AN ABSTRACT OF THE THESIS OF

Setsuwo Tsunoda for the Master of Science in Fisheries
(Name)   (Degree)   (Major)

Date thesis is presented _June 23, 1966_

Title MOVEMENTS OF SPAWNING SOCKEYE SALMON IN HIDDEN

CREEK, BROOKS LAKE, ALASKA

Abstract approved Redacted for Privacy
(Major professor)

The movements of a population of adult sockeye salmon
(Oncorhynchus nerka) were followed in a small tributary of Brooks
Lake, Alaska until spawning was nearly complete in 1963. The ob-
jectives of the study were to describe the movements of sockeye
salmon on the spawning ground of an entire small stream, to deter-
mine factors related to such movements, and to consider the sig-
nificance of the movements to the species.

The spawning run was inventoried at a weir located near the
mouth of the tributary. Portions of the run were sampled as they
immigrated, and the sampled fish were tagged to enable subsequent
identification of individual fish on the spawning ground. Following
the initial immigration, daily observations were made to ascertain
the location of all fish and the activities of the tagged fish. Tagging
had no material effect on either dispersal in the stream or pairing
of spawners.

The spawning run totalled 2,495; the ratio of males to females was 2.27:1.00. The run consisted preponderantly of males that had spent two winters in the ocean (two ocean-years) and females that had spent three winters in the ocean (three ocean-years). They entered the tributary over a period of 14 days in two waves separated by an interval of three days.

The overall median life span in the stream was 12 days in the first wave and eight days in the second wave. The difference was primarily due to predation on the salmon by the brown bear (Ursus arctos).

The average female established a redd in 1.4 days; thereafter the females rarely moved far from their redds. The average male required 2.3 days to establish himself in a spawning locale; thereafter most males remained within a relatively small area. The males showed a decided tendency to remain in areas with a high density of females on redds. Fewer females than males overshot their spawning sites.

No relation was found between the movements of spawners and either variations of water level or surface water temperature of the stream. Bear predation disrupted spawning activities only locally and temporarily.

Males of three ocean-years paired with more females per male than did males of one or two ocean-years. But because of their

greater numbers two-ocean-year males participated in more spawnings than did three-ocean-year males. The mean duration of pairing of a particular male with a particular female on a redd was 1.25 days.

I concluded that homing within the tributary did not occur; therefore its spawning stock must be a homogeneous unit. The role of the male is primarily one of fertilization of the eggs, not one of defense of territory. Because of the abnormally high ratio of males to females, competition between males for spawning partners resulted in most males of one or two ocean-years being relegated to attend females paired with larger males. Conflict among the males was apparently largely confined within two separate classes of males: males 50 cm or shorter jockeyed among themselves for seemingly preferred positions of attendance next to a pair on a redd, while males 51 cm or longer competed for spawning partners.

The polygamous habit in sockeye salmon usually results in a seeming excess of males on the spawning ground beyond the number required to fertilize the eggs. I propose that this "surplus" of males provides a safety factor in times of low numbers in a stock and the competition needed to disperse the males among the available females; both provisions insure fertilization of the available eggs. However, crucial experiments need to be done on an entire population of sockeye salmon with artificially reduced ratios of males to

females to determine whether the movements of the spawners would

result in an efficiency of egg fertilization sufficient to make harvest-

ing of the "surplus" males feasible.

MOVEMENTS OF SPAWNING SOCKEYE SALMON IN
HIDDEN CREEK, BROOKS LAKE, ALASKA

by

SETSUWO TSUNODA

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

MASTER OF SCIENCE

June 1967

APPROVED:

Assistant Professor of Fisheries
In Charge of Major

Head of Department of Fisheries and Wildlife

Dean of Graduate School

Date thesis is presented _June 23, 1966_

Typed by Opal Grossnicklaus

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

MOVEMENTS OF SPAWNING SOCKEYE SALMON IN HIDDEN CREEK, BROOKS LAKE, ALASKA

INTRODUCTION

Because most spawning grounds used by sockeye salmon

(<u>Oncorhynchus</u> <u>nerka</u>) are extensive, the movements of the salmon

on the spawning grounds must play a vital role in the propagation of

the species. In the spawning process the salmon must seek out a

suitable spawning area, and male and female must come together

for successful spawning to occur. Behavior of sockeye salmon on

the spawning ground has been studied by Schultz and students (1935),

Burner (1951), Mathisen (1962), and Hartman, Merrell, and Painter

(1964), but none of these workers considered relations among spawn-

ers of an entire, genetically separate population of sockeye salmon.

Numerous small, independent populations of sockeye salmon

spawn in lakes and streams throughout its range. The spawning

grounds are situated in that part of the Asian coast adjoining the

northern Bering Sea and extending south to the Kurile Islands and in

that part of the North American coast adjoining the northern Bering

Sea and extending south to the Columbia River drainage (Cleaver,

1964). The populations spawning in individual lakes and streams

are thought to be genetically separate. Thompson (1962) emphasized

the importance of studying individual small populations to elucidate

the factors causing fluctuations in numbers of this valuable species.

Associated with reproduction in anadromous salmonids are several activities that involve movement. The activities are: 1) migration to the home stream, 2) dispersal on the spawning ground, 3) spawning, and 4) defense of the redd. This study is concerned with movements associated with all but the first class of activities. The objectives of this study were to describe the movements of a population of sockeye salmon on the spawning ground of an entire small stream, to determine factors related to such movements, and to consider the significance of the movements to the species.

During the period 14-31 August 1963, I observed the movements of sockeye spawners in Hidden Creek, a small tributary of Brooks Lake in southwestern Alaska (Figure 1). The width of Hidden Creek averages about 12 feet and rarely exceeds 20 feet. In the portion used for spawning average depth of riffles was less than one foot and of pools was less than two feet. The gradient of the tributary does not exceed 2.5% (Hoopes, 1962). The tributary was open to salmon for 12,100 feet from Brooks Lake. A beaver dam obstructed further upstream movement during the period of study. Downstream from the beaver dam there was no obstacle to migration.
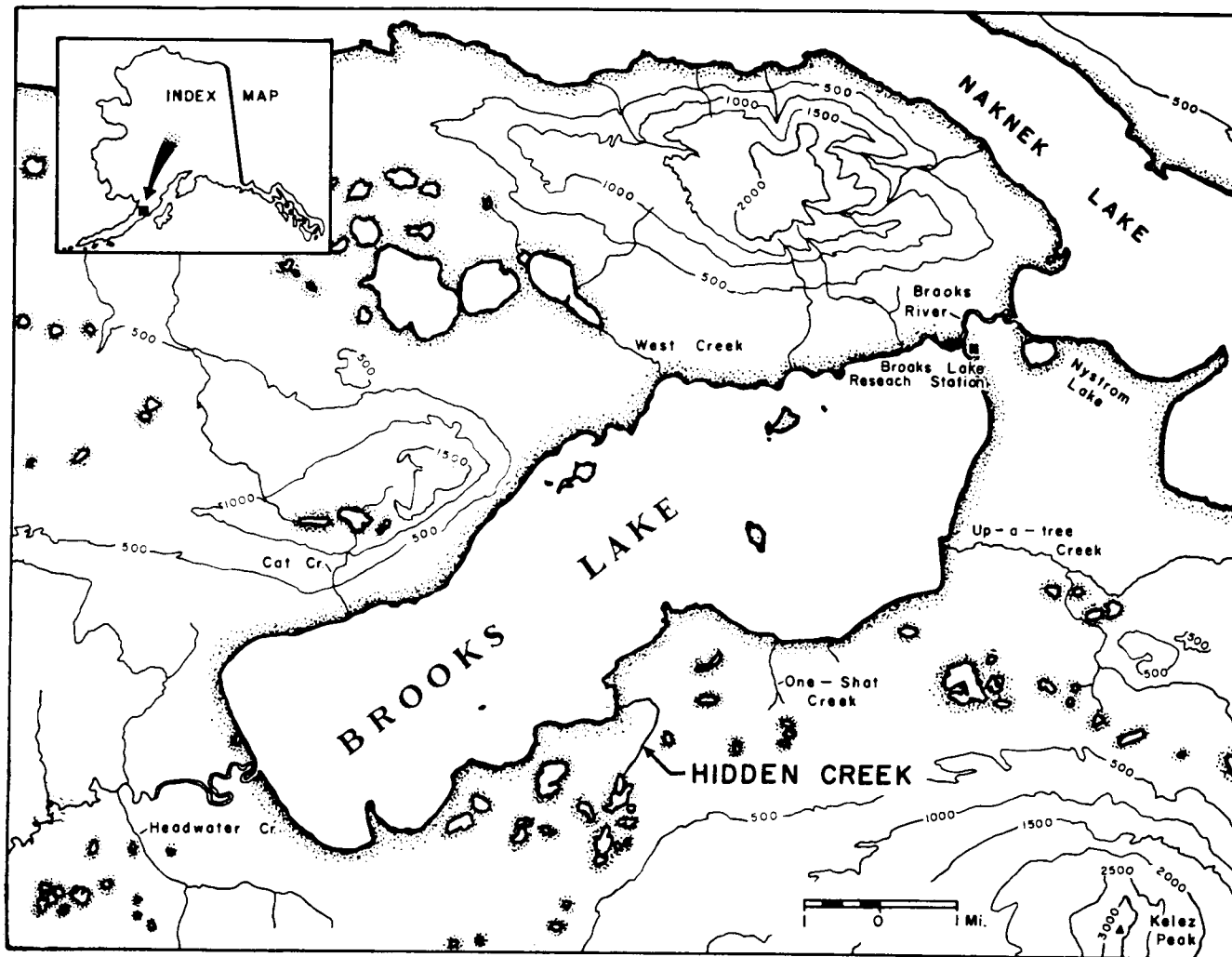
Figure 1. Location of Hidden Creek, a sockeye spawning tributary of Brooks Lake, Alaska. (After Hartman, Strickland, and Hoopes, 1962)

ESCAPEMENT

A total of 2,495 sockeye salmon entered Hidden Creek to spawn. Males and females were counted separately at a weir located 300 feet upstream from Brooks Lake; the ratio of males to females was 2.27: 1.00. The sexes are easily distinguished because secondary sexual characteristics are fully developed when the fish enter Hidden Creek to spawn. Most of the males had remained two winters in the ocean (two ocean-years), whereas most of the females had remained three winters (three ocean-years) (Figure 2).

Adult sockeye salmon began congregating at the mouth of Hidden Creek on August 11 and were continuously present there until immigration was complete. The fish entered the stream between August 14 and August 27 in two waves separated by an interval of three days (Figure 3). The bulk of the immigration occurred on August 17 and on August 22.

Six portions of the spawning run were trapped at the weir and tagged with plastic disks affixed through the dorsal musculature. A total of 573 fish (378 males and 195 females) constituting 23% of the run were tagged (Figure 3). Disks of two sizes and five colors were used in combinations of threes and fours to enable later identification of individual fish on the spawning ground. The sex and the distance between the middle of the eye and the fork of the tail were recorded
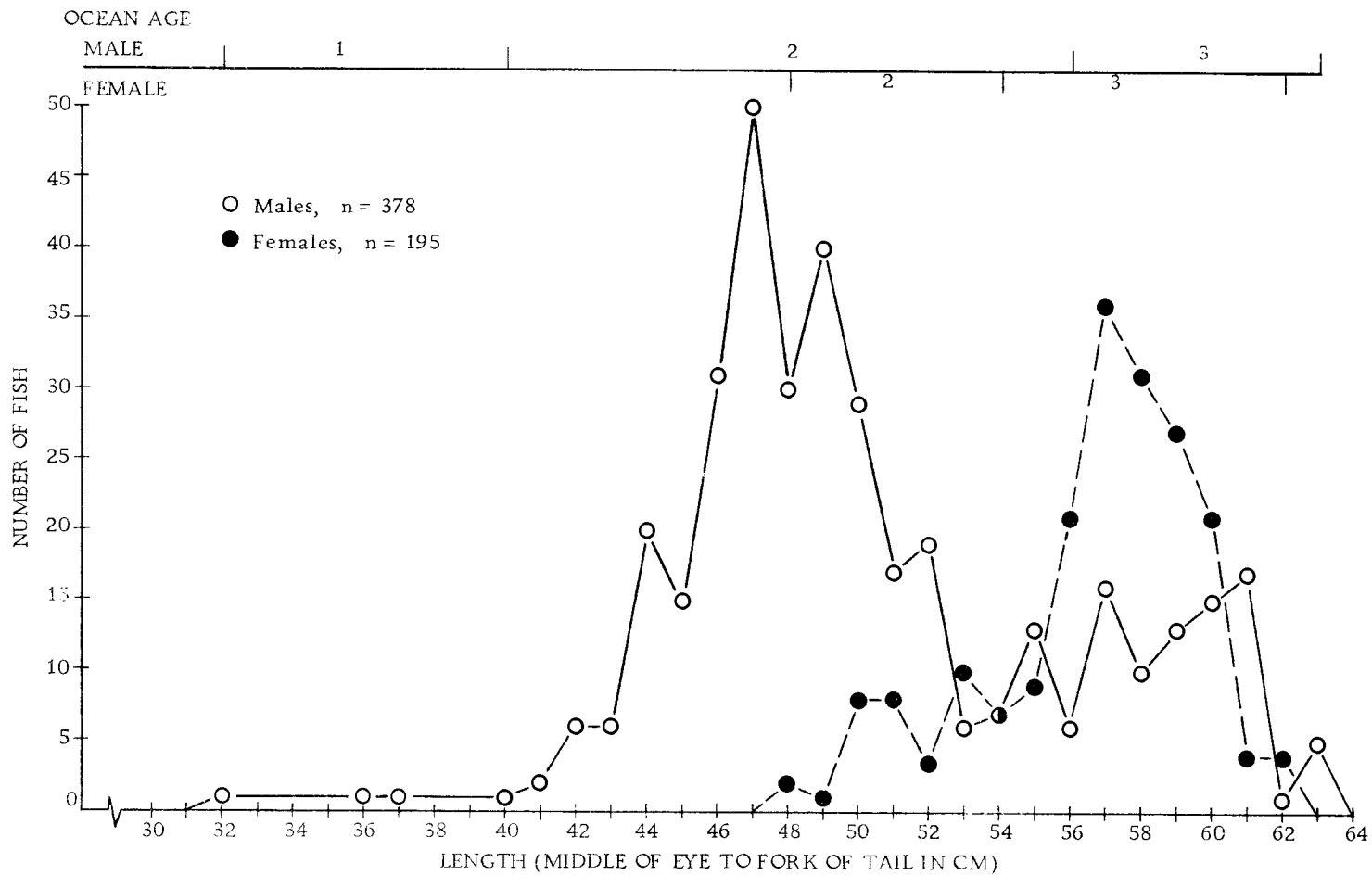
Figure 2. Length frequency distribution and ocean ages of adult sockeye salmon tagged at Hidden Creek weir. Ocean age classification is based on data from Hartman, Heard and Dewey (1964).
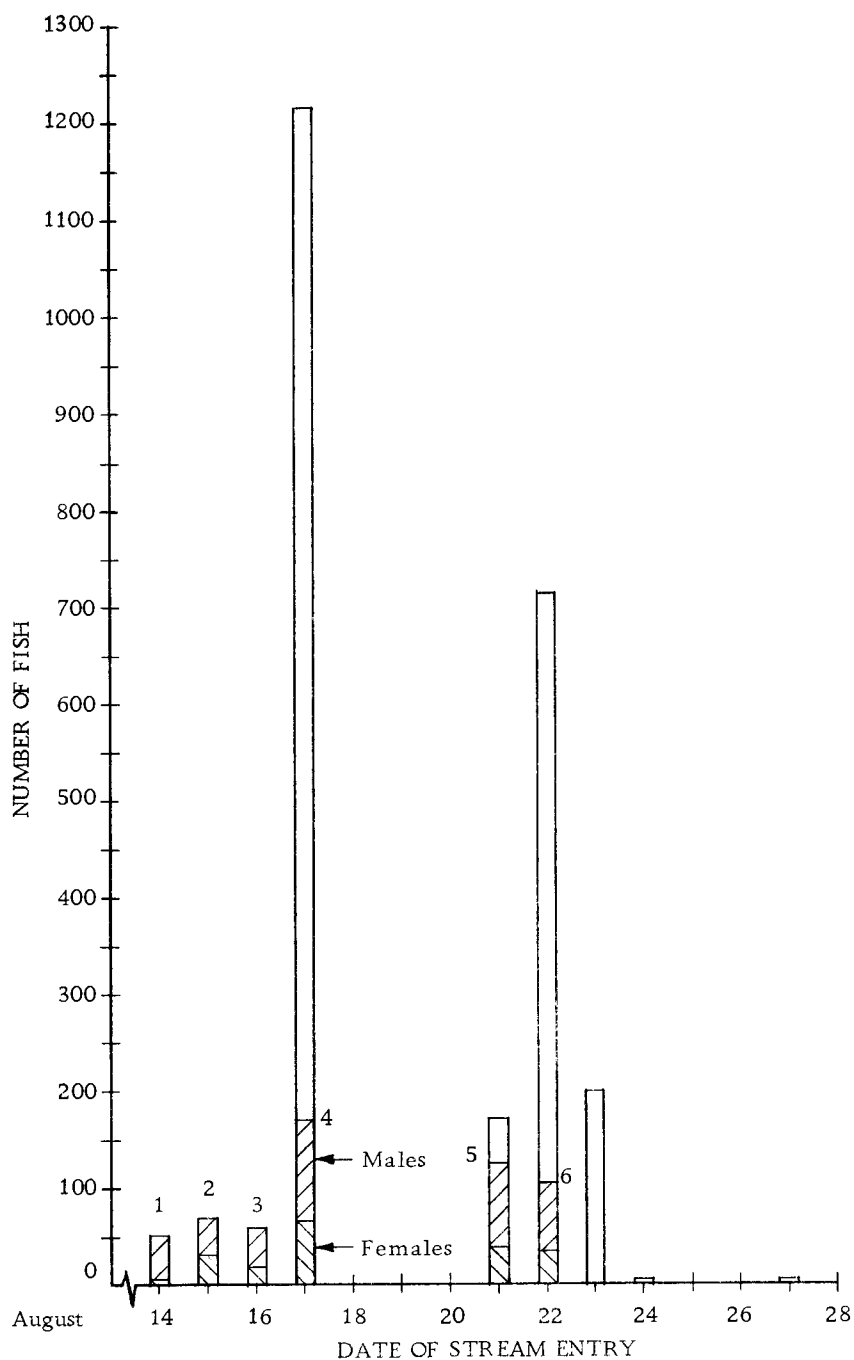
Figure 3. The Hidden Creek escapement in 1963. Hatched areas represent portions tagged; the number by each hatched area indicates the group.

for each tagged fish. All but the first few females tagged were anesthetized with quinaldine to prevent accidental voiding of eggs when handled. Because both sexes readily could be made to void sexual products, all immigrants were considered sexually mature.

LIFE SPAN OF SPAWNERS

The death of many tagged fish was not recorded and was attributed to predation on the salmon by the brown bear (Ursus arctos). A two-man team made daily observations of the fish in the stream. Visibility in the stream was such that prior to the onset of bear predation the daily observations accounted for an average of 92% of the tagged fish. Thereafter the efficiency of the daily observations diminished. Few of the tagged fish lost their tags prior to the start of bear predation. Often only the heads of fish killed by a bear remained, and seemingly bears readily swallowed tags because five sets of tags were found in one bear scat and three in another. Also, the bears carried salmon carcasses away from the immediate vicinity of the stream where they were not seen easily.

The median life span of the first wave of spawners in Hidden Creek was 12 days in the males and 12 to 14 days in the females (Figure 4). In the second wave the median life span was 9 days in the males and 7 to 8 days in the females. The overall median life span in the stream, adjusted for the untagged fish in each group, was 12 days in the first wave of spawners and 8 days in the second wave. For each tagged fish the median life span in the stream was calculated in hours from the middle of the tagging period of the group in which the fish was included to the middle of the daily observation
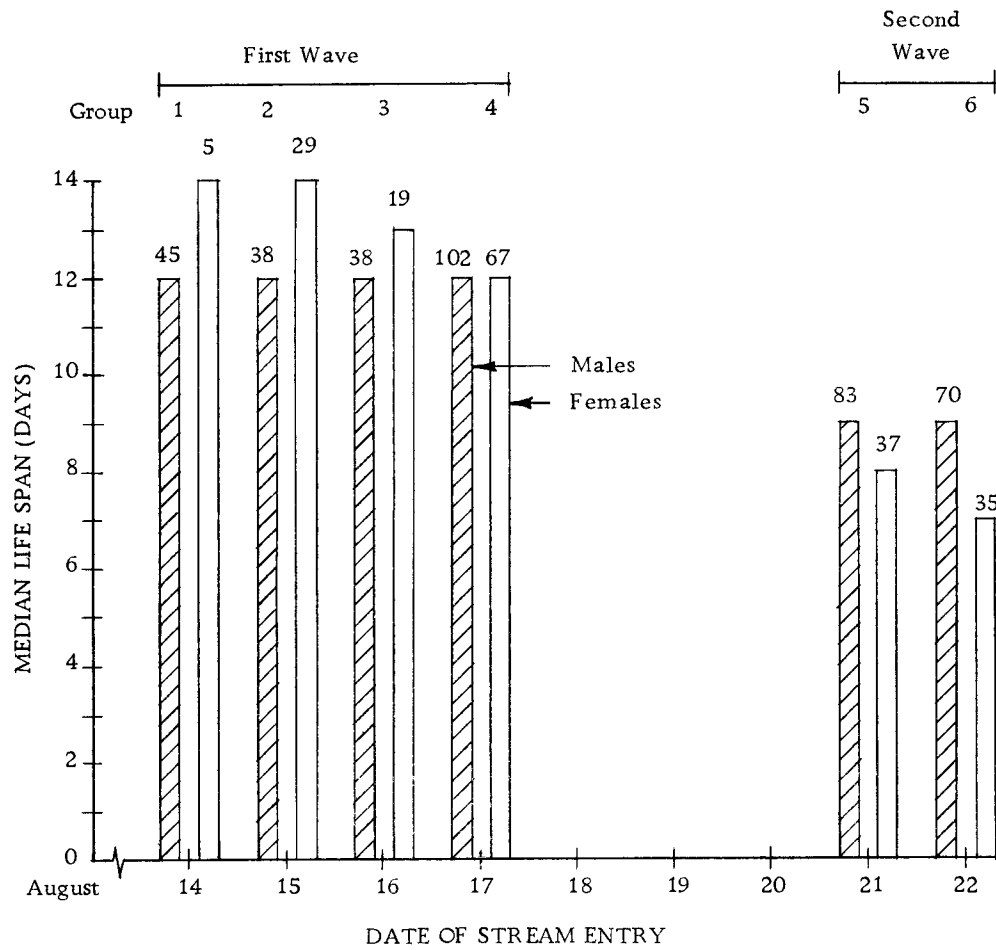
Figure 4. Relation between date of stream entry and median life span of spawners in Hidden Creek. The number above each bar indicates the number of spawners.

period in which the fish was last seen alive; then the hours were converted into days.

The difference between the median life spans in the stream of the two waves of spawners was primarily due to bear predation. Bear predation began on August 22, five days after immigration of the first wave of spawners was completed, but during the immigration of the second wave. No significant mortality due to tagging occurred; only two tagged fish died before spawning or the start of bear predation.

MOVEMENTS OF SPAWNERS

To study the movements of spawners I divided Hidden Creek into sections. Hoopes (1962) had divided the stream into 35 sections based on gradient. For my study I subdivided the 35 sections into a total of 103 sections and designated each section with a conspicuous marker. Lengths of stream sections were measured to the nearest foot down the center of the stream channel with a 100 foot steel tape. Widths of stream sections were measured to the nearest foot perpendicular to the banks wherever a marked change in width occurred. Though the resulting sections were of unequal length, this study was concerned primarily with the extent of movements, not with the exact absolute distances involved. The average length of the sections was about 120 feet. In some of the following analyses I combined the sections into 28 divisions averaging 375 feet long. Because no spawning occurred in the lowest 1,600 feet of the stream, movements of spawners within this area were disregarded, and division 1 begins at the upstream boundary of this area.

Following immigration of the first group of spawners, a two-man team made daily observations of the fish in the stream. The team recorded for each observation of a tagged or untagged fish the date, the time, the section of stream, the sex of the fish, and the activity of the fish. Each member of the team wore polaroid glasses

to enhance underwater vision. Care was exercised to avoid alarming the fish before their activities were recorded. The large number of fish to be observed each day precluded spending more than a minute or two observing any one fish; consequently the recorded activities were judged on only a few criteria (Table 1). About 7,000 observations of tagged fish were made.

Movement of a tagged fish could be detected only if the fish was observed in different stream sections on different days. Consequently movements out of a section and back occurring between daily observations and movements within a section were not detected.

Table 1. Activities of sockeye salmon spawners observed in Hidden Creek.

---

1. Migrating: either alone or with other spawners.

2. Resting: either alone or with other spawners; spawner usually in a pool away from immediate vicinity of spawning activity.

3. Male defending against male, but no associated female or redd evident.

4. Female on a redd but association with other spawners uncertain: female defending redd.

5. Male attending a pair on a redd: male adjacent to redd but off to one side; male often chased by the paired male or, less frequently, by the paired female.

6. Spawner paired: paired male and female lie immediately over redd; female digging or defending redd; male courting female or defending against other males.

7. Spawner on redd alone: usually a spent female; no associated spawner evident.

8. Death
   a. Natural death following spawning.
   b. Death from unknown cause before spawning.
   c. Killed by bear.

Before dealing with the movements of spawners it was neces-
sary to determine whether tagging materially altered their move-
ments. For this purpose the distributions in the stream of the tagged
and untagged immigrants of August 17 on August 18, 19, and 20 were
subjected to Chi-square tests of independence. Males and females
were treated separately. The differences between the distributions
were not significant ($p \geq 0.5$). Eicher (1951) and Mathisen (1962)
arrived at the same conclusion.

Another factor which could have influenced the interpretation
of the data was the unequal lengths of stream sections. Because
the upstream sections tended to be longest, movement in the upper-
most part of the stream was least likely to be detected. Congrega-
tion of either the shorter or longer fish in a particular part of the
stream could lead to differences in movement that were due more
to the lengths of stream sections than to the lengths of spawners.
By using the distribution of all tagged fish on August 23, treating
females and males separately, I found no relation between location
in the stream and length of fish.

Movements of the Female Sockeye

The average female had moved in 25% of the observations.
Almost all the movements occurred before the female established
a redd. Daily observations of tagged females, whose redd sites

became associated with certain landmarks, left no doubt that after
establishing a redd, the female rarely moved far from it as long as
she could maintain her position in the current. In Hidden Creek only
seven females moved from the immediate vicinity of their redds.
Five had returned by the following day, and the other two established
second redds elsewhere in the stream. Mathisen (1962) also noted
that after establishing a redd, the female sockeye rarely left its
immediate vicinity.

On the whole the females rapidly established their redds after
migrating into the spawning area, regardless of the chronological
order of their immigration, for 87.2% were observed on redds within
two days (Table 2). The mean time required to establish a redd site
was 1.4 days.

Table 2. Time from date of stream entry to time of redd establish-
ment by female sockeye spawners in Hidden Creek.

| | Group | Date of entry | Number of females establishing redds on day after entry | | | | Mean days required per female |
			1st	2nd	3rd	4th	
First Wave	1	Aug. 14	4		1		1.4
	2	15	26	1	4		1.3
	3	16	15	3			1.2
	4	17	34	14	12	4	1.8
Second Wave	5	21	34	2	1		1.1
	6	22	30	3	1		1.1

The fourth group of females took the longest time to establish

redd sites. Only 53% of these females were seen on redds within

one day of migration to the spawning ground, contrasted to over 80%

in all other groups. Two factors probably contributed to the longer

period. First, they were included in by far the largest group of

immigrants (Figure 3); consequently competition within the group for

spawning sites was no doubt especially keen. Second, their redds

were concentrated in the uppermost sections of the creek (Figure 5),

and they spent more time in migration. Also, they may not have

been as sexually mature at immigration and therefore not as highly

motivated to spawn as were later immigrants. The females of the

second wave of spawners established redds more quickly than the

females of the first wave (Table 2).

Some females migrated upstream beyond the location of their

redds before spawning. Hartman and Raleigh (1964) termed the behav-

ior of fish passing up through a spawning area and then returning

downstream to spawn "overshooting". In my study overshooting

only by at least 300 feet is considered. In Hidden Creek 18% of all

females overshot. That 76% of those that overshot were in group 6

suggests that these last arrivals on the spawning ground found it

more difficult to find an acceptable spawning site, though they es-

tablished redds as quickly as any other group (Table 2). The dis-

tance of female overshooting ranged up to 1, 800 feet, but less than
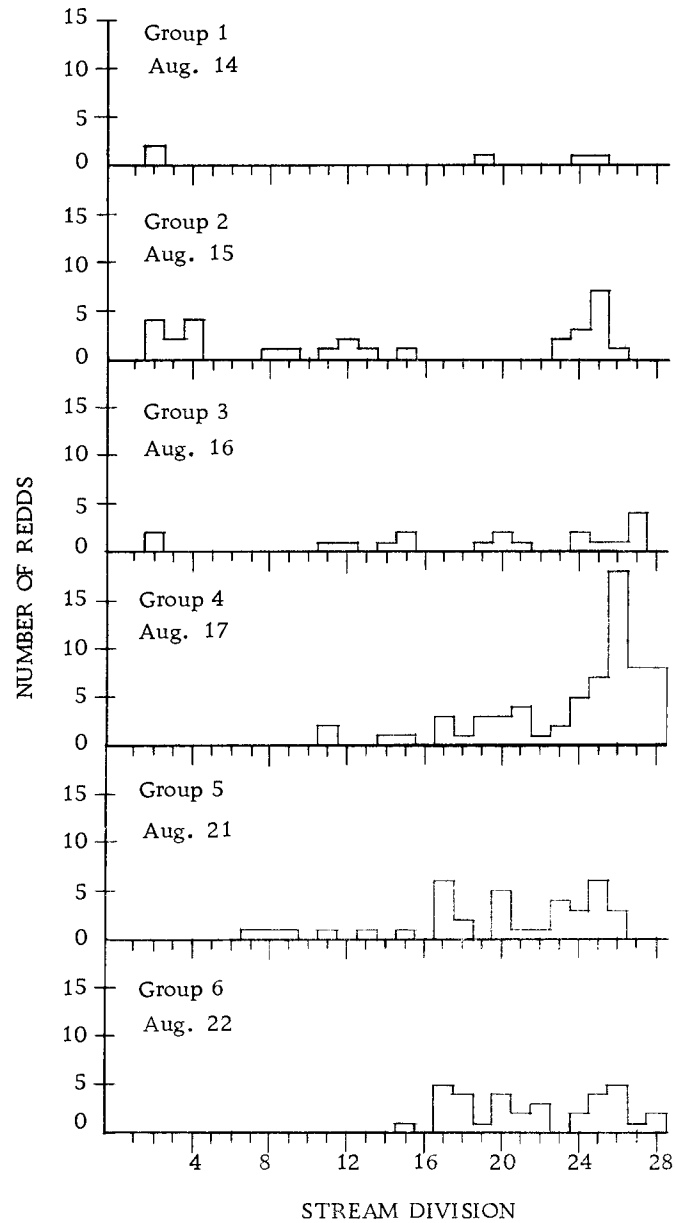
Figure 5. Relation between location of redd and chronology of
stream entry. The number of redds is based on
maximum counts per division of tagged females
judged to be on redds. Division 1 is the farthest
downstream.

5% of all females overshot more than 1,000 feet.

The females tended to concentrate in the upper part of the stream (Figure 6). The densest concentration of redd sites in a section was in the uppermost reaches of the spawning area where territories averaged 38.7 square feet as calculated from:

$$\frac{\text{maximum number of females judged to be on redds}}{\text{total area of section}} \qquad .$$

Because 93% of the females of the first wave of spawners were still alive when the last substantial numbers of the second wave had entered the stream, and because of the strong territoriality of established females, superimposition of redds probably was not extensive.

Movements of the Male Sockeye

The males moved about on the spawning ground much more than the females. The average male had moved in 55% of the observations (Figure 7) compared to 25% for the average female. The males did not limit their movements to the period before spawning as the females did.

The average male required 2.3 days to establish himself in a spawning locale, or to stabilize, after arriving on the spawning ground. I considered a male to have stabilized when the male was
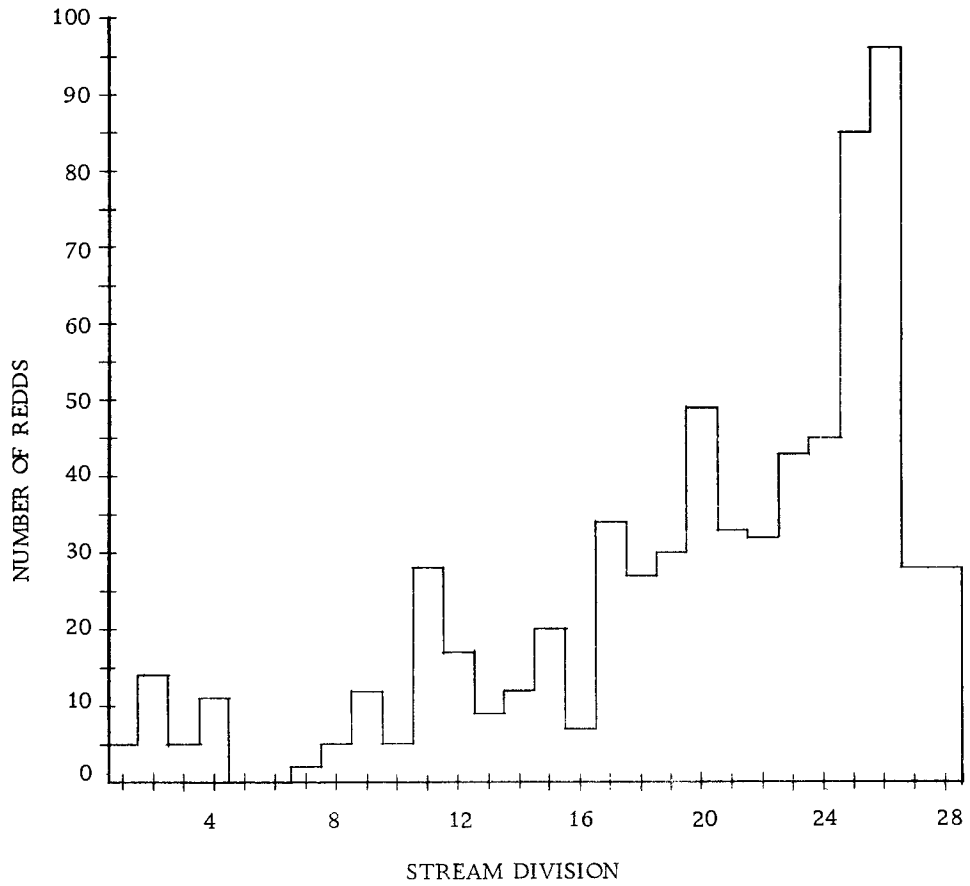
Figure 6. Final distribution of all redds. The number of redds
is based on maximum counts per division of all
females judged to be on redds. Division 1 is the
farthest downstream.
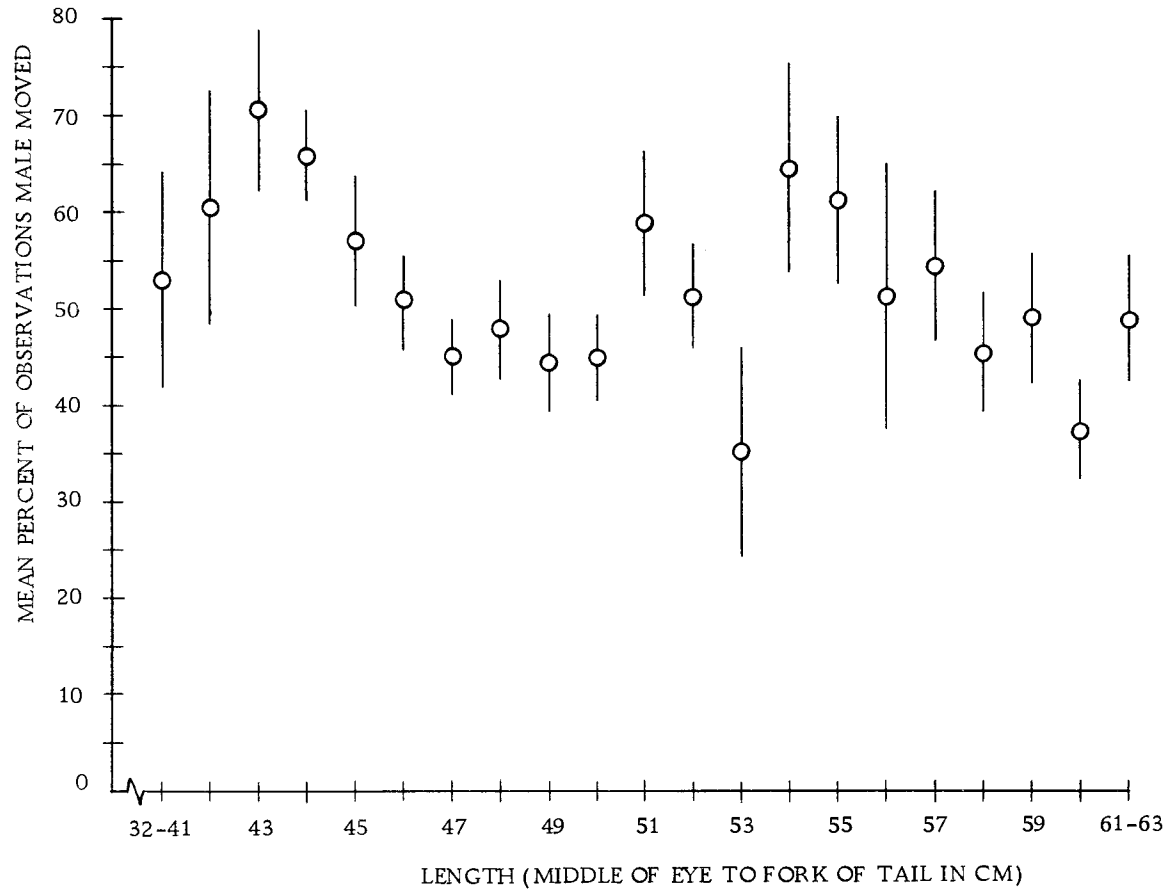
Figure 7. Relation between length of male and the percentage of observations in which the male had moved. Each vertical line represents one standard error on each side of the mean.

seen in the same section on at least two successive daily observations. The initial period required by the males to stabilize generally decreased from group 1 to group 6 (Figure 8). The decrease is most logically related to two factors. The ratio of males to females varied with the changes in the initial period required by the males in the first wave of spawners to stabilize. A lower ratio of males to females apparently affords more opportunity for a male to stabilize than does a higher ratio. But the abrupt decline of the initial period required to stabilize in groups 5 and 6 is greater than can be accounted for by the sex ratio alone, judged from the relation of these two statistics in the first wave of spawners. Also, smaller males ($\leq$ 54 cm) tended to take longer to stabilize than larger males ($>$54 cm) (Figure 9), yet these smaller males constituted a greater percentage of groups with the lower initial periods required to stabilize (groups 3, 5 and 6) than of groups with the higher initial periods required to stabilize (groups 1, 2 and 4) (Figure 8). For these reasons and because adult sockeye were assembled at the mouth of Hidden Creek during the three-day interval in the spawning run, I submit that the males in the second wave of spawners were probably more mature sexually and therefore more highly motivated to spawn than males in the first wave.

The distances of male movements were generally small after the males had initially stabilized. Seventy-nine percent of all males
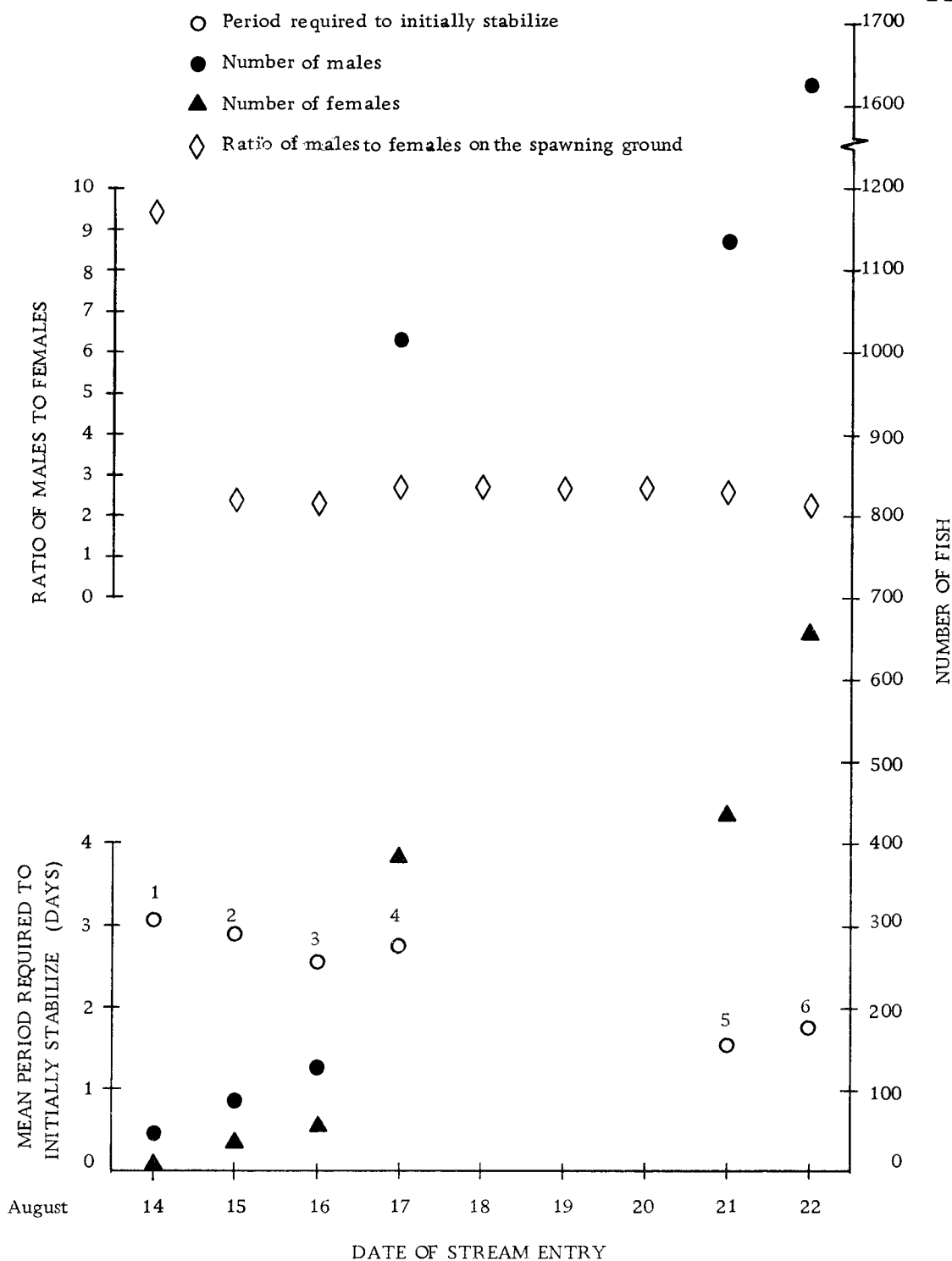
Figure 8. Relation between chronology of stream entry, ratio of males to females, and the period required by males to initially stabilize. The number by each open circle indicates the group.
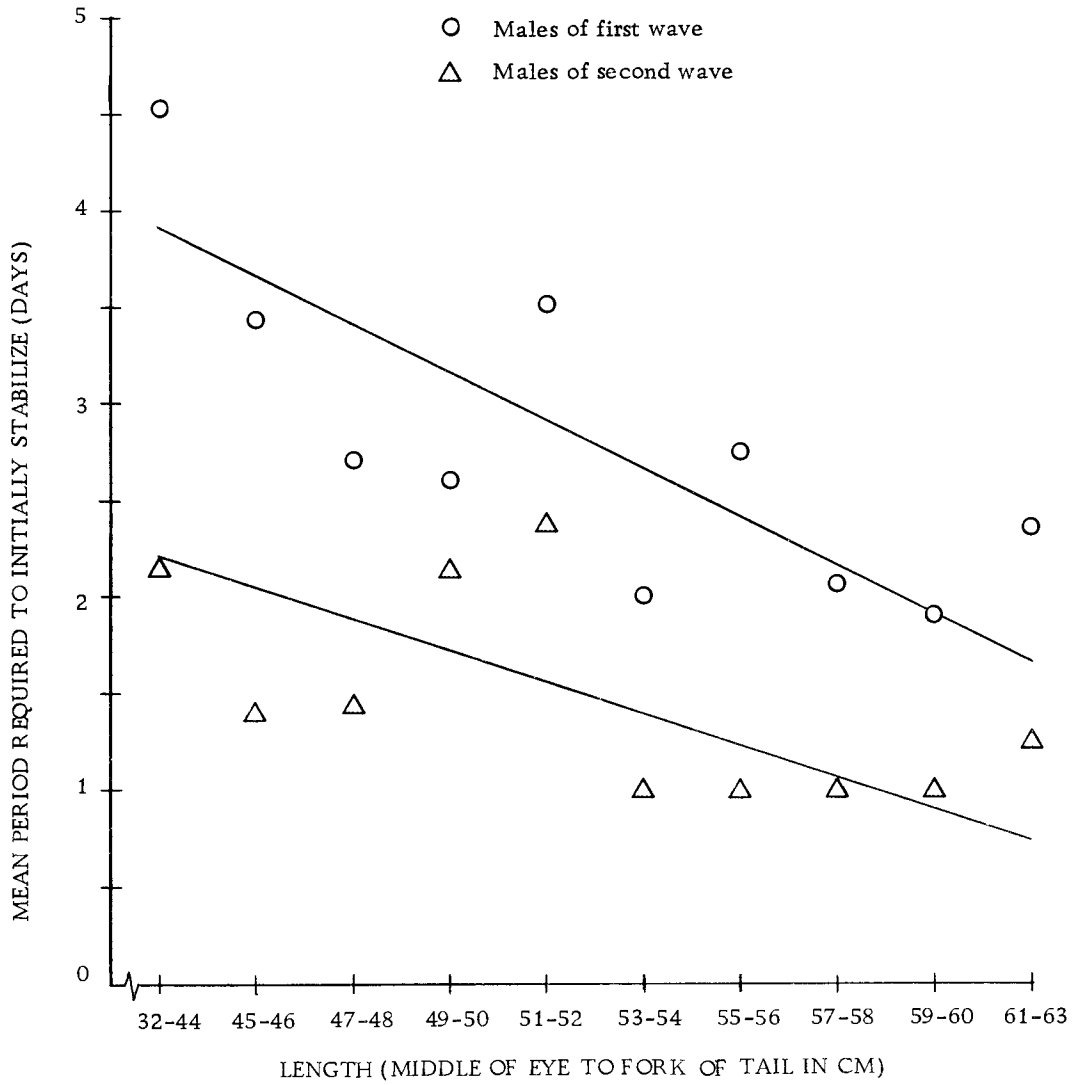
Figure 9. Relation between length of male and the period
required by the male to initially stabilize. Lines
drawn by inspection.

confined their movements within four divisions (about 1,500 feet)

or less after initially stabilizing (Figure 10).

The number of females on redds markedly influenced the

movement of males. The percentage of males leaving sections of

various densities of females showed a general decrease with in-

creased densities of females (Figure 11). It showed no relation to

the sex ratio. There was a difference in time spent on the spawn-

ing ground of four to seven days between males of the first wave of

spawners and males of the second wave. Therefore to avoid possible

differences in the vigor of males only tagged males of the second

wave of spawners were used in this analysis.

Thirty-one percent of all males overshot at least 300 feet, and

23% of all males overshot more than 1,000 feet. Males of all parts

of the run evidenced overshooting. More small males overshot than

large males; overshooting occurred in 29% of males 55 cm or shorter

compared to 17% of males longer than 55 cm.

In general the distribution of the males in the spawning areas

followed that of the females. In any area there were almost always

more males than females. The bulk of the females (over 62% of the

total) established redds in the uppermost 2,600 feet of the spawning

ground, and most of the males (68% of the total) migrated to the

same area.

Estimation of average values, however, fails to describe
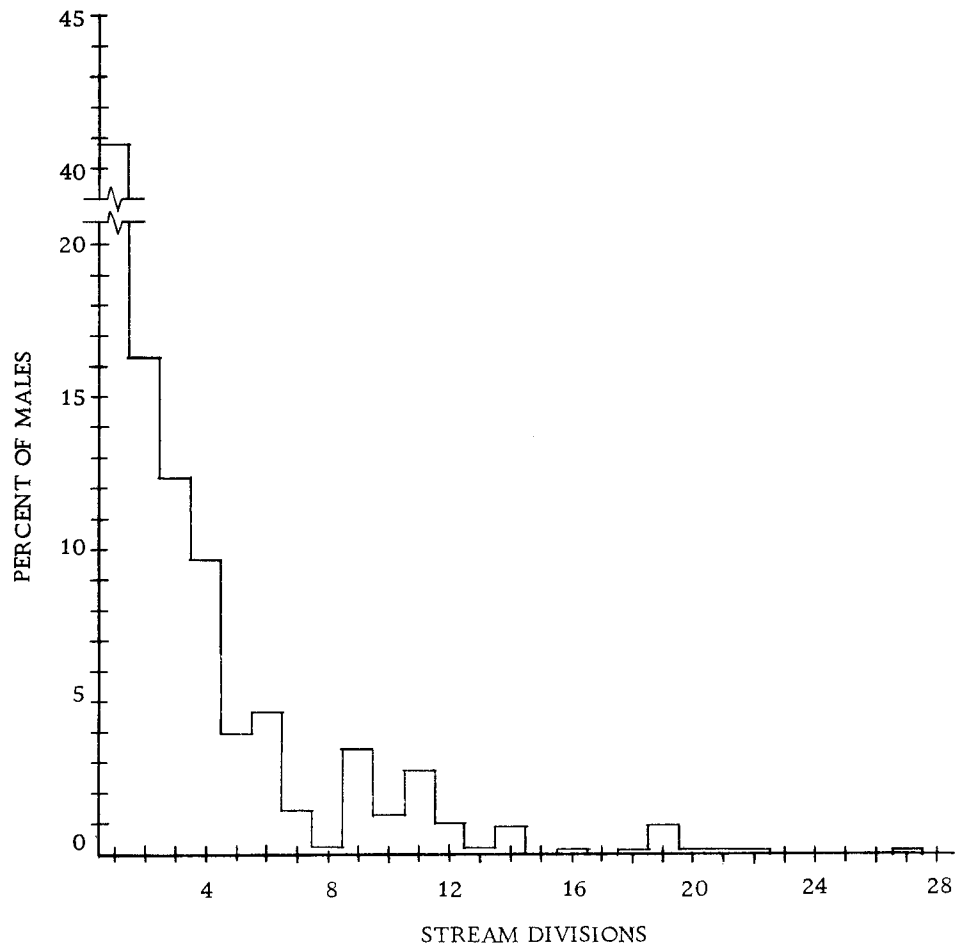
Figure 10. Percent of males that moved 1, 2, 3, . . . , n
divisions after initially stabilizing.
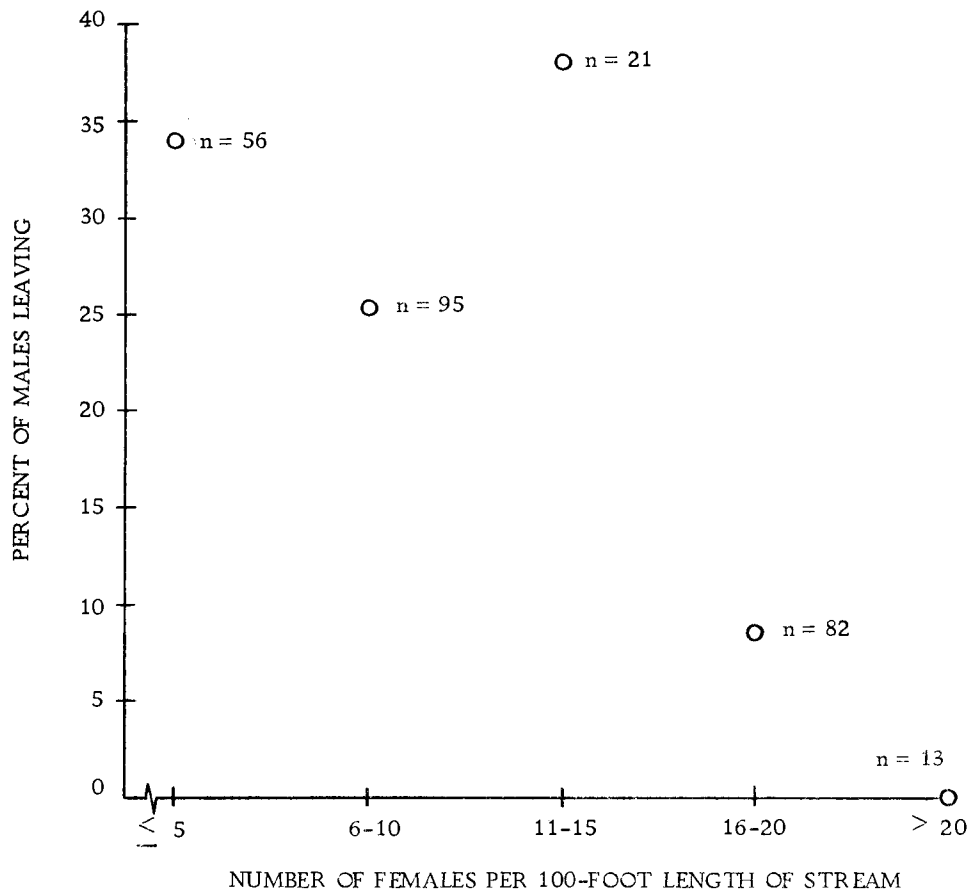
Figure 11. Relation between number of females per 100-foot length of stream and the percentage of males leaving the area.

adequately the variability in the movements of the males. There-
fore I looked for general patterns of movement, and several fairly
distinct types became perceivable when the sections were grouped
into the larger divisions.

Type 1: the male entered a division and was observed there

for the remainder of his spawning life except in a

few cases where the male was observed once outside

the division. This pattern included 49% of the males.

Type 2: the male entered a division, but his stay there was

interrupted after not less than two days by at least

two days outside the division, after which he returned

to the original division where he spent the remainder

of his life. This pattern included 3% of the males.

Type 3: the male entered a division and remained two to three

days, rarely more, before moving to another division

where he spent the remainder of his life. This pat-

tern included 33% of the males.

Type 4: the male entered a division and stayed there the major

part of his spawning life; two to three days of wander-

ing followed. This pattern included 6% of the males.

Type 5: the male never remained in any division more than

two consecutive days. This pattern included 8% of

the males.

The mean lengths of the males showing each pattern of movement were tested by analysis of variance and were found to be not significantly different ($F_{4, 256} = 0.57$).

Stream Characteristics and Movement of Spawners

I also examined variations of the water level and of the surface water temperature of the stream for possible effects on movements of spawners. The surface water temperature was measured at least twice daily, around 7:00 AM and 5:00 PM, with a pocket field thermometer. The water level was measured in the morning and afternoon at a gage located 750 feet upstream from Brooks Lake, above the influence of the water level of the lake on the water level of the stream. The gage consisted of a 2-inch iron pipe sunk into the bank of the stream with a welding rod, inserted into a styrofoam plastic float, indexing the water level on a rule.

Variations of the water level of the stream, either within a day or between days, showed no relation to movement of spawners within the stream. The greatest variation was 3 inches; otherwise the water level did not vary more than three-fourths of an inch.

I found no relation between the surface water temperature of the stream and movement of spawners. Variations of the surface water temperature within a day were greater than they were from day to day. The greatest variation was $4.5°$ C. The minimum temperature recorded was $7.0°$ C; the maximum temperature was $14.0°$ C.

Bear Predation and Movement of Spawners

Bear predation was another factor that could have influenced the movement of spawners. By comparing measurements of paw prints, I concluded that at least five bears frequented the stream during the study.

The first wave of spawners had sufficient time to stabilize by the time bears appeared on the creek. If the presence of bears had any effect on movement, the percentage of spawners showing movement should have been greater after the bears appeared. The percentage of males that moved each day did not increase. Further, the females showed virtually no movement at any time after they had established redds.

However, on several occasions the observers noted spawners rapidly swimming downstream. Later they noted that a bear had been present a short distance upstream. Since the presence of bears did not increase the percentage of spawners that had moved each day, bears may have disrupted spawning activities temporarily, but any spawners displaced by the bears either returned to their former location soon after the bears had left or did not leave the section entirely.

PAIRING

The observers judged a male to be paired with a female if he clearly demonstrated his dominance over any other males present or if he was attending a female in the absence of other males. Attendance of a female by a male does not necessarily mean that the male will spawn or has spawned with the female. But Mathisen (1962) stated, ". . . studies of the spawning act itself proved that a sexual bond between a male and a female generally was formed a short time prior to egg deposition and that an active attendance of a male evidenced by courtship and a regular defense of the redd indicated a participation in the following spawning act."

Before dealing with pairing of spawners it was necessary to establish that tagging had no effect on selection of spawning partners. For this purpose the number of tagged fish paired with untagged fish and the number of tagged fish paired with other tagged fish were subjected to Chi-square tests of independence on three successive days. Males and females were treated separately. In all cases the presence or absence of a tag made no significant difference in pairing $(p \geq 0.5)$.

In the course of his movements the male sockeye was attracted to many females, but rarely did he associate with any female for long. During the study 157 pairings of tagged males with different

tagged females were seen. In 82% of the observations the males

were seen with a particular female one day, in 13% two consecutive

days and in 4% three consecutive days. One male was seen four

consecutive days and another was seen five consecutive days with

a particular female.

All males were not equally successful in pairing. In fact a

social hierarchy based on size was evident when the percentage of

observations in which a male was seen paired was plotted against

length of male (Figure 12). Larger males were clearly more suc-

cessful in pairing than smaller males. A few cases of apparently

simultaneous pairing of one male with two females occurred. In all

cases the males were very large, and the redds were adjacent to

each other.

To determine the number of unspent females with which a male

paired, some means had to be devised to separate spent from un-

spent females. As the spawning season progressed, the number of

spent females present on the spawning ground increased, resulting

in an increased number of unattended females. But many females

known to have been spent were still attended by males, though none

of the males were observed more than once associated with any of

these spent females. Data from the study by Mathisen (1962) was

used to estimate four days as the average time required for comple-

tion of egg deposition. Then from the number of unspent, tagged
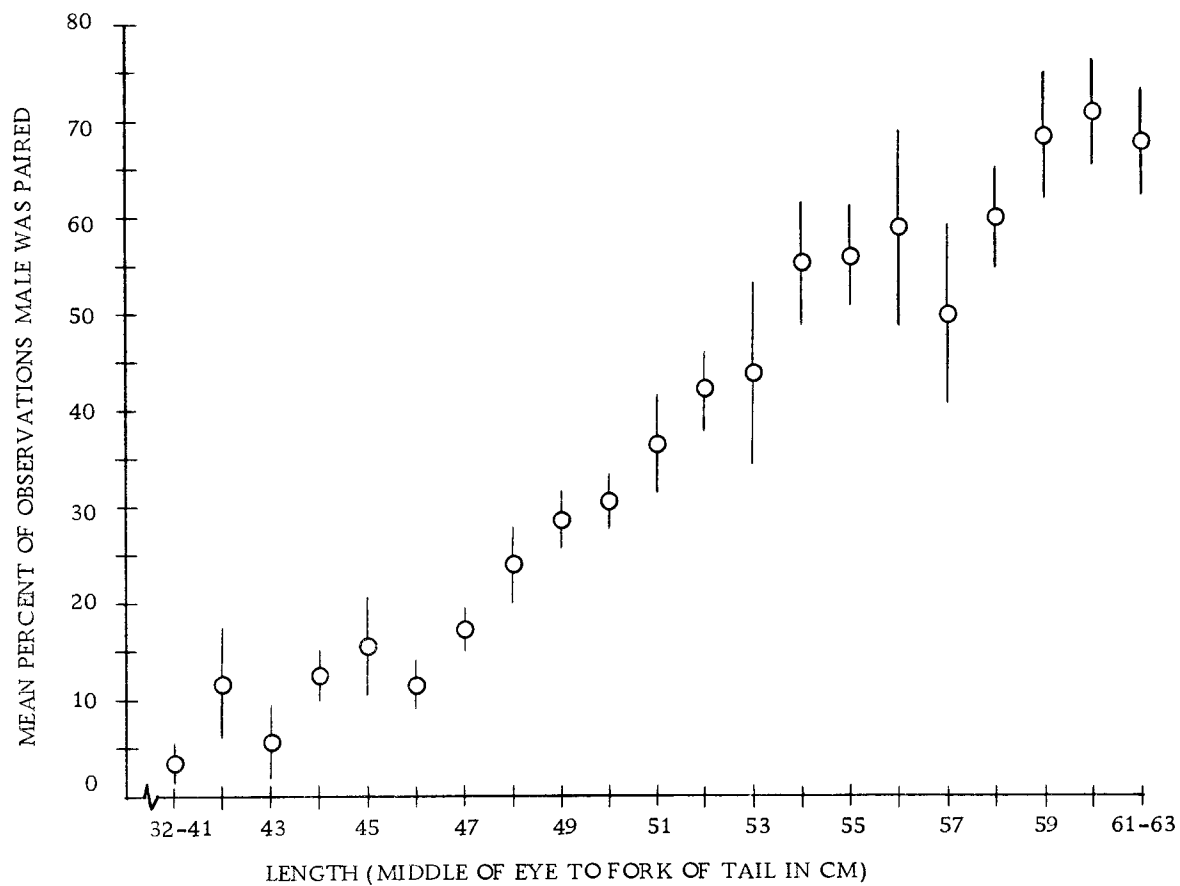
Figure 12. Relation between length of male and the percentage of observations in which the male was paired. Each vertical line represents one standard error on each side of the mean.

females with which tagged males had paired, the average number of

unspent females, both tagged and untagged, with which each male

had paired was calculated. The average number of unspent females

with which a male paired ranged from less than one for males 45 cm

or shorter to over five for males 60 cm or longer (Figure 13).

Despite social dominance in pairing by the larger three-ocean-

year males, they accounted for only 39% of all pairings. Because of

their greater numbers, the smaller two-ocean-year males took part

in more spawning acts. No relation was found between the sizes of

a male and a female that were paired.

Because the bulk of the spawners entered the stream within a

short time, considerable interbreeding between spawners of the two

waves was possible. Based on the observed pairings of tagged

spawners, males of the first wave accounted for 96% of the spawn-

ings by females of this wave and 66% of those by females of the

second wave. Conversely, males of the second wave accounted

for only 4% of the spawnings by females of the first wave and 34%

of those by females of the second wave. The comparatively small

percentage of spawnings in which males of the second wave partici-

pated was primarily due to the larger percentage of small males

in the second wave. These small males apparently could not com-

pete successfully with the larger males of the first wave despite

being fresher to the rigors of spawning.
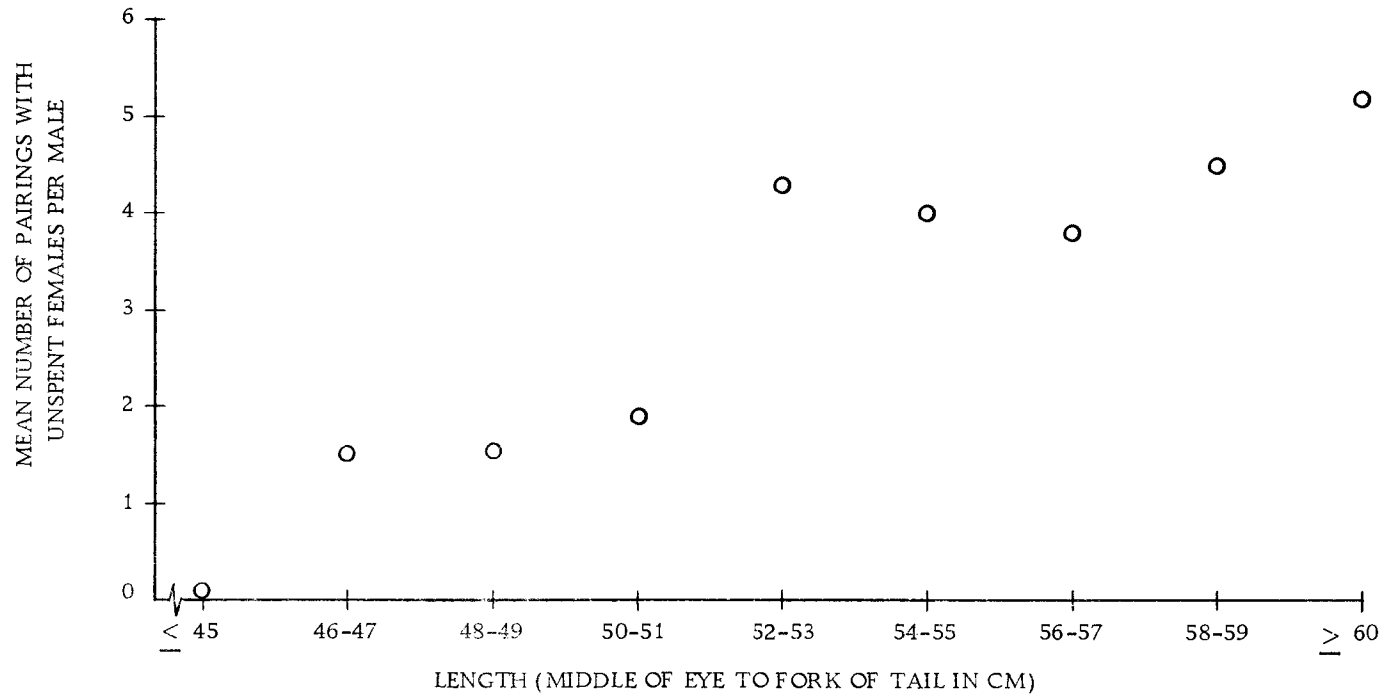
Figure 13. Relation between length of male and the number of unspent
females with which the male paired.

DISCUSSION

Homogeneity of the Hidden Creek Stock

In many salmonid stocks the theory of homing to parent streams is so well established that it is the basis of many of our current management practices. But the specificity of homing is still unknown. Hartman and Raleigh (1964) have shown that sockeye salmon are predisposed to spawn in a particular tributary prior to entry into a lake system. They concluded that the predisposition was due to homing and suggested that each lake or river tributary probably supports a discrete stock or a group of stocks of sockeye salmon.

There is some evidence for even higher specificity of homing in sockeye salmon. Transplantation of eyed eggs into waters devoid of salmon resulted in adults returning to spawn in the area of transplantation despite the availability of many miles of potential spawning gravels (International Pacific Salmon Fisheries Commission, 1955).

Female sockeye in Hidden Creek were strongly bound to a single redd following an initial migration. Male sockeye generally restricted their movements to a small portion of the spawning ground after an initial migration. Mathisen (1962) observed a similar pattern of movement in sockeye salmon in another small stream. For

these reasons and because of the apparently high specificity of homing

in sockeye salmon, they may not only home to a tributary, but also

to their natal gravels within the tributary.

However, the amount of overshooting, especially in the male,

does not support the hypothesis that sockeye salmon homed to parti-

cular sections of Hidden Creek. Also, McDonald and Shepard (1955)

reported major changes in the distribution pattern of sockeye salmon

within a stream because of altered environmental conditions. Flush-

ing of fine particles from gravels previously supporting only a small

percentage of the run resulted in the major portion of the run subse-

quently using those gravels. Therefore I consider homing highly

unlikely as a factor affecting the dispersal of adult sockeye salmon

within small tributaries like Hidden Creek and consider the Hidden

Creek stock to be a homogeneous unit.

Territoriality and Occupation of the Spawning Ground

A defended territory is maintained by the aggressive actions

of the territory holder. Species which exhibit aggressive tendencies

also show limited movement; thus aggressive action acts as a spacing

agent (Gerking, 1959). Such action is directed at competitors, most

often sexual competitors of the same species (Etkin, 1964).

The sockeye salmon is territorial only on the spawning ground;

during all other stages of its life history it is a schooling fish. On

the spawning ground migrating females were never seen trying to usurp the territory of an established female, which corroborates the observations of Mathisen (1962) and Merrell (1964). The time required for redd establishment by later arrivals on the spawning ground was less than that of earlier arrivals even though the later immigrants spawned mostly in the upper reaches of the stream. Although the paths of migrating females were frequently deflected, having to pass through vigorously defended territories apparently did not impede later migrants.

Sockeye salmon display territorial behavior on the redd site, but the role of the redd site and the sex partner in stimulating territorial behavior requires further study in view of somewhat conflicting reports. Mathisen (1962) stated that the male of a pair did most of the defending. The resident female frequently joined in driving off an intruding female, but in all but a few instances she left intruding males unmolested. Hoopes (1962) and Merrell (1964) observed that males defended against males and females defended against females. Rarely did they notice a resident fish defend against one of the opposite sex. Hartman, Merrell, and Painter (1964) reported that males defended almost entirely against other males, and females defended against both sexes.

In kokanee, the landlocked form of sockeye salmon, Schultz (1938) noted that females usually defended the upstream part of the

redd; the male defended the redd from intruders coming from any direction. Both drove away fish of either sex. Briggs (1953) in a study of the spawning behavior of coho salmon (Oncorhynchus kisutch) and chinook salmon (O. tshawytscha) stated, "It seemed clear, as a result of close observation, that the male exhibited no tendency toward territorial behavior but was merely interested in taking part in the spawning act."

My observations support Briggs' observations and attest that the male sockeye defends almost entirely against other males, while the female defends against other females and, to a much lesser extent, against males. The disparity between male and female sockeye in the strength of their association with a redd does not support a large role for the male in territorial defense. Other females pose a definite threat to excavation of deposited eggs; consequently strong territorial behavior in the female is advantageous for survival of the spawn. But males represent no threat to deposited eggs because their digging behavior apparently is activated only in the presence of an unspent female on a redd. Therefore the male must defend against other males to insure his participation in spawning rather than to protect the redd.

In sockeye salmon the female selects the redd site (Hoopes, 1962; Mathisen, 1962); consequently the dispersal of the female on the spawning ground is largely independent of the male. The female

apparently prefers certain sites for her redd, judged from the wide-
spread redd locations of the early immigrating females in Hidden

Creek. Fabricius and Gustafson (1954) demonstrated that the digging

response in a sexually mature female Arctic char (<u>Salvelinus alpinus</u>)

can be elicited by visual stimuli alone when she encounters a par-

ticular type of gravel bottom. Hoopes (1962) reviewed the various

hypotheses proposed to explain how female salmon and trout select

sites for their redds. The preference for particular sites for redds

results in a patchy distribution of sockeye salmon on the spawning

ground paralleling the distribution of preferred habitats in nature.

Territoriality alters somewhat the distribution of spawners

paralleling the distribution of preferred sites for redds. The se-

quence of occupation of various sections of the spawning ground in

Hidden Creek indicated that those sections with the highest densities

of spawners were among the first to be occupied. Hoopes (1962) and

Mathisen (1962) also noted this phenomenon. Therefore the distri-

bution of redds at the end of spawning must result from a compro-

mise between the preference of females for certain sites for their

redds and the vigor with which established females defend their

territories.

Territoriality in sockeye salmon causes the spawners to

spread over the available gravel. It also reduces superimposition

of redds, a potential cause of egg mortality, as was pointed out by

Hartman, Merrell, and Painter (1964).

Successive Mating

Successive mating with members of the opposite sex during a

single breeding season appears to require the existence of a male

hierarchy and is typically associated with highly developed secondary

sexual characteristics or enhanced male body size. Where the fe-

male is potentially able to get all her ova fertilized through a single

mating act, she is likely to need the services of only one male once.

Only where the eggs are laid in separate batches can the female ef-

fectively use the successive services of several males (Wynne-Ed-

wards, 1962).

All three characters, the hierarchy, the secondary sexual

characteristics during the spawning season, and the eggs being laid

in several batches, exist in sockeye salmon. Associated with these

characters in sockeye salmon is successive mating during spawning.

Others have also noted its occurrence in this species (Foerster,

1930; Mathisen, 1962). It has also been noted in kokanee (Schultz,

1938), in chinook salmon (Hobbs, 1937), in Atlantic salmon (Salmo

salar) (Belding, 1934; Jones and King, 1950), in brook trout (Salve-

linus fontinalis) (Hazzard, 1932), and in Arctic char (Fabricius and

Gustafson, 1954).

Foerster (1930) frequently observed the same male sockeye

consorting with two to three females. Mathisen (1962) reported as

many as ten females were actively courted by a single male sockeye;

the mode was five. Since Mathisen studied a sockeye population with

a 1:1 sex ratio, the calculated number of females with which Hidden

Creek males paired compares favorably.

As a consequence of successive mating in sockeye salmon the

duration of pairing is relatively short. In Hidden Creek it averaged

1.25 days, but this figure is probably high because the stream sur-

veys were conducted only once a day. Hoopes (1962) noted that

individual pairs may remain together for periods from several hours

to almost the entire period the female remains on the redd site.

Mathisen (1962) observed that males generally shifted attendance to

a different female daily, and he demonstrated that the post-spawning

association of male with female decreased with a small ratio of

males to females. He suggested that some means whereby a male

could locate females that are ready to spawn must exist.

Social Dominance in Pairing and Selection

The significance of dominance in social life is that it acts to

minimize aggression by effectively securing to the dominant members

the fruits of victory without disrupting group life by indiscriminate

conflict (Etkin, 1964). Because of the high ratio of males to females

in Hidden Creek, competition for females between males was keen.

Fights frequently developed, the most violent of which always oc-
curred between males of nearly equal size or between intruding,
larger males attempting to oust smaller males from females. When
the smaller males were not paired, they readily gave way before
the challenge of larger males.

Considering the primary form of defense by the male sockeye
against an intruding male, it is not surprising that the larger males
were more successful in pairing than the smaller males. Merrell
(1964) appropriately termed this conventional form of aggressive
behavior a "sidling bluff". It was also described in kokanee by
Schultz and students (1935), who termed it the "escorting act".
From my observations this male behavior does not necessarily
require the presence of either a female or a redd for its release.
But typically it began when an intruding male approached a pair
on a redd. The resident male quickly moved out to meet the in-
truder and lined up parallel and eye-to-eye with him. If the in-
truding male was not immediately intimidated by this act, both males
swam slowly upstream, still parallel and eye-to-eye, with jaws
slightly raised. Eventually one of the males retreated. Only where
the contest was prolonged did any violent attack by one or the other
male occur.

The small males, which included all the one-ocean-year males and most of the two-ocean-year males, were relegated to an attending role. But frequent conflicts arose even among these small, attending males over apparently preferred positions adjacent to and slightly downstream from a pair on a redd. In Atlantic salmon Jones (1959) observed that when several parr were attending a pair on a redd, one always assumed dominance over the others. Therefore some elucidation about the relationship between the size of male and frequency of movement (Figure 7) may be warranted.

Because of the direct, linear relation between size of male and the percentage of observations in which a male was seen paired (Figure 12), an inverse relation between size of male and the percentage of observations in which a male had moved could be expected. But such was obviously not the case. Then under the assumption that the percentage of observations in which a male had moved reflected the intensity of conflict among the males, two size classes of males are perceivable, one class including males up to 50 cm long and the other class including those from 51 to 63 cm long. The two size classes do not correspond to the ocean-age categories of the males.

Hence what may have occurred in Hidden Creek was a kind of intraclass dominance. In each of the two size classes, at the bottom there were the smaller males who competed little and consequently showed reduced movement, those of intermediate size who competed

but lost and were forced to move, and those larger males who were able to maintain their position.

In the sockeye salmon of Hidden Creek the three-ocean-year males probably fertilized more eggs per fish than the other males through social dominance in pairing. Merrell (1964) observed that large females were most sought by male sockeye resulting in the largest males spawning with the largest females. The sex ratio in that stream was usually 1:1. Though I found no evidence of this form of selection in Hidden Creek, the high ratio of males to females may have precluded it. Belding (1934) noted that the female Atlantic salmon favored large males and was intolerant of small males and grilse.

These forms of selection, however, are contravened by the selective action of the gill net fishery, which favors the escapement of the smaller, two-ocean-year fish of either sex (Petersen, 1954; Mathisen, 1955). Mathisen (1955) pointed out that little is known about the effects of these opposing forms of selectivity on sockeye stocks although gill net selectivity has operated since the beginning of the fishery over 60 years ago. If size of returning adults is even partly heritable, the significance of the problem to the fishery is obvious. Moreover, Hartman and Conkle (1960) showed a positive correlation between size of the female sockeye and fecundity. There may also be a positive correlation between size of the female sockeye

and size of egg as Allen (1958) and Koski (1966) have shown in coho

salmon.   Larger egg size may result in increased survival of the

progeny.

There is some evidence for growth rate as the prime factor

in inducing maturation.   Alm (1949), in studies of various species of

trout, and Parker and Larkin (1959), in a study of chinook salmon

and steelhead trout (Salmo gairdneri), concluded that the fastest

growing fish matured earliest.   But their studies did not indicate the

size of the parents of these earliest maturing fish.

However, since all females do not spawn simultaneously, and

given the polygynous habit of the male sockeye, each female usually

has more than one male attending her when she does spawn.   More

than likely one of the males attending her will be a small male   of

one or two ocean-years.   Under these conditions simultaneous ferti-

lization of the eggs of a single female by two or more males can and

does occur in sockeye salmon (Mathisen, 1962).   Consequently it re-

mains to be seen how effective social dominance in pairing is in re-

stricting egg fertilization by small males, and the role of inheritance

in influencing the size of returning adult sockeye salmon may be

further obscured.

Function of "Surplus" Males

Since pairing does not entail a continued association of two

individuals in monogamy, in a population with parity of the sexes there is frequently a pool of males available at any time to pair with a female ready to spawn, especially since all females are not ready to spawn simultaneously. Mathisen (1962) asserted that scattered observations of very small fish showed clearly that they formed the principal part of the pool. This situation also obtained in Hidden Creek.

Part of the functional value in retaining a seeming surplus of males may lie in maintaining a sufficiently high level of competition among the males to disperse them among the available females. Also, conditions are not always stable and optimal, and sometimes as a result of a catastrophe or where new habitats are being colonized, survival of the stock may depend on a few survivors. The smaller the ratio of males to females, the greater the chances that all the survivors might be females. Therefore preservation of parity of sexes could be of great importance where populations become sparse. Thompson (1962) reasoned to the same effect.

Mathisen (1962) demonstrated that in a closed area one male sockeye could fecundate up to 15 females with less than a 5% increase in egg mortality over that occurring with parity of sexes. He pointed out that successful fertilization of the eggs under a small ratio of males to females depends upon the speed and extent of coverage of the spawning ground by males together with the length

of time a female can delay spawning. He found that females would

delay spawning about ten days in the absence of males and that they

then proceeded to deposit unfertilized eggs. Because of the strong

bond between the female and her redd, the importance of the male's

movements in fertilizing the eggs is enhanced. Therefore the dis-

persive mechanisms among the male sockeye on the spawning ground

need to be clarified.

In Hidden Creek the various males classified into the five pat-

terns of movement constituted a system that acted to disperse the

males throughout the spawning ground. Competition between males

for females and the polygynous habit of the male were the driving

mechanisms of the system. Though homing could also act as a

dispersive agent, I have pointed out that homing within small tribu-

taries is unlikely to exist in sockeye stocks.

Dispersal of males, however, was also shown to be influenced

by the density of females on redds in an area. Most males, after an

initial migration, restricted their movements to a small area in

Hidden Creek, despite the greater than two-to-one ratio of males

to females and the resulting intense competition for females among

the males. Further, because Hidden Creek is narrow, there was

little opportunity for lateral movement by the males. Redds were

even situated not side by side, but oblique to each other. In larger

streams these conditions would not obtain; consequently less

longitudinal movement could be expected.

Mathisen (1962) concluded from his studies that there must be a potentially large harvestable surplus of males in the sockeye salmon escapement in Bristol Bay. However, I propose that the "surplus" males fill a biological need in sockeye stocks by insuring fertilization of the available eggs. In all stocks there should be a sex ratio sufficient to disperse the males among the available females and to act as a safety factor when spawners become sparse. This viewpoint is accentuated by the abnormally high 2. 27:1. 00 ratio of males to females in the Hidden Creek spawning run of 1963 notwithstanding a contemporary ratio of males to females of 0. 83:1. 00 in the overall Nahnek escapement (based on data from Alaska Department of Fish and Game, U. S. Bureau of Commercial Fisheries and Fisheries Research Institute, 1964). At the same time the Brooks River stock, which is one of the major sockeye stocks in the Naknek complex and which includes the Hidden Creek stock, had a 2. 20:1. 00 ratio of males to females, although the entire escapement was not inventoried (based on data from Hartman, Heard and Dewey, 1964). Therefore any practices in managing the fishery that could engender a large deviation from parity of the sexes in sockeye salmon stocks should be entered with caution.

However, the crucial experiment that remains to be done is to ascertain whether the movements of spawners in an entire population

of sockeye salmon with an artificially reduced ratio of males to

females would result in an efficiency of egg fertilization sufficient

to make harvesting of the "surplus" males feasible.

BIBLIOGRAPHY

Alaska Department of Fish and Game, U. S. Bureau of Commercial
    Fisheries and Fisheries Research Institute. 1964. Bristol
    Bay red salmon, 1963. A compilation of the catch and escape-
    ment data, ed. by Donald B. Siniff. Juneau. 181 p. (Alaska
    Department of Fish and Game. Informational Leaflet no. 35)

Allen, George H. 1958. Notes on the fecundity of silver salmon
    (Oncorhynchus kisutch). Progressive Fish Culturist 20:163-
    169.

Alm, Gunnar. 1949. Influence of heredity and environment on vari-
    ous forms of trout. Drottningholm, Institute of Freshwater
    Research, Report 29:29-34.

Belding, D. L. 1934. The spawning habits of the Atlantic salmon.
    Transactions of the American Fisheries Society 64:211-218.

Briggs, John C. 1953. The behavior and reproduction of salmonid
    fishes in a small coastal stream. San Pedro. 62 p. (Cali-
    fornia. Department of Fish and Game. Fish Bulletin no. 94)

Burner, Clifford J. 1951. Characteristics of spawning nests of
    Columbia River salmon. U. S. Fish and Wildlife Service.
    Fishery Bulletin 52:97-110.

Cleaver, Fred C. 1964. Origins of high seas sockeye salmon.
    U. S. Fish and Wildlife Service. Fishery Bulletin 63:445-476.

Eicher, George J. 1951. Effect of tagging on the subsequent behav-
    ior and condition of red salmon. Washington. 4 p. (U. S.
    Fish and Wildlife Service. Special Scientific Report--Fisher-
    ies no. 64)

Etkin, William. 1964. Co-operation and competition in social be-
    havior. In: Social behavior and organization among verte-
    brates, ed. by William Etkin. Chicago, University of Chicago
    Press. p. 1-34.

Fabricius, Eric and Karl-Jakob Gustafson. 1954. Further aquarium
    observations on the spawning behavior of the char, Salmo al-
    pinus L. Drottningholm, Institute of Freshwater Research,
    Report 35:58-104.

Foerster, R. E. 1930. An investigation of the life history and propagation of the sockeye salmon (Oncorhynchus nerka) at Cultus Lake, British Columbia. I. Introduction and the run of 1925. Contributions to Canadian Biology and Fisheries, n. s., 5:1-35.

Gerking, Shelby D. 1959. The restricted movement of fish populations. Biological Reviews 34:221-242.

Hartman, Wilbur L. and Charles Y. Conkle. 1960. Fecundity of red salmon at Brooks and Karluk Lakes, Alaska. U. S. Fish and Wildlife Service. Fishery Bulletin 61:53-60.

Hartman, Wilbur L. and Robert F. Raleigh. 1964. Tributary homing of sockeye salmon at Brooks and Karluk Lakes, Alaska. Journal of the Fisheries Research Board of Canada 21:485-504.

Hartman, Wilbur L., William R. Heard, and Robert Dewey. 1964. Sockeye salmon studies at Brooks Lake Biological Field Station. 1963. Auke Bay, Alaska. 36 p. (U. S. Fish and Wildlife Service. Bureau of Commercial Fisheries. Auke Bay Biological Laboratory. Manuscript Report no. 64-7)

Hartman, Wilbur L., Theodore R. Merrell, Jr. and Richard Painter. 1964. Mass spawning behavior of sockeye salmon in Brooks River, Alaska. Copeia, no. 2, p. 362-368.

Hartman, Wilbur L., Charles W. Strickland and David T. Hoopes. 1962. Survival and behavior of sockeye salmon fry migrating into Brooks Lake, Alaska. Transactions of the American Fisheries Society 91:133-139.

Hazzard, A. S. 1932. Some phases of the life history of the eastern brook trout, Salvelinus fontinalis, Mitchell. Transactions of the American Fisheries Society 62:344-350.

Hobbs, Derisley F. 1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. Wellington. 104 p. (New Zealand. Marine Department. Fisheries Bulletin no. 6)

Hoopes, David T. 1962. Ecological distribution of spawning sockeye salmon in three lateral streams, Brooks Lake, Alaska. Ph. D. thesis. Ames, Iowa State University. 235 numb. leaves.

International Pacific Salmon Fisheries Commission. 1955. Annual
      report for 1954. New Westminster, Canada. 43 p.

Jones, John W. 1959. The salmon. London, Collins. 192 p.

Jones, J. W. and G. M. King. 1950. Further experimental obser-
      vations on the spawning behaviour of the Atlantic salmon
      (Salmo salar Linn.). Proceedings of the Zoological Society of
      London 120:317-323.

Koski, K. V. 1966. The survival of coho salmon (Oncorhynchus
      kisutch) from egg deposition to emergence in three Oregon
      coastal streams. Master's thesis. Corvallis, Oregon State
      University. 84 numb. leaves.

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. Seattle, University of Washington. 285 numb. leaves.

Mathisen, Ole A. 1962. The effect of altered sex ratios on the
      spawning of red salmon. In: Studies of Alaska red salmon,
      ed. by Ted S. Y. Koo. Seattle, University of Washington
      Press. p. 137-245.

McDonald, J. G. and M. P. Shepard. 1955. Stream conditions and
      sockeye fry production at Williams Creek, Lakelse Lake, B. C.
      Fisheries Research Board of Canada, Pacific Coast Stations,
      Progress Report 104:34-37.

Merrell, Theodore R., Jr. 1964. Ecological studies of sockeye
      salmon and related limnological and climatological investiga-
      tions, Brooks Lake, Alaska, 1957. Washington. 66 p. (U. S.
      Fish and Wildlife Service. Special Scientific Report--Fisher-
      ies no. 456)

Parker, Robert R. and Peter A. Larkin. 1959. A concept of growth
      in fishes. Journal of the Fisheries Research Board of Canada
      16:721-745.

Petersen, Alvin E. 1954. The selective action of gill nets on Fraser
      River sockeye salmon. New Westminster. 101 p. (Interna-
      tional Pacific Salmon Fisheries Commission. Bulletin no. 5)

Schultz, Leonard P. 1938. The breeding habits of salmon and trout. Smithsonian Institution Annual Report for 1936/1937. Washington, D. C., Government Printing Office. p. 365-376.

Schultz, Leonard P. and students. 1935. The breeding activities of the little redfish, a landlocked form of the sockeye salmon, Oncorhynchus nerka. Mid-Pacific Magazine, 1935, p. 67-77.

Thompson, W. F. 1962. The research program of the Fisheries Research Institute in Bristol Bay, 1945-58. In: Studies of Alaska red salmon, ed. by Ted S. Y. Koo. Seattle, University of Washington Press. p. 1-36.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. New York, Hafner Publishing Company. 653 p.