of the means was only 9 percent through the entire night. The catch of yearlings was progressively less from net 1 to net 3. Fluctuations in the hourly percentages by net were so slight that no adjustment in the sampling technique was made. Sampling during any single hour yielded representative samples.

Net 1 was the only net fished for the entire season; its total catch for each nightly 1-hour sampling period provided an index to seasonal abundance (fig. 16). Probably some migration had already occurred when fishing began on May 20, since migrants were caught the first night of fishing. Peak migration occurred on May 29 when 343 sockeye salmon were captured during a 1-hour period.

In previous years, migrant sampling had been discontinued in mid-June, but in 1957 test

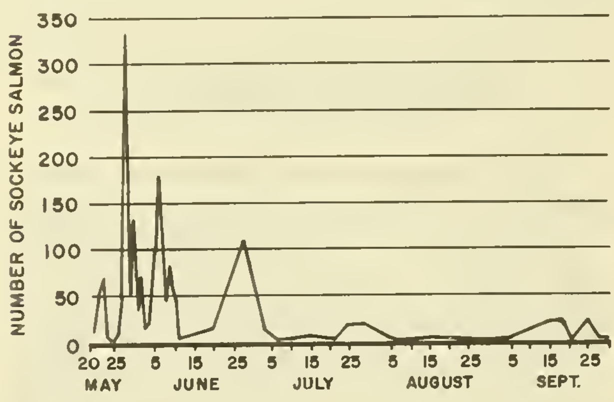

Figure 16.--Catch of downstream migrant sockeye salmon, Brooks Lake outlet, May 20 to September 25, 1957 (net 1 only, 1-hour catch each night).

fishing continued throughout the summer. A second major migration took place on June 28, and smaller migrations during the last of July and the middle of September. A few sockeye salmon migrated from the lake through the summer. Future programs requiring an estimate of total migration should take into consideration an extended migration period throughout the summer and fall. It is not known whether these summer migrants remained in Naknek Lake until the following spring, or whether they migrated immediately to the sea.

In addition to juvenile sockeye salmon seven other species of fish were caught in the nets: 881 sculpins *(Cottus* spp.); 57 coho salmon *(Oncorhynchus kisutch)*; 23 rainbow trout *(Salmo gairdneri)*; 9 Dolly Varden *(Salvelinus malma)*; 4 brook lamprey *(Entosphenus lamottei)*; 15 blackfish *(Dallia pectoralis)*; and 22 ninespine stickleback *(Pungitius pungitius)*. Almost all of the catches of these species were made at night. The coho salmon were caught from June 2 through 29, and some daytime migration of this species was observed by personnel counting adult sockeye salmon at the weir through June and July. Rainbow trout migrated sporadically from June 4 until October, and Dolly Varden first appeared at the end of September. A few lampreys were evident during May and early June, and blackfish appeared late in the summer. A few sticklebacks and large numbers of sculpins were caught intermittently throughout the summer.

MIGRATION OF JUVENILE SALMON UPSTREAM

The question had been raised as to whether juvenile sockeye salmon originating in Brooks River or Naknek Lake might migrate upstream into Brooks Lake. Such a phenomenon has been noted at some lakes, notably Karluk Lake on Kodiak Island, Alaska, and Babine Lake in British Columbia (Roy Jackson, personal communication). An upstream migration on a large scale at Brooks Lake would seriously complicate studies of survival and production of the indigenous lake population.

By the very nature of Brooks River this is not likely to happen. In the first place, juveniles attempting to swim from lower Brooks River or Naknek Lake would encounter Brooks Falls, which is about 8 feet high. An efficient gravity flow fish ladder enables adult salmon to bypass the falls, but it would be extremely difficult for juveniles to do so. Furthermore, several stretches of Brooks River have rapids so swift that it is difficult for a man to keep his footing.

Although it was deemed unlikely that small salmon, particularly fry, could migrate upstream, a stationary trap was constructed to intercept a portion of small fish that might do so and so provide a measure of the seriousness of the problem. The trap was located on a small point of land about 100 yards below the outlet of Brooks River on the right bank (fig. 17). It was simply constructed with two rigid leads of 1/4-inch-mesh wire cloth trap and a box trap of 3/8-inch-mesh wire cloth lined with 1/8-inch-mesh nylon bobbinet. One lead intersected the shore at an angle, and the other extended toward midstream where the current was too swift for fry to swim upstream. We assumed that small fish attempting an upstream migration would seek a path of least resistance along the shore. The trap was usually emptied and cleaned twice daily. Fish entering the trap eventually escaped, but a relative index of migration was obtained from fish remaining in the trap at the time of checking. The trap was installed June 2 and removed September 14. The catch by month is shown in table 8.

Three features of the trapping study are of particular interest: (1) The maximum catch of sockeye fry (244) was in July but was insignificant compared with the total probable downstream migration from Brooks Lake; (2) the catch of fry in June was small despite the fact that maximum downstream migration was observed during this period; and (3) threespine stickleback *(Gasterosteus aculeatus)* and ninespine stickleback, which do not usually occupy the same waters, were captured together.

Observations of Brooks River incidental to other activities supported the conclusion that the upstream migration of sockeye salmon

Figure 17.--Stationary trap for catching juvenile sockeye salmon migrating upstream in Brooks River, 1957.

juveniles is insignificant. At no time was any large migration upstream noticed, although personnel particularly watched for it. The few sockeye salmon fry that were caught in the trap probably originated in Brooks Lake, since the area below the trap provided an excellent resting place out of swift water for fish pausing during their downstream migration.

MIGRATORY BEHAVIOR OF JUVENILES AS DETERMINED FROM OBSERVATIONS

Observations of the migratory behavior of juvenile sockeye salmon were made 39 times between May 18 and September 27 on Brooks River and Brooks Lake and its tributaries. They are summarized as follows:

1. Yearling and 2-year-old sockeye salmon were evident to observers in appreciable numbers in Brooks Lake or River only at night at the outlet during the period of peak outmigration in late May and early June.

2. Large schools of sockeye salmon fry were observed at the outlet of Brooks Lake and at the mouth of Brooks River, particularly from mid-May to mid-June and again in September. These schools sometimes consisted of thousands of fish.

3. There was never any evidence of significant upstream migration from Naknek Lake or from Brooks River into Brooks Lake. On the contrary, whenever fry were evident, there was a continual downstream displacement as indicated in part by (2) above.

4. Sockeye salmon yearlings and 2-year-olds migrated from Brooks Lake to Naknek Lake within a single night.

5. Lake *(Salvelinus namaycush)* and rainbow trout, which lie in schools at Brooks Lake outlet during May and June, fed mainly on floating insects drawn to the outlet by surface current, but sometimes ate young salmon.

6. Sockeye salmon fry in Brooks Lake fed voraciously on periphyton, which breaks

TABLE 8.--Trap catches (by month), upstream migrant fish, Brooks River, June to September 1957

Species	June 2-30	July 1-31	Aug. 1-31	Sept. 1-14	Total
Sockeye salmon fry	54	244	2	2	302
Sockeye salmon yearlings		10			10
Coho salmon juveniles		1			1
Rainbow trout fry	2	151	47	7	207
Rainbow trout		3		1	4
Dolly Varden	2	3	3	1	9
Sculpin	135	137	59	46	377
Lamprey	2				2
Northern pike			1		1
Blackfish			1		1
Unidentified stickleback	7				7
Threespine stickleback	12	17	2	1	32
Ninespine stickleback	10	4	4	3	21

loose from the shallow bottom adjacent to the lake outlet on calm days.

7. All fry migrated out of Brooks Lake tributaries by the first of June.

8. The shallow shoreline areas of Brooks Lake were almost devoid of rooted aquatic vegetation for cover or food until July.

9. Downstream migrating salmonids were very reluctant to pass between weir pickets during daylight.

10. Rainbow trout fry were much more evident than sockeye salmon fry in streams and in the shallow shoreline areas except during May and June.

11. During their nesting periods, Arctic terns *(Sterna paradisaea)* and greater yellowlegs *(Totanus melanoleucus)* fed actively on concentrations of sockeye fry at the mouth of Brooks River. Their predation was minor, considering the tremendous numbers of fry and small numbers of birds.

12. Migrations of sockeye salmon from Brooks Lake occurred in May and June, and again in late July and mid-September.

PART III. JUVENILE SOCKEYE SALMON LAKE RESIDENCE

Sockeye salmon are unique among the Pacific salmon in their habits during the first year or two of life. Immediately after emerging from the natal gravels, most stocks migrate to a lake where they live for 1 or 2 years. This is an important and critical period in their life because during this time, when they are growing to migratory size, they are vulnerable to predators coexisting in the lake with them and to competition for food between themselves and other fishes. Until 1957 no investigation of lake-dwelling juveniles had been undertaken at Brooks Lake.

The objectives of the studies were to (1) evaluate the relative merits of tow nets, beach seines, and fine-mesh gill nets as tools for sampling fish; (2) determine seasonal and diurnal changes in vertical and horizontal distribution; (3) determine length and weight by age class; (4) determine food and its availability through the summer growing season; (5) evaluate the kinds and incidence of parasites; and (6) evaluate SCUBA (self-contained underwater breathing apparatus) as a means of observing natural behavior.

SAMPLING GEAR

Tow Net

One of three types of sampling gear used was a small high-speed tow net identical to that used by Canadian biologists (Johnson, 1956). The net was a cone-shaped fine-mesh nylon bag 9 feet long with a rigid ring 3 feet in diameter holding the mouth open. It was towed through the water as fast as possible by two boats powered with large outboard motors.

Tows were made on 12 nights for a total of 7-1/2 hours of actual fishing. Only 10 sockeye salmon were caught, and 5 of these were taken in one 15-minute tow. Most tows were made during twilight (the time when the Canadians caught most fish) but were also made at other times. Weather ranged from flat calm to very rough, and lake areas fished ranged from shoal to midlake. All tows were at the surface. The catch of fish per hour was 1.3, compared with a maximum of 384 per hour in the Canadian studies.

Further experimentation with modified tow nets might produce better catches, but from our experience it is apparent that catches are affected by many variables. Often the lake was too rough to operate boats, particularly at night. Since our net was only 3 feet in diameter, a slight shift in depth of concentration of fish could greatly affect the catch (it was learned in gill net sampling that weather affects vertical distribution). Probably the major contributing factor to our lack of success was the low density of resident sockeye salmon at Brooks Lake in contrast to the high density encountered by Johnson (1956).

Beach Seines

A second sampling gear, used on 11 occasions, was a 50- by 5-foot nylon beach seine with 1/4-inch mesh (bar measure). The net proved to be unsatisfactory as a sampling tool because young-of-the-year were able to swim through the mesh during the early part of the season, and yearlings were seldom present along the shoreline--the only place a seine could be used.

Only one beach seine haul resulted in a large catch. A comparison of the length frequencies of juveniles in this catch (fig. 18) with those of juveniles in July gill net catches (fig. 19) indicates considerable disparity, probably reflecting different growth from gill net-caught fish because of their atypical diet in the shallow (less than 3 feet) beach environment. Selectivity of gill nets undoubtedly accounted for the lack of a mode at 50 mm., representing the fry population (fig. 19). Beach seine-caught fish had this 50-mm. mode, but lacked a mode at 85 to 100 mm., probably reflecting slower growth of beach-dwelling yearlings (fig. 18).

Gill Nets

Gill netting proved to be the best method of catching pelagic juvenile sockeye salmon, and most of our data on abundance, size, and food were from gill net samples. Similar nets had been used successfully for sampling salmonids by the Washington State Department of Fisheries in forebays of high dams (Rees, 1957).

The gill nets were of three basic types. By modification and combination, seven types of sets were possible (fig. 20):

Type I--Floater, graduated mesh. Five 15-foot-square panels of white nylon mesh, sizes 1/2, 3/4, 7/8, 1, and 1-1/8 inches, a total length of 75 feet.

Type II--Floater, graduated mesh. Six 15-foot-square panels of brown nylon mesh, sizes 1/2, 3/4, 1, and 1-1/2, 2, and 3 inches a total length of 90 feet.

Type III--Floater, uniform mesh. A 50- by 6-foot white nylon mesh net, 3/4 inch.

Type IIIa--Same as type III, but submerged, fishing on bottom.

Type IV--Combination floater and submerged. A type I and type II net attached end to end and suspended vertically with one end at the surface and the other submerged. Total length, 165 feet. Used only in deep water.

Type V--Combination floater and submerged. A tandem arrangement of three type I

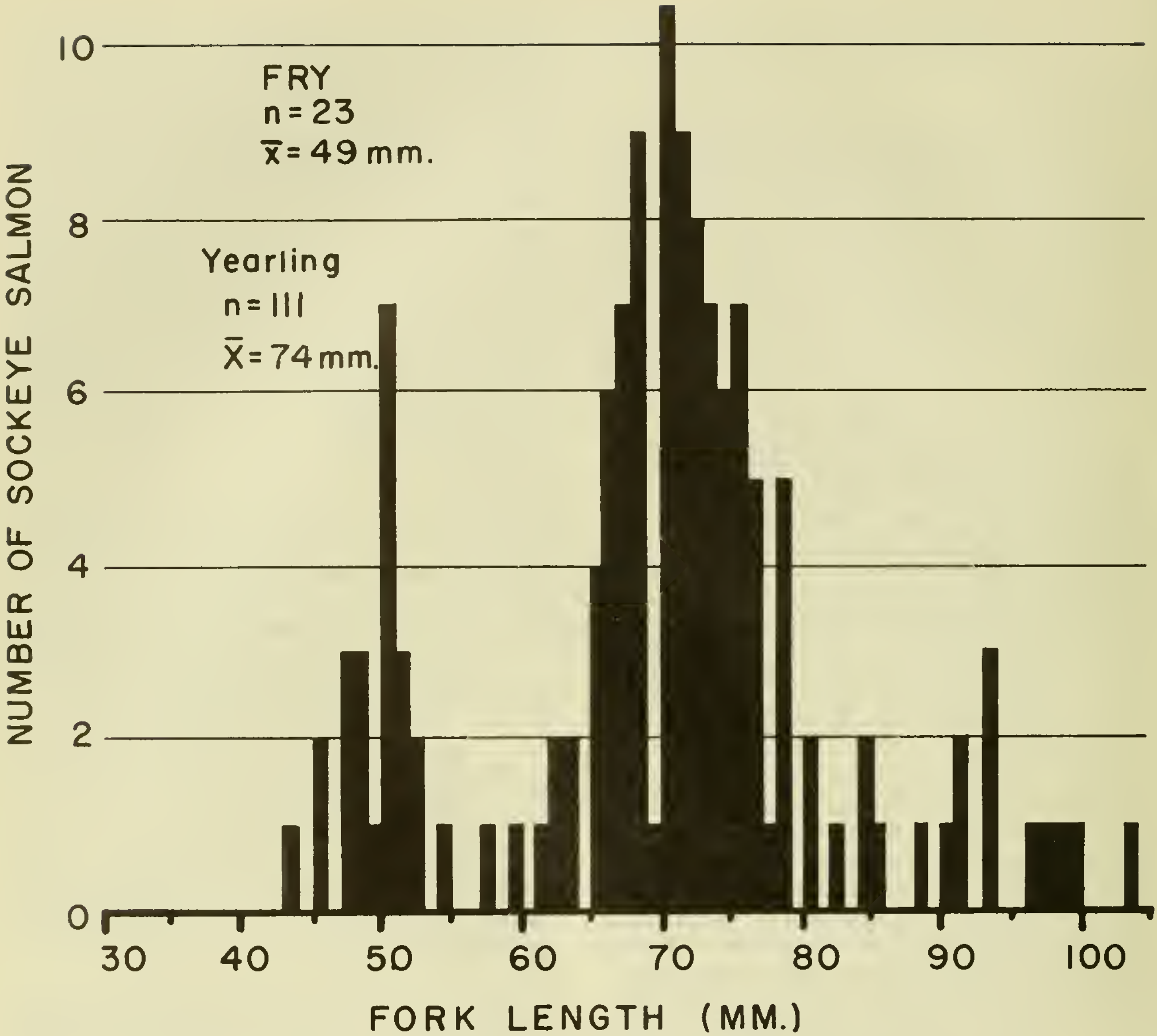

Figure 18.--Lengths of juvenile sockeye salmon caught in beach seine, Brooks Lake, July 3, 1957.

nets adjoining each other but fishing at three depths: 0-15 feet, 15-30 feet, and 30-45 feet.

Type VI--Floater. Two type III nets attached end to end, 100- by 6-foot white nylon mesh, 3/4 inch.

Type VII--Submerged. A type II net with an extra lead line that caused it to sink and fish the bottom.

Fishing began June 12 and continued until October 6. During June and the first part of July, sets were made at various depths from shore to midlake and from one end of the lake to the other at locations shown in figure 21 to determine where sockeye salmon could be found. Stations I, II, and III in figure 21 were also used in the limnological studies that will be discussed later. From mid-July through mid-September fishing was continued at only two general locations: At station I, in the littoral zone from shoreline to dropoff; and at station II or III in midlake. From mid-September to October 6, only the midlake locations were fished. By fishing a littoral and a deep-water area simultaneously, however, limited comparisons of abundance in the two habitats could be made.

The efficiency of the nets was greatest when they were new at the start of the season and least at the end of the season, owing to a gradual increase in number of holes and mended sections. No correction was applied for reduced efficiency; it is not believed to be a major factor because nets were discarded when they reached a point where major repairs were needed. On a few days nets over the shallow littoral area were fouled with detached periphyton, which also probably reduced efficiency. No correction was practical in this case either. Good catches were often made under these conditions, suggesting that the fouling did not appreciably reduce a net's catching ability.

Fish were removed from the nets daily, usually between 9:30 and 11 a.m., except when bad weather occasionally made boating unsafe. At the start of the season nets were checked morning and evening, but so few fish were caught during the day that the evening check was discontinued. One or two men checked the nets (fig. 22); two men were necessary in rough water and desirable even when the water was calm. Nets were left in the water continuously, except when repairs were made or the location changed.

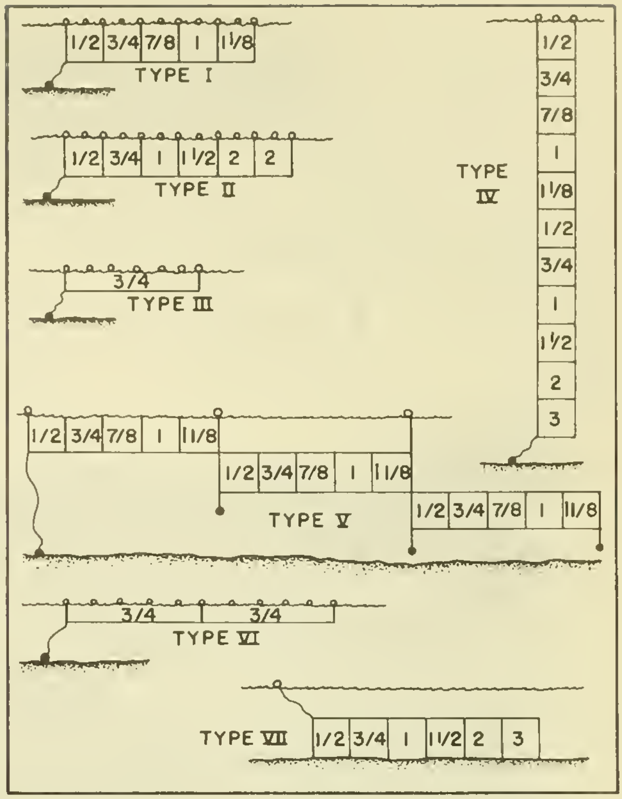

Figure 20.--Diagrammatic sketch of seven types of gill net sets used in sampling lake-resident juvenile sockeye salmon in Brooks Lake in 1957. (All sizes are stretch measure in inches.)

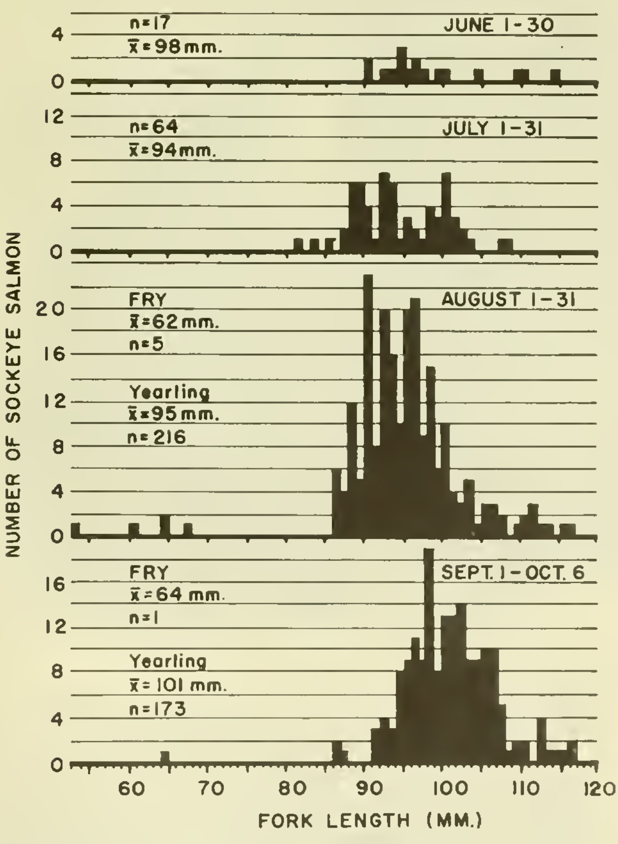

Figure 19.--Lengths of juvenile sockeye salmon caught in gill nets, Brooks Lake, June 1 to October 6, 1957.

For each fish captured a record was made of the species, net type, mesh size, and location of fish in mesh (top, middle, or bottom), fork length, weight, location and depth of water of the set, and wind. Scales were taken for age analysis.

Five hundred and five juvenile sockeye salmon were caught during the season in all types of gill nets (table 9), with August being the most productive month. Other species also were caught and processed in the same way as were the juveniles, with the exception of adult sockeye salmon which were counted and released. Scales were not preserved from species other than sockeye salmon.

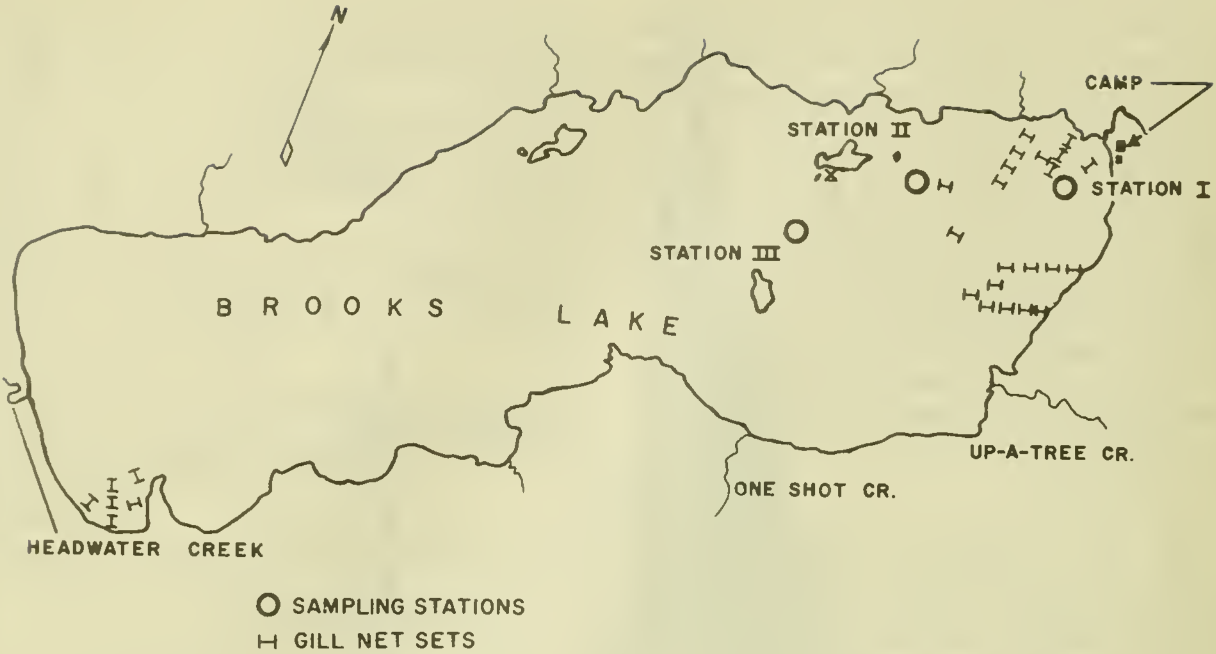

Figure 21.--Gill net and limnological sampling stations, Brooks Lake, 1957.

TABLE 9.--Gill net catches of all species by month, June to October 1957, Brooks Lake

Species	June	July	August	Sept.	Oct.	Total
Juvenile sockeye salmon	20	73	232	178	2	505
Adult sockeye salmon	0	36	94	7	1	138
Coho salmon	5	13	8	0	0	26
Rainbow trout	6	16	32	8	0	62
Dolly Varden	0	3	0	1	0	4
Lake trout	4	16	1	2	0	23
Round whitefish	5	36	74	5	0	120
Pygmy whitefish	0	25	0	1	0	26
Sculpins	1	52	19	6	0	78
Unidentified sticklebacks	0	3	5		0	8
Threespine sticklebacks			3	6	0	9
Ninespine sticklebacks			3	2	0	5
Blackfish	0	0	0	1	0	1

An unusual finding in the gill net catches was the occurrence of pygmy whitefish *(Coregonus coulteri)*, which were previously unreported in this region of Alaska. They were caught both in shoal areas in Headwater Bay and in deep sets in other parts of the lake. What little is known of the life history and distribution of this species has been summarized by Eschmeyer and Bailey (1954).

The catches of each species in table 9 are not directly comparable because some species were not usually associated with juvenile sockeye salmon. For instance, lake trout

Figure 22.--Checking experimental gill net, Brooks Lake, 1957.

and round whitefish *(Coregonus cylindraceum)*, which are usually deep-water species, would probably have been caught in greater numbers had more deep sets been made (Rawson, 1951). Furthermore, fish larger and smaller than juvenile sockeye salmon were not as likely to be caught because of mesh selectivity. All species known to be in the lake were caught in the gill nets with the exception of northern pike *(Esox lucius)* and Artic grayling *(Thymallus arcticus)*, which are both rare.

The incidental catch of 138 adult sockeye salmon did not significantly detract from the production of the 1957 brood year because most of them were released alive.

Mesh sizes larger than 1 inch were relatively unproductive except for adult sockeye salmon. The 3/4-inch size was by far the most efficient for juvenile sockeye salmon, catching 91 percent of the total catch. Sockeye salmon fry were not successfully sampled because the twine on the 1/2-inch size was too thick in proportion to the interstices.

SEASONAL AND DIURNAL CHANGES IN VERTICAL AND HORIZONTAL DISTRIBUTION

To make valid comparisons of catches it was necessary to equate nets of different sizes to a standard unit. A standard unit was defined as 75 square feet of mesh; thus each 15-foot-square panel of type I, II, IV, V, and VII nets was equal to three units, and each 50-foot length of Type III and VI nets was equal to four units (fig. 20).

Even though most catches were made at night, a 24-hour period was used as the standard time unit. Nets were checked once each 24-hour period. Thus, a unit of effort was the catch per 75 square feet of a given mesh size in a 24-hour period. Catches of species other than sockeye salmon did not warrant detailed catch per unit of effort analysis, nor did catches of juvenile sockeye salmon, except for those taken in nets of 3/4-inch mesh.

A comparison of the monthly catch of sockeye salmon from nets in the littoral area with the catch from nets in midlake shows that littoral sets produced a relatively constant catch of about 0.6 sockeye salmon per 75 square feet per day, whereas the midlake net's catch increased steadily from 0 to 0.65 sockeye salmon per unit per day (table 10). This indicates that sockeye salmon inhabit the shallow shoreline areas in the summer and increasingly disperse into deep water as the season advances. Food studies, as shown later, further substantiated this conclusion. Krogius and Krokhin (1956a) found the same general pattern of progressive migration from littoral to pelagic regions in Lake Dalnee, Kamchatka, suggesting that this is a universal behavior trait of juvenile sockeye salmon. If littoral and midlake nets were sampling the same population in proportion to its density, one would expect the catch per hour on littoral sets to diminish as the catch in midlake nets increased. This did not occur, and no explanation is offered.

Table 11 shows the depth distribution of sockeye salmon caught between the surface and the 45-foot depth at midlake stations for 28 days on which catches were made. From July 21 through August 22, a type V net was used, simultaneously sampling all depths from 0 to 45 feet. Fifteen, or 79 percent, of the sockeye salmon were caught in the surface net (0-15 feet), while only 4, or 22 percent, were caught from depths of 15 to 45 feet. This is in complete agreement with results from Lake Dalnee, Kamchatka, during the summer months (Krogius and Krokhin, 1948).

From August 29 through October 6 a type I net was used, permitting sampling only of the 0- to 15-foot level (table 11). When catches of the surface net of the entire period are combined, the catch distribution by 5-foot intervals in the upper 15 feet substantiates the conclusion that juvenile sockeye salmon were concentrated near the surface to 10 feet, where 91 percent were caught, while only 9 percent were caught between 10 and 15 feet.

To determine the optimum time of day to catch fingerlings with the tow net, three gill nets were checked every 2 hours on August 15 and 16. These consisted of two type II nets and one type III net, and all were fished in water less than 15 feet deep. The entire catch was made between midnight and 4 a.m. The night was moonlit and calm, making locating and checking the nets easy. This night's catch indicated that best success with tow nets at the surface in shallow water could be expected around 2 a.m.

LENGTH AND WEIGHT BY AGE CLASS

It has been previously shown that age groups of juveniles in Brooks Lake in 1957

TABLE 10.--Comparison of monthly littoral and midlake catches of sockeye salmon in Brooks Lake from June to September 1957 (3/4-inch mesh only)

[N= number salmon; S= number sets; U= units of 3/4-inch mesh (one unit is 75 square feet of net)]

Net type and item	June		July		August		September	
	Littoral	Midlake	Littoral	Midlake	Littoral	Midlake	Littoral	Midlake
I								
N	11		11	0		12		33
S	7		7	2		3		17
U	21		21	6		9		51
II								
N	0		19	0	39			
S	5		17	1	49			
U	15		51	3	147			
III and IIIa								
N	7		32		130		18	
S	11		7		35		20	
U	44		28		140		80	
IV								
N		0		0				
S		2		4				
U		6		12				
V								
N				6		14		
S				10		19		
U				90		171		
VI								
N					29		105	
S					2		11	
U					16		88	
VII								
N					0		0	
S					2		11	
U					6		33	
Total								
N	18	0	62	6	198	26	123	33
S	23	2	31	17	88	22	42	17
U	80	6	100	110	309	180	201	51
Catch per unit 3/4 inch mesh	0.23	0	0.62	0.05	0.64	0.14	0.61	0.65

TABLE 11.--Number of sockeye salmon caught by depth at stations II and III (midlake) for 28 days with complete data, July 21 to October 6, 1957

Date	Depth (feet)								
	Surface net			Middle net			Deep net		
	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45
				Number of fish					
July									
21-22	0	1	0	0	0	0	1	0	0
24-25	0	1	0	0	0	0	0	0	0
30-31	1	0	0	0	0	0	0	0	0
31- 1	0	0	1	0	0	0	0	0	0
August									
4- 5	0	1	0	0	0	0	0	0	0
6- 7	0	0	0	0	0	0	0	1	0
8- 9		(1)[1]		0	0	0	0	0	0
9-10		(1)		0	0	0	0	0	0
11-12		(4)			(1)		0	0	0
13-14	1	0	0	0	0	0	0	0	0
14-15	2	1	0	0	0	0	0	0	0
21-22	0	0	0	0	1	0	0	0	0
Total	4	4	1	0	1	0	1	1	0
August									
29-30	6	0	0						
30-31	0	6	0						
31- 1	0	1	0						
September									
1- 2	0	3	0						
4- 5	1	2	0						
5- 6	3	0	0						
6- 7	4	1	0						
7- 8	0	3	0						
9-10	5	0	0						
15-22	0	10	0						
23-25	1	0	3						
25-26	1	0	1						
26-27	0	3	0						
27-28	1	0	0						
29-30	0	2	1						
October									
4- 6	0	2	0						
Grand total	26	37	6						
Percent	27	54	9						

[1] Numbers in parenthesis indicate that the exact depth was not recorded; not included in totals.

could be distinguished by length-frequency distributions; therefore, gill net-caught fry and yearling fish were distinguished on the basis of size alone without recourse to scale reading (fig. 19).

The decrease in mean length in June and July may be explained by the inclusion in June samples of larger 2-year-olds which subsequently migrated from the lake and were no longer available in August. Yearlings increased in mean length from 95 mm. in August to 101 mm. in September. Two-year-olds of the same age class in the 1957 spring outmigration (fig. 12) were only 109 mm. long, or only 8 mm. longer than these fish in the fall. If it is assumed that yearlings of each of these year classes grew at the same rate, the fish we sampled in the fall of 1957 would gain only an additional 8 mm. during the ensuing 7 winter months. This projected slow winter growth contrasts with the 6 mm. of rapid growth in only 1 month during the latter part of the summer of 1957.

The average daily weight of combined samples of gill net-caught fingerlings is shown in figure 23. Points are scattered, indicating

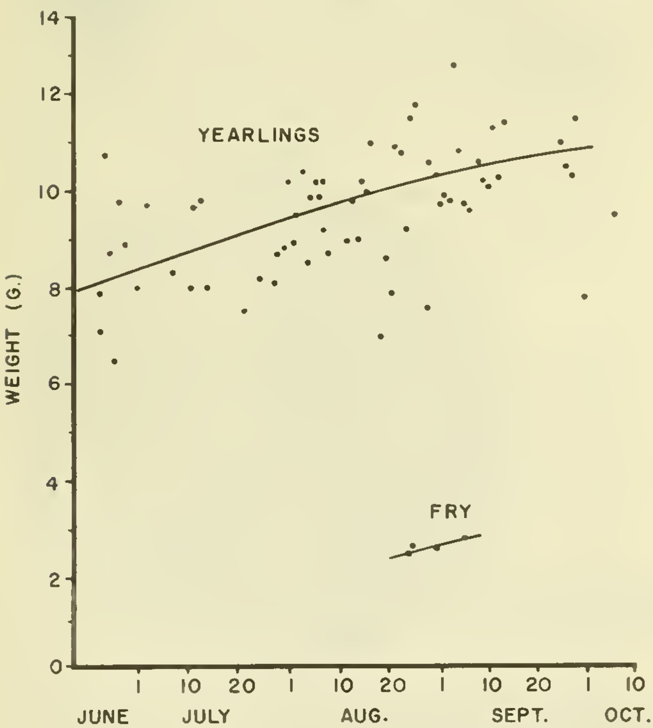

Figure 23.--Average daily weights of sockeye salmon caught in gill nets in Brooks Lake, from June to October 1957. (Curves fitted by inspection.)

variable growth, possibly because of differences in diet. This contrasts with more uniform weights of the 1957 outmigration (fig. 13). Any final conclusions based on these limited 1957 weight data would be premature, but one may speculate that fish far below average weight either perish during the winter, or compensatory growth allows them to catch up with the rest of the fish by the time of spring migration. Apparently growth conditions in Brooks Lake were about the same in 1957 as in 1956 since the 2-year-olds of the 1954 brood were the same weight at the start of the 1957 outmigration as were the 1955 brood fish at the end of the 1957 summer season. This conclusion assumes that little weight gain occurred during the winter of 1957-58, as indicated by the flattening out of the weight curve in figure 23. Too few fish were caught from the 1956 brood to draw any conclusions on their growth.

FOOD AND ITS AVAILABILITY THROUGH SUMMER GROWING SEASON

Stomach contents of all fish from gill nets were examined. Each fish was weighed and measured, and a scale sample was taken for mounting in the same manner as previously described for fyke net-caught fish. Stomachs were then excised with a small scissors, and the estimated percentage of fullness recorded (empty = 0 percent, distended = 100 percent). The contents were placed on paper towels and allowed to drain, after which they were placed in graduated centrifuge tubes where total volumes were measured by water displacement to the nearest 0.05 ml. At the beginning of the season an attempt was made to measure volumes for each food organism, but the volumes were so small that they could not be accurately measured with available equipment.

After total volume was measured, counts of each organism were made. Zooplankters were classified by genus and insects by common names (or orders, if specific identification was in doubt). Only whole or major portions of insects were counted as individuals. When insect fragments occurred, no attempt was made to estimate the original number. This procedure prevented errors of duplication but made the totals minimal.

Because zooplankters usually were too numerous to count, their numbers were estimated as follows: The bottom of a petri dish was marked into 1-cm. squares with a diamond-tipped pencil; plankters were uniformly distributed over the dish; and at least four squares were counted through a binocular microscope. The average of the counted squares was then multiplied by the area of the petri dish (64 cm.^{2}) to estimate the total numbers.

To compare changes in diet, the season was arbitrarily separated into three periods (July, August, and September), and food of all gill net-caught fish from each period was combined (fig. 24). The following significant facts are apparent:

1. Contrary to the usual belief that sockeye salmon are primarily plankton feeders, insects were found in an even greater percentage of stomachs examined during the season than was plankton--30.2 as opposed to 26.2.

2. There was a well-defined progressive seasonal shift in the diet from insects during the first part of the summer to plankton during the latter part of the summer. This same shift in diet was also found by Russian investigators at Lake Dalnee, Kamchatka (Krogius and Krokhin, 1956a).

3. Incidence of empty stomachs increased progressively through the season.

4. A few sockeye salmon were piscivorous and even cannibalistic, as indicated in the "other" category in figure 24, which comprised mostly fish remains.

Speculation on the implication of these facts leads to some interesting tentative conclusions:

1. The period of insect feeding corresponds to the period of most rapid growth of juveniles during the spring and early summer, indicating that availability of insects during a given year may be more important to the juveniles' well-being than availability of plankton.

2. Winged insects, which make up the bulk of the diet, are generally more abundant over the littoral areas adjacent to land. Thus, preference (or availability) of insects near shore during the early summer is conducive to concentrating sockeye salmon near the shoreline (table 10).

3. The simultaneous movement to mid-lake areas, decrease in insect feeding, increase in plankton feeding, and increased incidence of empty stomachs all contribute to slower growth and early formation of an annulus.

4. Availability is probably the governing factor in the lower incidence of insect feeding as the season progresses. Gross observations indicate that the peak of insect production is in June, coinciding with the period of maximum daylight. By October very few winged insects are evident at Brooks Lake.

5. Sockeye salmon select individual food organisms, even species of plankton. In many instances stomachs of fish caught at the same time and place contained entirely different organisms. Sometimes a stomach from a fish would contain only one species of plankton in large numbers, while a fish captured in adjacent meshes of a gill net would contain another species.

The shift from insects to plankton through the season in terms of total numbers is shown in table 12. Total numbers of organisms are shown rather than frequency of occurrence as in figure 24. The overall ratio of individual insects to plankton organisms was 1:25. The percentage fullness of stomachs through the season was also measured (fig. 25). Sockeye salmon ate less as the season progressed, with the incidence of 0 to 10 percent fullness more than doubling, from 22 percent in June and July to 59 percent in September. This slackening of feeding further explains the late summer decrease in growth rate and fall annulus formation.

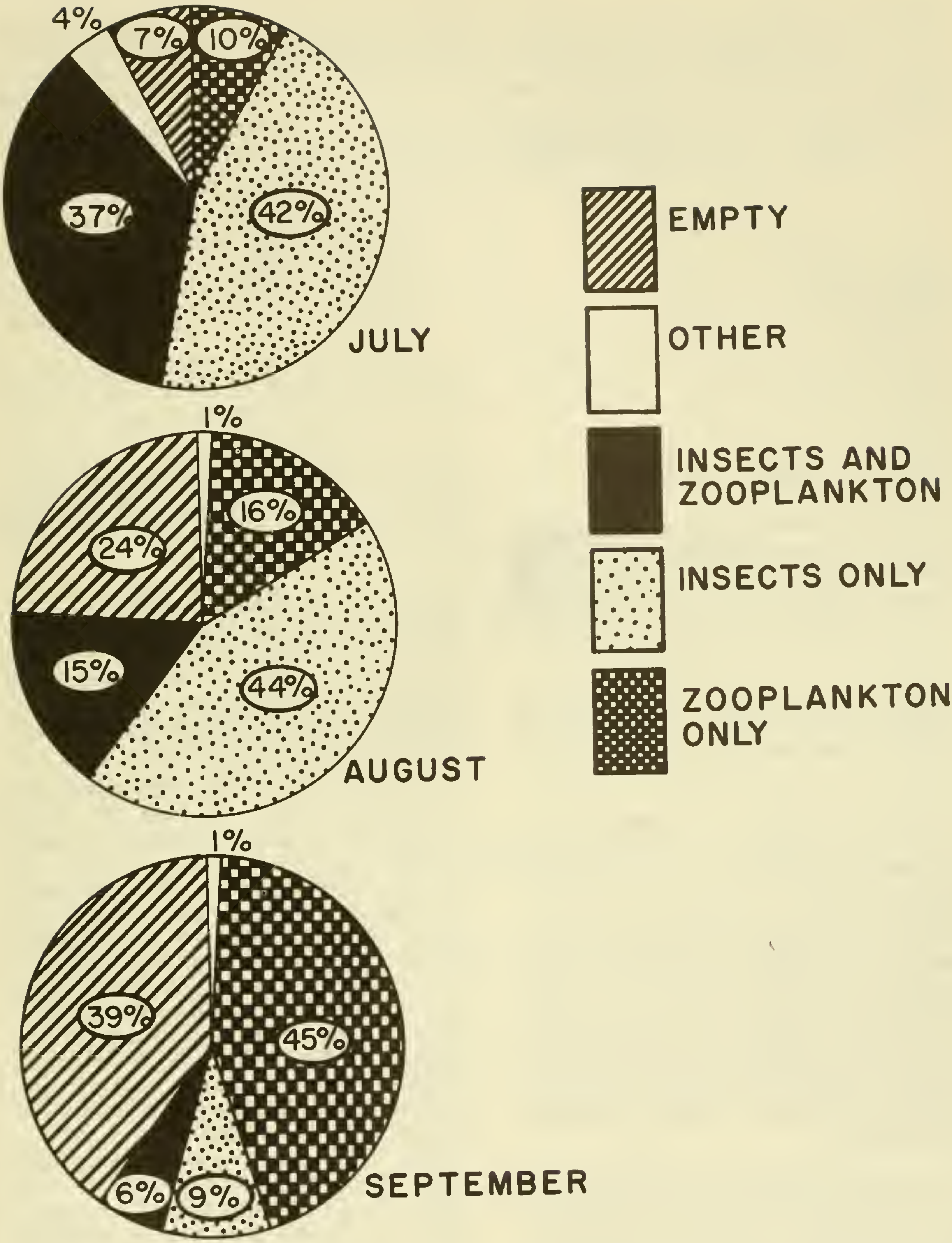

Figure 24.--Percentage of total stomachs by month containing each type of food, gill net-caught sockeye salmon, July to September 1957, Brooks Lake.

TABLE 12.--Frequency of occurrence of insects and plankton in sockeye salmon captured in Brooks Lake, June 27 to September 12, 1957

Period	Individual fish containing-- Plankton	Individual fish containing-- Insects	Total plankters	Total insects	Plankters per fish	Insects per fish
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
June 27-July 31	49	83	45,042	1,850	919	22
August 1-31	64	120	36,576	5,202	572	43
September 1-12	89	27	101,289	314	1,138	11
Total	202	230	182,907	7,366	905	32

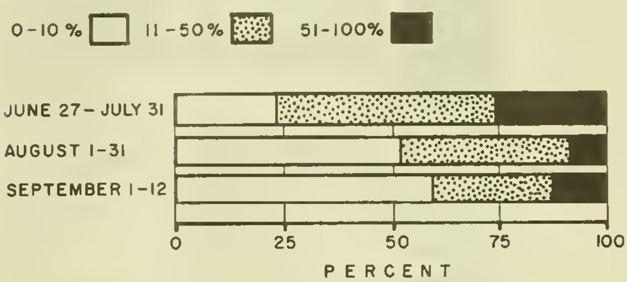

Figure 25.--Percent fullness of stomachs from gill net-caught juvenile sockeye salmon, Brooks Lake, June 27 to September 12, 1957.

The species composition of food items was also compared through the season (table 13). Four species of zooplankton (*Daphnia longispina, Bosmina longirostris, Bosmina coregoni*, and *Cyclops* sp.) made up over 96 percent of the plankton. The relative percentages of each species were almost identical in July and September, whereas in August, *Cyclops* doubled in frequency of occurrence and *Daphnia* occurred only one-third as often. During this time no major fluctuations in actual abundance of plankton occurred in the lake, as shown in part IV, the section on plankton distribution and abundance.

More than 76 percent of the insects eaten by juvenile salmon were midges. This high ratio of midges to other insects in stomachs was quite constant through the summer in contrast to marked differences in the species composition of plankton in the diet from month to month. The abundance and availability of midges is apparently an important factor in sockeye salmon ecology at Brooks Lake.

The absolute number of each kind of organism in stomachs probably is of little significance, except as a relative measure of the number of separate ingestions or food selections made. Ninety-six percent of individual organisms were plankters, and only 4 percent were insects (table 13).

Sockeye salmon juveniles fed upon a greater variety of food than any other fish species present in Brooks Lake (table 14). This food included 9 different planktonic forms (10 including copepod nauplii), 19 insects, and 3 identified fish (sockeye salmon, sculpins, and pygmy whitefish). Two other fish species in Brooks Lake (whitefish and sticklebacks) are competitors for plankton food. This competition was probably of little consequence in 1957, considering the high density of zooplankton and low density of sockeye salmon, whitefish, and sticklebacks. In years of greater densities of juvenile sockeye salmon, however, competition from sticklebacks might be a serious problem. Krogius and Krokhin (1956a, 1956b) and Krogius (1951) found in Lake Dalnee, Kamchatka, that survival of sockeye salmon is directly related to the abundance of threespine sticklebacks.

All fish except blackfish were insectivorous, and competition for winged insects may have been acute. We had no direct way of detecting such competition, but despite the superabundance of insects in the area, no quantities of floating dead insects were observed on the lake. If a surplus of insects were present, such concentrations would have been visible on the surface in calm weather. Most species of fish were easily caught with an artificial dry fly anywhere on the periphery of the lake, and trout were often observed feeding on insects along the lake shore near the field station, suggesting high utilization of floating insects.

There was no indication of serious predation by other fish on sockeye salmon, although lake trout, which are voracious fish-eaters, could be a serious threat if present in sufficient numbers. Lake trout, however, are not numerous and do not grow as large in Brooks Lake as in adjacent lakes. Rainbow trout were mainly insectivorous in Brooks Lake in 1957, corresponding with findings in British Columbia lakes by Idyll (1942), who cites six papers documenting the preference of rainbow trout for insects, even when fish are readily available.

Many of the statements in the foregoing section on juvenile sockeye salmon in their lacustrine environment are based on limited data, and some of the conclusions are in the realm of conjecture. Further, food relationships may be entirely different during the winter (which has not been studied) or during other years. Nevertheless, factual published data on this subject are scant, and findings presented will be useful in future comparative studies at Brooks Lake and elsewhere.

PARASITES

A record was kept of external parasites whenever they were seen and of internal parasites encountered during the analysis of stomach contents of fish caught in Brooks Lake. Table 15 lists the parasites and their hosts. The occurrence of the cestode *Triaenophorus* indicates that sockeye salmon are occasionally piscivorous because the adult *Triaenophorus* requires an intermediate fish host for maturation. Young sockeye salmon could only have become infected by eating an infected fish. Lake trout contained both larval and mature forms of *Triaenophorus*, as might be expected since they occasionally feed on sculpins, sockeye salmon, and sticklebacks.

The parasitic copepod *Salmincola edwardsii* was commonly found around the mouths and gills of adult sockeye salmon in the lake but was never found on adults examined as they entered the lake at the weir trap. This indicates

TABLE 13.--Plankters and insects contained in stomachs of sockeye salmon captured in Brooks Lake, June 27 to September 12, 1957

Period and number stomachs examined	Plankters						Insects			Total plankters	Total insects
	Total	*Cyclops*	*Diaptomus*	*Daphnia*	*Bosmina.*	Other	Total	Midges	Other		
	Number	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*
June 27 to July 31 105	45,042	37.90	0.74	44.77	16.23	0.36	1,850	77.89	22.11	96.05	3.95
August 1-31 202	36,576	66.19	2.25	12.38	14.42	4.76	5,202	76.23	23.76	87.55	12.45
September 1-12 158	101,289	37.64	3.60	41.10	17.58	0.08	314	80.57	19.43	99.69	0.31
Entire season 465	182,907	43.41	2.63	36.26	16.62	1.09	7,366	76.84	23.16	96.13	3.87

TABLE 14. --Checklist of organisms found in stomachs of fish caught by gill nets, beach seines, and tow nets, Brooks Lake, 1957

Organisms	Juvenile sockeye salmon	Coho salmon	Rainbow trout	Dolly Varden	Lake trout	Round whitefish	Pygmy whitefish	Sculpins	Stickle-backs	Black-fish
Zooplankton										
Bosmina coregoni	x						x		x	
Bosmina longirostris	x						x		x	
Ceriodaphnia	x									
Chydorus	x					x				
Conochilus	x									
Cyclops sp.	x					x	x		x	
Daphnia longispina	x					x	x		x	
Diaptomus	x								x	
Eurycercus						x				
Holopedium gibberum	x								x	
Copepod nauplii	x									
Plecoptera (Stoneflies)	x		x		x					
Odonata										
Damselflies			x							
Dragonflies			x							
Dragonfly naiads				x	x					
Coleoptera										
Beetles			x					x		
Hemiptera										
Back swimmers	x		x							
Waterboatmen			x							
Waterstriders	x									
Fragments	x	x	x			x				
Homoptera										
Leafhoppers	x							x		
Fragments	x	x	x							
Neuroptera										
Lacewings	x	x	x							
Trichoptera (Caddisflies)	x	x	x	x	x	x		x		
Lepidoptera										
Moths			x							
Diptera										
Crane flies	x		x							
Deer flies	x									
Horn flies					x					
Horse flies	x		x							
Midges (larvae)	x		x	x		x	x	x	x	
Midges (winged)	x	x	x	x		x	x	x		
Mosquitoes	x									
Fragments	x	x	x			x		x		
Hymenoptera										
Ants (winged)	x		x			x				
Bees			x							
Wasps	x	x	x					x		
Amphipods			x			x				
Clams						x		x		
Leeches								x		
Mites	x									
Snails						x		x		x
Spiders	x		x							
Pygmy whitefish	x				x					
Salmon eggs								x		
Salmonids	x	x	x		x					
Sculpins	x		x		x			x		
Sticklebacks				x	x					

TABLE 15.--Parasites and their hosts found in catches of fish from Brooks Lake, 1957

Name and type of parasite	Stage of maturity	Juvenile sockeye salmon	Adult sockeye salmon	Rainbow trout	Lake trout	Dolly Varden	Sculpins	Sticklebacks
Salmincola edwardsii								
External	Mature		x	x	x			
Triaenophorus sp.								
Internal	Mature[1] and larval	x			x[2]		x	x
Eubathrium sp.								
Internal	Mature	x		x	x	x		
Dibothriocephalus latus								
Internal	Pleurocercoids	x		x				
Schistocephalus solidus								
Internal	Larval						x	x
Trematodes								
Internal	Mature						x	

[1] Mature forms in sockeye salmon and immature forms in sculpins and sticklebacks.
[2] Lake trout stomachs contained immature and adult forms.

that they acquire the parasite after entering the lake and that infestation is very rapid. There were no apparent effects from these ectoparasites, and they probably do little harm. Infestations were heaviest during July and diminished in August and September.

Sculpins and sticklebacks were often heavily infested with trematode cysts and the trematode *Schistocephalus solidus.*

Lake trout were t ıe most heavily parasitized fish in Brooks Lak , most commonly by the cestode *Eubothrium* ;p., but also by *Salmincola* and *Triaenophorus.* These same parasites are characteristic in lake trout of Great Bear Lake (Miller and Kennedy, 1946). The large heads and thin, emaciated bodies of the trout were evidence of the infestation.

The occurrence of plerocercoids of *Dibothriocephalus latus* in sockeye salmon and rainbow trout was expected because adults of this parasite were often observed in bear feces in streams where bears fed on salmon.

Probably parasites have little effect on sockeye salmon in Brooks Lake, except beneficially in possibly limiting the predatory lake trout population.

SCUBA

SCUBA has been used with considerable success in fish behavior research in relatively warm tropical and temperate waters wherever transparency is high enough to permit good visibility. A limited trial was made at Brooks Lake in 1957 to evaluate its potential in observing, in cold water, the distribution and behavior of sockeye salmon during their lacustrine life. Equipment included the following: compressed air tanks and regulator, rubber dry suit with hood and gloves, long wool underwear, wool socks, swim fins, face mask, and safety line.

On the afternoon of August 3, three dives were made in calm water under an overcast sky. Figure 26 shows the diver preparing to dive. His verbatim description of each dive follows:

Dive 1--Dive was of 10 minute's duration and extended from station I in 5 to 6 meters of water 100 yards south along the bottom, which was completely covered with a mat of vegetation. No fish were observed.

Dive 2--Dive was made in immediate vicinity of station II over 120 feet of water.

Figure 26.--Preparation for dive with use of SCUBA gear to observe behavior of fish in Brooks Lake, 1957.

Depth of dive extended to 30 feet. Plankton was very evident. The experimental gill nets were fishing properly but no fish of any kind were seen in or near the nets.

Dive 3--Dive was begun at station 11 over 120 feet of water; 150 adult sockeye salmon were observed swimming parallel to the shore.

A description of a second series of dives made on August 30 under the same conditions as on August 3 follows:

Dives 1 and 2--Each dive was of 15 minute's duration, between 2 and 3 p.m., on the edge of the shelf (where shallow littoral zone ends) down to 45 feet. The purpose of the dives was to determine whether sockeye salmon fry were inhabiting the dense vegetation blanketing the bottom. The only live fish observed were one nearly dead blackfish and one adult male sockeye salmon at a depth of 30 feet. The bottom was very soft, and a cloud of sediment was stirred up with each step. Aquatic plants (predominantly *Myriophyllum*) formed a thick mat on the bottom. Three dead sculpins were seen as were large thin-shelled snails.

This very limited diving indicated that SCUBA may be useful as an observation method at Brooks Lake, and an expanded SCUBA program will be undertaken in the future.

PART IV. LIMNOLOGY AND ITS RELATION TO SOCKEYE SALMON

Limnological data were collected in 1957 concurrently with studies of the biology of sockeye salmon discussed in Parts I, II, and III. One form of Liebig's Law, or the Law of the Minimum, states that productivity is limited by the nutrient present in the least amount at any given time. If one essential element is in short supply, regardless of the abundance of other essential elements, production may be limited. Part IV describes the limnology of the lake and stream environments and the significance of selected key factors, including nutrients, in the biology of sockeye salmon (fig. 27).

The objectives of the studies were to: (1) Measure relative seasonal abundance of zooplankton and phytoplankton at three representative stations and relate to the distribution and the diet of juvenile sockeye salmon; (2) determine the bottom morphometry of Brooks Lake by surveys with a recording echo sounder; (3) determine the relative abundance of bottom fauna and through food studies, relate to utilization by sockeye salmon; (4) determine the following qualities that influence productivity by analyzing lake water at 2-week intervals at representative midlake stations--temperature, phosphorus, nitrogen, silica, turbidity, transparency, oxygen, hydrogen ion concentration, and alkalinity and total hardness; (5) determine the primary productivity of Brooks Lake by the carbon^{14} method; (6) record continuously the temperature of the gravel water of Brooks River and One Shot Creek; (7) record fluctuations in lake level; and (8) record climatological data and solar radiation.

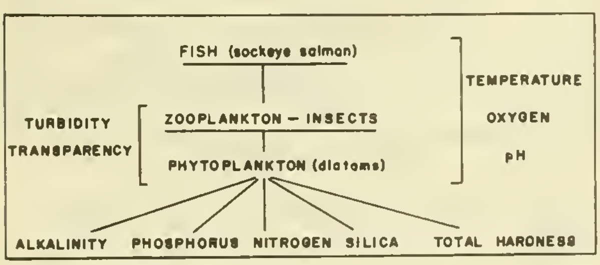

Figure 27.--Probable relation of sockeye salmon production and chemical and physical water qualities in Brooks Lake.

PLANKTON AND ITS RELATION TO JUVENILE SOCKEYE SALMON

Information was needed on the kinds and abundance of zooplankton in Brooks Lake because, as previously discussed in Part III in the section on food of juvenile sockeye salmon, it is an important food item. Phytoplankton are not usually eaten by juveniles, but information on kinds and abundance gives useful clues to basic productivity and to limiting chemical constituents of the water.

Beginning June 27, when weather permitted, plankton collections were made at 10-day intervals at three stations (fig. 21). Zooplankton was collected with a Clarke-Bumpus sampler with a number 10 net, and phytoplankton was collected with a 3-liter Kemmerer water sampler.

Station I was located on the edge of the littoral area in 5 m. of water; station II, southwest of station I in 35 m.; and station III, in midlake southwest of station II in 67 m. Depths sampled were as follows: station I, surface and 5 m.; station II, surface, 5, 10, and 25 m.; station III, surface, 5, 10, 25, 35, and 50 m. All tows were made between 10 a.m. and 1 p.m.

Zooplankton

The Clarke-Bumpus sampler was an open, nonclosing type and was operated according to recommendations of the inventors (Clarke and Bumpus, 1950). To ensure that the mouth of the instrument remained perpendicular to the flow during horizontal tows and to prevent water from entering the net while it was being raised or lowered to the desired sampling depth, a 20-pound weight was fastened to the lower edge of the sampler frame.

After each haul the net and bucket were rinsed with lake water and the contents drained into a small screw-top jar containing a solution of 3 percent formalin. Plankters were then transferred to an alcohol solution for storage until counts and identifications could be made. Identifications were made from keys by Pennak (1953). Numbers of plankters were estimated as follows: The volume of preserved concentrate was measured with a graduated cylinder, and the number of each organism determined by the formula

$$\underline{n} = \frac{cv}{1}$$

in which n = number of plankters per liter of original water; c = number of plankters in 1-ml. cell; v = volume of concentrate in milliliters; and 1 = volume of original water sampled in liters. For example, if the sampler recorded 75 revolutions (1 revolution = 4 liters), the sample measured 100 ml., and the count was 60 plankters in a 1-ml. Sedgwick-Rafter cell, the calculated number of organisms per liter of lake water would be

$$\underline{n} = \frac{60 \times 100}{300}$$

$$\underline{n} = 20 \text{ organisms per liter.}$$

Counts were made by filling a 1-ml. Sedgwick-Rafter cell with thoroughly mixed concentrate. Guidelines were scored on the underside of the cell with a diamond-tipped pencil to help prevent duplication of counts. Total numbers of each species in the cell were counted. Initially, duplicate samples of concentrate were counted to check the technique and develop skill in counting. Since counts of organisms in duplicate samples were found to be consistent, counts were later made only on single samples of concentrate.

The following six genera and species of zooplankters were collected: *Daphnia longispina*, *Bosmina longirostris*, *Bosmina coregoni*, *Holopedium gibberum*, *Cyclops* sp., and *Diaptomus* sp. Species identification of *Cyclops* and *Diaptomus*, could not be made with the microscopes available at the field station. *Eurycercus* was found in stomachs of round whitefish but never in plankton collections, and the rotifer *Conochilus* was found once in a sockeye salmon stomach; therefore, the two zooplankters were present in the lake in 1957 but were not abundant.

An unidentified cladoceran was found in stomachs and plankton collected between water depths of 5 and 25 meters at stations II and III. Samples of live and preserved individuals of this species were sent to D. K. Hilliard of the Arctic Health Research Center at Anchorage, Alaska, but he was unable to identify them. At Hilliard's suggestion, samples were sent for identification to Kaj Berg, Freshwater Biology Laboratory, University of Copenhagen, Copenhagen, Denmark. Berg and a colleague, Mr. Ren, identified it as an arctic form of *Holopedium gibberum*. An excerpt from Berg's letter follows: "The Cladoceran in question belongs to the species *Holopedium gibberum* Zaddach. However, they do deviate from the typical form of the species as the gelatinous case is considerably lower and the abdomen somewhat slimmer than on this species. It is a hunger form or what the Germans call 'Kummer form.' But these differences are not enough to establish a variety or subspecies on the existing material, as there is an even transition from the typical form to the one present, which is of Arctic origin. It turns on a form, which--owing to the short period of activity in the Arctic fresh waters--must carry out its development and reproduction in the shortest time possible and with a minimum of use of material on account of the low content of food in the Arctic lakes. From a biological point of view the animal can furthermore do without the big gelatinous case in the fairly cold water, as the viscosity here is great. We know analogous forms of the species from Greenland."

The average numbers of zooplankters per liter of water sampled for each of the three stations were significantly different (fig. 28).

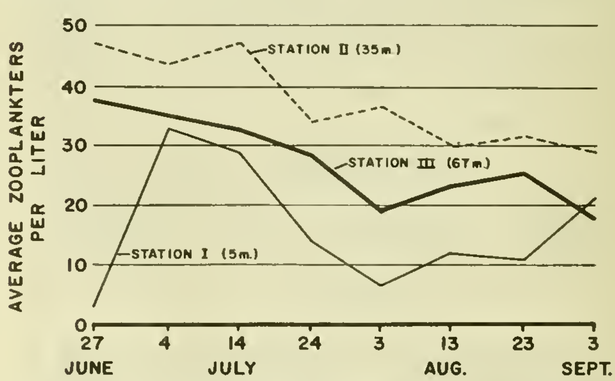

Figure 28.--Numbers of zooplankters per liter of lake water, averages of all depths for each sampling date, June 27 to Sept. 3, 1957, Brooks Lake.

There was a general decline at stations II and III in midlake throughout the season, whereas at station I in shallow water, two maxima occurred, one in early July and the other in September. Zooplankton density was highest at station II. Part of the differences between stations may be explained by the fact that station III samples were weighted by the inclusion of deeper plankton-scarce samples. If only the surface and 5-m. samples for each station are plotted, however, plankton density at station II remains highest (fig. 29). A possible explanation of this phenomenon is that station II may be in a region of upwelling cool water resulting from deflection of water masses upward along the dropoff near station II.

The significant points of figures 28 and 29 are: the general decline in zooplankton abundance through the season and the consistently high plankton density at station II. The second point has no obvious significance in the ecology of sockeye salmon, but the first has the following significant implications.

The seasonal decline in zooplankton must have been caused either by progressively less favorable conditions for plankton production or by cropping by fish. If the former is true, insects are the preferred food and plankton is second choice, as evidenced by the fact that in the spring when zooplankton is most abundant juvenile sockeye salmon feed much more heavily on insects (figs. 24 and 28).

If pelagic sockeye salmon (and other competing species) are cropping the zooplankton

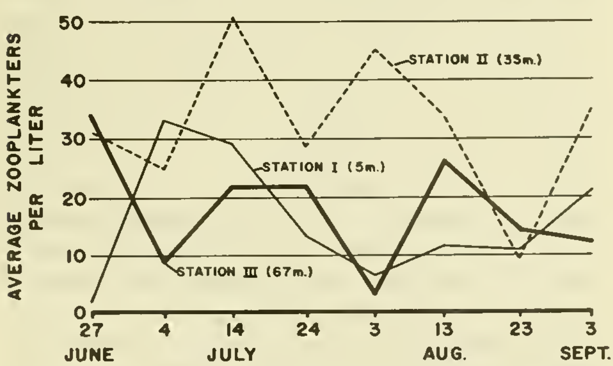

Figure 29.--Numbers of zooplankters per liter of lake water, averages of surface and 5-m. depths only, June 27 to Sept. 3, 1957, Brooks Lake.

population as the season progresses, plankton could be a limiting factor under conditions of high densities of sockeye salmon. The plankton-feeding sockeye salmon contained from 3,000 to 5,000 plankters, and one contained more than 10,000. At an average density of 40 zooplankters per liter in lake water, a fish containing 10,000 plankters would have to ingest the entire population from 250 liters of water.

Zooplankton depth distribution is characterized by large fluctuations resulting from diurnal vertical migrations, with least numbers near the lake's surface during midday (Welch, 1935). All plankton samples at Brooks Lake were collected around midday, and as might be expected, abundance of copepods and cladocerans was usually least at the surface (fig. 30). On the other hand, all gill net catches of juvenile sockeye salmon were at

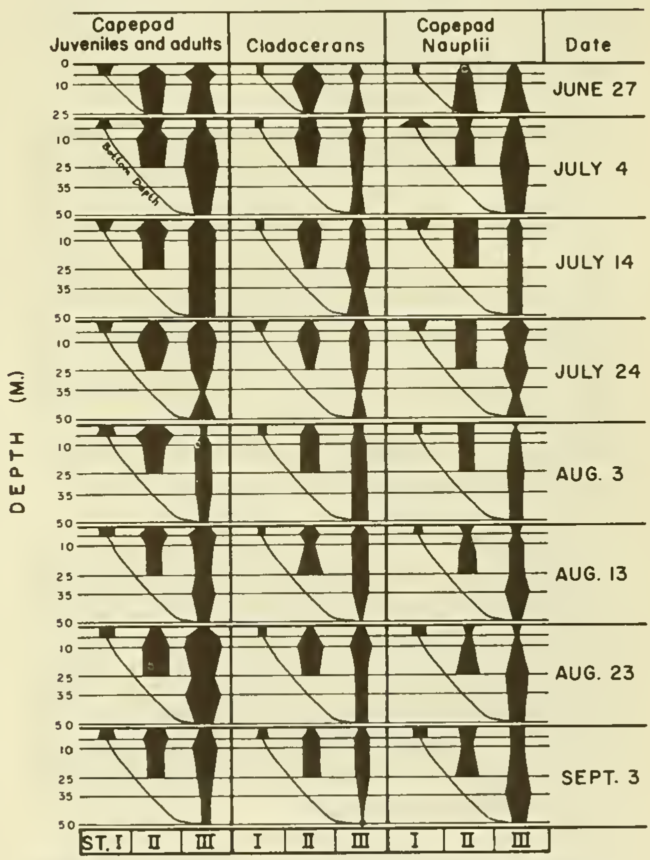

Figure 30.--Daytime seasonal and vertical distribution of zooplankton groups at three stations in Brooks Lake, June 27 to September 3, 1957. Width of each spherical curve corresponds to the cube root of individuals per liter at the indicated depths.

night. They were mostly captured near the surface (table 10) where they fed on plankton, especially in late summer (fig. 24). Presumably sockeye salmon juveniles were attracted to the surface waters by the nighttime concentration of plankton. Because our plankton samples were taken in the day and our fish samples at night, it is not surprising that the depths of maximum density of sockeye salmon and zooplankton did not coincide. It would be enlightening to obtain a series of day and night plankton samples at Brooks Lake to compare abundance at different depths through a series of 24-hour periods but we were unable to undertake this in 1957.

On the eight sampling dates weather ranged from clear and calm to rough and windy. There was no discernible relation of weather conditions and horizontal or vertical plankton distribution. This is not surprising since the maximum concentrations occurred at depths of 5 m. and more, below the influence of surface water conditions.

Of zooplankters eaten by sockeye salmon, 46 percent were the copepods, *Cyclops* and *Diaptomus*, and 54 percent were the cladocerans, *Daphnia* and *Bosmina*. This implies that plankton-feeding sockeye salmon definitely prefer cladocerans to copepods, because copepods were invariably more abundant than cladocerans in samples (fig. 30). Salmon seldom ate copepod nauplii, and therefore the significance of their distribution and abundance to sockeye salmon is only indirect in ultimate abundance of copepods.

Figure 30 requires some explanation and interpretation. The black shapes are spherical curves (Birge and Juday, 1922). They represent three-dimensional columns of relative plankton densities in a vertical water column at each of the three stations. The water column at each station was sampled at each indicated depth. The bottom depth was 5 m. at station I; 35 m. at II; and 67 at III.

The significant points in figure 30 are:

1. Samples at station I are not representative of the main body of the lake. Except for copepod nauplii on July 4 and 14, zooplankters were less dense at station I than at II and III.

2. Zooplankters were usually less abundant in the surface 5 m. of water at midday than at lower depths, probably because of the inhibiting effect of light. Usually the region of highest concentrations was from 5 to 10 m.

3. Plankton density was greatest during the early summer and decreased gradually through the summer and fall.

4. Copepod juveniles and adults were always more abundant than cladocerans or copepod nauplii.

5. Relative vertical distribution showed little stratification, indicating that the lake contained zooplankton throughout the season at all depths.

From 1926 to 1930, limnological studies were conducted at Karluk Lake on Kodiak Island (Juday, Rich, Kemmerer, and Mann, 1932). Karluk Lake was then a major producer of sockeye salmon; conditions for sockeye salmon production were presumably satisfactory. Since Karluk and Brooks Lakes are in the same general geographic area and are approximately the same size, general comparisons should be useful and valid. *Bosmina*, *Daphnia*, *Cyclops*, and *Diaptomus* were the dominant forms in both lakes. Maximum abundance of *Daphnia* was considerably greater in Brooks Lake: 21 per liter compared with 9 per liter in Karluk Lake. The largest catch of *Bosmina* in Karluk Lake was 13 per liter compared with 11 in Brooks Lake. Maximum abundance of *Diaptomus* in Karluk Lake was 22 per liter compared with 53 per liter in Brooks Lake, and for *Cyclops*, it was 145 per liter compared with 31 in Brooks Lake. For copepod nauplii, maximum abundance in Karluk Lake was 100 per liter; in Brooks Lake it was 56. The one striking difference between Brooks and Karluk Lakes is that at Karluk Lake rotifers reportedly were the most abundant form of all zooplankters, while at Brooks Lake rotifers were scarce and were never found in net or centrifuge samples (they were found in stomach samples).

Further comparisons could be made, but it is clear that the zooplankton of Brooks and Karluk Lakes are generally similar. It is not known whether the abundant rotifers in Karluk Lake were utilized by sockeye salmon. In conclusion, there is no evidence of a deficiency in numbers of genera or actual abundance of zooplankters utilized by Brooks Lake sockeye salmon in 1957.

Zooplankton probably do not limit sockeye salmon production at Brooks Lake where fish densities are low. Even the lowest plankton densities measured were relatively high and were similar to densities in Karluk Lake during its period of high sockeye salmon production (Juday, Rich Kemmerer, and Mann, 1932).

Phytoplankton

To measure the relative abundance of phytoplankton and protozoa, samples were taken at the same sampling times and locations as for zooplankton, as described on page 43. Only 2 liters of each 3-liter sample were used to measure phytoplankton abundance, the third liter being utilized for chemical analyses. Samples were transported to the lakeside laboratory as quickly as possible, and the entire 2 liters was immediately centrifuged in a high-speed plankton centrifuge. The volume of plankton for each sample was determined by transferring the concentrate from the metal centrifuge cup into a small graduated glass centrifuge tube and recentrifuging in a geared hand-operated centrifuge. After the volume was determined, a measured quantity of 3 percent formalin was added to preserve the sample for later counting and identification.

Counts were made with a large-aperture pipette by placing 1 ml. of the concentrate into a Sedgwick-Rafter cell and counting random fields until a minimum of 100 individual plankters (or colonies in multicellular species) were counted. Many green algae and protozoa were fractured during the centrifuging. *Botryococcus* colonies in particular were evident in uncentrifuged samples but were rarely seen afterward.

The underside of the Sedgwick-Rafter cell was marked with a diamond-tipped pencil to partition the sample into sections as an aid in preventing counting fields more than once.

Counts were converted to plankters per liter with this formula:

$$\underline{n} = \frac{K\bar{x}v}{l}$$

in which $\underline{n}$ = number of plankters per liter of original water, K = a constant, $\bar{x}$ = average count per field, v = volume of original preserved concentrate, and l = volume of original water sample (in liters).

The constant (K) was the number of fields of view in the entire cell. It was calculated by first measuring in millimeters the diameter of a field of view under the microscope and then calculating the area of the circular field of view. The area of the entire cell (1,000 square mm.) was then divided by the area of a single field; the resulting quotient was K. The average count per field ($\bar{x}$) was the quotient resulting from dividing the total count (about 100) of each plankter by the number of fields of view examined.

This procedure produced a relative measure of seasonal and depth distributions of phytoplankton and protozoa but was only an approximation of actual numbers per original liter of lake water. Only recognizable fragments or cells were counted, which tended to minimize counts; on the other hand, counts were increased by regarding as individuals each fragment of colonial phytoplankton broken apart during centrifuging. The numbers per liter of each of the three most abundant phytoplankton groups (green algae, blue-green algae, and diatoms) and protozoa were plotted in the same way as were zooplankton (fig. 31). A checklist was compiled of all genera of phytoplankton and protozoa encountered (table 16).

Phytoplankton and protozoan distributions, both vertically and in relative seasonal abundance, were much more variable than zooplankton (figs. 30 and 31). Since diatoms were abundant at all depths throughout the season, zooplankters had sufficient diatoms for food.

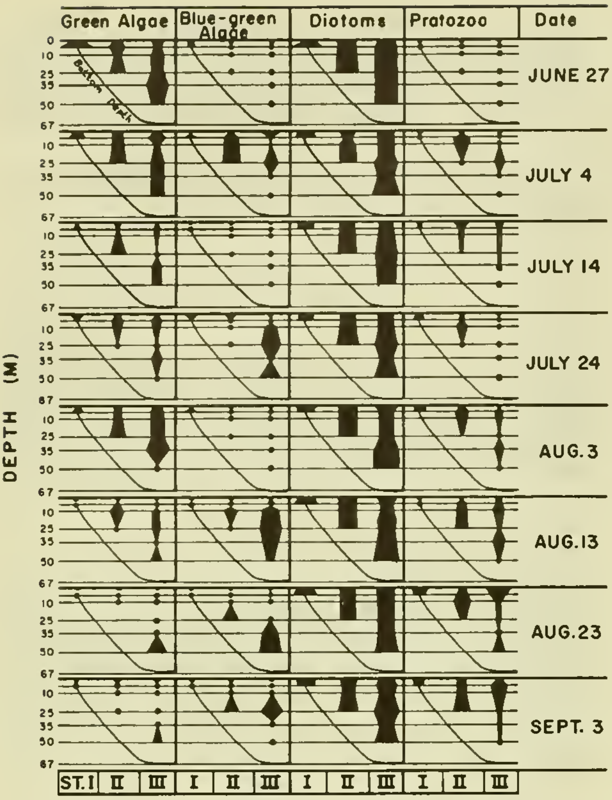

Figure 31.--Seasonal and vertical distribution of phytoplankton and protozoan groups at three stations in Brooks Lake from June 27 to September 3, 1957. Width of each spherical curve corresponds to the cube root of individuals per liter at the indicated depths. Dot indicates absence of representatives of a group in that sample.

Green algae showed two pulses in abundance, the larger in late June and early July and the smaller in early August. Maximum density of the June pulse of green algae was 147,000 individuals per liter at station I and was coincident with a dense bloom of green algae on the littoral zone.

Blue-green algae (two genera, *Microcystis* and *Lyngbya*) also showed two pulses, one on July 4 and the other in mid-August. This abundance of blue-green algae is interesting because oligotrophic lakes such as Brooks are usually deficient in blue-green algae (Rawson, 1956). Maximum density of blue-green algae was 57,000 individuals per liter at the 50-meter depth at station III on August 23.

On the basis of phytoplankton population, Brooks Lake does not entirely fit the traditional oligotrophic classification. Throughout the summer, diatoms were the dominant form, and *Melosira* was usually the dominant genus. *Melosira* is usually regarded as an indicator of eutrophy rather than oligotrophy, but at Brooks and Great Slave Lakes *Melosira* was the dominant diatom. Other eutrophic indicators were also found, namely, *Synedra, Fragillaria,* and *Asterionella.* Maximum density of diatoms was 181,000 per liter at station I on June 27. Possibly an even greater density occurred in the spring before sampling began.

TABLE 16.--Genera of plankton found in water samples from Brooks Lake, 1957

Green algae	Blue-green algae	Diatoms	Protozoa
Ankistrodesmus	*Lyngbya*	*Asterionella*	*Ceratium*
Botryococcus	*Microcystis*	*Cyclotella*	*Dinobryon*
Closterium		*Cymbella*	*Vorticella*
Pediastrum		*Diatoma*	
Phacotus		*Fragillaria*	
Pleurococcus		*Gomphonema*	
Scenedesmus		*Melosira*	
Spirogyra		*Navicula*	
Staurastrum		*Stephanodiscus*	
		Synedra	
		Tabellaria	

Protozoa formed a small and variable portion of the total plankton, reaching maximum abundance of 17,000 individuals per liter on August 23 at the 5-meter depth at station II.

The total plankton of Brooks Lake in 1957 was generally abundant throughout the season and well distributed to all depths.

MORPHOMETRY

The bottom morphometry of Brooks Lake had to be determined before we could make a map on which we could base planning of future biological and chemical sampling programs. A Raytheon portable recording echo sounder model DE 119B, which could be read to within half a foot over a range of 0 to 245 feet, was used. A hand-sounding line was used to calibrate the sounder and to sound the areas beyond maximum range of the instrument.

A bracket consisting of a 1/4-inch bolt through the left gunwale, with the outer end embedded in a small wooden fairing block, was used to mount the transducer rod on the boat. The transducer rod was clamped to the outside of this block so that it pivoted on this point (fig. 32). The upper projecting end of the transducer rod was guyed in place by two stout lengths of twine secured to the gunwale fore and aft. When not in use the transducer rod was pivoted so that its axis lay along the gunwale.

Sounding techniques and construction of the map followed the methods described by Warner (1953). Fifty-seven sounding transects were made across Brooks Lake (fig. 33). Based on these transects, a large-scale master map was drawn with contour intervals of 10 feet, which are increased to 40-foot intervals in figure 34 for clarity.

The surface area of the lake is 28.9 square miles, excluding the islands. Maximum length is 10.7 miles and maximum width, 4.1 miles. Mean width is 2.7 miles. Maximum depth is 258 feet at the point indicated on figure 34, and mean depth is 148 feet. Length of shoreline is 31.5 miles and shoreline development, 1.7. The volume is 2,745,600 acre feet. The surface altitude is 62 feet above sea level.

BOTTOM FAUNA

A limited number of samples were taken with an Ekman dredge at stations I, II, and III (fig. 21) to learn the general composition and distribution of bottom fauna. In general, bottom fauna (mainly Diptera larvae) was abundant at station I (5 m.) but decreased to almost none at station III (67 m.). Our studies of sockeye salmon food indicate that bottom fauna is not directly important to sockeye salmon. This finding agrees with the Cultus Lake studies of Ricker (1952).

WATER QUALITY

Temperatures and chemical qualities of Brooks Lake water were determined at stations I, II, and III, which were selected as representative of the shallow-, medium-, and maximum-depth areas of the lake. Samples at each station were taken at 10-day intervals between July 4 and September 3. The water qualities chosen for measurement were those believed to be most likely to be limiting factors or to affect production of sockeye salmon. Samples were collected with a 3-liter Kemmerer water sampler, transferred immediately to brown, ground-glass stoppered bottles and were analyzed within 30 hours. Samples kept overnight before being analyzed were kept cool by storing in a refrigerator. Glassware was scrupulously cleaned with detergent and rinsed with distilled water immediately before use.

To insure use of identical techniques for comparative purposes in future years, a detailed description of each analytical technique was prepared. Pertinent data were recorded at the time a sample was taken.

Temperature

Water temperature is of vital importance to the entire biota of a lake and is one of the principal factors in determining overall production.

Figure 32.--Sounding Brooks Lake with portable echo sounder. Transducer rod is on right, over side of boat. Point of land in background is reference point (transect 41).

Temperatures of Brooks Lake water were taken with a pocket thermometer which was immersed in each sample immediately after it reached the lake's surface. This procedure resulted in warming of the sampler and its contents whenever the lake water was colder than overlying water through which it passed en route to the surface. (See comparative

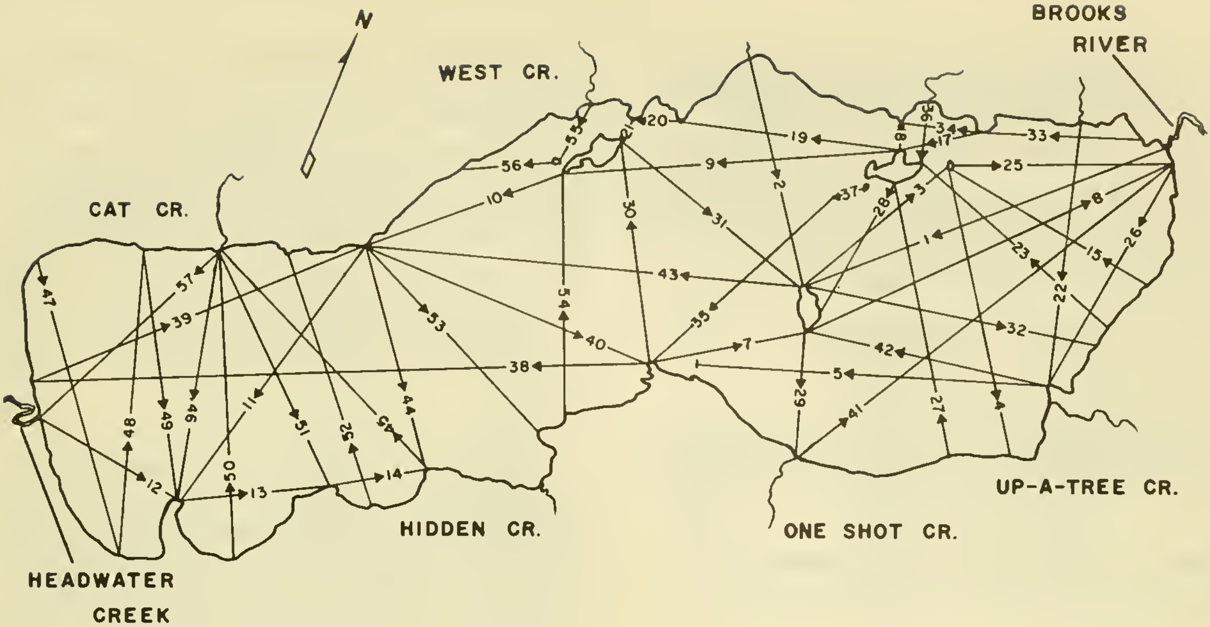

Figure 33.--Sounding transects of Brooks Lake made in 1957 with portable echo sounder.

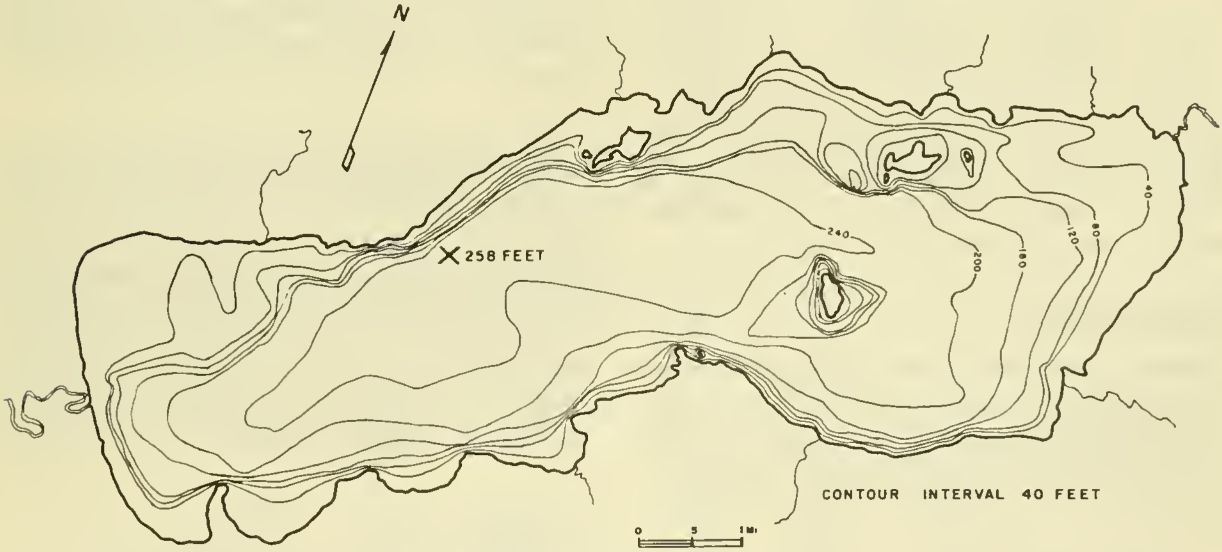

Figure 34.--Bottom contour map of Brooks Lake.

readings October 3 in figure 35.) For this reason, actual temperatures at deeper points were slightly lower than indicated.

Figure 35 shows the temperature profiles at each station for successive dates of sampling. Because temperatures were recorded only for selected depths, and no continuous temperature profiles were obtained, little was learned on presence of or characteristics of the thermocline. The range of temperatures from surface to bottom was quite small, indicating that thermal stratification was not pronounced; the maximum range was 17° F. in 65 m. on August 23.

From July 24 through August 23, surface temperatures at station II were less than at I

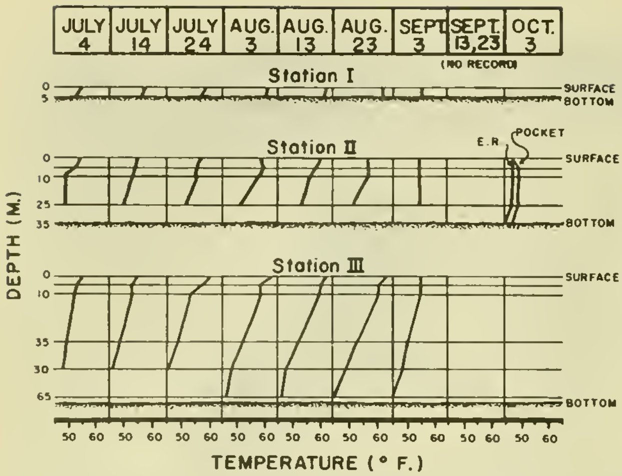

Figure 35.--Brooks Lake vertical temperatures, stations I, II, and III, July to October 1957.

or III. This corresponds with greater zooplankton densities at station II over those of I and III (figs. 28 and 29). It is conjectured that station II is in a region of upwelling of cold water masses originating from the depths. From the bottom configuration, as indicated by the contour map (fig. 34), and from the action of submerged gill nets at station II, such upwelling is likely when strong winds sweep the lake. Further study is needed to learn the reasons for the measured differences between stations II and III.

Phosphorus

Soluble phosphorus was measured with a Klett-Summerson photoelectric colorimeter as described by P. R. Nelson. [4] Great care was required in analysis because of microquantities present and the danger of contamination.

Phosphorus and nitrogen (together with carbon and hydrogen) are the principal constituents of living cells and are usually present in extremely small quantities in lake waters. It is likely that if a nutrient deficiency were present, one of these would be in short supply.

The range of phosphorus was from 0 to 0.0152 p.p.m., and amounts were quite uniform at all depths and dates (table 17). These data indicate that when relatively few spawners are present, as was the case in 1957, carcasses of spawners do not contribute a measurable amount of phosphorus to the lake. On the contrary, phosphorus declined slightly through the season, with the least amounts on September 3. This conclusion was also reached in Cultus Lake studies by Ricker (1937).

Organic bottom sediments probably play a more important part in supplying available phosphorus than do salmon carcasses. Our quantitative phytoplankton sampling indicates that the biomass of the standing crop of phytoplankton must be much greater than that of salmon carcasses at any one time, and over a period of a year it must be vastly greater. It is probable that renewal of the supply of phosphorus is not dependent on salmon carcasses in a large lake such as Brooks, with relatively abundant plankton and small salmon runs.

Since phosphorus is present throughout the season, it is probably not a limiting factor on plankton production. Phosphorus is one of the principal living cell constituents and is taken up and readily stored by phytoplankton (Ruttner, 1953). If it were a limiting factor, measurements would be zero because phytoplankton would utilize all of it as soon as it appeared. Thus, if it is present in detectable quantities, it may be regarded as being in adequate supply.

Nitrogen

Nitrite nitrogen was measured with a Klett-Summerson photoelectric colorimeter according to directions in Nelson's compilation. [5] As with phosphorus, great care was required in the analysis.

Nitrite ranged from 0 to 0.0050 p.p.m. and was relatively uniform in quantity and vertical

[4] Compilation of field methods for water analysis. 1952. [Unpublished typewritten report.] On file at BCF Biological Laboratory, Auke Bay, Alaska.

[5] See footnote 4.

TABLE 17.--Soluble phosphorus determinations, July 24 to October 3, 1957, Brooks Lake

[In parts per million]

Station and depth (m.)	Soluble phosphorus					
	July 24	Aug. 3	Aug. 13	Aug. 23	Sept. 3	Oct. 3
I						
0	0.0038	0.0091	0.0114	0.0053	0.0015	
5	.0083	.0114	.0076	.0061	.0000	
II						
0	.0099	.0091	.0038	.0091	.0008	0.0039
5	.0121	.0061	.0053	.0046	.0008	
10	.0076	.0152	.0046	.0121	.0015	
25	.0114	.0129	.0061	.0053	.0015	
35						.0066
III						
0	.0121	.0099	.0053	.0061	.0008	
5	.0121	.0083	.0008	.0046	.0000	
10	.0061	.0076	.0099	.0046	.0023	
50	.0129	.0061	.0091	.0053	.0015	
65		.0144	.0091	.0053	.0046	

TABLE 18.--Nitrite determinations (NO_2), July 4 to October 3, 1957, Brooks Lak

[In parts per million]

Station and depth (m.)	Nitrite							
	July 4	July 14	July 24	Aug. 3	Aug. 13	Aug. 23	Sept. 3	Oct. 3
I								
0	0.0008	0.0017	0.0025	0.0017	0.0017	0.0017	0.0008	
5	.0008	.0017	.0017	.0025	.0008	.0008	.0008	
II								
0	.0008	.0017	.0017	.0008	.0008	.0000	.0017	0.0008
5	.0000	.0025	.0017	.0008	.0008	.0000	.0008	
10	.0000	.0017	.0017	.0025	.0017	.0000	.0008	
25	.0000	.0017	.0017	.0041	.0008	.0008	.0008	
35								.0008
III								
0	.0017	.0017	.0017	.0008	.0008	.0000	.0008	
5	.0017	.0017	.0017	.0017	.0017	.0000	.0017	
10	.0017	.0017	.0017	.0008	.0008	.0008	.0017	
50	.0025	.0017	.0017	.0025	.0025	.0008	.0017	
65				.0025	.0025	.0025	.0017	

distribution through the summer (table 18). Nitrite was detected at each station on every sampling date, although it was not found at certain depths on July 4 and August 23. The zero measurements may not be absolute because 0.0008 p.p.m. was the smallest quantity our equipment could detect. Quantities between absolute 0 and 0.0008 were recorded as zero.

The absence of an increase of nitrite in the autumn indicates that decaying salmon carcasses are not important in increasing detectable nitrogen supplies in the lake, at least when relatively small numbers of salmon are present, as they were in 1957. If appreciable nitrogen had been added, its effects should have been apparent on the August 23 and September 3 sampling dates. Furthermore, the prime source of nitrogen in lakes is probably from the atmosphere rather than through organisms (Ruttner, 1953).

Silica

Silica determinations (table 19) were made with a Klett-Summerson photoelectric colorimeter. Silica is the major constituent of the skeletal structure of diatoms, which are usually the principal phytoplankton food for zooplankton in oligotrophic lakes. A major decrease in silica often occurs after a bloom of diatoms (Ruttner, 1953), so a shortage of silica could limit diatom production.

Silica ranged from a low of 9.4 to a high of 12.0 p.p.m. SiO_2 and was relatively uniform throughout the season and at all water depths. This is consistent with the uniform distribution and abundance of diatoms, which are the main cause of variations in silicon content. Brooks Lake has a high silicon content compared with many other lakes, probably because of the presence of volcanic ash on the watershed from the eruption of nearby Katmai Volcano in 1912 and subsequent continuing minor eruptions of several nearby volcanoes. This explanation is suggested by the fact that tropical lakes with volcanic watersheds have high silicon contents (Hutchinson, 1957), and the material from the 1912 eruption was 60 to 75 percent silica (Griggs, 1922). The Brooks

TABLE 19.--Silica determinations (SiO_2), July 4 to October 3, 1957, Brooks Lake

[In parts per million]

Station and depth(m.)	Silica							
	July 4	July 14	July 24	Aug. 3	Aug. 13	Aug. 23	Sept. 3	Oct. 3
I								
0	10.7	10.7	9.4	11.0	10.2	9.9	10.1	
5	10.7	10.7	10.4	11.3	10.6	9.9	10.3	
II								
0	10.8	10.8	10.5	11.1	10.7	10.0	10.3	11.2
5	10.6	10.8	9.7	10.5	10.7	9.8	10.4	
10	10.6	11.0	10.4	10.8	10.9	9.7	10.5	
25	10.8	10.7	10.6	11.0	11.4	10.4	10.5	
35								11.2
III								
0	10.5	10.7	10.2	11.2	10.9	9.8	10.4	
5	11.3	10.9	10.8	10.8	10.8	10.2	10.4	
10	10.9	10.6	10.6	11.1	10.5	10.2	10.5	
50	10.6	10.6	12.0	11.6	10.8	10.4	10.9	
65				11.5	10.6	10.5	11.0	

TABLE 20.--Turbidity determinations in terms of silica (fuller's earth), July 4 to October 3, 1957, Brooks Lake

[In parts per million]

Station and depth (m.)	Turbidity							
	July 4	July 14	July 24	Aug. 3	Aug. 13	Aug. 23	Sept. 3	Oct. 3
I								
2	2.4	2.4	0.8	0.8	0.5	1.0	0.4	
5	2.7	2.4	0.7	0.7	0.7	0.7	0.6	
II								
0	2.1	1.4	0.8	0.6	0.6	0.7	0.6	0.4
5	2.4	2.1	0.5	0.7	0.7	0.6	0.6	
10	2.7	2.4	0.8	0.7	0.5	0.5	0.5	
25	2.7	2.4	0.7	0.8	0.6	0.4	0.6	
35								0.5
III								
0	2.4	2.4	0.8	1.1	0.8	0.6	0.7	
5	2.4	2.4	0.5	0.7	1.0	0.5	0.7	
10	2.4	2.4	2.7	0.8	0.5	0.5	0.6	
50	2.4	2.4	1.4	4.0	0.6	0.4	0.7	
65				10.3	0.7	2.8	0.7	

Lake silica content from year to year fluctuates but is always high. In determinations made at Brooks Lake between 1947 and 1955, the range was 7.0 to 16.2 p.p.m. SiO_2.[6] Even this lowest figure is far greater than in most North American and European lakes and contrasts with relatively small amounts found in Karluk Lake (Barnaby, 1944).

Turbidity

The amount of turbidity provides a measure of total particulate matter in the water. In Brooks Lake this material is mostly plankton and so provides a check on quantitative plankton measurements.

Turbidity was measured July 4 and 14 with a Klett-Summerson photoelectric colorimeter, and for the remainder of the summer, starting July 24, with a turbidimeter, as described by Welch (1948). The method was changed because the colorimeter was not sensitive enough to measure accurately the extremely low turbidities. The results of July 4 and 14 were corrected by using the turbidimeter as a standard and calibrating the colorimeter. Turbidities were extremely low, ranging from 0.4 to 10.3 (p.p.m. silica (fuller's earth)) with only a single sample exceeding 4.0 (table 20). Most of the particles were plankton, although spruce pollen was also present early in the season.

Transparency

Transparency, as measured by Secchi disk visibility, is a widely used and simple determination for comparing relative water transparencies of different lakes. Usually, low visibility indicates high productivity and vice versa.

Secchi disk visibility measurements were made only at stations II and III. The readings

[6] Theodore R. Merrell. 1956. Evaluation of Brooks Lake Research Station. [Typewritten report.] On file at BCF Biological Laboratory, Auke Bay, Alaska.

TABLE 21.--Secchi disk visibility, July 4 to September 2, 1957, Brooks Lake

[In meters]

Station	Visibility						
	July 4	July 14	July 24	Aug. 3	Aug. 13	Aug. 23	Sept. 2
II		10.5	10.8	16.5	12.5	16.4	13.0
III	11.5	10.5	11.0	15.0	13.5	16.7	13.5

varied little seasonally and ranged from 10.5 to 16.7 m. (table 21). These high readings are within the range for large subalpine lakes in Europe (Hutchinson, 1957) but are almost double those at Karluk Lake (Juday, Rich, Kemmerer, and Mann, 1932) and more than double those of Great Slave Lake (Rawson, 1956). Great Slave Lake is not directly comparable, however, because of the possible influence of a large turbid tributary that adds inorganic silt to the lake.

Oxygen

Oxygen in parts per million was determined by the unmodified Winkler method (American Public Health Association, American Water Works Association, 1946).

Oxygen was abundant at all depths and stations on all dates, suggesting that the lake's water mass was in constant circulation (table 22). Percentage saturation values (Lagler, 1949: fig. 51) were always high, and most samples were supersaturated even at 65 m. The lowest saturation was 88 percent at 5 m. on July 14. These facts would place Brooks Lake in the extreme (or α-orthograde) classification typical of oligotrophic lakes (Hutchinson, 1957). Abundance of oxygen at all depths was consistent with small vertical temperature gradients (fig. 35).

Hydrogen Ion Concentration (pH)

A limited number of pH measurements were made with a Heilige colorimetric comparator at all regular sampling depths on July 14 and 24 and on August 3, and at 0, 7, and 15 m. on September 6. The range for all samples was only 7.1 to 7.3, again indicating thorough circulation of the lake at all depths throughout the summer and uniform distribution of dissolved nutrients.

Alkalinity and Total Hardness

Methyl-orange alkalinity was determined according to the method specified by the American Public Health Association and American Water Works Association (1946: p. 31-32). Total hardness from all sources was measured with a standard chemical testing kit.

Alkalinity and total hardness were each determined because hardness of natural water is an index of productivity. Generally, moderately hard waters are more biologically productive than soft waters (Lagler, 1952). Methyl-orange (normal carbonate, CO_3) hardness and total hardness were measured, the former being the major component of total hardness in Brooks Lake. Water samples were tested several times for phenolphthalein alkalinity (hydroxide); none was ever detected, so it was not measured regularly.

Methyl-orange alkalinity was quite uniform through the season at all depths, ranging from 28.0 to 35.6 p.p.m. (table 23). Values found in 1957 agree closely with those measured from 1947 to 1955, indicating that the hardness of Brooks Lake has remained stable for the past 10 years. On the basis of these data, Brooks may be classified as a soft-water lake, of rather low productivity.

Primary Productivity

The measurement of primary productivity of Brooks lake through the summer by the $Carbon^{14}$ technique described by Nielsen (1952) was a major phase of the overall Brooks

TABLE 22.--Oxygen content and percent saturation, July 4 to October 3, 1957, Brooks Lake

Station and depth (m.)	July 4		July 14		July 24		Aug. 3	
	Content	Saturation	Content	Saturation	Content	Saturation	Content	Saturation
I	*P.p.m.*	*Percent*	*P.p.m.*	*Percent*	*P.p.m.*	*Percent*	*P.p.m.*	*Percent*
0	11.1	102	10.6	101	10.4	102	10.0	100
5	12.3	112	9.3	88	10.4	100	10.2	100
II								
0	10.8	100	11.0	102	10.3	99	10.1	100
5	11.6	105	11.0	102	10.4	100	10.2	102
10	12.3	107	11.2	104	10.6	102	10.3	102
25	12.2	106	12.1	106	10.4	93	12.0	107
III								
0	11.3	104	11.0	100	10.2	102	10.0	101
5	11.6	105	11.1	102	10.4	100	10.9	107
10	12.0	107	11.2	103	10.4	95	11.0	108
50	13.0	106	12.0	103	12.1	103	12.2	105
65							11.8	101

Station and depth (m.)	Aug. 13		Aug. 23		Sept. 3		Oct. 3	
	Content	Saturation	Content	Saturation	Content	Saturation	Content	Saturation
I	*P.p.m.*	*Percent*	*P.p.m.*	*Percent*	*P.p.m.*	*Percent*	*P.p.m.*	*Percent*
0	10.0	100	11.3	113	10.6	99		
5	10.4	103	10.6	105	10.6	99		
II								
0	10.2	102	10.3	104	10.7	100	11.0	
5	10.1	101	10.5	105	10.7	100		
10	10.2	100	10.6	105	10.6	99		
25	11.8	106	11.9	106	10.6	99		
35							11.1	
III								
0	10.0	101	10.7	106	10.6	99		
5	10.1	101	11.3	102	10.6	99		
10	10.3	101	10.5	104	10.7	100		
50	12.3	108	12.1	105	12.0	102		
65	12.3	104	11.8	97	11.8	98		

TABLE 23.--Alkalinity and total hardness determinations, July 4 to October 3, 1957
Brooks Lake

[MO = methyl orange; T = total hardness]

Station and depth (m.)	July 4		July 14		July 24		August 3	
	MO	T	MO	T	MO	T	MO	T
I	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
0	31.2		35.6		30.0	32.8	31.8	34.6
5	31.2		35.2		32.0	33.6	32.2	34.6
II								
0	30.6		35.2		31.3	32.4	31.0	34.2
5	29.2		34.8		30.5	32.2	32.2	36.0
10	30.8		34.4		31.3	33.6	32.0	34.6
25	30.8		34.2		31.0	35.0	31.2	35.6
III								
0	31.0		34.8		32.3	30.8	33.0	35.8
5	31.6		34.6		32.3	32.4	31.6	34.6
10	30.4		33.8		29.3	32.8	32.0	33.8
50	28.2		34.0		31.8	32.0	31.2	35.4
65							31.4	33.6

Station and depth (m.)	August 13		August 23		September 3		October 3	
	MO	T	MO	T	MO	T	MO	T
I	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
0	31.6	35.4	30.4	42.0	28.4	31.8		
5	30.2	35.0	30.0	41.0	28.8	31.8		
II								
0	31.8	36.2	29.4	37.4	28.2	31.8	31.2	31.8
5	31.0	33.8	29.8	37.2	28.0	32.2		
10	31.6	35.2	29.2	36.8	28.4	31.6		
25	30.8	34.8	31.2	37.8	28.4	31.8		
35							30.0	31.6
III								
0	31.2	35.2	30.4	39.4	29.2	31.8		
5	31.6	36.0	29.6	39.4	29.0	32.0		
10	31.6	35.8	30.0	37.0	29.2	31.8		
50	31.0	34.6	31.6	39.8	29.0	32.4		
65	30.0	36.4	30.6	38.6	29.2	32.4		

Lake program in 1957, and was accomplished by arranging to support a project by a University of Michigan graduate student, Charles R. Goldman. The results have been published separately (Goldman, 1960), but because this work is interrelated with the rest of the program reported here, a summary of the technique and results follows. The primary productivity program was planned and executed by Goldman and was the subject of his Ph. D. thesis.

Determining primary productivity by means of radioactive carbon tracers is a rapid and sensitive technique for measuring rate of organic increase at the lowest trophic level (phytoplankton). Because production at this base of the food chain may limit production of successive trophic levels (e.g., sockeye salmon) a measure of its production may be a valuable key to assessing the productive potential of an entire lake's biomass. However, this technique has limitations similar to those characteristic of other food pyramid analyses. Even when a good measure of primary productivity is obtained, to be of practical use in production of sockeye salmon the intermediate steps through each trophic level must be related to each other. Thus, it is possible that a highly productive lake might have its productivity concentrated in some presently economically useless end product. The 1957 program was designed to develop suitable field techniques and compare primary productivity seasonally and in different locations in Brooks Lake. Collection of limnological data and fish samples was made concurrently with the primary productivity work.

Determining primary productivity consists essentially of measuring the rate of uptake of radioactive tagged carbon atoms by phytoplankton during the process of photosynthesis--the greater the rate of uptake, the more productive the water.

Primary productivity measurements with sodium carbonate C^{14} began on June 14. A second measurement was made on the 18th, and thereafter determinations were made every fifth day throughout the summer under all weather conditions. Duplicate determinations were made at each Brooks station once during the season to assess experimental error.

The three limnological and gill net sampling stations (fig. 21) were also used for primary productivity samples. Two additional stations were established exclusively for primary production measurements, one in Naknek Lake which was sampled every 15 days and the other near the south shore of Brooks Lake which was sampled once a month.

Primary productivity was measured at 1-m. intervals from surface to 5 m. at all stations, and below this depth, at 10, 15, 20, 25, and 35 m. At station III measurements were also made at 50 and 65 m.

The following successive steps were taken in the primary productivity determination:

1. Clear glass 150-ml. bottles, numbered and with ground glass stoppers and ties, were washed in detergent and rinsed with distilled water.

2. A metal harness snap was tied to the neck of each bottle so that it could be readily attached to hog-ring loops at intervals on a line that was run from the surface to bottom of the location where a measurement was desired.

3. The bottles were placed in numerical order in a heavy wooden box, which acted as an insulated carry-case, and transported by boat to the sampling station.

4. A light reading was taken with an ordinary photographic photoelectric light meter, always in the same direction (on Brooks Lake samples the reading was always on Mt. Katolinat (fig. 1).)

5. A Secchi disk reading was taken.

6. At the station where a measurement was desired a sample was taken with a Kemmerer bottle from each depth and transferred to a numbered bottle.

7. To each sample bottle was added 2 ml. of sodium carbonate C^{14} (5 microcuries).

8. The bottle was snapped to the line at the depth corresponding to the depth at which

the sample was taken, and the series of bottles was then lowered to incubating depths.

9. Samples were allowed to incubate for 4 hours at the selected depths.

10. In the same sequence as incubation was started, bottles were picked up at the end of 4 hours and immediately placed in the dark sample box.

11. Samples were rushed back to the laboratory, and 100 ml. of each were vacuum-filtered through millipore filters again in the same order as originally set out.

12. Very dilute Janus Green B dye (2 ml.) was added to the sample being filtered to detect leaks in the vacuum system.

13. Ten ml. 0.003 HCL (normal) were pipetted onto the filter to remove residual carbonate or organisms adhering to the funnel surface.

14. Ten ml. 3 percent formalin were pipetted onto the filter to preserve organisms and prevent bacterial activity.

15. The millipore filters were placed in individual shallow aluminum sample pans to dry.

16. Millipore filters were glued to shallow sample pans, on the back of which were inscribed the station, date, depth, and ml. of sample (if different from 100 ml. normal).

17. Sample pans were mailed to the University of Michigan where radiation of each was later measured.

An example of one series of comparative data between Naknek and Brooks Lakes demonstrates a typical situation (fig. 36). Productivity is measured in terms of beta radiation counts per second. Highly turbid Naknek Lake is much more productive than clear Brooks Lake in the upper 10 m., but below that depth, because of deeper light penetration, Brooks Lake is the more productive. The striking differences shown are all the more significant when one considers that Brooks Lake temperatures were higher (which would increase production) and that the Brooks experiment was on a bright day, while that for Naknek Lake was on a cloudy day. This example served to

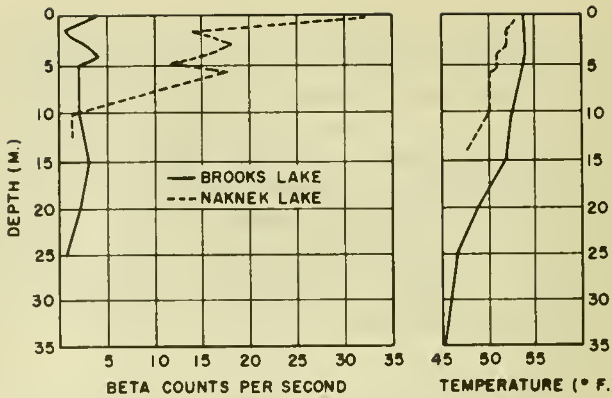

Figure 36.--Relative primary productivity and temperature of Brooks and Naknek Lakes on 2 days in July 1957.

show how great differences may be in primary productivity between adjacent lakes in the same system.

Summary of Water Quality Analysis

The following may be concluded from the water analyses studies:

1. None of the qualities measured were in short supply nor did they fluctuate greatly, indicating that lack of these essential nutrients is not the primary cause of current low production of sockeye salmon in Brooks Lake.

2. The entire water mass is in constant circulation with no stratification (except possibly thermally for short periods).

3. Compared with other lakes of the world, Brooks Lake would be classified as a moderately productive, soft-water, oligotrophic lake, supplied with all essential nutrients and able to support a healthy fish population.

The three points above are based on data taken between July and October during the summer growing season. Measurements of the same water qualities should be made periodically throughout the year to establish the validity of my conclusions. Ruttner (1953: p. 55) says, "Only those dissolved substances which are either of no importance for life or are present in amounts in excess of those necessary do not undergo a marked change in their amounts and states." If the same uniformity of distributions and amounts of dissolved substances which characterized the summer period continues year around, we must search for causes other than lack of dissolved nutrients to explain Brooks Lake's low fish production.

TEMPERATURE OF BROOKS RIVER AND ONE SHOT CREEK

Thermographs were operated continuously as in previous years on Brooks River and One Shot Creek to record water temperatures.

CLIMATOLOGICAL DATA

A weather station was operated throughout the summer, recording daily rainfall, maximum and minimum temperatures, 6 p.m. temperature, and observations of unusual weather. Data for all year may be found in "Climatological Data, Alaska," the monthly summary published by the U.S. Weather Bureau.

Solar radiation in terms of incident radiation in gram calories per square centimeter was recorded continuously during the last part of the summer with a pyrheliometer. These data will be extremely useful in the future when several years of comparative seasonal totals have been collected. The weather in 1957 was exceptionally clear and sunny at Brooks Lake, and we might expect that phytoplankton production would be greater under such conditions than it would during a cloudy summer with less solar radiation reaching the lake's surface.

FLUCTUATIONS IN LAKE LEVEL

A lake-level recorder and still well was installed on a rock ledge near Brooks Lake outlet to record fluctuations in Lake level. Its exact elevation was surveyed to an improvised permanent bench mark embedded in the ledge of the north end of the weir so that when it is removed for winter storage it can be reestablished each spring at the identical level.

SUMMARY AND CONCLUSIONS

1. The adult sockeye salmon run into Brooks Lake extended from June 25 to October 4 with a peak migration in early July.

2. The 1957 run of 31,597 sockeye salmon was one of the smallest spawning escapements since 1940 when counting began. After recounting 27,183 downstream, a net total of only 4,414 remained in the lake. This total proved to be incorrect.

3. Many sockeye salmon escaped upstream unobserved; the true escapement was estimated to be 29,000 sockeye salmon, based on tagging at the weir and recovery on the spawning grounds.

4. About half of the sockeye salmon that entered the lake later returned to spawn in Brooks River.

5. Other salmon species counted through the weir were: 7 chum, 18 king, 461 coho, and 1 pink.

6. A sample of 704 adult sockeye salmon was taken at the weir to determine the age and length composition, sex ratio, and potential egg deposition of the run.

7. Age composition of the run was: 27 percent 5_2, 8.1 percent 5_3, and 62.1 percent 6_3.

8. The sex ratio of the 1957 adult run was 1:1.

9. Mean mideye-fork length of males sampled at the weir was 55.9 cm. and of females, 55.4 cm.

10. Calculated numbers of eggs in female sockeye salmon in the run ranged from 3,044 to 5,060 per female with a mean of 4,115.

11. Potential egg deposition in the Brooks Lake system (not including Brooks River) was estimated to be 57 million.

12. The early run of sockeye salmon consisted mostly of lake tributary spawners; the middle run was a mixture of tributary and Brooks River spawners; and the late run was primarily Brooks River spawners. This differential distribution by time period suggests that the Brooks run is composed of several races, each with different migratory habits.

13. Egg retention by Brooks spawners is low, suggesting successful egg deposition.

14. By marking dead salmon with distinctive fin clips on successive stream surveys, we determined that within 7 days the dead fish disappeared almost completely. Thus, counts of dead fish on successive weekly surveys are additive for minimum total counts.

15. Bears eat many sockeye salmon spawners but take mostly spent fish.

16. Because of removal of salmon from the streams by bears, tag ratio samples from dead fish in Brooks tributaries are impractical.

17. On the basis of 2,333 observations of spawning activity on Brooks River, the following conclusions were made: (a) A 1:1 sex ratio was most common; (b) males were twice as aggressive as females in defending a redd territory; (c) three separate and distinct spawning waves occurred on Brooks River on the same spawning area; (d) there was a relation between downstream weir counts and spawning waves in Brooks River; (e) there was no relation between measured environmental factors and spawning behavior; (f) females lived considerably longer than males and defended a redd until death; and (g) females averaged 7.75 days on a redd from time of selection through spawning to death.

18. Diurnal mass movements of sockeye salmon spawners in and out of One Shot and Hidden Creeks did not occur in 1957.

19. Fewer than 400 sockeye salmon spawned on Brooks Lake beaches in 1957, indicating that beach spawning was of negligible importance.

20. Peak migration of juveniles out of Brooks Lake occurred on May 29, but some migration continued all summer and fall.

21. Throughout the season, 1,293 outmigrant sockeye salmon were caught with fyke nets.

22. Outmigrants during the main migration were composed of two distinct age and size groups: 2-year-olds, averaging 109 mm. mid-eye-fork length, and yearlings, averaging 83 mm.

23. The total season's outmigrant age composition was 2 percent fry, 42 percent yearlings, and 56 percent 2-year-olds.

24. Representative daily samples were obtained from samples with as few as five fish, taken at any location at Brooks Lake outlet.

25. Sockeye salmon fry and fingerlings emerging from Brooks River gravels migrate downstream into Naknek Lake and do not migrate upstream into Brooks Lake in significant numbers.

26. Sockeye salmon migrants feed actively and grow rapidly up to the time of seaward migration.

27. Sockeye salmon fry in Brooks Lake tributaries migrated completely out of small tributaries by June 1.

28. Canadian tow nets and beach seines were unsatisfactory for representative sampling of sockeye salmon in Brooks Lake.

29. Small-mesh gill nets, although subject to limitations, are the most practical gear for sampling lake-dwelling sockeye salmon in Brooks Lake.

30. In nylon gill nets, 3/4-inch stretch mesh was the most efficient size for capturing yearling sockeye salmon.

31. Five hundred and five juvenile sockeye salmon were caught in gill nets during the summer. Other catches included: 138 adult sockeye salmon, 26 coho salmon, 62 rainbow trout, 4 Dolly Varden, 23 lake trout, 120 round whitefish, 26 pygmy whitefish, 78 sculpins,

1 blackfish, 5 ninespine stickleback, and 9 threespine stickleback.

32. Sockeye salmon fry were not successfully caught in gill nets because the smallest mesh size was too large to hold them.

33. Juvenile sockeye salmon were nearly absent from midlake areas in early summer but gradually adopted a pelagic life as the season progressed.

34. In midlake 79 percent of the sockeye salmon were captured between the surface and 15 feet, and only 21 percent from 15 to 45 feet.

35. Increases in weight of lake-dwelling juvenile sockeye salmon level off during August and September when initial formation of an annulus occurs.

36. Of sockeye salmon caught in the lake more were feeding on insects than on plankton.

37. Incidence of empty stomachs increased through the season.

38. Four varieties of zooplankton and one of insects made up the bulk of sockeye salmon food in the lake.

39. Sockeye salmon in the lake had no serious parasite infestations.

40. SCUBA is a practical method of observing fish in the natural aquatic environment in Brooks Lake.

41. Brooks Lake zooplankton and phytoplankton were well distributed at all depths and stations through the season and, compared with other North American lakes, were relatively abundant.

42. A large-scale contour map of Brooks Lake was completed based on 57 transects made with an echo sounder.

43. Periodic chemical and physical measurements were made of the following water qualities from surface to bottom at three stations: temperature, transparency, phosphorus, nitrogen, silica, turbidity, oxygen, pH, and total hardness. Each of these was adequate to support fish and was well distributed at all depths through the summer.

44. Primary productivity of Brooks Lake was measured throughout the summer by the Carbon^{14} technique of Nielsen (1952) at 5-day intervals at three stations from surface to bottom; measurements in Naknek Lake were made every 15 days for comparison. Primary productivity was moderately low but extended to a much greater depth in Brooks Lake than in Naknek. Rate of production in Naknek Lake in the surface region was greater than in Brooks, but production in Brooks extended to a greater depth.

ACKNOWLEDGMENTS

The enthusiasm and technical competence of the six college students who assisted me at Brooks Lake made possible the successful accomplishment of program objectives. Each assistant was responsible for one phase or more of the program, and under my direction each prepared an analysis and report when the project was completed. Their reports are the basis for this paper. Their individual principal contributions and college or university origins are as follows: W. L. Hartman, Cornell University, contour map and spawning behavior observations; C. R. Goldman, University of Michigan, primary productivity; W. H. Pogue, Humboldt State College, counts, tagging, stream surveys, adult samples, and climatological instruments; R. E. Painter, University of Michigan, primary productivity, spawning observations, and chemical water analyses; J. A. Harbour, Eastern Washington College, fingerling outmigration; F. P. Meyer, Iowa State College, gill net sampling, food studies, upstream migration of juveniles in Brooks River, plankton, and fish parasites; G. Y. Wong, University of Washington, chemical water analyses.

F. F. Hooper recommended instruments and procedures for some of the chemical analyses. Warren Steenberg, Katmai National Monument Ranger, piloted his personal plane for aerial surveys of beach spawning on September 14. W. E. Johnson of the Fisheries Research Board of Canada supplied the Canadian tow net.

LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION.
1946. Standard methods for the examination of water and sewage. 9th ed. Lancaster Press, Inc., Lancaster, Pa., 286 p.

BARNABY, JOSEPH T.
1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum), of the Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 39, vol. 50, p. 237-295.

BIRGE, E. A., and C. JUDAY.
1922. The inland lakes of Wisconsin. The plankton. I. Its quantity and chemical composition. Wisconsin Geological and Natural History Surveys, Bulletin 64, Science Series No. 13, 222 p.

BRETT, J. R.
1952. Skeena River sockeye escapement and distribution. Journal of the Fisheries Research Board of Canada, vol. 8, no. 7, p. 453-468.

CLARK, WEBSTER K.
1957. Seasonal food habits of the Kodiak bear. Transactions of the Twenty-Second North American Wildlife Conference, p. 145-151

CLARKE, G. L., and D. F. BUMPUS.
1950. The plankton sampler--an instrument for quantitative plankton investigations. American Society of Limnology and Oceanography, Special Publication No. 5, 8 p.

CLUTTER, R. I., and L. E. WHITESEL.
1956. Collection and interpretation of sockeye salmon scales. International Pacific Salmon Fisheries Commission, Bulletin 9, 159 p.

EICHER, G. J., Jr.
1951. Effects of tagging on red salmon. U.S. Fish and Wildlife Service, Special Scientific Report--Fisheries No. 64, 4 p.

ESCHMEYER, P. H., and R. M. BAILEY.
1954. The pygmy whitefish, *Coregonus coulteri*, in Lake Superior. Transactions of the American Fisheries Society, vol. 84, p. 161-199.

FOERSTER, R. E.
1936. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. Journal of the Biological Board of Canada, vol. 2, no. 3, p. 311-333.

GILBERT, CHARLES H., and WILLIS H. RICH.
1927. Investigations concerning the red salmon runs to the Karluk River, Alaska. Bulletin of the U.S. Bureau of Fisheries, vol. 43, p. 1-69. [Document No. 1021, issued July 27, 1927.]

GOLDMAN, CHARLES R.
1960. Primary productivity and limiting factors in three lakes of the Alaska Peninsula. Ecological Monographs, vol. 30, no. 2 (April), p. 207-230.

GRIGGS, ROBERT F.
1922. The valley of ten thousand smokes. The National Geographic Society, Washington, D.C., 341 p.

HUTCHINSON, G. E.
1957. A treatise on limnology. John Wiley and Sons, Inc., New York, 1015 p.

IDYLL, C.
1942. Food of rainbow, cutthroat and brown trout in the Cowichan River system, B.C. Journal of the Fisheries Research Board of Canada, vol. 5, no. 5, p. 448-458.

JOHNSON, W. E.
1956. On the distribution of young sockeye salmon *(Oncorhynchus nerka)* in Babine and Nilkitkwa Lakes, B. C. Journal of the Fisheries Research Board of Canada, vol. 13, no. 5, p. 695-708.

JUDAY, C., WILLIS H. RICH, G. I. KEMMERER, and ALBERT MANN.
1932. Limnological studies of Karluk Lake Alaska, 1926-1930. Bulletin of the U.S. Bureau of Fisheries, vol. 47, no. 12, p. 407-436.

KROGIUS, F. V.
1951. O dinamike chislennosti krasnoi *(Oncorhynchus nerka* (Walbaum)). [On the dynamics of abundance of the sockeye salmon (*Oncorhynchus nerka* Walb.).] Izvestiia Tikhookeanskovo Nauchno-issledovatel'skovo Instituta Rybnovo Khoziaistva i Okeanografii, vol. 35, p. 1-16. [Fisheries Research Board of Canada, Translation Series No. 101.] (Translation examined only.)

KROGIUS, F. V., and E. M. KROKHIN.
1948. Ob urozhainosti molodi krasnoi (*Oncorhynchus nerka* Walb.) [On the production of young sockeye salmon (*Oncorhynchus nerka* Walb.).] Izvestiia Tikhookeanskovo Nauchno-issledovatel'skovo Instituta Rybnovo Khoziaistva i Okeanografii, vol. 28 p. 3-27. [Fisheries Research Board of Canada, Translation Series No. 109.] (Translation examined only.)

1956a. Rezultaty issledovanii biologii nerki-krasnoi sostoainiia ee zaposov i kolebanii chislennosti v vodakh Kamchatki. [Results of a study of the biology of sockeye salmon, the condition of the stocks, and the fluctuation in numbers in Kamchatka waters.] Voprosy Ikhtiologii, no. 7, p. 3-20. [Fisheries Research Board of Canada, Translation Series No. 176.] (Translation examined only.)

1956b. Prichiny kolebanii chislennosti krasnoi na Kamchatki. [Causes of the fluctuations in abundance of sockeye salmon in Kamchatka.] Trudy Problemnikh i Tematicheskikh Soveshchanii ZIN, No. 6, p. 144-149. [Fisheries Research Board of Canada, Translation Series No. 92.] (Translation examined only.)

LAGLER, KARL F.
1949. Studies in freshwater fishery biology, 3d ed. J. W. Edwards, Ann Arbor, Mich., 231 p.

1952. Freshwater fishery biology. William C. Brown Co., Dubuque, Iowa, 360 p.

MATHISEN, OLE A.
1955. Studies on the spawning biology of the red salmon, *Oncorhynchus nerka* (Walbaum), in Bristol Bay, Alaska, with special reference to the effect of altered sex ratios. Ph. D. Thesis, University of Washington, Seattle, 285 p.

MILLER, R. B., and W. A. KENNEDY.
1946. Observations on the lake trout of Great Bear Lake. Journal of the Fisheries Research Board of Canada, vol. 7, no. 4, p. 176-189.

NIELSEN, E. STEEMANN.
1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer, vol. 18, p. 117-140.

PENNAK, ROBERT W.
1953. Freshwater invertebrates of the United States. The Ronald Press Co., New York, 769 p.

RAWSON, D. S.
1951. Studies of the fish of Great Slave Lake. Journal of the Fisheries Research Board of Canada, vol. 8, no. 4, p. 207-240.

1956. The net plankton of Great Slave Lake. Journal of the Fisheries Research Board of Canada, vol. 13, no. 1, p. 53-127.

REES, W. H.
1957. The vertical and horizontal distribution of seaward migrant salmon in the forebay of Baker Dam. Washington Department of Fisheries, Fishery Research Paper, vol. 2, no. 1, p. 5-17.

RICKER, W. E.
1937. Physical and chemical characteristics of Cultus Lake, B. C. Journal of the Biological Board of Canada, vol. 3, no. 4, p. 363-402.

1952. The benthos of Cultus Lake. Journal of the Fisheries Research Board of Canada, vol. 9, no. 4, p. 204-212.

ROUNSEFELL, GEORGE A.
1957. Fecundity of North American salmonidae. U.S. Fish and Wildlife Service, Fishery Bulletin 122, vol. 57, p. 451-468.

RUTTNER, FRANZ.
1953. Fundamentals of limnology. University of Toronto Press, Toronto, Canada, 242 p.

SCHAEFER, MILNER B.
1951. A study of the spawning populations of sockeye salmon in the Harrison River system, with special reference to the problem of enumeration by means of marked members. International Pacific Salmon Fisheries Commission, Bulletin 4, 207 p.

WARNER, KENDALL.
1953. The use of a graphic-recording echo sounder on Maine lakes. Progressive Fish-Culturist, vol. 15, no. 4, p. 170-174.

WELCH, PAUL S.
1935. Limnology. McGraw-Hill Book Co., New York, 471 p.

1948. Limnological methods. The Blakiston Company, Philadelphia, 381 p.

MS #1002

Created in 1849 the Department of the Interior--a department of conservation--is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States--now and in the future.

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BUREAU OF COMMERCIAL FISHERIES
WASHINGTON, D.C. 20240

POSTAGE AND FEES PAID
U.S. DEPARTMENT OF THE INTERIOR