SELECTION OF SPAWNING SITES BY SOCKEYE SALMON IN SMALL STREAMS

DAVID T. HOOPES[1]

ABSTRACT

This study was undertaken in three small western Alaska streams to identify factors that influence selection of spawning sites by sockeye salmon. Temporal and spatial distribution patterns were relatively constant from year to year despite large fluctuations in the number of spawners. The selection of a spawning site was more closely related to composition of the stream bottom than to gradient, water depth and velocity, or cover.

The selection of spawning sites by salmon and the factors that influence selection bear directly on the problem of estimating the carrying capacities of spawning grounds. Such estimates cannot be developed for returning adults without knowledge of what constitutes an acceptable spawning area. In this study I relate the distribution of spawning sockeye salmon, *Oncorhynchus nerka*, in three small streams to the physical characteristics of the streams. The work reported was done at Brooks Lake, Alaska, in 1959, 1960, and 1961 and is one phase of an overall investigation by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) on the freshwater ecology of sockeye salmon.

The three study streams, Hidden, Up-a-tree, and One Shot Creeks, are lateral[2] tributaries of Brooks Lake (Figure 1). Hidden Creek enters Brooks Lake in the southeastern shore about 10 km from the outlet, Brooks River. The other two streams lie between Brooks River and Hidden Creek. Up-a-tree Creek, the longest lateral stream in the Brooks Lake system, enters the lake at the southeastern corner; One Shot Creek, the shortest of the major spawning tributaries, flows into the lake on the south shore not far from Hidden Creek. Some physical features of the portions of the three streams accessible to salmon are presented in Table 1. Included in the table is the pool-riffle ratio, an indicator of the proportion of stream length composed of pools. What constitutes a pool is somewhat subjective, but I considered a pool to be a place where the stream was deeper and wider than average, the current was appreciably slower than immediately upstream or downstream, and hiding places for fish were more extensive than in adjacent parts of the stream.

The three streams were alike in two significant aspects—volume of flow and presence of beaver dams. Flows in each stream varied from 0.23 to 0.34 m^3s (cubic meter per second) (8.2 to 12.1 cfs) throughout the spawning season except for some short periods of higher flows during freshets. Beaver dams blocked the upstream migration of salmon except during brief periods of unusually high water.

DISTRIBUTION OF SPAWNERS

The distribution of adult sockeye salmon was observed closely and recorded from the time fish arrived off the stream mouths until they had all spawned. I recorded the number of fish ascending the streams each day and the distribution of spawners along each stream on an average of every 3 days.

Sockeye salmon school off the mouths of tributaries to Brooks Lake 1 to 3 weeks before ascending the streams to spawn (Hartman and

[1] National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821.

[2] The term "lateral tributaries" refers to streams entering a lake from shores that lie roughly parallel to the lake's long axis.

Manuscript accepted January 1972.

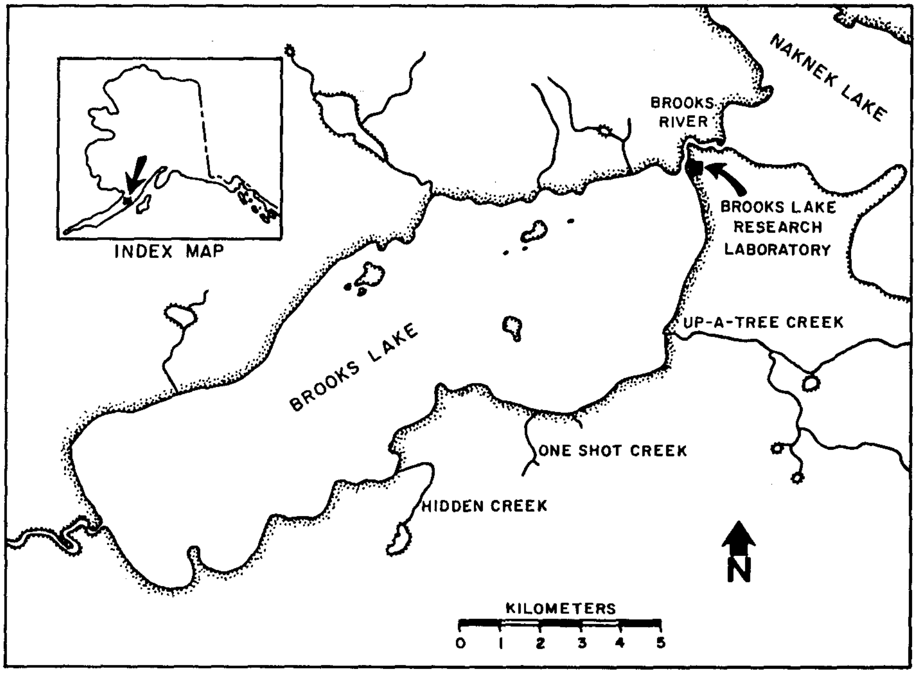

FIGURE 1.—Brooks Lake, Alaska, showing three lateral tributaries where spawning sockeye salmon were studied in 1959, 1960, and 1961.

Raleigh, 1964). I observed fish joining schools off the stream mouths even after some fish had entered the streams and begun spawning. These late-arriving fish usually spent several days in the school before they ascended the stream.

In some years all adult sockeye salmon that entered the study streams were passed through weirs. Weirs were operated at Up-a-tree and One Shot Creeks in 1961 (Table 2) and at Hidden Creek in 1959, 1960, and 1961 (Table 3). To insure that all fish in the run were counted, the weirs were closed when fish first appeared off the stream mouths. The fish were allowed to pass upstream through a counting gate whenever 10 or so appeared immediately downstream from the weir.

Although spawning sockeye salmon were constantly present in each study stream for several weeks, they tended to enter the streams in waves or pulses. Fish entered Hidden Creek in several distinct waves in 1959 and 1960 but not in 1961 (Table 3). However, the weir records for Up-a-tree and One Shot Creeks suggest the presence of more than one major influx of spawners in

TABLE 1.—Watershed area, total length, and physical characteristics of portions of streams accessible to salmon in Hidden, Up-a-tree, and One Shot Creeks, tributaries to Brooks Lake, Alaska.

			Portion accessible to salmon					
Stream	Watershed area (km^2)	Total length (*km*)	Stream length (*km*)	Range of stream width (*m*)	Pool-riffle ratio	Range of pool depths (*cm*)	Range of riffle depths (*cm*)	Percent gradient in spawning areas (*range*)
Hidden Creek	28	13	3.9	3-6.0	4:6	50- 80	15-30	0.74-1.45
Up-a-tree Creek	75	24	8.0	3-4.5	3:7	60-100	25-35	0.36-0.72
One Shot Creek	13	6.5	3.8	3-4.0	3:7	60- 90	25-35	0.84-1.30

TABLE 2.—Number of sockeye salmon passed upstream through the weirs each day and cumulative upstream count at Up-a-tree and One Shot Creeks, 1961.

Stream and date	No. of fish through weir	Cumulative count	Stream and date	No. of fish through weir	Cumulative count
Up-a-tree Creek			One Shot Creek		
July 28	1	1	July 30	1	1
29	0	1	31	10	11
30	135	136			
		[1]521	Aug. 1	14	25
31	[2]121	642	2	146	171
			3	6	177
Aug. 1	1	643	4	9	186
2	35	678	5	3	189
3	0	678	6	0	189
4	0	678	7	0	189
5	10	688	8	85	274
6	3	691	9	1	275
7	0	691	10	0	275
8	26	717	11	4	279
9	59	776	12	11	290
10	0	776	13	0	290
11	9	785	14	0	290
12	2	787	15	1	291
13	3	790	16	0	291
14	19	809	17	0	291
15	10	819	18	5	296
16	0	819	19	0	296
17	12	831	20	4	300
18	0	831	21	0	300
19	0	831	22	0	300
20	0	831	23	0	300
21	0	831	24	0	300
22	0	831	25	0	300
23	0	831	26	0	300
24	0	831	27	1	301
25	0	831	28	2	303
26	0	831	29	0	303
27	1	832	30	2	305

[1] At 7:30 a.m. on July 30 the Up-a-tree Creek weir was washed out because of high water. The weir was replaced and a stream survey made on July 31 after the water receded and cleared. An estimate of 521 fish was obtained. This figure was used for subsequent cumulative counts.
[2] Counted upstream after survey.

these two streams in 1961 (Table 2). Three distinct waves of spawners were observed in studies on nearby Brooks River by Hartman, Merrell, and Painter (1964).

The distribution of spawners over the length of each stream was determined from repeated counts of occupied redds in survey sections which were established for measuring stream gradients.[3] The counts were summed by section and totaled for the entire stream. The percentage of this total occurring in each section was calculated for the year, and these percentages were used as indicators of the distribution of each year's run. Distribution was not uniform among the three study streams during the 3 years of this study but was generally consistent for each stream (Figures 2, 3, 4) despite marked differences between years in the number of spawners (Table 4).

In 1959, when occupied redd sites were counted at 2-day intervals, the distribution of spawners in Hidden Creek changed very little after the first week. Counts were combined to show the similarity in distribution of occupied redds at the end of the first, second, and third week of spawning (Figure 5). By the end of the first week (early period), 2,625 sockeye salmon had ascended the stream to select redd sites and spawn. An additional 1,239 fish entered and began to spawn during the second week (middle period), and 694 more entered during the third week (late period). Thus, substantial numbers

[3] These survey sections will be described in more detail later. They consist of 100- to 200-m-long segments of stream channel extending from the mouths of the study streams to the first beaver dam judged to be normally impassable to migrating salmon.

TABLE 3.—Number of sockeye salmon passed upstream through the weir each day and cumulative upstream count at Hidden Creek, 1959, 1960, and 1961.

Date	1959		1960		1961	
	No. of fish through weir	Cumulative count	No. of fish through weir	Cumulative count	No. of fish through weir	Cumulative count
August						
9	--	--	--	--	38	38
10	1,240	1,240	--	--	0	38
11	0	1,240	--	--	39	77
12	0	1,240	--	--	1	78
13	547	1,787	--	--	383	461
14	40	1,827	23	23	417	878
15	574	2,401	1,216	1,239	0	878
16	224	2,625	269	1,508	0	878
17	0	2,625	6	1,514	8	886
18	1,217	3,842	42	1,556	130	1,016
19	0	3,842	0	1,556	0	1,016
20	0	3,842	0	1,556	0	1,016
21	0	3,842	319	1,875	0	1,016
22	22	3,864	158	2,033	0	1,016
23	0	3,864	.0	2,033	0	1,016
24	0	3,864	110	2,143	0	1,016
25	0	3,864	43	2,186	7	1,023
26	0	3,864	1	2,187	46	1,069
27	0	3,864	15	2,202	3	1,072
28	694	4,558	37	2,239	0	1,072
29	--	--	10	2,249	1	1,073
30	--	--	26	2,275	0	1,073
31	--	--	--	--	1	1,074
September						
1	--	--	--	--	4	1,078
2	--	--	--	--	0	1,078
3	--	--	--	--	0	1,078
4	--	--	--	--	0	1,078
5	--	--	--	--	13	1,091

TABLE 4.—Sockeye salmon escapements into Hidden, Up-a-tree, and One Shot Creeks in 1959, 1960, and 1961.

Stream and year	Method of enumeration	No. of fish in escapement[1]
Hidden Creek		
1959	Weir count	4,558
1960	Weir count	2,275
1961	Weir count	1,078
Up-a-tree Creek		
1959	Stream survey[2]	542
1960	Stream survey	1,334
1961	Stream survey and weir	653 (832)
One Shot Creek		
1959	Stream survey	246
1960	Stream survey	269
1961	Stream survey and weir	221 (305)

[1] Figures in parentheses are weir counts.
[2] Highest single count during any one season.

of fish ascended the stream and occupied redd sites while other fish were already spawning. Some late fish spawned adjacent to previous arrivals, and others continued on to the upstream spawning areas. This distribution of spawners was not measurably altered by differences in their numbers, as evidenced by the distribution throughout the season of the considerably fewer fish in 1961.

Although the distribution of spawners from year to year varied more in Up-a-tree than in Hidden Creek, Up-a-tree Creek had areas of consistently high and consistently low spawning density (Figure 3). More spawners entered Up-a-tree Creek in 1960 than in 1959 or 1961, and the 1960 spawners were distributed more uniformly along a greater length of stream than either the 1959 or 1961 spawners. In 1961, relatively few fish spawned in the lower sections of the stream.

The distribution and number of spawners in One Shot Creek was similar for the 3 years of the study (Figure 4, Table 4)—here spawners consistently concentrated in the upper and lower ends of the stream.

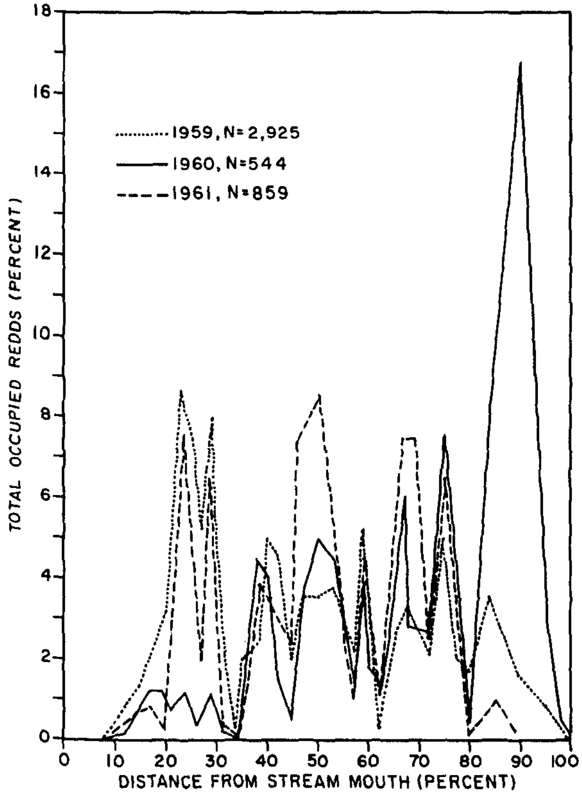

FIGURE 2.—Distribution of redds occupied by sockeye salmon in Hidden Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

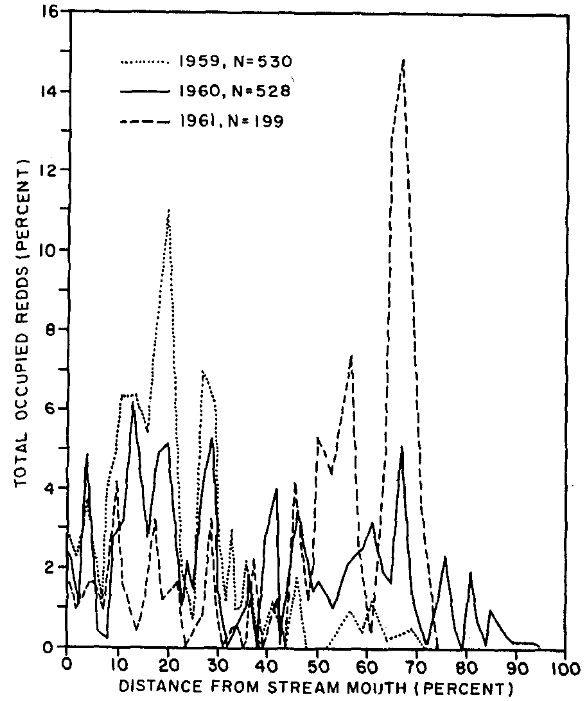

FIGURE 3.—Distribution of redds occupied by sockeye salmon in Up-a-tree Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

PHYSICAL CHARACTERISTICS OF STUDY STREAMS IN RELATION TO SPAWNING

To determine relationships between the location of spawning sites and physical characteristics of the streams, I measured the gradient, size composition of the bottom materials, and water depth and velocity of spawning areas in the three streams. Velocity and volume of streamflow, stream width, and stream gradient are known to affect the size composition of materials in the streambed, but velocity is considered to be the dominant factor (Krumbein and Pettijohn, 1938; Rubey, 1938; Hjulstrom, 1939; Krumbein and Sloss, 1951). A reduction in stream gradient is accompanied by a reduction in water velocity and in the average size of bottom particles.

STREAM GRADIENT

Gradients were measured in each study stream from the mouth to the first beaver dam judged normally impassable to migrating salmon. Gradients were calculated between convenient points (stations) that were 100 to 200 m apart along the stream. The relative elevation of the water surface was measured with a surveyor's level, and the distance between stations was measured along the center of the streambed with a surveyor's chain. Stream width was also measured at each station. The survey sections were numbered consecutively upstream from the mouth of each creek.

Survey sections were often too long to reveal variations in gradient and distribution of spawn-

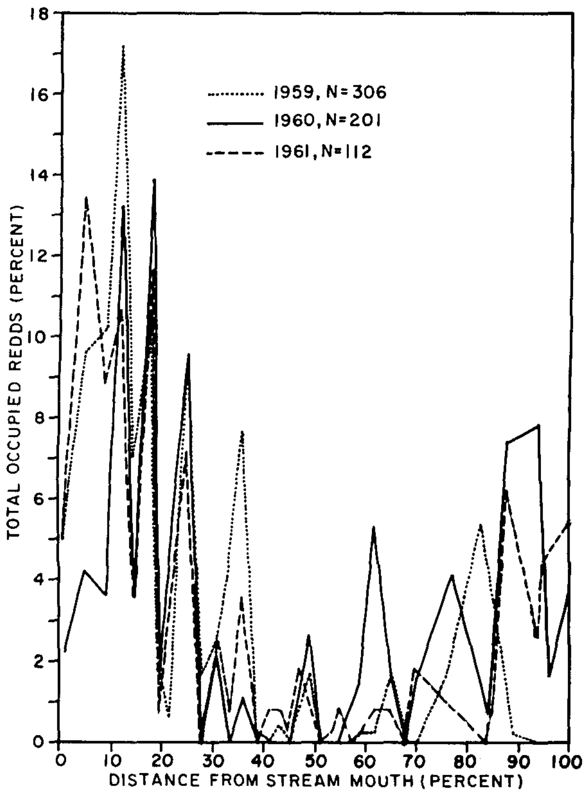

FIGURE 4.—Distribution of redds occupied by sockeye salmon in One Shot Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

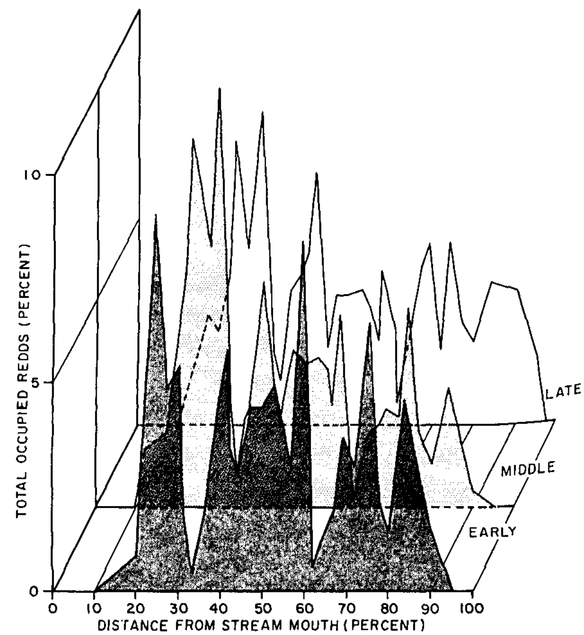

FIGURE 5.—Temporal and spatial distribution of redds occupied by sockeye salmon during the early, middle, and late periods of the 1959 spawning season in Hidden Creek, Brooks Lake, Alaska.

ers in great detail. For example, some had so many steep runs and falls that the average gradient appeared to be too high for spawning, although the sections contained one or two short reaches of stream with gradients acceptable to spawning fish. Other sections had long reaches of generally too low gradient but had one or two short steep falls, so that little acceptable spawning ground was actually available even though the average gradient appeared suitable for spawning. Despite these problems in methodology, after comparing the density of spawning females and stream gradients section by section in the three study streams for all 3 years, I found that little or no spawning occurred in areas having average gradients of less than 0.5% or more than 2.0%.

SIZE OF STREAMBED MATERIALS IN SELECTED SECTIONS

I made detailed studies of bottom composition in eight of the sections surveyed for gradient.[4] Sections were selected for these detailed studies on the basis of their relative amounts of use by spawning salmon so that areas having high and low spawning densities could be compared. Two sections with high and two with low densities of spawners were selected in Hidden Creek, and one each was selected in Up-a-tree and One Shot Creeks.

From six to nine samples of the streambed were collected in each of the eight sections. The samples were taken from both pools and riffles at locations where salmon spawned in 1959. Each sample consisted of the top 20 to 30 cm of bottom materials (gravel and sand) from an area 1 m^2. The material was removed from the

[4] Observations were also made on water depth and velocity and availability of streambank cover.

streambed with a shovel and placed in a cotton soil sample bag. It was later washed into individual 19-liter tins, drained, and allowed to air dry. The dried samples were separated into 10 size classes by passing them through a stacked series of square-meshed 20-cm U.S. Standard sieves. After the sample was placed on the top sieve, the series was agitated for 10 min in a hand-powered portable sieve shaker. The materials retained on each sieve were weighed to the nearest gram on a triple-beam trip scale.

I describe the particle size distribution of the streambed by relating the percent of the total sample weight retained on each sieve to the logarithm of its mesh size. This method of analysis is described more fully by Spangler (1951) and by the American Society for Testing Materials (1958).

Because the particle composition of streambed samples from pools and riffles was so similar within each section, I combined the data by section. I then derived a cumulative size distribution for each section by summing the weights retained by each sieve size in all samples for a section. These data were used to construct cumulative distribution curves with which I could compare the composition of the stream bottom in sections of high spawning density (Figure 6) with that in sections of low spawning density (Figure 7).

The curves for sections of high spawning density (Figure 6) show that bottom composition was quite similar in all three streams. The only difference among the four sections was the slightly higher percentage of small particles and the somewhat lower percentage of large particles in section 9 of Hidden Creek, as evidenced by the lateral displacement toward the left of the composition curve for this section.

The cumulative curves for sections with low spawning density (Figure 7) showed that particle size distribution was similar in three of the sections (one from each stream) but quite different in the fourth section (Hidden Creek, 2). It is clear that spawner density was low in Hidden Creek in areas where particle sizes were either very large or very small.

Sockeye salmon spawned most frequently in areas where the particles were intermediate in size. In sections of high spawning density and intermediate gradient, cobbles larger than 7.6 cm in diameter made up about 6% of the bottom, cobbles from 2.5 to 7.6 cm about 50%, particles 1.3 to 2.5 cm about 20%, and particles less than 1.3 cm the remainder (Figure 8A). The bottom in sections of low spawning density and high gradient was made up of almost 40% cobbles exceeding 7.6 cm in diameter and contained very little material less than 2.5 cm in diameter (Figure 8B). The bottom in sections of low spawn-

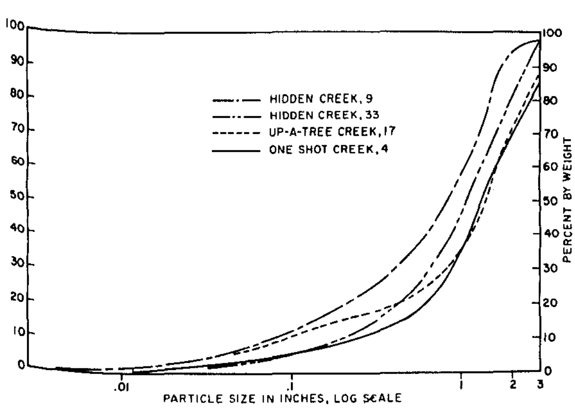

FIGURE 6.—Curves of cumulative particle size distribution in four sections with high-spawning density, Hidden Creek sections 9 and 33, Up-a-tree Creek section 17, and One Shot Creek section 4. All four sections had intermediate stream gradients.

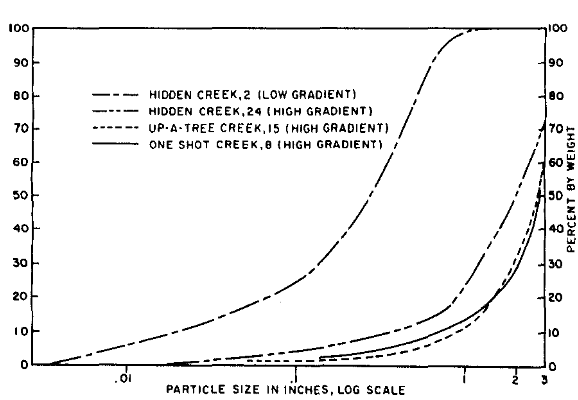

FIGURE 7.—Curves of cumulative particle size distribution in four sections with low-spawning density, Hidden Creek sections 2 and 24, Up-a-tree Creek section 15, and One Shot Creek section 8. All of the sections had high gradients except Hidden Creek section 2, which had low.

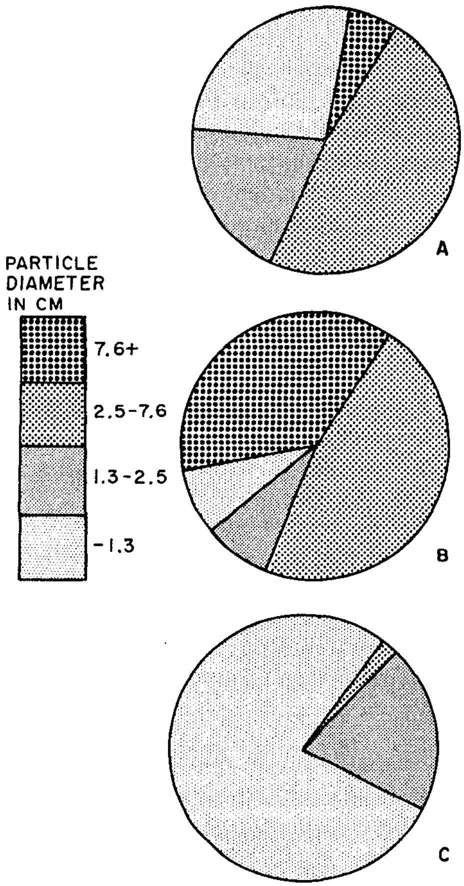

FIGURE 8.—Particle composition by percent weight of bottom materials in study sections having (A) high spawning density and intermediate gradient, (B) low spawning density and high gradient, and (C) low spawning density and low gradient.

ing density and low gradient contained 80% particles under 1.3 cm in diameter (Figure 8C).

WATER DEPTH AND VELOCITY

Water depth and velocity were measured in 1960 in each of the eight study sections (Table 5). Three to five transects about equidistant from each other were laid out across the stream in each section. Velocity and depth were measured at about 0.3-m intervals along these transects with a Gurley impeller-type current meter[5] mounted on a graduated rod and set at 12 cm above the streambed, described as "fish depth" for Pacific salmon.[6] Volume of flow was computed from the velocity and depth data collected. The values presented are assumed to reflect conditions normally encountered by fish selecting spawning sites in the study sections, although pronounced changes in water depth and velocity may occur briefly during the spawning season as a result of heavy rains. Sections with high and low densities of spawners often had similar water depths and velocities (Table 5: Depths—Hidden Creek, section 9 versus 24; One Shot Creek, section 4 versus 8. Velocities—Hidden Creek sections 9 and 33 versus Up-a-tree Creek section 15 and One Shot Creek section 8).

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

[6] J. S. Chambers, R. T. Pressey, J. R. Donaldson, and W. R. McKinley. Washington State Department of Fisheries, Annual Report, 1954, submitted to U.S. Army Corps of Engineers, 145 p.

TABLE 5.—Average depth, velocity, and volume of flow in sections of high and low spawning densities of Hidden, Up-a-tree, and One Shot Creeks, Brooks Lake, Alaska, 1960.

Stream and section	Level of spawning density	Average depth (*cm*)	Water velocity (*mps*)	(*fps*)	Volume of flow (m^3s)	(*cfs*)
Hidden Creek						
9	High	15	0.59	1.9	0.27	9.6
33	High	23	0.45	1.5	0.31	11.1
24	Low	15	0.70	2.3	0.25	8.9
2	Low	28	0.39	1.3	0.28	10.0
Up-a-tree Creek						
17	High	24	0.36	1.2	0.29	10.3
15	Low	23	0.47	1.5	0.31	11.1
One Shot Creek						
4	High	32	0.35	1.1	0.37	13.2
8	Low	28	0.54	1.8	0.44	15.7

FACTORS AFFECTING SPAWNING SITE SELECTION

Salmon and trout usually spawn in a specific type of microenvironment within a broadly uniform environment. One such type of microenvironment occurs at the downstream ends or tails of pools, just upstream from the point where the flow breaks over the lip of the pool into the riffle below (Needham and Taft, 1934; Schultz and students, 1935; Smith, 1941; White, 1942; Briggs, 1953; Shapovalov and Taft, 1954). Riffles may also contain microenvironments attractive to spawning salmon[7] (Belding, 1934; Burner, 1951; Needham and Vaughan, 1952; Briggs, 1953; see also footnote 6.)

Variations in streambed slope are important in the selection of spawning sites because these variations cause exchange in intragravel and stream water (Vaux, 1962) and affect the stability of the bottom. In pools, spawning sites were usually located where the bottom sloped upward slightly in the direction of flow, as in pool tails. Even in riffles, fish observed during this study seldom constructed redds where the bottom sloped steeply but rather chose gently sloping sites where the excavated tailspill provided a slight rise. The preferred streambed was also nearly level across the stream, although moderate to steep lateral inclines were occasionally used in crowded areas.

In 1959, sockeye salmon first entered and began spawning in Hidden Creek on August 11. On August 13, I marked 14 redds in an area of high spawning density after taking detailed notes on the exact location of each spawning site and the features of the immediate environment. I assumed that the first fish in an area selected the preferred sites, so that these 14 sites represented preferred habitat. All of the sites were at or near the tails of pools and along the bank adjacent to the main streamflow. I observed the sites until August 25, when high water precluded further study.

[7] J. S. Chambers, G. H. Allen, and R. T. Pressey. Washington State Department of Fisheries, Annual Report, 1955, submitted to U.S. Army Corps of Engineers, 175 p.

Observations in the immediate vicinity of the 14 study redds showed that late-arriving fish spawned upstream from the initial redd at the tail of each pool. When the pool was filled with redds for its entire length and pool width permitted two or more redds side by side, late arrivals chose spawning sites sequentially upstream, again beginning at the tail but across the stream from the original site. No salmon spawned in unstable gravels usually associated with the shallow sides of pools.

Riffles made up 60 to 70% of the stream length accessible to salmon in the three study streams, and many fish spawned in these riffles. As in the pools, spawning salmon preferred definite parts of the riffles. The first fish invariably chose sites along the deeper side and higher bank. Salmon also preferred certain riffles over others. Short riffles with water of moderate depth and flow were used as readily as pool tails. Long shallow riffles with some cover along adjacent banks were occupied next. The last sites used were those in long shallow riffles without nearby pools or cover.

The significance of cover in the selection of a spawning site by sockeye salmon is hard to evaluate. Hourston and MacKinnon (1957) found that pink salmon, *O. gorbuscha,* spawning in an artificial channel selected sites adjacent to cover rather than those distant from cover. I frequently observed that sockeye salmon, especially those that arrived early when a wide choice of sites was available, selected a site that had good cover. The absence of cover did not necessarily prevent early spawners from selecting a particular site, but given two adjacent locations apparently equal with regard to water depth and flow and gravel composition, the fish tended to select the site nearer to cover. Favored sites were near deeply undercut banks, banks overhung with tall grass and herbaceous plants, holes washed under tree roots, log and brush jams, and deep pools.

Cover that attracts alarmed fish may not actually afford protection, because concealment alone does not insure safety. I have observed brown bears, *Ursus gyas,* systematically search for salmon under overhanging vegetation and undercut banks. In my three study streams, cover that would protect a salmon from bears was quite scant, and even when such cover was available, alarmed fish often sought the shaded area provided by overhanging herbs and grasses as refuge rather than places of comparatively greater security such as undercut banks and logs.

The selection of a site by a spawning sockeye salmon seemed to be more closely related to the composition of the stream bottom than to any other single factor studied. Work done with fish closely related to salmon supports this view (Hobbs, 1940; Fabricius, 1950; Fabricius and Gustafson, 1954; Needham, 1961). This preference by salmon for areas having bottom materials of intermediate composition explains why the density of spawners was high in sections with moderate gradient and low in sections with either high or low gradient. When more desirable bottom material was lacking, fish spawned in excessively coarse material (higher gradients) before excessively fine (lower gradients). In this respect, my observations indicated that gradient was related to the selection of spawning sites by sockeye salmon. The observations by Trautman (1942) and Huet (1949, 1959) showing that distribution of several species of fish permanently resident in lotic environments is closely related to stream gradient may well have resulted from a preference by those fish for a particular substrate.

Factors other than physical conditions in the spawning grounds may also influence the selection of redd sites by sockeye salmon. Briggs (1955) stated that among anadromous fishes, the earliest arrivals in a particular spawning tributary traveled to the most distant spawning grounds and the later arrivals occupied areas closer to the stream mouth. In the three streams I studied, however, early arrivals did not necessarily ascend to the uppermost spawning areas. Moreover, the sites selected by later arrivals often were located between sites chosen by the earlier spawners.

The female sockeye salmon selects the spawning site, usually near other spawners (Noble, 1938). The presence and stimulation of other spawners may be necessary for successful spawning even though much effort is expended in territorial defense. I seldom saw single spawning pairs but observed rather that fish tended to form more or less isolated groups of several pairs. How much of this behavior is due to preference for certain physical characteristics of the spawning grounds and how much to innate social behavior is not known.

SUMMARY

1. Spawning site selection by sockeye salmon in three small lateral tributaries entering Brooks Lake, Alaska, was studied from 1959 through 1961.

2. Several waves of sockeye salmon spawners ascended the principal study stream in 1959 and 1960 when the numbers of fish were moderate and high but not in 1961, a year of relatively few fish.

3. Both temporal and spatial distribution patterns were defined and found to be relatively constant despite large fluctuations in the number of spawners.

4. The distribution of spawning fish was correlated with stream gradients. Little or no spawning occurred in areas having gradients of less than 0.5% or more than 2.0%.

5. In preferred spawning areas, cobbles from 2.5 to 7.6 cm in diameter made up about 50% of the bottom, materials 1.3 to 2.5 cm about 25%, and particles less than 1.3 cm the remainder.

6. Spawner distribution was more closely related to the composition of the stream bottom than to any other single factor studied.

7. Given two adjacent locations equally desirable with regard to hydrological conditions and bottom composition, sockeye salmon tended to select the site with the most nearby cover and concealment.

8. Early arrivals did not necessarily use the uppermost spawning areas, and later arrivals primarily filled in acceptable areas already in use.

ACKNOWLEDGMENTS

This study was conducted while the author was employed as a seasonal fishery aid at the National Marine Fisheries Service Field Station, Brooks Lake, Alaska. The author is indebted to Wilbur L. Hartman, Charles J. DiCostanzo, and George Y. Harry, Jr., for making available the time, equipment, transportation, financial aid, and editorial assistance required. The author is particularly grateful to Milton B. Trautman, Curator of Vertebrate Zoology at the Ohio State University Museum, for his guidance in formulating the study and carrying out portions of the field work and to Kenneth D. Carlander, Professor of Zoology at Iowa State University, for his critical review of the doctoral dissertation from which this paper was prepared.

LITERATURE CITED

AMERICAN SOCIETY FOR TESTING MATERIALS.
1958. Book of A.S.T.M. Standards, part 4.

BELDING, D. L.
1934. The spawning habits of the Atlantic salmon. Trans. Am. Fish. Soc. 64:211-218.

BRIGGS, J. C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. Calif. Dep. Fish Game, Fish Bull. 94, 62 p.
1955. Behavior pattern in migratory fishes. Science (Wash., D.C.) 122:240.

BURNER, C. J.
1951. Characteristics of spawning nests of Columbia River salmon. U.S. Fish Wildl. Serv., Fish. Bull. 52:97-110.

FABRICIUS, E.
1950. Heterogeneous stimulus summation in the release of spawning activities in fish. Inst. Freshwater Res. Drottningholm, Rep. 31:57-99.

FABRICIUS, E., AND K.-J. GUSTAFSON.
1954. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. Inst. Freshwater Res. Drottningholm, Rep. 35: 58-104.

HARTMAN, W. L., T. R. MERRELL, JR., AND R. PAINTER.
1964. Mass spawning behavior of sockeye salmon in Brooks River, Alaska. Copeia 1964:362-368.

HARTMAN, W. L., AND R. F. RALEIGH.
1964. Tributary homing of sockeye salmon at Brooks and Karluk Lakes, Alaska. J. Fish. Res. Board Can. 21:485-504.

HJULSTROM, F.
1939. Transportation of detritus by moving water. (Translated from Swedish by Parker D. Trask.) *In* Recent marine sediments, a symposium, p. 5-31. American Association of Petroleum Geologists, Tulsa, Okla.

HOBBS, D. F.
1940. Natural reproduction of trout in New Zealand and its relation to density of populations. N. Z. Mar. Dep., Fish. Bull. 8, 93 p.

HOURSTON, W. R., AND D. MACKINNON.
1957. Use of an artificial spawning channel by salmon. Trans. Am. Fish. Soc. 86:220-230.

HUET, M.
1949. Apercu des relations entre la pente et les populations piscicoles des eaux courantes. Rev. Suisse Hydrol. 11:332-351.
1959. Profiles and biology of Western European streams as related to fish management. Trans. Am. Fish. Soc. 88:155-163.

KRUMBEIN, W. C., AND F. J. PETTIJOHN.
1938. Manual of sedimentary petrography. Appleton-Century-Croft, Inc., N.Y., 549 p.

KRUMBEIN, W. C., AND L. L. SLOSS.
1951. Stratigraphy and sedimentation. W. H. Freeman and Company, San Franc., 497 p.

NEEDHAM, P. R.
1961. Observations on the natural spawning of eastern brook trout. Calif. Fish Game 47:27-40.

NEEDHAM, P. R., AND T. M. VAUGHAN.
1952. Spawning of the Dolly Varden, *Salvelinus malma*, in Twin Creek, Idaho. Copeia 1952: 197-199.

NEEDHAM, P. R., AND A. C. TAFT.
1934. Observations on the spawning of steelhead trout. Trans. Am. Fish. Soc. 64:332-338.

NOBLE, G. K.
1938. Sexual selection among fishes. Biol. Rev. (Camb.) 13:133-158.

RUBEY, W. W.
1938. The force required to move particles on a stream bed. U.S. Geol. Surv. Prof. Pap. 189: 121-140.

SCHULTZ, L. P., AND STUDENTS.
1935. The breeding activities of the little redfish, a landlocked form of the sockeye salmon, *Oncorhynchus nerka*. Mid-Pac. Mag. 48:67-77.

SHAPOVALOV, L., AND A. C. TAFT.
1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish Game, Fish. Bull. 98, 375 p.

SMITH, O. R.
1941. The spawning habits of cutthroat and eastern brook trouts. J. Wildl. Manage. 5:461-471.

SPANGLER, M. G.
1951. Soil engineering. International Textbook Company, Scranton, Pa., 458 p.

TRAUTMAN, M. B.
1942. Fish distribution and abundance correlated with stream gradient as a consideration in stocking programs. Trans. North Am. Wildl. Conf. 7: 211-223.

VAUX, W. G.
1962. Interchange of stream and intragravel water in a salmon spawning riffle. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 405, 11 p.

WHITE, H. C.
1942. Atlantic salmon redds and artificial spawning beds. J. Fish. Res. Board Can. 6:37-44.