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The Behavior and Reproduction of Salmonid Fishes in a Small Coastal Stream

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INTRODUCTION

Perhaps the first, and certainly one of the most fundamental steps in the management of any animal resource is a detailed study of the life cycle of the species under consideration, the basic purpose of such a study being to discover the limiting factors on the population and, if possible, to weigh their effects. As Leopold (1933) has pointed out, "Game management consists largely of 'spotting' the limiting factor and controlling it."

In regard to salmonid fishes, it was frequently supposed, until very recently, that by far the greatest losses took place during the egg and larval stages, and that once the young fish were free swimming they were relatively safe from predation. This belief of most early authorities gave impetus to the practice of artificial hatching. The advantage of artificial rearing during the early stages of the life cycles was fully accepted by most biologists, in spite of some evidence to the contrary, until Hobbs (1937, 1940) published the results of his extensive New Zealand redd sampling projects on introduced salmonid species.

The impact of Hobbs' work was felt almost immediately and was reflected in the changing attitudes of a great many persons concerned with the management of salmonid fisheries. In many parts of the world, the status of salmonid culture underwent a fundamental change, evidently due to the influence of these New Zealand investigations, as well as recent evidence indicating relatively poor survival for the liberated hatchery product. The nature of this change has been well expressed by Lagler (1949) as follows:

> "The status of fish culture and stocking as a fish management tool has changed rapidly during recent years. Stocking is no longer regarded as the principal means for generally maintaining and improving fishing; it has been shown at times to be unnecessary, wasteful, and even harmful. Fish culture and planting of fish are now being related more and more carefully to research and to other management practices. As an art, the artificial propagation of fishes will continue to have a place of some importance because: (1) fish will be needed for restocking following pollution, winter-kill, experimental poisoning, etc.; (2) stocking to maintain the supply is needed where natural spawning is inadequate; (3) there are continuous experimental requirements—as for studies involving the tagging or marking of large numbers of fish; (4) some seasonal fishing for highly preferred species can be provided in waters near centers of human population; (5) ornamental and bait fish propagation is big business."

It is true that Hobbs (*loc. cit.*) showed substantial evidence that trout and salmon were capable of producing young at an extremely high rate of efficiency under natural conditions. However, the fact that all of this author's work was done in New Zealand should have made it necessary to regard the results with some caution until similar studies could be accomplished in the native habitat of the species under consideration. Unfortunately, this has not always been done, some workers having tended to accept Hobbs' results with little reservation, and to apply them to management problems in North America.

The present study was undertaken principally in order to obtain information regarding the extent of natural mortality during the egg and larval stages of certain salmonid fishes in a small California stream, to gather essential knowledge of the spawning behavior of these fishes, and to compare the results of such observations with similar evidence from other waters.

Daily stream observations were conducted during the fall, winter, and spring of two separate seasons. The study was begun on October 15, 1948, and continued until June 1, 1949. It was resumed on October 20, 1950, and was finally concluded on May 30, 1951. The sampling of natural redds was accomplished at the times indicated in Tables 4, 5, and 6 (pages 42-44). During the 1950-51 season temperature and flow records (Figure 1) were taken at a centrally located station (near the confluence of Godwood and Prairie Creeks) which was close to the spawning areas of the species being studied. The water temperatures in nearby parts of the watershed rarely varied more than 1 degree F. from those taken at this station.

The temperature (F.) was taken at midday with a standard laboratory thermometer immersed in the center of the stream. The volume of flow was calculated by means of a standard float method over a 50-foot section.

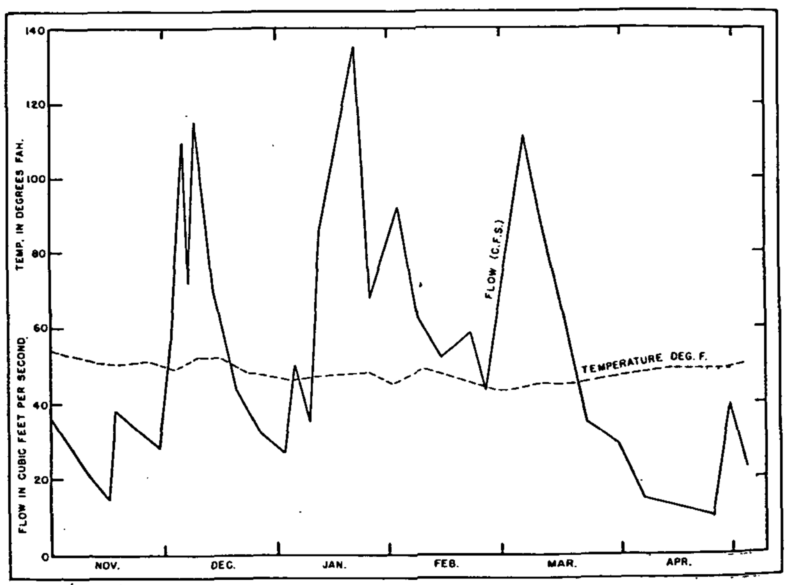

FIGURE 1. Temperature and flow of Prairie Creek in 1950-51 season.

THE STREAM

The entire study was conducted within the watershed of a small stream named Prairie Creek. This tributary enters another stream called Redwood Creek a short distance above tidewater, which in turn flows into the Pacific Ocean near the town of Orick, Humboldt County, California.

The Prairie Creek drainage basin lies within the Coast Redwood Belt of the Humid Transition Life Zone. In places pure stands of redwood (*Sequoia sempervirens*) were found, but along the stream edges other species such as the red alder (*Alnus rubra*) were abundant, as well as several shrub species comprising a dense thicket called "soft chaparral" by Jepson (1925).

The altitude ranges from sea level to about 1,000 feet and the rainfall of the area is comparatively high, averaging about 75 inches annually. The stream itself is only 14 miles in length and drains an area of about 30 square miles.

Prairie Creek was selected for this study because of its small size and because it was evidently subject to less winter flooding than many other coastal streams. The presence of four native species of salmonid fish (three of them abundant) offered an excellent opportunity for observation of specific differences in behavior and reproduction, since all these forms were exposed to more or less the same ecological factors.

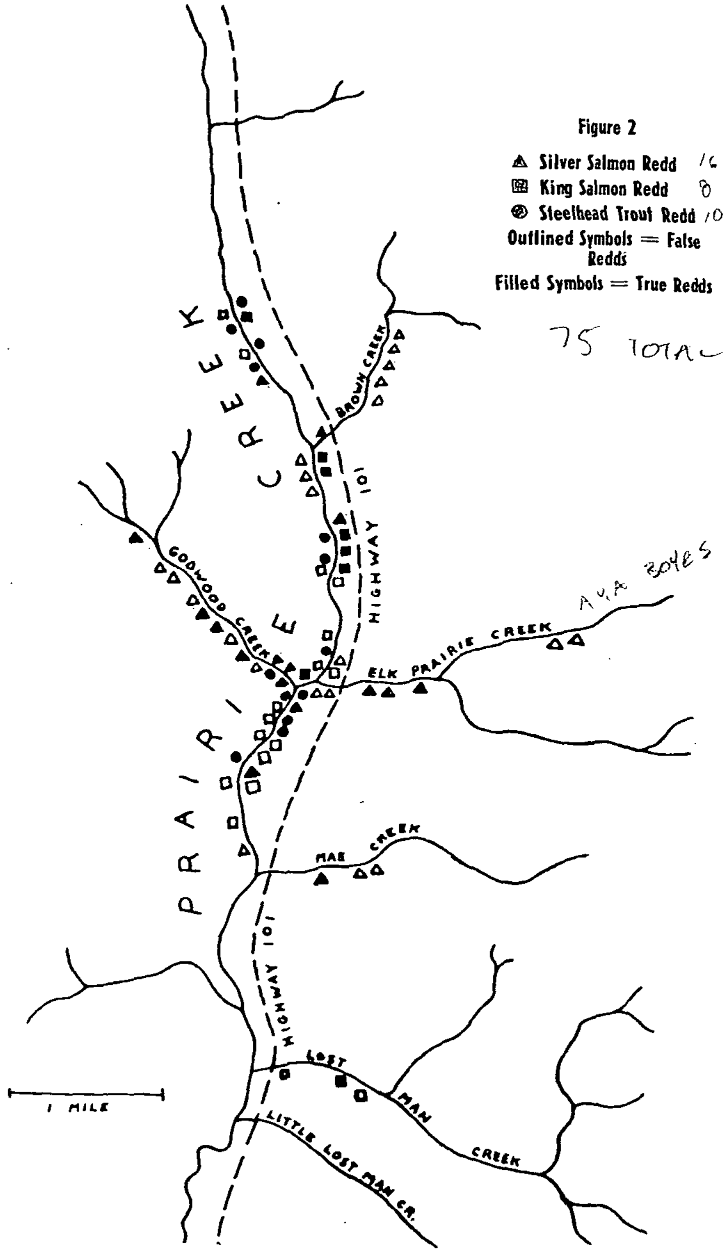

FIGURE 2. Portion of the Prairie Creek drainage utilized by spawning salmonid fishes.

PART I

BEHAVIOR

SILVER SALMON, *ONCORHYNCHUS KISUTCH* (WALBAUM)

Range

This species is found throughout the North Pacific and evidently has a wider range than the other native salmonids. It spawns in streams tributary to Monterey Bay and has been recorded at sea as far south as the Coronado Islands, Mexico. It seems to be common from Central California northward through the Bering Sea and south along the Asiatic coast to the Japanese Islands. Jordan, Tanaka, and Snyder (1913) list it from Otaru, the Ura River, Osatsubo, and the Province of Shinano, Japan.

Time of Migration

Many of the smaller coastal streams in California do not contribute a large enough flow during the summer months to maintain an open passage to the ocean. During this period a sandbar, thrown up across the mouth by wave action and ocean currents, is usually effective in preventing any stream flow from entering the sea except by seepage. Consequently, anadromous fishes are denied access to these streams until fall rains create sufficient flow to wash out the sand barriers. A large proportion of California's silver salmon spawn in such small streams. Most of the remainder spawn in small tributaries of streams which are large enough to keep the bar open at all times.

In streams which are seasonally closed by bars the initial entry of the adults into fresh water is usually dependent upon the occurrence of the first heavy fall rains. These usually take place in October or November but may arrive as early as the middle of September.

Snyder (1931) reports that in the Klamath River, California, an occasional silver salmon is caught prior to September 6th. The mouth of this large river is always open and the fish are free to enter at any time. Marr (1943) has observed that the silver salmon runs occur earlier in the year with increasing latitude of the stream in which they spawn and that in the Yukon River, Alaska, the major part of the run takes place in July and August. Taft and Shapovalov (1945) reported that the first fish were noted to enter Redwood Creek in September. In Prairie Creek a few individuals were seen on the spawning areas as early as the third week of October. However, the largest runs did not reach the upper portions of the creek until the second week of November. The majority of these fish migrated well into the headwaters of Prairie Creek or ascended its smaller tributaries.

Many of the late October and November arrivals migrated as far up the small tributaries as it was physically possible for them to do so and stopped only when confronted by impassable barriers, such as log jams or waterfalls. They often showed remarkable persistence in swimming up riffles where the flow was as low as two cubic feet per second and the water depth as little as two inches.

In most cases the fish did not attempt to enter these smaller tributaries until a heavy rain had increased the flow to some extent. Then they exhibited a tendency to make their ascent in a "run" composed of at least several pairs. These runs occurred at nonrelated intervals in each of the principal tributaries. For example, in 1948 the first run appeared in Godwood Creek on November 15th, in Brown Creek on November 22d, in Elk Prairie Creek on December 3d, and in Mae Creek on December 8th.

During the 1948-49 season spawning silver salmon were present in Prairie Creek most of the time from October through the first week of February. In 1950-51 the run was slightly shorter, ending by the middle of January. In 1949 the run was interrupted for nearly the entire month of January during a prolonged spell of dry, cold weather.

Migratory Stimuli

The effects of various migratory stimuli upon certain salmonid fishes have been discussed a number of times in the literature. Several theories have been formulated to provide a mechanistic explanation for the "homing" ability of this group. Curtis (1949) has presented an excellent summary of the most prevalent of these ideas.

The possible effects of some environmental factors upon the movements of adults in the freshwater streams is of close concern to the problem at hand and should be carefully considered. Calderwood (1903) found that Atlantic salmon (*Salmo salar* Linnaeus) ascended the Tay River from the estuary during times when there was either a rise in water level and temperature or a rise in temperature unaccompanied by a rise in water level. Mottley (1938) during his work with rainbow trout at Paul Lake concluded that the factor which controlled the high intensity of migration in the early afternoon appeared to be associated with the temperature of the water. Davidson, Vaughan, and Hutchinson (1943) observed that pink salmon sometimes will not enter a stream until a freshet occurs and that changes in temperature alone seemed to have no effect in promoting migratory movement. By contrast, Neave (1943), during his work on the silver and king salmon, found no correlation at all between migration numbers and water temperatures or flow. Huntsman (1945) experimented with the effects of artificial freshets upon Atlantic salmon and found evidence that all stages of this fish responded more or less to freshets by ascent of streams. He further stated that these ascents occurred chiefly as the high water was subsiding.

In connection with this question an interesting phenomenon took place on the Mad River during a dry, cold spell in January, 1949. This river is a coastal stream which enters the Pacific near the town of Arcata, California, about 30 miles south of Prairie Creek. The runs of anadromous fishes are counted as they pass through the fish ladder at the Sweasey Dam, about 25 miles from the river mouth. From the unpublished records kept by the California Department of Fish and Game it could be seen that for the 10 previous years a large portion

of the annual steelhead run had been passing over the dam during the four-week period from January 15th to February 15th.

The steelhead in 1949 appeared in the lower reaches of the river at about the usual time and good catches were made by anglers all along the stretch below the dam. During the cold weather of January there were no major increases in water flow and, as expected, only a very few fish came over the ladder. However, a large rise of cold water did occur as the result of mixed rain and snow on February 4th, 5th, and 6th. The fish did not react to this situation and the only obvious explanation was that the flow increase was not accompanied by the usual temperature rise because of the unusually cold precipitation. By February 8th only one trout had reacted to the water rise by passing over the ladder despite the fact that large numbers of fish, perhaps two to four thousand, were quiescent in the river immediately below the dam. As soon as the cold period was over and the water temperature rose several degrees, beginning February 9th, the fish ascended the ladder in great numbers.

These observations might constitute some evidence to support the findings of Calderwood (1903) and Mottley (1938) indicating that migrating salmonids may react more closely to temperature changes than to fluctuations in water volume. In the California north coastal region the stream rises in the winter time almost always seem to be accompanied by sharp temperature increases (the temperatures shown in Figure 1 were taken weekly and do not demonstrate this). This fact makes it difficult to separate the effects of these two environmental factors.

Roule (1933) is responsible for the theory that salmon migrate upstream in pursuit of an improved oxygen supply because of a physiological need for this element by the maturing adults. He assumes the presence of an oxygen gradient extending from the ocean to the spawning grounds in the headwaters of the streams. However, it can be shown that such a gradient does not always exist and that the migrants frequently pass from waters of comparatively high oxygen content to those which have less.

Rate of Migration

In Elk Prairie Creek it was possible to time the progress of the silver salmon run from the mouth of the stream to the spawning area two miles distant. In this stream the fish took approximately two full days to travel the last two miles of their journey. However, it must be borne in mind that this last portion was the most difficult because of the smaller flow of water and the comparatively great number of obstacles, including log jams, small waterfalls, and shallow water areas.

Age and Size

Evidence from various scale study projects has indicated that the silver salmon, over the major part of their range, usually return to spawn in the third year of life. The young fish almost invariably spend their first year in fresh water and migrate to sea in the spring. A small percentage of the males may mature precociously and leave the ocean in their second year. Taft and Shapovalov (1945) determined the ages of 2,218 adults from Waddell Creek on the Central California coast, and found that all of them returned either as males in the season following downstream migration or as males and females in the second season following the downstream migration. Their data showed that 17.4 percent of the 2,397 adults observed over a nine-year period were precocious males (grilse) in their second year of life.

Marr (1943) has presented information from his Columbia River studies which is very useful from a comparative standpoint. He concluded that only 6.1 percent went to sea and returned in their second year (grilse) and but 83.9 percent went to sea in their second year and returned in the third. Of the remaining 10.0 percent, almost all (9.7 percent) did not leave fresh water until they were in their third year and returned to spawn in the fourth. The remaining 0.3 percent also spent nearly three years in fresh water but came back in their third year.

A further south to north change in proportions of the different age groups is indicated through the work of Gilbert (1924). He found that in the Yukon River in Alaska the silver salmon usually did not leave fresh water until the beginning of their third year and spawned principally in their fourth year.

Marr (*op. cit.*) also indicated the presence of a south to north change in size when he showed that British Columbia fish were significantly heavier for their length than were those from the Columbia River.

Considering the information listed above it seems logical to assume that the Prairie Creek silver salmon are almost all referable to the two life history categories that have been listed by Taft and Shapovalov (*op. cit.*) for the Waddell Creek population. Prairie Creek is similar in size to this stream and its location is comparatively close.

During the 1950-51 season it was possible to obtain length and weight measurements from a few of the adults shortly after they had finished spawning. Four normal size males averaged 33.2 inches in total length and 13.2 pounds in weight. The one small male was 24 inches in total length and weighed 5.9 pounds. Six females averaged 29.7 inches total length and 9.3 pounds.

Sexual Dimorphism

The dimorphism between the sexes in silver salmon is very marked, being more extreme in some respects than in any of the other American salmon. Except for the grilse, the breeding male is usually noticeably larger than the female. In addition, the sides of the male are suffused with color ranging from a deep purple to a brilliant red; the color of the female is considerably duller although a great deal of variation is demonstrated. Some of the females, after losing their silvery marine coloration, remain a drab olive-green while others develop a bronze or reddish tint on their sides. A few of them demonstrate a well-defined, longitudinal stripe of a deep red or purple shade which extends from the opercle region to the base of the caudal fin.

Some change in general body contour can usually be seen in the male. The dorsal anterior region between the head and the first dorsal fin has a tendency to become ridged and projected slightly upward

giving this part of the body an increase in depth. No such body change is observed in any of the females.

By far the most striking breeding modification of the male is the prolongation and hooking of the upper jaw and the appearance of the large breeding teeth. The lower jaw also becomes elongated and slightly hooked but to a much lesser degree. Tchernavin (1938b) examined five species of *Oncorhynchus* (including the silver salmon) and found that a large portion of the skull elements were more or less affected by breeding changes and that those parts which underwent the greatest modification were the ethmoid region of the chondrocranium and all of the tooth-bearing bones. He stated that these changes consisted mainly of a lengthening of the affected parts and the formation of new breeding teeth. A great deal of the lengthening of both jaws and the accompanying hooking effect is apparently due mostly to the development of enormous, ossified bases for these breeding teeth. These bases are closely applied to the premaxillary and the dentary, but project a considerable distance beyond these bones when their growth is completed. The breeding teeth, many times larger than those once used for feeding, project well out from their bases and give the male a very formidable appearance. In addition, long needleshaped teeth are said to develop on the pharyngeal plates. These jaw modifications are always most marked in the largest of the males. The females demonstrate little or no apparent change in the head structures.

There has been considerable speculation in the literature regarding the origin and possible use of these secondary sex characters in the salmon. Cunningham (1900), in discussing the Atlantic salmon, observed that the males fought constantly with one another and that the enlarged tip of the lower jaw must have resulted from blows afflicted against the bodies of rivals. In the same year Barrett-Hamilton (1900) suggested that both the hypertrophy of the head and the development of livid colors were the result of a pathological condition because of the inability of the excretory organs to do their required work. His observations were based upon examination of several species of *Oncorhynchus* in Alaskan waters.

As late as 1936, Mottley (1936) maintained that these secondary sex characters were neither adaptive nor purposeful from an evolutionary standpoint. He inferred that growth of the snout took place to utilize excess supplies of albuminoid material not required for energy or the manufacture of sex products. He explained that the female does not show this development because the material is utilized by the developing ovaries. Even Tchernavin (1938a) was of the opinion that the origin of the hooked jaw in the Atlantic salmon could not be due to sexual selection or competition between males because the fish were not able to harm each other with this device.

In view of the above statements it seems necessary to emphasize that secondary sex characters need not be utilized as weapons for actual combat in order to be successful from a sexual selection standpoint. Such color and structural modifications have a definite display value for the benefit of the female in many animals, although in the case of the salmon this is probably true to but a limited extent, if at all. Noble (1945) is of the opinion that sex colors aid sex recognition and intimidation of other males in salmon and trout but do not attract the female.

As Huxley (1938) has pointed out, there are three main types of characters concerned with rivalry between males of a polygamous species: first, those affecting mere strength and size; second, those concerned with threat; and third, those special weapons used for actual combat. In the case of the Pacific salmon the characters operating in "intrasexual selection" (in Huxley's terminology) seem to be closely analogous to those seen in the deer. The antlers of the male deer may be used as weapons for actual combat but usually subserve the more common function of threat from a distance. The heavily armed, hooked jaw of the male salmon also constitutes a seemingly usable weapon for actual combat but it is scarcely ever employed as such (see data on page 19).

As a result of the Prairie Creek observations and a review of work with other animals in regard to the function of the secondary sex characters, it has been concluded that such modifications in the salmon are of definite value in intrasexual selection and did not evolve merely in order to utilize excess waste materials or as a result of any physical blows or irritations. These characteristic changes in size, body shape, coloration, and head structure are obviously utilized mainly for threat, although the teeth may rarely be employed as actual combat weapons, and they may also have some value for display purposes.

Breeding Ratio

It was not possible to obtain a sex determination of all the migrants because Prairie Creek was not supplied with a ladder or weir at which such counts could be accurately taken. Counts were recorded of the number and size of the males that were attending 10 different females. The average number per female was 1.5. In four cases it was noticed that only a single grilse was present, indicating perhaps a temporary shortage of the large males. The greatest number of attending males observed was three, and this took place on only one occasion.

Taft and Shapovalov (1945) list data from three places where accurate records of the population sex ratio were maintained: Of 2,397 fish counted in Waddell Creek over a nine-year period, 17.4 percent were male grilse, 40.5 percent large males, and 42.1 percent females. In Scott Creek, California, 1,568 fish were counted over a three-year period and 17.6 percent were male grilse, 35.1 percent large males, and 47.3 percent females. At Benbow Dam on the Eel River, California, 60,479 fish were counted over five seasons and 25.3 percent were male grilse, 32.2 percent large males, and 42.5 percent females. Taft and Shapovalov (*op. cit.*) also noted that the males predominated in the early portions of the runs while the females were most numerous in the latter parts.

Location of Spawning Areas

In California the silver salmon are common in almost all of the small coastal streams as far south as Monterey Bay. However, they are very rarely found in the Sacramento-San Joaquin River system, the largest in the State. They do enter the Klamath River but seem to prefer the smaller tributaries that are located near the mouth of this stream. Jordan and Evermann (1902) have noted that this species enters the shorter coastal streams late in the fall. Chamberlain (1907) observed that silver salmon frequently continue up the smaller streams and may be seen in water too shallow to cover them. Carl and Clemens (1948) state that these fish spawn mainly in small tributaries and often only a short distance from the sea. Burner (1951) related that this species apparently prefers small streams flowing only three or four cubic feet a second.

The distribution of this species in the Prairie Creek watershed fits in well with the above observations. In spite of the fact that Prairie Creek itself is quite a small stream (Figure 1), the majority of these fish migrated up into the smaller tributaries or into the headwaters of the main stream above the junction of the principal tributaries (Figure 2).

The earliest running fish, arriving in October, November, and the first part of December, were the ones that traveled to the farthest reaches of the watershed and the later arrivals usually utilized the lower parts of the tributaries and even the lower section of Prairie Creek itself.

Many of the early observers placed great emphasis on the many difficulties encountered by migrating salmon and described in detail the various types of injuries which were supposed to have been received on the journey to the spawning grounds. It remained for Evermann and Scovell (1896) to discover that such injuries and deterioration did not ordinarily take place even on extensive journeys to the breeding areas but occurred after arrival. These observations were made on the sockeye salmon, *Oncorhynchus nerka* (Walbaum) and later, Evermann (1897) on the king salmon, *Oncorhynchus tshawytscha* (Walbaum). All of the newly arrived silver salmon seen in Prairie Creek were in perfect condition with no sign of any type of injury.

Physical Characteristics of the Redds

At the time the fish were engaged in breeding activities, notes were taken on the important physical characteristics of the individual spots selected for redd construction. The characteristics of those redds which were later excavated and found to contain eggs are summarized in Table 1.

The data in Table 1 are arranged in chronological order. The water velocity was computed by timing the progress of a float over the redd surface. The gravel size refers to the average diameter of the large rocks which formed the most conspicuous part of the redd structure. The interspaces between the larger stones were always filled with smaller stones, sand, and silt. The "depth of eggs" indicates the vertical distance below the gravel surface at which the eggs were found at the time of excavation. Ten out of the 16 redds were located at the downstream ends of pools, the rest lying in riffle stretches. Burner (1951) has noted that in the Toutle River, Washington, the silver salmon selected an average water depth of 7.8 inches and placed their eggs an average of 8.0 inches below the gravel surface.

Breeding Activities

Shortly after the arrival of the salmon run in the general vicinity of the spawning area the females started their digging action in various spots that were apparently suited to the purpose. However, they would

TABLE 1

Physical Characteristics of the Productive Redds of the Silver Salmon

Stream	Date	Water depth	Velocity (feet/ second)	Gravel size	Depth of eggs	Location
Godwood Creek	10/24/48	5"	2.5	1.5"	10"	End pool
Prairie Creek	11/18/48	8"	2.0	4"	7"	End pool
Godwood Creek	11/25/48	5"	2.0	3"	11"	End pool
Godwood Creek	12/15/48	6"	2.0	3"	15"	Riffle
Mae Creek	12/16/48	4"	2.0	2"	10"	Riffle
Elk Prairie Creek	12/25/48	6"	2.0	5"	11"	Riffle
Elk Prairie Creek	2/ 6/49	5"	2.0	3"	12"	Riffle
Godwood Creek	2/ 7/49	7"	1.5	2"	11"	End pool
Prairie Creek	10/21/50	--	--	3"	8"	Riffle
Prairie Creek	11/28/50	7"	2.0	3"	8"	End pool
Prairie Creek	11/28/50	6"	1.5	3"	8"	End pool
Elk Prairie Creek	12/10/50	8"	2.0	4"	9"	End pool
Godwood Creek	1/ 6/51	6"	2.0	2"	7"	End pool
Godwood Creek	1/ 6/51	5"	1.5	2"	10"	End pool
Brown Creek	1/ 8/51	7"	2.5	2"	8"	Riffle
Godwood Creek	1/13/51	8"	1.0	3"	12"	End pool
Averages		6.2"	1.9	3.7"	9.8"	

often leave their initial location and move elsewhere before any eggs were deposited. Unspawned females that were sexually mature enough to begin the digging action were always closely attended by one or more males.

It seemed quite apparent that the female alone was responsible for the selection of the proper site at which to bury her eggs. After the territory was once selected she vigorously defended it against all others of her sex, the males being generally unmolested. In some cases this female territorial behavior continued for as long as two weeks after all the eggs were deposited and until the fish became too weak to maintain a position against the current.

Although territorial behavior has been recognized in other groups of fishes it seems to have gone almost unnoticed in the salmonids. Burner (1951) mentioned that the female salmon "had a natural tendency to guard the privacy of the redd area." Allee (1949) has emphasized that more is known about the territorial organization of birds than of most nonhuman groups, and that their defended areas can be classified as follows:

1. Mating and nesting plus food collection space.
2. Mating and nesting with food collected elsewhere.
3. Mating station only.
4. Nesting region only.
   a. Solitary individuals.
   b. Colonies.
5. Nonbreeding territories.
   a. Roosting territories.
   b. Feeding territories.

The areas selected by the salmon seem to be closely analogous to category No. 2. The attempt of the female to hold the territory long after spawning has been completed makes it obvious that the territory fulfills the dual purpose of both a mating and nesting area.

As in other closely related species, all of the redd construction was accomplished by the female. At fairly regular intervals, once every two to three minutes, she turned on her side and dug vigorously. This "digging" was accomplished by placing the tail flat against the substrate and suddenly lifting it upward with a powerful muscular contraction. The resultant hydraulic suction was generally strong enough to loosen stones and finer materials and to move them several inches upward. This material, once having been detached from the redd surface, was then carried by the current for a short distance before coming to rest again. This motion of the tail was usually repeated very rapidly five or six times, after which the individual rested before continuing the process.

This disagrees with some earlier descriptions. For example Chamberlain (1907) was under the impression that the spawning fish moved the gravel by forcing the body and tail against it. Bean (1893) asserted that both sexes of this species take part in the redd construction and that they use their snouts in collecting material for the nest. There was no evidence of such activities in Prairie Creek.

As the digging process was repeated time and again over the same spot, a well defined pit gradually became apparent. During this period the male was always in close attendance, usually to the side and slightly behind the female. He showed his attention by a characteristic quivering motion of his body, and by swimming close to her, first on one side then the other. Ordinarily, the male exhibited but little activity compared to his mate. However, if any smaller males or grilse were present he would display great energy in chasing these rivals to keep them away from the female. It seemed clear, as a result of close observation, that the male exhibited no tendency toward a territorial behavior but was merely interested in taking part in the spawning act. The contests between males were almost invariably decided following assumptions of threatening attitudes and displays of teeth. Even in the rare cases when the breeding teeth were actually used as weapons, no apparent physical injuries resulted. In fact, no injuries were ever found on any of the males which could be clearly ascribed to a rival fish.

When the nest was finished it usually consisted of a pit, slightly oblong in shape with the long axis parallel to the flow of water. For 37 redds observed the length of the pit averaged around three feet while the width was about two feet. Depth measurements were taken of two of these pits before eggs were placed in them and they extended, respectively, eight and ten inches below the surface of the substrate.

Soon after completion of the egg pit, the spawning act itself took place. The following account is the result of observations conducted on Godwood Creek on January 13, 1951, at 3.10 p.m.: The male quickly swam close to the female and took up a position exactly beside her. Both fish seemed to press well against the bottom of the nest so that their genital openings were slightly upstream from the center and deepest portion of the pit. The large cloud of milt expressed by the male was immediately apparent. Both individuals opened their mouths wide and remained in position, with no noticeable movement, for about two seconds. As soon as the act began, a small grilse quickly came up on the unoccupied side of the female and evidently also liberated some spermatozoa. The excess milt was rapidly carried off by the current, but a good portion remained at the bottom of the pit, effectively obscuring the eggs. As soon as the sex products were liberated, the female immediately moved forward and started digging about six inches above the upstream edge of the pit. She continued this, at more than usual rapidity, until the ova seemed to be well covered in less than a minute's time. As the female moved out of the nest a single small trout dashed into the pit and was probably successful in securing one or two eggs. No other evidence of predation was seen and the eggs were so rapidly covered that it seemed extremely improbable that this type of action could ever account for the loss of any significant number. No ova could be seen floating from the nest as it was being covered over.

This observation agrees with those of Greeley (1932) who observed spawning in rainbow, brook, and brown trout. He stated that at most, a very slight percentage of the eggs deposited in the pit are taken, in the short interval between spawning and covering of the eggs. There seems to be no basis for accepting the view of Fraser (1917) that trout follow this species to the spawning beds and devour so many of the eggs that the possible number of fry is at once very much reduced, unless the behavior of this fish in British Columbia waters is considerably different. Taft and Shapovalov (1945) express the opinion that at least 97 percent of the eggs lodge in the pit and are properly buried.

Peart (1920) was the first to recognize that the egg pit, due to its characteristic shape, afforded a highly efficient device for the retention of the sex products until they were covered over. Through the introduction of India ink into the bottom of these depressions, he was able to explain and diagram the action of the water currents. He found that the fluid within the confines of the pit was quite still, with only a very slight movement in a direction opposite to that of the main stream flow. He also introduced milt into artificial pits and found that it remained visible for a period of two to four minutes.

Although Peart's work was concerned with *Salmo salar* his results have been found to be applicable to other salmonid species as well. Hobbs (1937) introduced potassium permanganate crystals into pits constructed by king salmon and found that the current behaved in essentially the same manner. In a later work Hobbs (1948) investigated the nests of *Salmo trutta* Nilsson and presented a diagram of the flow which looks about the same as that drawn by Peart in 1920. Burner (1951) also gave a similar diagram which illustrated the currents in a typical Pacific salmon redd.

In Prairie Creek, the nests of the two salmon species, as well as those of the steelhead trout, were carefully examined. It was found that the flow within all of these structures was basically the same as that described by the above three authors. The slight lifting force of the reverse current along the bottom of the pit was not strong enough to float any eggs out of the nest, although it did cause them to concentrate somewhat along the upstream edge of the pit. It seems likely that the action of this reverse current lends a certain amount of mechanical aid to the spawning process in holding the newly laid eggs in the most advantageous position. The ova that are closest to the upstream edge of the pit are those that become buried most rapidly as soon as the female resumes her digging activity. Such eggs are also the least likely to be buried at an insufficient depth or consumed by a predatory fish.

In general, pairs of this species demonstrated breeding activity from two to four days, although, as Taft and Shapovalov (*loc. cit.*) have noted, they may continue for as long as a week or more. As soon as the female had discharged her complement of eggs the male seemed to become immediately aware of the situation and left. Other males, in the course of their wanderings, sometimes paused and paid only momentary attention to such abandoned females. Their company was readily accepted, but they seemed to be able to sense that the female had already performed her reproductive function.

No correlations of breeding activities with the relatively small water temperature variations were evident. The midday temperature of Prairie Creek during the silver salmon spawning run of 1950-51 ranged from 46 degrees F. to 56 degrees F. Burner (1951) reported that these fish spawned in the Toutle River, Washington, with the temperature ranging from 42 degrees F. to 58 degrees F. Chamberlain (1907) found this species spawning at 46 degrees F. in Alaska.

Postspawning Activities

The spawned-out females usually continued to perform the digging action at irregular intervals until they finally died. This activity was continued whether or not any male fish were in the vicinity. Even when females grew very weak and started to drift downstream with the current they often paused to dig at various places.

Virtually all of the silver salmon females gave no external indications of physical deterioration until after all of the spawning activities had been finished. Five of these fish were killed and examined immediately after they were abandoned by the male and all of them were found to have completed deposition of their eggs. Most of the well known symptoms of salmon nearing the end of their life cycle, such as frayed fins, loss of skin in places, fungus infection, and sometimes blindness, affected the females during the guarding of the redd area only after spawning had taken place.

By way of comparison, the males continued to demonstrate courting actions even after they began to undergo physical degeneration and maintained these actions until they became helpless and began to drift with the current.

Redd Classification

The term "redd" is usually applied, in a general sense, to those stream bed areas which have been disturbed by the digging action of the female, whether or not eggs are actually deposited therein. Since the circumstances under which these redds are constructed are apt to vary, it seems advantageous to propose the following classification:

I. True redd—actually contains or has contained eggs.
II. False redd—no eggs ever deposited.
   a. "Trial redd" (term introduced by Hobbs, 1937)—area which is worked by female before spawning takes place.
   b. Postspawning redd—area dug up by female after egg complement has already been deposited elsewhere.

In many cases it was noted that trial redds were fully as extensive, in regard to the amount of surface area covered, as the true redds. Also the construction of these trial redds seemed to be, in general, a well established procedure with both the silver and king salmon. The habit of digging postspawning redds seemed to be equally well established and large gravel areas were sometimes affected.

During the two seasons of the Prairie Creek study, a total of 37 silver salmon redds was marked. These were all at localities where unspawned females accompanied by males were apparently engaged in the construction of true redds. All of these areas were thoroughly excavated later, and 20 of them (54.0 percent) were found to be only trial redds, containing no eggs at all. Furthermore, it is estimated that at least half of the spent females dug postspawning redds, in areas well separated from the place of egg deposition, which would be conspicuous enough to be counted by a casual observer. Therefore, it can be seen that a procedure of counting a pair of adults for each well defined redd area would clearly constitute a serious overestimate of perhaps 150 percent, at least insofar as Prairie Creek silver salmon are concerned.

Summary

The silver salmon evidently has a wider range than the other North Pacific salmonids. It prefers the smaller coastal streams for reproductive purposes and migrates from the ocean after the fall rains begin to have their effect on the runoff. The spawning migration in Prairie Creek extended from three to four months.

Almost all of the individuals returning to California streams are evidently in their third year of life, except a small portion of male grilse which are in their second year. Further north, substantial numbers of this species delay spawning until their fourth year.

Sexual dimorphism is very marked, especially in regard to the head structures. The secondary sex characters are used mainly for threat, and have a definite value in intrasexual selection. A small excess of males is apparently the usual condition in a breeding population.

In Prairie Creek the majority of the adults migrated up into the smaller tributaries or into the headwaters of the main stream. The earliest arrivals traveled to the farthest reaches of the watershed while individuals of the later runs found spawning areas farther downstream. Apparently all fish arrived on the spawning beds with no physical injury.

The female alone was responsible for the selection and defense of a territory which filled the dual purpose of both a mating and nesting area. The female also performed the entire operation of redd construction. The ova and sperm were released simultaneously into the bottom of a well defined egg pit. This pit was immediately covered and there was little or no egg loss. In general, the breeding activity lasted from two to four days.

Virtually all of the spent females gave no indication of physical deterioration until after egg deposition had been completed. It was also observed that these females usually continued to perform the digging action at irregular intervals until they died.

The construction of trial and postspawning redds, neither of which contained eggs, was found to be a well established procedure. It was estimated that perhaps three-fourths of all the redds constructed by this species in Prairie Creek fell into these two categories.

KING SALMON, *ONCORHYNCHUS TSHAWYTSCHA* (WALBAUM)

Range

The king salmon is native to the North Pacific. According to Roedel (1948) it rarely enters streams south of San Francisco Bay but has been taken at sea off Southern California. Croker (1936) states that a few are taken nearly every summer in the neighborhood of San Pedro, California. Jordan, Tanaka, and Snyder (1913) list it from the east coast of Siberia and south to Hokkaido, Japan.

Time of Migration

There are two quite well defined populations of this species along the American coast, each with its own characteristic time of migration. The spring run king salmon is typical of the largest rivers, where there is enough flow in the headwaters for these fish to live through the summer. This spring run may begin as early as February or March. The fish evidently travel upstream slowly and have a protracted resting period in the pools near the spawning grounds. They usually do not spawn before August and continue spawning through November.

On the other hand, fish belonging to the fall run population do not enter fresh water until autumn. This form is found in both the large rivers and the small coastal streams; it seems to move fairly rapidly to the spawning areas, where the eggs are deposited without much delay. Snyder (1931) recorded these fall fish in the Klamath River in August or early September, while the greatest numbers are usually found entering the Sacramento River in the latter part of September and early October. The fish which utilize the smaller coastal streams begin their migration as soon as the fall rains provide sufficient flow.

Only the fall king salmon are found in Prairie Creek, the stream being much too small to maintain any large fish over the summer drought period. Most of the individuals comprising the first main run arrive on the spawning area during the first and second weeks of November. However, many of them may have first entered fresh water in the lower reaches of the stream some time in October. New arrivals were seen after almost every high water period from November to January. In the 1948-49 season the run continued through the first week of January, but in 1950-51 it was concluded by the last day of December.

Migratory Stimuli

The effects of the various stimuli which are said to operate in the freshwater environment have been discussed in connection with the description of the silver salmon run (page 12). The remarks and references recorded there apply generally to this species.

Rate of Migration

The rate of upstream migration evidently varies widely in different localities. Curtis (1949) stated that in the Yukon River, Alaska, the king salmon have been known to travel at the rate of 50 miles per day. He also observed that in this particular river speed is essential, since many of the individuals must travel 2,000 miles in the relatively short period the river is unfrozen. Stone (1897) estimated the speed in the lower part of the Columbia River at slightly over three miles per day. Jordan and Evermann (1902) concluded that those fish entering the Columbia and ultimately spawning in Idaho must average nearly four miles per day. Rutter (1904) found that the fall run fish ascended the Sacramento River, California, at the rate of four or five miles a day. All of these rates should probably be considered no more than rough estimates, since apparently none of them resulted from a well designed mark and recovery program.

Age and Size

Many scale studies have been made for the purpose of obtaining life history data on this species. In general, these have usually borne out the contention of Gilbert (1914) that spawning may take place in the third, fourth, fifth, sixth, or seventh year, but usually occurs in the fourth or fifth year (it is now known that some males may spawn in their second year in the Sacramento River). However, it should be mentioned that Gilbert (1924) found that in the Yukon River the king salmon usually spawn in their fifth and sixth years rather than the fourth or fifth, and that seven-year fish were quite abundant. These facts indicate that there may be a south to north change in the proportion of the different age groups, similar to that pointed out by Marr (1943) for the silver salmon.

During the 1950-51 season it was possible to obtain length and weight measurements from a number of the adult fish after they had finished spawning. Eighteen females averaged 35.8 inches in total length and 16.9 pounds. Ten males averaged 32.6 inches in total length and 15.7 pounds. Hobbs (1937) listed a table which showed that 17 spent females from the Broken River system, New Zealand, averaged 31.2 inches in total length and 9.6 pounds. An interesting comparison was given between eight of these spent fish and eight fresh females of the same length from the mouth of the Broken River. The average weight difference between these two categories was 23.7 percent. Rutter (1904) weighed a large number of specimens from the Sacramento River and found that the average male underwent a weight loss of 26 percent from the "fresh" condition to death. The average female was found to suffer a 19 percent weight loss over the same period (not including the weight of the ova).

The work of Belding (1934) showed that many Atlantic salmon lost as high as 31 to 44 percent of their total weight during their freshwater existence. He concluded that, since death takes place in many other animals when the body weight is reduced approximately 40 percent, many of this species die either from too much weight loss or from other causes indirectly affected by their weakened physical condition.

Sexual Dimorphism

In general, the large males seemed to be of a slightly greater size than the females, although the discrepancy was not as apparent as in the silver salmon. Structural dimorphism, while noticeable, was also not as pronounced in this species. Following the loss of the silvery guanine layer, a large portion of the males developed a slight reddish tint on the sides; others, however, remained a dark olive-green. This red coloration was not seen on any of the females.

As in the silver salmon, some change in general body contour could usually be seen in the male. The dorsal anterior region of the body between the head and first dorsal fin had a tendency to become ridged and projected slightly upward, giving this region an increase in depth. No such body change was observed in any of the females.

No visible head modifications were noticed in the females, but the jaws of the males became somewhat prolonged and hooked (less so than in the silver salmon) and were provided with large breeding teeth. Information and conclusions regarding the origin and use of such secondary sex characters are listed under the description of the history of the silver salmon (page 15).

Breeding Ratio

Because Prairie Creek was not supplied with a ladder or weir, it was not possible to determine the numbers or the sex of all the migrants. However, it was noticed that the supply of all sizes of males seemed to be proportionally more plentiful than of females, in contrast to the breeding ratio of the silver salmon. Counts were recorded of the number and size of the males that were attending 15 different females. The average number per female was 2.1. In one case only a single grilse was present, but in two other instances a total of four males was noted.

Location of Spawning Areas

The fall population of king salmon inhabits many of the smaller coastal streams as well as the large river systems in California. Prairie Creek, however, probably comes quite close to the minimum size of stream which is normally utilized. Most tributaries which have noticeably less flow are not adopted by this species, but may be well populated by both the silver salmon and the steelhead trout. The distribution of the spawning area in Prairie Creek clearly indicates the preference of the king salmon for areas of comparatively greater flow (Figure 2).

King salmon were seen in only the one large tributary to Prairie Creek (Lost Man Creek). They did not enter any of the smaller creeks of the upper watershed, which were sought by the silver salmon. Consequently, the populations of these two species were quite compatible, even though their spawning periods coincided.

The distribution of the early arrivals was not noticeably different from the later running individuals. Stone (1884) and Hobbs (1937) noted that the earlier runs of king salmon go farther upstream and later fish take places below them. A conflicting observation has been recorded by Brice (1898), who stated that the first fish take up the first available spawning sites and force the newcomers farther upstream, until finally the highest points are reached.

This phenomenon of differential distribution between early and late running groups (with the early arrivals showing the longest migration) may be applicable to many species of anadromous fishes. This same type of behavior has been seen in the sea lamprey (*Petromyzon marinus* Linnaeus) by Applegate (1950) and was observed by the author in the Pacific lamprey, *Entosphenus tridentatus* (Gairdner), the silver salmon, and the steelhead trout (*Salmo gairdneri* Richardson).

Physical Characteristics of the Redds

Table 2 summarizes the characteristics for each of the redds that later proved to be productive (true redds).

TABLE 2

Physical Characteristics of the Productive Redds of the King Salmon

Stream	Date	Water depth	Velocity (feet/second)	Gravel size	Depth of eggs	Location
Prairie Creek	11/22/48	10"	2.5	6"	14"	Riffle
Lost Man Creek	12/22/48	16"	2.0	6"	14"	End pool
Prairie Creek	11/14/50	12"	2.0	3"	12"	End pool
Prairie Creek	11/17/50	14"	2.5	4"	12"	End pool
Prairie Creek	11/17/50	11"	2.0	4"	10"	End pool
Prairie Creek	11/20/50	12"	1.5	4"	10"	End pool
Prairie Creek	11/22/50	12"	1.5	3"	8"	Riffle
Prairie Creek	11/23/50	15"	2.0	4"	11"	Riffle
Averages		12.7"	2.0	4.2"	11.2"	

The data in Table 2 are arranged in chronological order. The gravel size refers to the average diameter of the large rocks which formed the most conspicuous part of the redd structure. The "depth of eggs" indicates the vertical distance below the gravel surface at which the eggs were found at the time of excavation. Finally, the "location" column indicates whether the redd was located in a riffle stretch or at the downstream end of a pool where the water was beginning to gather momentum.

According to Hobbs (1937), in Winding Creek (New Zealand) practically all of the material in redds was less than three inches in diameter, although many of them had odd stones of considerably larger size.

Burner (1951) gives some interesting comparative data from his work on the fall run king salmon of the Kalama and Toutle Rivers in

the State of Washington. He found that in the Kalama River this species selected an average water depth of 14 inches, an average velocity of two feet per second, and placed eggs an average of 10 inches below the gravel surface. In the Toutle River he found this fish preferred an average water depth of 11.6 inches, an average velocity of 1.3 feet per second, and placed eggs at an average of 10.7 inches below the gravel surface.

Other observers have noted that the king salmon will accept deeper water for spawning purposes. Chamberlain (1907) found that in Alaska spawning took place in water two to three feet deep and Walford (1937) listed a depth of one to four feet as a general requirement. Chapman (1943) gave the first report of individuals of this species spawning in the main Columbia River. He found them constructing redds at a depth ranging from 2 to 15 feet just below Kettle Falls, Washington.

Breeding Activities

Many of the king salmon arrived on the spawning area in a more or less immature state, indicated by a large amount of silvery coloration on the back and sides. These fish could be seen lying in the deepest pools, where they waited until they were ripe enough to spawn.

The selection of territory, redd construction, and breeding behavior were almost identical with that of the silver salmon, previously described, with the exception of the following few important points: The digging labors of the female were conducted at a more leisurely pace than was noted with the silver salmon, the time interval between such actions being usually five minutes or more instead of every two to three minutes. The resultant nest or egg pit was generally larger, about three feet wide and four feet in length, compared to the 2- x 3-foot structure of the silver salmon. Two of these egg pits were measured when they were apparently excavated to their maximum depth. One extended 11 inches below the gravel surface and the other 14 inches (somewhat greater depths than were recorded for the silver salmon).

Although no complete, detailed description of the breeding habits of the king salmon exists in the literature, a number of authors have given brief accounts, most of which, obviously, resulted from casual observations. Some authors were under the impression that redd construction is accomplished by the male. Jordan (1885) told how the male excavated a broad, shallow nest with his tail and snout. Furthermore, he reiterated this observation in many of his subsequent important works; see Jordan 1894, 1902, 1905, and 1907. As late as 1937, Walford (1937) repeated this same description.

Stone (1884, 1897), as well as Brice (1898), believed that both sexes took part in the nest building and that the fish somehow hollowed out cavities with their heads and tails. Bean (1893) also thought that both male and female participated in the nest construction, but said nothing about how it was done. Riddle (1917) maintained that both sexes excavated a pit by pushing on the bottom with their heads and the sides of their bodies.

Others finally recognized that the digging activity was performed by the female but completely misinterpreted the action. Downing (1900) thought that the work of the tail was part of the process of egg ejection. Townsend and Smith (1902) and Rutter (1904) believed that the digging movements were performed merely for the purpose of looosening the eggs from the ovaries. The authors of all three of these works were under the impression that the eggs were left exposed on the surface of the stream bed. In fact, Rutter (*loc. cit.*) stated that any covering of over an inch of even fine gravel would kill the eggs. Townsend and Smith (*loc. cit.*) also believed that death resulted if the eggs were covered.

None of these early writers indicated that the act of egg laying and that of fertilization were simultaneous. Apparently most of them believed that either the male deposited milt on the eggs after they were laid or that he fertilized them as they were being carried downstream by the current. Downing (*loc. cit.*) was of the opinion that fertilization depended upon the entire stream becoming permeated with sperm. The belief that females would spawn alone, with no male in the vicinity, was common and was due to a confusion of the digging action with the spawning act.

It remained for Hobbs (1937) to give the first accurate, although brief, description of the breeding activities of this species. He recognized, through work on New Zealand streams, the true significance of what he was able to observe. The only other accurate, but also brief, account was given by Haig-Brown (1941), in a popular book on the life history of this salmon.

The egg liberation itself was not witnessed in the king salmon, but the remarks of Hobbs (*loc. cit.*) and of Haig-Brown (*loc. cit.*) indicate that this process is the same as that seen in the silver salmon. Therefore, it can probably be safely assumed that the eggs are placed in the pit and covered over with very little resultant mortality. Haig-Brown indicated a belief that over 99 percent were successfully buried. In general, pairs of this species demonstrated breeding activity for a week or more. Hobbs has noted that the greater part of the ovaposition seems to occur within seven days. The males deserted the female as soon as she had finished discharging her egg complement, and, evidently, searched for other unspawned females.

The midday temperature of Prairie Creek during the king salmon spawning run of 1950-51 ranged from 48 degree F. to 51 degrees F. Chamberlain (1907) stated that in the McCloud River (a tributary of the Sacramento River) this species begins spawning at 56 degrees F. and finishes within three or four degrees of this. However, Jordan and Evermann (1902) maintained that spawning will not begin until the temperature drops to 54 degrees F. and Walford (1937) repeated this same statement. Burner (1951) found this species spawning within a range of 42 degrees F. to 61 degrees F. in the Kalama and Toutle Rivers in the State of Washington. Mattson (1948) found that the temperature ranged from 43 degrees F. to 64.5 degrees F. during the spawning period in the Willamette River in Oregon.

Virtually no external indications of physical deterioration could be seen in the females until after the spawning activities had been completed. A large number of these fish were killed and examined immediately after they were abandoned by the male and all of them were found to have completed deposition of their eggs. The males, on the

other hand, continued to demonstrate courting actions even after they bore such outward markings as loss of skin, frayed fins, fungus infection, and sometimes blindness.

Postspawning Activities

This part of the adult existence also closely paralleled that of the silver salmon. The spent females usually continued to perform the digging action at irregular intervals until they died. This activity was continued independently of the presence of any male fish. Usually, the period of postspawning life extended from two to four weeks (compared to several days to two weeks for the silver salmon). Hobbs (1937) found that in New Zealand the redd life (including the spawning period) usually did not extend beyond three weeks.

The territorial behavior of this species seems to be more highly developed than that observed in the silver salmon, especially during the postspawning period. Several of the redds in Prairie Creek were located quite close to one another and the behavior of the guardian females was carefully watched.

The spent females not only sought to defend the immediate redd area itself but the surrounding territory as well, as much as 20 feet on all sides. These territories were held chiefly against other females of the same species, the males being unmolested. However, both sexes of the silver salmon were usually chased off when they appeared.

Desperate contests were often waged between females that happened to be guarding redds that were less than 40 feet from one another. These individuals were occasionally seen to charge an opponent full tilt and to strike with such force that the recipient of the blow would be projected half out of the water. They were also seen to bite with such effect that actual physical injury resulted. The savagery of this type of fighting offered a distinct contrast to the mild contests between males for the right to participate in the spawning act.

It seems clear that such behavior must have a positive effect in increasing the reproductive efficiency in this species. It is well known that the most vulnerable period in the progress of the fertilized eggs is the so-called "tender stage," which usually extends over the initial two or three weeks of the embryonic development. The disruption of a redd by subsequent spawners during this period could cause significant losses by unearthing the ova or even killing them by shock.

Hobbs (1937) and Haig-Brown (1941) have both mentioned tha the tendency of the female to retain its position on the redd afte spawning may be interpreted as evidence of parental care. This i contrary to the opinion of Needham (1938) who, referring to th habits of all salmon and trout, stated that once the eggs are deposite no further parental care is given them.

The various types of redds have been previously classified (page 22) and these categories are suited to the redds of the king salmon a well. During the two seasons of the Prairie Creek study, a total of 2 redds was marked. These were all localities at which unspawne females, attended by males, were apparently engaged in the construc tion of true redds. All of these areas were thoroughly excavated late and 17 of them (68.0 percent) were found to be only trial redds

Furthermore, it is estimated that at least half of the spawned-out females dug conspicuous postspawning redds in places well separated from the area of egg deposition. Therefore, if the total size of the run in Prairie Creek was estimated by counting a pair of fish for each conspicuous redd, as is sometimes done, a serious error (perhaps over 200 percent) would result.

Summary

The king salmon is native to the North Pacific but its range is not quite as extensive as that of the silver salmon. The Prairie Creek individuals belong to a fall run population, which enters fresh water in the autumn and completes breeding activities before spring. The spawning migration in Prairie Creek lasted a little over two months.

Spawning in Pacific Coast streams usually occurs in the fourth or fifth year, but may take place from the second to the seventh year. There is probably a south to north change in abundance of the different age groups, with the fish of the most northerly streams showing the greatest average age.

Sexual dimorphism was not as marked as in the silver salmon, but differences were noted in size, body contour, color, and head structure. The use and value of the secondary sex characters were apparently the same as that listed for the silver salmon. The supply of males seemed to be relatively more plentiful than was the case with the latter species. The king salmon were usually found spawning in the lower portions of the main stream and did not enter any of the smaller tributaries of the upper watershed, which were selected by many of the silver salmon. The phenomenon of differential distribution between early and late running groups (with the early arrivals showing the longest migration) was not noticed in the king salmon of Prairie Creek.

There were noticeable differences in the physical characteristics of the redds between the two salmon species. The king salmon selected areas with a greater water depth and velocity, a larger gravel size, and buried the eggs considerably deeper. Also, the digging labors of the female were conducted at a more leisurely pace and the resultant nest or egg pit was larger. In general, pairs of this species demonstrated breeding activity for a week or more.

The females usually showed no external indications of physical deterioration until after the spawning activities had been completed. The postspawning period usually extended from two to four weeks (compared to several days to two weeks for the silver salmon) and the females commonly continued to perform the digging action at irregular intervals until they died.

The territorial behavior seemed to be more highly developed than that observed in the silver salmon, especially during the postspawning period. It seems clear that such behavior must have a positive effect in increasing the reproductive efficiency in this species.

As was the case with the silver salmon, the construction of trial and postspawning redds was found to be a well established procedure. It was estimated that well over three-fourths of the redds constructed by this species in Prairie Creek fell into these two categories.

STEELHEAD TROUT, *SALMO GAIRDNERI* RICHARDSON

Range

This species is native only to the Pacific American coast. Barnhart (1936) lists the southern limit as San Diego County, California. Evermann and Goldsborough (1907) have found that it extends northward as far as central Alaska, but not beyond the Alaskan peninsula.

Time of Migration

Most individuals of this species, especially those fish inhabiting the smaller coastal streams, migrate upstream during the late fall or winter and spawn in the early spring. However, a population of so-called "summer steelhead" is found in some of the large rivers. These fish usually ascend to the headwater streams in the early spring in a comparatively immature condition and postpone spawning until fall. These two populations can be considered more or less analogous to the fall and spring types of king salmon.

It should be mentioned that it seems quite probable that a good chronological separation may exist between breeding populations of these two types. If so, they must be considered distinct for purposes of study and eventual management. Also, it is entirely possible that a morphological basis for separation might eventually be found.

The Prairie Creek steelhead were only of the fall or winter run type and they usually spawned between the last week of February and the last week of April, although in 1951 a single pair was observed on a redd in Lost Man Creek on January 1st. In Waddell Creek, Taft and Shapovalov (1945) have noted that the run is sometimes spread over a long period of time; 96 percent of the fish usually entered the stream between December 3d and May 5th. Carl and Clemens (1948) state that spawning takes place during January, February, and March in the Cowichan River, British Columbia. In Alaska, near the northern limit of the species' range, the breeding time is somewhat later in the spring. Evermann and Goldsborough (1907) list data which indicate that spawning takes place throughout the month of May in Central Alaska.

Steelhead and Rainbow

S. gairdneri may be considered separable into two distinct types on yet another basis. Most of the coastal streams seem to have numerous individuals of this species that are permanent fresh-water residents. These are commonly called "rainbow trout," leaving the designation "steelhead" for the anadromous type.

As a consequence of field studies conducted at Prairie Creek and elsewhere it is believed that these two types are not representative of a single, homogeneous population, and that a distinct barrier to gene flow between the two groups does exist.

Among trout in general, a positive correlation seems apparent between the size of the spawning female and the size of the stream selected for redd construction. There are several logical reasons for this behavior. Small fish build small redds and utilize finer gravel. Considering the locations which stream spawning trout almost always occupy in riffle stretches and downstream ends of pools, another positive correlation is usually evident between the average gravel size and the stream size. Also, smaller fish do not bury their eggs as deep as their larger relatives, and the lesser tributaries usually offer greater protection from floods, which can erode the gravel to such an extent that eggs may be lost. Finally, the success of the defense of the breeding territory often depends on the size of the female. In places where the spawning areas are quite well populated a large percentage of the smallest females may be forcibly prevented from occupation of any areas except those of comparatively low flow.

The difference in size between the female rainbow of the coastal streams and the female steelhead is generally very marked. This vast difference in size seems to be accompanied by an almost equally great difference in the location of redd sites. As a result, there is apparently a good spatial separation insofar as the females are concerned.

In regard to the males, a similar, although probably not as complete, separation seems to be effected. There is no recorded instance of a large steelhead male attending a rainbow female, probably because the large fish would not be able to move easily into the comparatively shallow water which is usually selected. On the other hand, it is often assumed that rainbow males may attempt to participate in the spawning act with the steelhead female. It is entirely possible, however, that such small males may actually be young steelhead, since a few sometimes attain sexual maturity before their initial descent to the ocean. Nevertheless, in the majority of such cases these attempts are probably not successful because the large male is very active in driving off his smaller rivals. Even if the rainbow was able to approach at the necessary moment, the number of sperms produced by the steelhead, and consequently the number of eggs fertilized, would be considerably greater. Therefore, it seems evident that a noticeable amount of spatial isolation does exist between breeding populations of these two forms of *S. gairdneri.*

It does not necessarily follow that such distinct populations need to demonstrate morphological differentiation (or that such differentiation be required as proof of separation), even though anatomical differences usually eventually develop as a result of any long continued barrier to gene flow. The discovery of Neave (1944) is of great importance because it shows that at least in the Cowichan River, British Columbia, such a barrier must have existed for a long time. He found that significant differences existed between average scale counts of rainbow and steelhead from this stream, and most important, that these differences, both in scale number and migratory habit, were maintained in hatchery-raised offspring of these two forms.

Neave (*loc. cit.*) did state that the two forms often spawned on the same grounds, but he did not indicate whether this procedure was the rule or the exception. In the absence of more exact information, it seems most likely that the cause of the population separation here must also be spatial isolation, rather than a partial psychologic or genetic isolation as was thought by Emerson (1949). In Prairie Creek no evidence was found of any small size trout (either rainbow or cutthroat) ever spawning in the same habitat selected by the steelhead.

As Neave (*loc. cit.*) has emphasized, two such self-perpetuating stocks must be regarded as separate species from a management standpoint. It may be added that, due to highly significant differences in the scale counts, there seems to be some basis for considering the two forms as distinct entities from a taxonomic standpoint as well.

Migratory Stimuli

The effects of various stimulatory agents operating in fresh water have been previously discussed in connection with the silver salmon (page 12). The factors considered there can be applied generally to the steelhead trout.

Rate of Migration

Only a single reference to the rate of upstream migration in this species could be located. Needham (1938) states that the rate of ascent of the Klamath River has been determined by competent observers as approximately 2.5 to 3.0 miles per day.

Age and Size

Scale studies undertaken on the Pacific coast have shown that the majority of this species spend two years in the ocean before their first spawning, although fish remaining either one or three years are common. Sumner (1948) found that over 80 percent of the Oregon fish that he examined showed two ocean annuli on their scales. Meigs and Pautzke (1940) found that 67.4 percent of their fish from Puget Sound, Washington, fell into this category.

The period of freshwater residence before descent to sea is also quite variable, ranging from one to four years. However, in this environment as well the greatest numbers seem to respond to the migratory urge after two years. This was apparent in the two above mentioned papers dealing with conditions in Oregon and Washington. In addition, Dr. Willis H. Rich (private communication based on studies made between 1910 and 1913) reported that the main migration of steelhead in Scott Creek, California, took place when the fish were a little over two years old. The fish of the Cowichan River, British Columbia, show a little different behavior, according to Neave (1940). He found that about 60 percent of the steelhead from this stream went to sea as yearlings.

It can probably be concluded that, at least in the coastal streams of California, most steelhead first spawn at the age of four years, after having spent two years in the stream and two years in salt water. Taft and Shapovalov (1945) state that the great majority of first spawners from Waddell Creek were three or four years old.

The age distribution of the adults is complicated in this species because some fish survive more than one spawning. Taft and Shapovalov (*loc. cit.*) studied scales from 3,888 mature fish and found that 3,222 (82.8 percent) were first spawners, 583 (15.0 percent) second spawners, 80 (2.1 percent) third spawners, and 5 (0.1 percent) fourth spawners. The great majority of those spawning the second time were four or five years old, while most of the third spawners were five or six years old, and the fourth spawners were mainly six years old. Neave *(loc. cit.)* found that Cowichan River fish also demonstrated a three- to six-year range in age, and that first spawners comprised 93 percent of the adult population.

Since almost all of the steelhead migrated rapidly downstream immediately following spawning, it was not possible to obtain measurements from a series of the spent fish. However, a single female was killed following the completion of its redd. This individual was 29.5 inches in total length and weighed 7.5 pounds. Needham (1938) states that the usual weight of returning migrants is from 3 to 12 pounds, although they have attained as much as 42 pounds. Jordan and Evermann (1902) found that the average size of the fish reaching the Sawtooth Mountains, Idaho, was about 8 pounds, the range being from 2 to 14 pounds.

Sexual Dimorphism

Judging from stream-side observations, the size of the adults appeared to be quite uniform, with no apparent difference between the average size of the males and the females. There was no sign of any smaller males comparable to the salmon grilse. Furthermore, there was no noticeable dimorphism in the general body shape, as was usually the case with the two salmon species.

Both sexes, when ripe enough to spawn, showed the characteristic rainbow stripe on the side extending well up on the opercles. However, most of the males showed additional red coloration in a second stripe, ventral and parallel to the main, mid-lateral one.

The breeding modifications in the skull and jaws of the male were much less marked than in the genus *Oncorhynchus*. However, some changes, which were apparently somewhat similar to those described for *Salmo salar* by Tchernavin (1938b), could usually be found. He found that Atlantic salmon lost their feeding teeth just before entering fresh water and that these were replaced by a special set of "breeding teeth." He also noted that these breeding teeth were set in sockets in the premaxillary and the dentary; a condition not found in *Oncorhynchus*. The rostrum, premaxillaries, and dentary bones all become quite elongated and the anterior part of the snout grew upward, giving a curve to the upper jaw. Tchernavin *(loc. cit.)* considers these general changes to be applicable to all species of *Salmo*.

In the large males of *S. salar* the tips of the dentaries have a tendency to grow upward into a knob-like structure which may be further enlarged by an extension of the connective tissue. This peculiar, hook-shaped apparatus has not been seen in *S. gairdneri*. It may be well to note that despite the fact that the Atlantic salmon and steelhead are known to be ordinarily very difficult to separate morphologically, the large breeding males are dissimilar in a number of characters.

The importance of such secondary sex characters has been previously discussed (page 16) and the conclusions reached there may be considered fully applicable to this species.

Breeding Ratio

In general, the supply of males seemed to be plentiful, although no facilities where an accurate count could be taken were available at Prairie Creek. The sex ratio of the run in Waddell Creek was about 49 percent males and 51 percent females according to Taft and Shapovalov (1945). These authors also noted that the males predominated in the early stages of the run and were in the minority in the latter portion. Jordan and Evermann (1902) examined 4,179 Columbia River steelhead at The Dalles, Oregon, in September and October only. They found that only 1,531 (36.6 percent) were males.

Location of Spawning Areas

It was surprising to find that the distribution of steelhead on the spawning grounds almost exactly duplicated that of the king salmon, which was seen earlier in the season (Figure 2). With the single exception of a redd in Godwood Creek, all of this species spawned either in Prairie Creek itself or in its one large tributary, Lost Man Creek. This preference for comparatively deep water is also reflected in the data of Table 3, showing the various physical characteristics of the productive redds.

The earliest arrivals tended to spawn farther upstream than did the later ones. This phenomenon of differential distribution in anadromous fishes was previously discussed (page 26).

Physical Characteristics of the Redds

As with the two salmon species, notes were taken on the important physical characteristics of each spot selected for redd construction. Table 3 lists these characters for each of the redds that later proved to be productive (true redds).

TABLE 3

Physical Characteristics of the Productive Redds of the Steelhead Trout

Stream	Date	Water depth	Velocity (feet/ second)	Gravel size	Depth of eggs	Location
Prairie Creek	2/20/49	8"	2.0	2"	11"	End pool
Godwood Creek	2/21/49	10"	2.5	3"	10"	End pool
Prairie Creek	3/ 1/49	12"	2.5	5"	10"	Riffle
Prairie Creek	3/ 8/49	14"	2.5	4"	9"	End pool
Prairie Creek	3/10/49	8"	2.5	3"	7"	Riffle
Prairie Creek	3/10/49	12"	2.0	5"	9"	End pool
Prairie Creek	3/12/49	11"	2.0	3"	9"	End pool
Prairie Creek	3/30/49	13"	2.5	4"	11"	End pool
Prairie Creek	3/21/51	9"	1.5	2"	6"	End pool
Prairie Creek	3/27/51	9"	2.0	2"	6"	End pool
Prairie Creek	3/26/51	7"	2.0	2"	7"	Riffle
Prairie Creek	3/26/51	8"	2.0	3"	8"	End pool
Prairie Creek	3/26/51	--	--	--	6"	End pool
Averages		10.1"	2.2	3.2"	8.4"	

The data in the table are arranged in chronological order. The gravel size refers to the average diameter of the large rocks which formed the most conspicuous part of the redd structure. The "depth of eggs" indicates the vertical distance in inches, below the gravel surface, at which the eggs were found at the time of excavation. Finally, the "location" column indicates whether the redd was located in a riffle stretch or at the downstream end of a pool where the water was beginning to gather momentum. It may be noted that 10 out of the 13 redds were located at the ends of pools. This preference for an "end of pool" situation was also recognized by Needham (1938), who examined 20 redds in Waddell Creek and found that all were located at such places.

Breeding Activities

A good many of the fish arrived in the vicinity of the spawning area in a relatively immature state and remained in the deeper pools until they were ready to deposit their eggs. For example, in 1949 it was noticed that one of the new arrivals had a characteristic scar on its back. It was possible to keep track of this particular fish until it took part in the spawning activities. In this case, the time interval between arrival at the redd area and the actual spawning was exactly two weeks.

The selection of territory, redd construction, and breeding behavior followed the same general pattern that was observed in individuals of the two salmon species. Nevertheless, some distinct differences were observed. First, the time interval between digging actions was usually from about 30 seconds to one and one-half minutes, considerably more rapid and irregular than for the salmon. Second, the body of the female seemed to be bent at a more abrupt angle as the tail was placed against the substrate before the start of the lifting action, although during the lifting action itself the tail did not seem to be raised as far in a vertical direction as was the case with the salmon; consequently, the surface of the water was apt to be less distributed and a comparatively small amount of splashing resulted. Third, when viewed from above, the egg pits tended to be circular in shape instead of oblong, as was typical with the salmon, the horizontal dimensions being usually about three feet by three feet. A nest that looked to be complete was found to extend eight inches below the normal gravel surface.

The adult trout were quite wary, especially when the water was clear. They could be approached only with great caution, even when they were engrossed in breeding activities. In general, the periods of greatest activity on the redds were the early morning and evening. During the middle of the day many of the fish left the redd area and sought a hiding place in the vicinity, either in deeper water or under an overhanging bank.

The most accurate and detailed account of the breeding habits of any salmonid fish is that given by Needham and Taft (1934), based on observations of a pair of steelhead trout in Waddell Creek. This same description was repeated by Needham (1938) and was given in a somewhat modified form by Curtis (1949). It was also quoted by Schultz (1938).

Apparently the process of egg deposition is fully as efficient as was noted with the salmon females. Needham and Taft (*loc. cit.*) stated that not a single egg was seen to be swept out of the nest by the current.

Taft and Shapovalov (1945) related that scarcely any of the eggs are swept out of the nest, and that apparently both eggs and milt are held in the pit by current eddies below the stream bed level.

The redds in Prairie Creek were usually occupied by breeding fish from two or three days to as long as a week. Curtis (1949) stated that complete spawning may take from one to seven days. Needham and Taft (1934) recorded a female that completed its redd in slightly less than 24 hours, although in this case the fish had been held in a trap for some time before it was allowed to spawn.

Steelhead will spawn at comparatively low temperatures, according to Evermann and Goldsborough (1907), who found them on redds in Alaska between 38 degrees F. and 39 degrees F. In Prairie Creek the midday temperature varied from 46 degrees F. to 47 degrees F. during the spawning period in March, 1951.

No external indications of physical deterioration could be seen in either sex during the existence on the redd.

Postspawning Activities

When the spawning was completed most of the fish moved immediately downstream. Some of them were seen swimming rapidly with the current, rather than drifting backwards. Most of the few individuals that remained upstream eventually developed fungus patches, but no carcasses were found. Evidently, a large proportion of the spent fish were successful in reaching the ocean.

None of the females remained on the redd or attempted any defense of the territory after the eggs were all deposited. In addition, none of them were seen to continue the digging action into the postspawning period, as was the case with the salmon species. In fact, there was little or no construction of false redds, postspawning or trial, by the steelhead. It was possible to recover eggs from every one of the large redds that was constructed. A few spots were disturbed by the females during their search for a proper redd location, but all of these were quite small and ordinarily could be distinguished from true redds.

Of the three species so far discussed, this is the only one for which it might be possible to directly estimate the size of the spawning run by counting the numbers of the large redds. However, even in this case the estimate would be apt to be too high, since a few of the females apparently place their eggs in more than one redd.

Summary

The steelhead trout is native only to the American coast in the North Pacific, its range being quite restricted in comparison with that of the silver salmon and king salmon. The Prairie Creek individuals belong to a population which migrates upstream in the late fall or winter and usually spawns in the early spring. The spawning activities in this stream lasted mainly from March through April.

Members of this species that are permanent fresh-water residents are commonly called "rainbow trout," leaving the designation "steelhead" for the anadromous type. It is believed that these two types are representative of two homogeneous populations, and that a distinct barrier to gene flow between the two groups does exist.

In California most steelhead first spawn at the age of four years, after having spent two years in the stream and two years in salt water. The great majority of breeding fish range in age from three to six years.

Sexual dimorphism was not as noticeable as in either of the salmon species. The size of the sexes was quite uniform and there was no apparent difference in general body contour. In general, the dimorphism was confined to coloration and head structure. The use and value of the secondary sex characters was evidently the same as that listed for the silver salmon. Despite the fact that the Atlantic salmon and steelhead are known to be ordinarily very difficult to separate morphologically, the large breeding males are dissimilar in a number of characters.

The spatial (but not temporal) distribution of steelhead on the spawning grounds almost exactly duplicated that of the king salmon. The earliest arrivals tended to spawn farther upstream than did the later ones. The physical characteristics of the redds agreed fairly well with those listed for the king salmon and showed a marked contrast to those recorded for the silver salmon.

The digging actions of the female on the redd were usually conducted at a considerably more rapid and irregular pace than was observed for the salmon. Also, the egg pits tended to be circular in shape instead of oblong, as was typical with the salmons. During the middle of the day many of the fish left the redd area and sought hiding places in the vicinity. The redds in Prairie Creek were usually occupied from two to three days to as long as a week. No external indications of physical deterioration could be seen in either sex during the existence on the redd.

After the eggs were all deposited none of the females remained on the redd or attempted any defense of the territory. In addition, none of them was seen to continue the digging action into the postspawning period, as was the case with the salmon species. There was little or no construction of false redds, postspawning or trial, by the steelhead. It was possible to recover eggs from every one of the large redds that was constructed.

PART II

REPRODUCTION

REDD SAMPLING PROGRAM

Marking Procedure

Upper Prairie Creek and its tributaries were frequently inspected in order to locate pairs of spawning fish and to mark the places of egg deposition. This activity involved covering, at frequent intervals, about 20 miles of apparently suitable spawning area. It was always necessary to proceed with caution to avoid alarming the fish before they could be seen. In many places the undergrowth was almost impenetrable and progress could be made only by wading the stream channel itself. As a result, it took approximately five days to cover adequately this area once. Had more frequent inspections been possible, a somewhat greater number of redds could have been marked.

Both species of salmon were present in the watershed over most of the fall and early winter period. Consequently, it was considered necessary to witness the spawning activity to obtain a positive identification of the species involved before any redd was actually marked. This procedure also eliminated any chance of being misled by postspawning redds, which were usually similar in appearance to the true type.

The steelhead trout, however, was the only large salmonid found in upper Prairie Creek during the spring, so that its redds could not be mistaken for those of any other species. Also, this fish did not show any tendency to construct postspawning redds. Therefore, it was possible to mark a few of the steelhead redds immediately after the fish departed or during the middle part of the day when the redd was sometimes temporarily abandoned.

The marking was done with redwood stakes, about 18 by 3 by $\frac{1}{2}$ inches, which were usually painted white on the top and supplied with black numerals. These markers were driven into the bank well above the high water mark and as close to the redd as possible. Various measurements at each marker were then taken with a steel tape, so that the exact spot of redd construction could be relocated at a later date. Notes were also taken at this time on the various physical characteristics of each area, including water depth and velocity, size of the gravel, and general location. In addition, it was usually possible to obtain information on breeding habits, sex ratio, territorial behavior, and physical condition of the mature fish.

Equipment

The equipment used in this operation was simply a steel tape for accurate location of marked redds, a sharp-pointed shovel, and a net which was especially designed to collect samples of the eggs and larvae.

The basic design of the net was taken from that described by Hobbs (1937), but was somewhat modified so that it could be anchored in the stream bed without requiring the services of an extra person merely to hold it in place. The frame for this apparatus was shaped from a rectangular piece of iron bar, $\frac{1}{2}$ x $\frac{1}{4}$ inches and 10 feet long. This piece was bent and the ends welded to give a rectangular frame four feet wide and one foot high. Four metal loops were then welded on the front to accommodate two 18-inch iron rods which served to anchor the net in place in the stream bed. Four panels of tapered nylon netting, with a $\frac{1}{10}$-inch mesh, were then sewn together and attached to the frame. The finished net (Figure 3) proved to be quite practical for most of the places where it was used. The entire apparatus was comparatively

FIGURE 3. Net in position.

light and easy for a single person to handle. The netting was strong enough to withstand fairly swift water up to a depth of about 18 inches.

Sampling Technique

It was initially planned to sample all redds at both the eyed and larval stages of development. However, it was found that abnormally high flows would greatly interfere with the process of excavation. The net was too fragile to be used much of the time, and when the water was unusually turbid the eggs or lavae could not be seen. In most locations the water was low and clear enough to permit excavation work on the redds only a comparatively small amount of the time. Accordingly, it was impossible to obtain as many samples as originally desired.

The following general procedure was developed for the removal of the samples from the redds: The first step consisted of shoveling across the width of the redd at a depth of about two feet. Then the gravel was slowly turned over, both up and down the length of the

redd at this depth, until the eggs or larvae were contacted. The removal of the gravel from a lateral direction instead of from directly above seemed to cause less damage to the contents (Figure 4).

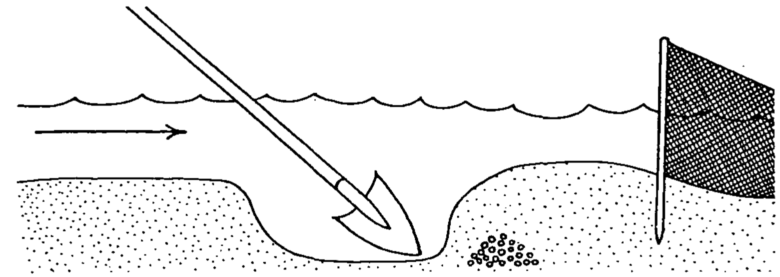

FIGURE 4. Method of removing gravel over eggs.

At the time the eggs or larvae were discovered, the net was set about five feet below the site of excavation. For purposes of separation, the material from the redd was thrown up into the current. Since the eggs (or larvae) were much lighter than the gravel, they were usually carried down into the net while almost all of the heavier contents fell short. When it appeared as though about one hundred eggs (or larvae) had floated into the net, it was removed and the specimens counted. The dead individuals were preserved, and the live ones were put back in the gravel and covered.

Sampling Results

The results are summarized in Table 4 for silver salmon, Table 5 for king salmon, and Table 6 for steelhead trout.

All of the samples were taken either at the eyed stage, usually from 30 to 40 days after deposition, or at the larval stage, usually between 50 and 75 days after deposition.

One additional productive redd for each of the salmon species was found. The king salmon redd was located in Lost Man Creek in an area where bulldozer operations had extensively altered the stream bed. It was believed that the results of the sample from this redd should not be listed because of this alteration of the natural structure of the spawning ground. The data from the additional silver salmon redd were not included because the sample was taken at the sensitive pre-eyed stage. The redd could not be resampled because a large loss was evidently created when the area was first disturbed.

In order to find a sound average redd mortality figure for each species based on these tables, some additional factors were taken into consideration. First of all, there was the possibility that some decomposition of the dead eggs might have taken place before the sampling date. Some of the eggs that were recovered at the larval stage were quite soft and there was little doubt that a small percentage had disintegrated to the extent that they were no longer recoverable.

The following experiment was set up to obtain an idea of the rate of decomposition of dead eggs in Prairie Creek: Three large, round, tin cans about 12 inches deep and six inches in diameter were selected. About 200 holes, one-eighth inch in diameter, were punched through

TABLE 4

Sampling Results for Silver Salmon Redds

Redd No.	Location	Deposition date	Sample No.	Approximate days after deposition	Live eggs	Dead eggs	Live larvae	Dead larvae	Percent mortality (uncorrected)
2	Godwood Creek	12/15/48	1	34	192	15	--	--	7.2
3	Godwood Creek	11/25/48	2	55	119	17	2	--	12.5
4	Elk Prairie Creek	12/25/48	3	29	129	18	--	--	12.2
5	Prairie Creek	11/18/48	4	67	237	22	69	4	7.8
6	Godwood Creek	10/24/48	5	93	--	5	748	12	2.2
3	Godwood Creek	11/25/48	* 6	82	--	15	361	25	10.0
5	Prairie Creek	11/18/48	* 7	100	--	15	480	12	5.3
2	Godwood Creek	12/15/48	* 8	106	--	1	25	--	3.8
7	Elk Prairie Creek	2/ 6/49	9	65	--	32	31	--	50.8
4	Elk Prairie Creek	12/25/48	*10	106	--	14	126	1	9.2
8	Godwood Creek	2/ 7/49	11	65	--	1	91	--	1.1
9	Prairie Creek	10/22/50	12	61	--	9	91	--	9.0
16	Prairie Creek	11/28/50	13	29	161	6	--	--	3.9
17	Prairie Creek	11/28/50	14	60	--	1	29	--	3.3
16	Prairie Creek	11/28/50	*15	61	--	29	72	--	28.7
29	Godwood Creek	1/13/51	16	27	40	1	--	--	2.4
26	Godwood Creek	1/ 6/51	17	38	88	2	--	--	2.2
27	Godwood Creek	1/ 6/51	18	38	233	15	--	--	6.0
28	Brown Creek	1/ 8/51	19	37	58	27	--	--	31.8
22	Elk Prairie Creek	12/10/50	20	65	--	1	179	--	0.5
27	Godwood Creek	1/ 6/51	*21	71	--	230	--	--	100.0
26	Godwood Creek	1/ 6/51	*22	71	--	99	59	--	62.6

* Indicates a sample from a redd that had been sampled once before.

TABLE 5

Sampling Results for King Salmon Redds

Redd No.	Location	Deposition date	Sample No.	Approximate days after deposition	Live eggs	Dead eggs	Live larvae	Dead larvae	Percent mortality (uncorrected)
1	Prairie Creek	11/22/48	1	53	117	11	--	--	8.6
3	Prairie Creek	11/17/50	2	32	88	6	--	--	6.4
2	Prairie Creek	11/14/50	3	37	35	10	--	--	22.2
6	Prairie Creek	11/17/50	4	34	21	0	--	--	0.0
8	Prairie Creek	11/22/50	5	31	96	8	--	--	7.7
10	Prairie Creek	11/23/50	6	31	219	75	--	--	25.5
4	Prairie Creek	11.20/50	7	39	149	2	--	--	1.3
4	Prairie Creek	11/20/50	* 8	67	--	8	92	--	8.0
3	Prairie Creek	11/17/50	* 9	70	--	16	87	4	18.7
10	Prairie Creek	11/23/50	*10	65	--	2	31	--	6.1

* Indicates a sample from a redd that had been sampled once before.

TABLE 6

Sampling Results for Steelhead Trout Redds

Redd No.	Location	Deposition date	Sample No.	Approximate days after deposition	Live eggs	Dead eggs	Live larvae	Dead larvae	Percent mortality (uncorrected)
1	Godwood Creek	2/21/49	1	51	--	12	187	--	6.0
3	Prairie Creek	3/ 8/49	2	35	506	14	--	--	2.7
4	Prairie Creek	3/ 1/49	3	44	50	15	160	--	6.7
5	Prairie Creek	3/10/49	4	34	50	51	3	--	49.0
6	Prairie Creek	3/10/49	5	35	233	22	--	--	8.6
7	Prairie Creek	2/10/49	6	66	--	8	51	--	13.6
8	Prairie Creek	3/12/49	7	35	137	39	--	--	22.2
3	Prairie Creek	3/ 8/49	* 8	63	--	1	108	--	0.9
2	Prairie Creek	3/30/49	9	41	--	5	93	--	5.1
33	Prairie Creek	3/26/51	10	29	--	60	177	--	25.3
34	Prairie Creek	3/26/51	11	29	--	1	95	--	1.0
31	Prairie Creek	3/21/51	12	36	--	64	--	--	100.0
35	Prairie Creek	3/26/51	13	31	--	45	11	--	80.4
32	Prairie Creek	3/27/51	14	63	--	104	3	--	97.2

* Indicates a sample from a redd that had been sampled once before.

the bottoms of these containers. Each was then filled half full of redd gravel and supplied with 100 dead silver salmon eggs. After being filled to the top with gravel, each can was then buried in a location which closely simulated that of most of the natural redds. The containers were placed in a vertical position with the tops lying about two inches below the stream bed surface and under about four inches of flowing water. No lids were used on these cans and presumably the perforated bottoms allowed a fair amount of water to percolate past the eggs.

The first of the containers was excavated after 30 days. A total of 99 sound eggs was counted. None of them appeared excessively soft and all of the shells were intact. In the work on the natural redds most of the eyed stage samples were taken close to 30 days after the deposition date, at which time the dead eggs were almost always in excellent condition. On the basis of evidence from the entire sampling program and the relatively insignificant 1 percent decomposition of dead eggs in the experiment, it was decided that any adjustments of the results from eyed stage samples to account for decomposition losses were unnecessary.

After 60 days the second can was unearthed and a total of 91 eggs was counted, indicating a 9 percent loss. This time many of the eggs were quite soft, but most of the shells were still intact. The contents of the third can were examined after 90 days. Eighty-seven eggs were recognizable as individuals, but all were very soft and extensively decomposed. Only a few remained with unbroken shells. Hobbs (1937) placed freshly killed king salmon eggs in perforated canisters and buried them in a New Zealand stream. He discovered that all eggs of one lot were still intact after being buried 55 days. It is difficult to account for the disagreement between this information and that from Prairie Creek, where a 9 percent loss was recorded after 60 days. The eggs of the two salmon species are almost identical in appearance and structure, and the water temperature was virtually the same in both localities. It is possible that the variation was due to the difference between eggs of the two species or to the effects of different bacteria and/or fungi on the rate of decomposition.

Since most of the larval stage samples were taken from 50 to 75 days past the deposition date (an average of 65 days), it seemed proper to assume that roughly 9 percent of the dead eggs would have disintegrated to the extent that they could no longer be counted. Therefore, in order to include all loss from this source, it was considered necessary to increase all larval stage mortality figures by this amount before proceeding to calculate the average redd loss for each species. It is assumed that both the dead king salmon and dead steelhead eggs decompose at about the same 9 percent rate that was determined for the silver salmon eggs. No evidence appeared during the course of this study to invalidate this assumption. An exception was made in some cases in which extremely large losses of eyed eggs occurred in worm-infected redds; presumably none of these dead eyed eggs would have had time to decompose before the sampling was accomplished.

These larval stage samples were mostly taken a comparatively short time after hatching had occurred. This made it necessary to consider the problem of adding another correction to account for a possible loss of larval fish between the hatching and the emergence periods. In connection with this problem, the results of observations conducted with the experimental burial of eyed eggs are of interest. Immediately after the young fish emerged from a plant of 2,907 king salmon eggs, the gravel of the redd area was carefully searched but no dead larvae were found. The same result was realized from a plant of 1,580 silver salmon ova, and only a single dead larva resulted from 1,416 eyed steelhead eggs. In addition, dead larvae were either absent or occurred in very small numbers when natural larval stage redds were excavated (only six out of 26 such samples produced dead larvae and in none of them was the number significantly large). It can probably be assumed that if there had been a noticeable mortality during the early part of the larval stage it would have been detected in some of the samples, and if such a mortality had taken place in the latter portion of this stage, more evidence probably would have been found in the gravel after the emergence had occurred. Thus, there is good evidence to show that such losses are quite rare and would not materially affect the eyed stage (or corrected larval stage) mortality figures.

The dependence upon such samples for a total redd loss figure might be criticized because of the possibility of some of the eggs or larvae having been carried out of the redds as the result of erosion due to flooding. The Prairie Creek study was conducted with this possibility in mind. All marked redds were repeatedly observed with special attention to the effects of high water upon the general gravel contour. Usually, the stream width did not extend over 10 or 12 feet in the redd vicinity and the water was always comparatively shallow. Therefore, there is no reasonable doubt that if the gravel was eroded to a depth where egg loss would result it would have been easily noticed. In some places, especially where the eggs were deposited in an unusually wide stream bed, lengths of metal pipe were driven close to the redd to serve as reference points, so that the extent of gravel displacement could be measured. In no case during the development of the eggs or larvae did this displacement measure more than two inches (vertically). It is certainly possible that in larger streams a considerable amount of erosion may take place before the change of contour becomes apparent to the casual observer. In these cases it would be appropriate to locate the surface accurately, either by means of surveying equipment or through the use of a reference point on a pipe driven near each redd.

In considering the above evidence it is probable that eyed stage samples, taken just before hatching time, give a very close approximation of the loss which can be expected to take place during the productive existence of the redd. Also larval stage samples, taken shortly after the hatching period, seem to give a good measure of total redd mortality if corrected by 9 percent.

The data from the tables listing the sampling results for each of the three species can now be analyzed. Since several of the redds were sampled twice, it should be noted that in these instances the larval stage was the one utilized to obtain the total mortality figure. This was considered the best procedure, since in some localities large losses were accompanied by infestations of an unidentified oligochaete worm during the interval between the two samples (see following section). It should be mentioned that if such worms are found in an eyed sample it is

essential that the redd be resampled after hatching, so that the full mortality may be recorded. In the case of the silver salmon a total of 22 samples was taken from 15 true redds, and larval stage data were available for 13 of the localities. The average corrected mortality was 25.7 percent. With the king salmon 10 samples were taken from seven true redds, and larval stage data were used for three localities. The average

TABLE 7

Average Redd Mortalities

Species	Samples	Number of redds	Average mortality (corrected)
Silver salmon	22	15	25.7%
King salmon	10	7	14.0%
Steelhead trout	14	13	35.1%

corrected mortality, in this case, was 14.0 percent. With the steelhead 14 samples were taken from 13 true redds, and larval stage data were used for nine of the localities. The average corrected mortality, calculated for this species, was 35.1 percent. This information is summarized in Table 7.

Effects of Oligochaete Worms

In the latter part of each season, usually from February to May, some of the redds become infested to depths sometimes exceeding one foot with various numbers of a single species of oligochaete worm. This worm was the only representative of the stream bottom fauna ever found to penetrate the substrate more than superficially (one or two inches). Moreover, it soon became apparent that abnormally high redd losses were recorded when the worms were present. It was found that most of the dead eggs, in these cases, had undergone normal development to the eyed stage. In fact, large numbers of dead eyed eggs were found only in these infested redds.

It has not been possible to have this worm identified, since it apparently represents an unknown species. It will be named and classified whenever sexually mature specimens can be found. In the meantime, for the benefit of fishery workers the following brief description (plus Figure 5) is presented: average length about 100 mm. and average width about 1.5 mm.; body composed of about 433 segments; first segment enlarged into a prominent proboscis; mouth opening appears to be at third segment; setae in the form of strong chitinous hooks, two rows on the ventral side of the body and two more dorsally; the ventral hooks are the largest and extend the full length of the body, the dorsal rows terminate at about one third of the distance from the anterior end. The color is an iridescent pink and the body wall is somewhat translucent. No clitellum was apparent, although it may appear on sexually mature individuals.

In general, the amount of mortality discovered in any particular redd tended to show a positive correlation with the degree of infestation. In some cases, over 400 individual worms were removed from one egg pit

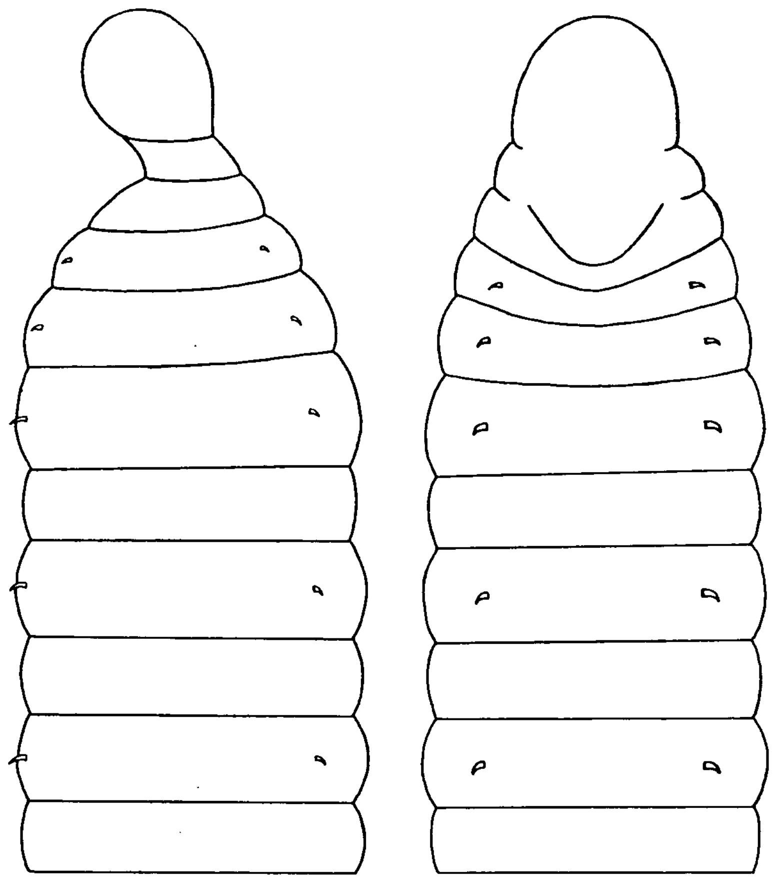

FIGURE 5. Lateral (left) and ventral (right) views of anterior end

during the collection of a single sample. When only five individuals or less were taken while obtaining a sample the mortality was not abnormally high and the redd was regarded as "noninfested."

An indication of the effect of the worm on natural redds can be presented by a comparison of the mortalities in infested redds with those from noninfested redds. In reference to Table 4 (page 42), giving the sampling results for the silver salmon, four of the samples (numbers 15, 19, 21, and 22) were taken from infested redds. The average mortality for these redds alone was 55.8 percent, compared to a 14.8 percent loss for the 11 which were not infested. In the case of the steelhead trout redds a similar effect can be demonstrated. Seven of the samples (numbers 4, 6, 7, 10, 12, 13, and 14) represented infested redds which had an average mortality of 55.4 percent. In comparison, the six clean redds gave an average mortality of only 13.7 percent.

Almost all of the instances of contamination were discovered during the spring from February to May. The tendency of the worm population to increase at this time of the year is in general accord with the seasonal population increase of most of the other bottom fauna forms. None of the king salmon redds was found to be infested. The spawning of this species was evidently completed early enough in the season, so that effective concentrations of the worm were avoided. Apparently for the same reason, those silver salmon nests which were constructed during the first portion of the run also remained unaffected. However, the steelhead run occurred at about the time of year that the bottom fauna (probably including the worm in question) achieves a noticeable population peak. It is presumed that this is the reason that seven out of the 13 productive steelhead redds showed this oligochaete infection.

When the average mortality in the noninfested redds of each of the three species is compared (king salmon, 14.0 percent; silver salmon, 14.8 percent, and steelhead, 13.7 percent) the percentage of loss is remarkably uniform. This evidence strongly suggests that almost all of the interspecific variation previously shown in the redd mortality of these fishes (page 47) was due solely to the effects of this particular worm. The evidence so far accumulated indicates that the silver salmon and the steelhead trout suffer about equally when the redds are contaminated (the average mortality of infested redds of the former being 55.8 percent, compared to 55.4 percent for the latter).

When more than one sample was removed from some of the redds it was noted that numbers of worms in a given location can sometimes increase with great rapidity. For example, in silver salmon redd No. 27, only a few individuals were found when the area was first excavated on February 14th, but on March 17th, only 30 days later, a very heavy infestation, which resulted in a 100 percent mortality, was discovered. This rapid increase in numbers, which was not accompanied by an appearance of large quantities of young individuals, suggests that this species is able to migrate through the gravel with some facility and perhaps is able to detect the eggs for a considerable distance. It is noteworthy that heavy concentrations of the worms appeared only where there were eggs; very few worms were ever found in false redds or other stream bed areas.

In view of this information it was decided to set up a controlled experiment, whereby something more could be learned about the effect of this annelid species upon the developing eggs. Therefore, in the spring of 1951, a trough at the Prairie Creek Fish Hatchery was made available for the following work: Two small canisters about four inches high and three inches in diameter were selected. Numerous small holes, each about one millimeter in diameter, were punched in both the bottoms and lids. Some fine gravel from a nearby stream bed was used to fill each can one-third full. Twenty-five healthy, eyed, king salmon eggs from the Prairie Creek Hatchery supply were added to each container. In addition, 10 of the live oligochaete worms were placed on top of the eggs in one of the cans. After this, more gravel was added so that the containers were each filled two-thirds full. Then the same procedure was repeated, 25 more eggs being alloted to each canister and 10 more worms placed in the same one which previously received these animals. Both cans, each containing 50 eggs, were then completely filled with gravel and placed on their sides in the hatchery trough, which was supplied with running water. Thirty days later these cans were opened and the contents inspected. All of the eggs in the container supplied with worms were dead. In the other can, seven hatched larvae and three-eyed eggs survived. Even though a detrimental effect by the worm was demonstrated, the eggs in both containers were evidently not supplied with a sufficient flow of water. Upon examination of the holes in the bottoms and tops of the cans it was discovered that a large number of them had become rusted shut during the period of immersion.

Therefore, the experiment was repeated. This time the holes were slightly enlarged (to about 1.5 mm.) and were kept open during the progress of the problem. The experiment followed the same procedure as was described above, except that the eggs used were from steelhead trout instead of king salmon, and the time interval was reduced to nine days. When the cans were opened on this occasion the one without the worms contained only four dead eggs while the one with worms showed 49 dead eggs. A third trial with steelhead eggs resulted in 49 dead eggs in the worm-laden receptacle, while only 17 dead individuals were found in the control can.

It was not possible to determine conclusively the method whereby the developing embryos were killed. There was no evidence that the living eggs were directly attacked mechanically. The worms evidently did not consume any of the yolk material until the tough, outer chorion had become naturally ruptured during the slow process of decomposition. The lethal agent may well be found in the copious quantity of mucus which is exuded continuously by this oligochaete. When large numbers of worms were dug out of the stream bed, the gravel was found to be well permeated by the mucus. Also, when a few individuals were placed in a glass of water the surrounding fluid soon became quite viscous. The effect upon the eggs could be due to the presence of an actual poison, but, more likely, the mucus either prevented an adequate oxygen supply from reaching the ova or had a detrimental effect on the osmotic balance.

The results of both the hatchery experiments and the work on natural redds indicate that such worms can have rapid and sometimes catastrophic effects upon developing salmonid eggs. In the case of the steelhead especially, it is quite possible, in Prairie Creek, that this annelid may constitute an important limiting factor on the population.

Sampling Results From Other Areas

As was mentioned in the introduction, the only thorough work on the pre-emergence portion of the life cycle of salmonid fishes was done by Hobbs (1937, 1940) in New Zealand. However, it was evidently Chamberlain (1907) who supplied the first published data from the sampling of naturally constructed redds. He examined 58 red salmon (*Oncorhynchus nerka*) nests in a tributary to Karluk Lake, Kodiak Island, Alaska, and found that two-thirds of the eggs were "in good condition." He also noted that those eggs buried deepest developed with the least loss.

It seems that no further work was done along this line until White (1930) sampled a single redd of the brook trout, *Salvelinus fontinalis* (Mitchell), in a stream on Prince Edward Island, in the Gulf of St. Lawrence, Canada. He removed eggs from the nest and let them develop in a hatchery trough, where 79 percent hatched successfully. This procedure may be criticized, of course, because the loss might have been increased by the removal and handling of the eggs. Hazzard (1932) took occasion to excavate 21 redds of the same species near Ithaca, New York. The eggs were examined at the eyed stage and 79.8 percent were found to be alive. This particular study was undertaken to determine the percentage of fertilization under natural conditions. Samples at this stage may or may not indicate the nonfertilization loss, but do give an idea of the mortality which takes place up to the eyed stage for this particular species and locality.

Foerster (1938) held red salmon in prepared cages while they spawned and stated the result of such reproduction as follows: "From several general tests, it would appear that under natural conditions the successful deposition, fertilization, and development of eggs would approximate 70 percent." While this figure is of interest, it is certainly possible that examination of redds where the fish were allowed to choose their own spawning location would give considerably different results.

In 1942, White told of removing eggs from a new Atlantic salmon redd and obtaining a 78 percent hatch in a trough. Apparently, the most recent work was done by Hunter (1948), who found that 10 redd samples indicated only a 13.73 percent survival for chum salmon, *Oncorhynchus keta* (Walbaum), and 3.18 percent for pink salmon, *Oncorhynchus gorbuscha* (Walbaum). The results of this work on the British Columbia coast, indicating extreme losses, offer a distinct contrast to all other such investigations. It hardly seems possible that the redd mortality in these two forms could normally be so great, especially since other species of closely related fishes, with apparently almost identical spawning habits, all show a survival that is very high in comparison.

In 1948, Hobbs summarized the results of his entire redd sampling program, which had been carried on over several years. His total collection consisted of samples from 711 redds (mostly of brown trout, although some of rainbow trout and king salmon were included). Of the 503,139 specimens collected, 92.4 percent were living. Hobbs (*loc. cit.*) also calculated that not over 1 percent average additional loss could have occurred before the time of emergence. Therefore, the figure of 8.6 percent can be safely accepted as the average total redd mortality figure for his New Zealand investigations.

In recent years there has been a tendency among fishery biologists to apply the findings of Hobbs (*loc. cit.*) to reproduction of salmonid fishes in North America with little or no qualification. Experience with the introduction of other vertebrate animals from North America to New Zealand and elsewhere has shown, in some cases, that the normal efficiency of natural reproduction was greatly increased. There is no reason to believe that this same phenomenon could not be applicable to some of the fishes as well. In fact, such a condition might well have been expected from the evidence afforded by the outstanding success of some of the introductions.

The results of the sampling program in Prairie Creek, together with the small amount of previous work done in North America, offer a decided contrast to Hobbs' figures and indicate, so far, that a great many less young fish are added to the salmonid populations via natural reproduction in their native range than is the case in New Zealand.

The Degree of Natural Fertilization

Some work has been done on the extent of fertilization accomplished under natural conditions, but it is here considered separately because sometimes the nonfertilization loss may have but little influence upon the percentage of total redd mortality. Hobbs (1937) was apparently the first to employ the sampling technique on redds within a short time after construction in order to record the efficiency of this process. In five New Zealand king salmon redds he found an average fertilization of 98.24 percent. In 1940, the same author investigated 48 trout (brown and rainbow) redds which showed a 98.99 percent fertilization.

In the same year two other papers which dealt with the same subject appeared. Cameron (1940) found a 98.2 percent fertilization based on an average of five samples of pink salmon eggs and a 98.6 percent average from 10 red salmon nests. Cramer (1940) dug up four coastal cutthroat nests and discovered the fertilization varied from 93.0 to 98.6 percent.

During the work on Prairie Creek in 1950-51, a method (based on the suggestion of Mr. Stephen Smedley), whereby the nonfertile ova could be separated from the remainder of the dead specimens, was utilized. The technique consisted of immersing all the dead eggs in a saturated NaCl solution for about two hours at room temperature. In eggs in which the chorion was still intact the coagulation of the yolk became entirely reversed, so that the transparency was equal to that of live individuals. In the case of partially decomposed ova the technique was effective, but the clearing was not quite as complete. By careful examination through a binocular dissecting microscope it was possible to identify the embryos down to a very small size. It is believed that this method provided a basis for separating the infertile specimens with a fair degree of accuracy.

The dead eggs from six king salmon, eight silver salmon, and three steelhead trout redds were examined, using the above described technique. The percentage of fertilization recorded, including both live and dead eggs, was 92.4, 93.4, and 96.2 percent, respectively; the average from the redds of all three species was 94.0 percent.

In the light of these recent investigations the statements of some of the earlier authorities may accordingly be discounted. For example: Downing (1900) gave the opinion that not one egg in a thousand was fertilized naturally, and Townsend and Smith (1902) were also confident that only a small percentage of the eggs were ever fertilized. Gray (1920) wrote that a comparatively low percentage of the eggs in a redd appeared to be fertilized and quoted a figure of 8 to 10 percent, which he had received from an unidentified authority. Apparently the estimates of none of these authors were based on samples from natural redds.

LOSS IN ARTIFICIAL PROPAGATION

In spite of the fact that hatcheries for salmonid fishes have been operating on the Pacific Coast of the United States for over 80 years, there has been *no successful attempt* to maintain records which satisfactorily show just how efficiently such installations can carry out their functions. Virtually all of these fish cultural stations attempt to note mortalities which occur once the eggs have been collected and placed in the hatching baskets, and some keep count of the number of females from which the eggs were taken. However, this is usually the limit of the recorded information.

If the efficiency of the artificial propagation method is to be compared among various hatcheries or with natural reproduction, then some additional, and highly important, factors must be considered. Before eggs are taken for hatchery use the adult fish must usually be held in specially constructed ponds or behind a weir across a stream until the individuals become mature enough so that their sex products are easily obtained. During this period, when the large fish are forcibly prevented from completing their spawning migration, a significant mortality can be expected. This is usually the result of physical injuries sustained in constant attempts to escape confinement. In addition, in many localities a large, unrecorded loss of eggs occurs when females attempt to spawn on the bottom of the holding ponds or below the obstructing weirs. In these cases the chance for development is slight, since such places are usually totally unfit for the continued survival of the eggs.

During the process of manual spawning further losses are to be noted in the case of the Pacific salmons. Regardless of the experience of the egg-taking crew, once in a while a "green" female, in which the eggs are too immature for use, is killed. Also, the work of excision and removal is generally done in a hurry and some of the eggs are almost always left adhering to the connective tissue of the ovary or else under part of the viscera. The steelhead trout female is not cut open; consequently, the process of egg removal may be incomplete, with a comparatively large number of ova left in the abdominal cavity.

There is no doubt that under ordinary conditions the loss of eggs from the above causes will greatly exceed that which takes place through the egg and fry stage in the hatchery trough. The assignment of even tentative values to these initial categories of loss is by far the greatest problem in attempting a diagnosis of the efficiency of the artificial hatching procedure.

Letters of inquiry were sent to both state and federal agencies concerned with fish hatchery operation in California, Oregon, and Washington. The individuals contacted were usually very cooperative but they generally did not have much information available regarding losses before the eggs reached the hatchery. Therefore, the small amount of data which could be gathered was utilized with recognition of the fact that the conclusions may be somewhat modified when more detailed studies of artificial propagation can be made.

Silver Salmon

In accordance with the plan to list mortality causes in chronological order, the first type considered is that occurring as the result of confinement in holding ponds or by weirs across streams. The Oregon Fish Commission supplied data from two hatcheries which indicated an average loss of 6.9 percent. The Washington Department of Fisheries gave information on two silver salmon runs at Minter Creek which demonstrated a similar loss of 14.2 percent. On the other hand, the mortality in the very small, crowded holding area on the Mad River, California, ran about 50 percent (personal observations during a single run).

For the sake of selecting a single figure to represent the mortality realized during the retaining period, it was decided to take the average of the data from the three sources listed above. Therefore, pending the receipt of further information for this species, the amount of 23.7 percent will be utilized to represent mortality during this stage of operation.

It should be emphasized that the extent of this "holding" mortality evidently varies widely with both the length of the retaining period and the size of the holding ponds (if ponds are used). The length of the retaining period, in turn, seems to be well correlated with the topographic location of the egg taking station. When such stations are located well upstream (in the vicinity of the natural spawning grounds) it is necessary to hold the adult fish but a short time, compared to the more or less lengthy process required farther downstream.

There is no information at all available regarding the numbers of eggs lost (through natural spawning attempts) when females are retained. At this time, therefore, no figure can be added for this category, although it should be borne in mind that large losses can occur in this manner, especially behind weirs.

The communication from the State of Washington indicates that about 2.5 to 3.7 percent of the females will be found immature (and their eggs not usable) after having been killed. A 3.0 to 5.0 percent loss is evidently common in Oregon, while a mortality of about 5.0 percent was observed on the Mad River, California. On the basis of these figures it seems fair, at this time, to allot an average loss of about 4.0 percent to this cause.

The number of eggs lost during the spawn-taking process is usually small, but nevertheless important. The results of investigations conducted with one large run at Minter Creek, Washington, gave an average mortality of 3.8 percent. At Mad River, California, this type of loss represented about 2.0 percent of the total egg content of each fish. Information on losses from these two sources indicates an average loss of 2.9 percent for this category.

Finally, the hatchery loss (up to the time of the yolk sac absorption) remains to be considered. The average from data supplied by seven Oregon hatcheries was 13.3 percent. Washington gave a figure of about 25.0 percent, based on an average from two years operation at Minter Creek. A mortality of about 15.0 percent was realized at the Prairie Creek Hatchery in California. The mean from all three places is 17.8 percent.

The crude average survival, for the portion of the life cycle under consideration, was computed as follows: 100—23.7=76.3; 4.0 percent of 76.3=3.0; 76.3—3.0=73.3; 2.9 percent of 73.3=2.1; 73.3—2.1=71.2; 17.8 percent of 71.2=12.7; 71.2—12.7=58.5 percent.

King Salmon

The large U. S. Fish and Wildlife Service installations at Leavenworth, Entiat, and Winthrop (in the State of Washington) reported an average holding pond loss of about 50 percent. Casual observations on the Mad River, California, revealed about a 15 percent mortality, while data from two runs at the Coleman Station (U. S. F. W. S.), California, averaged 18.2 percent. Eight Oregon Fish Commission hatcheries reported an average loss of 13.9 percent, and Mattson (1948) told of a 15 percent estimated mortality below weirs in the Willamette Valley in Oregon. The average for all these sources is 22.6 percent.

As was the case with the silver salmon, there was no information available on the number of eggs lost (through natural spawning attempts) by females being retained.

Information from Oregon reveals that about 3.0 to 5.0 percent of the females killed are still too immature to have usable ova. On the other hand, the Coleman Station listed only a 0.1 percent loss from this cause, while about 5.0 percent seemed to be normal for the Mad River, California, operation. On the basis of these data, a figure of 3.0 percent represents the average.

Observations at Mad River showed that about 2.0 percent of the eggs were lost during the manual spawning operation. The Oregon Fish Commission, the only other agency to give an estimation in this category, indicated a 0.5 to a 10.0 percent mortality, depending upon how fast the work was done. A tentative average in this case is 3.6 percent.

Finally, information on the hatchery loss (up to the time of the yolk sac absorption) was available as follows: The Leavenworth, Washington, hatchery records showed a 6.0 to 9.0 percent loss for this species, while an 8.6 percent average was calculated from data supplied by nine Oregon hatcheries. In California, the Coleman station gave 6.6 percent as an average loss for the past five years, and the Prairie Creek Hatchery loss was about 10.0 percent. Hobbs (1948) listed a mortality of 17.6 percent for the New Zealand hatcheries. The average figure from all of these localities is 10.1 percent.

The crude average survival, for the portion of the life cycle under consideration, was computed as follows: 100—22.6=77.4; 3.0 percent of 77.4=2.3; 77.4—2.3=75.1; 3.6 percent of 75.1=2.7; 75.1—2.7=72.4; 10.1 percent of 72.4=7.3; 72.4—7.3=65.1 percent.

Steelhead Trout

Information available from the Washington Department of Game gave data from the holding of summer run fish which showed an average loss of about 50.0 percent. However, it must be emphasized that these fish were retained for comparatively long periods of time (eight months in some cases). Approximately this same amount of loss was observed at Mad River, where the spring-run fish were held but a short time. In this case the holding areas were extremely small and crowded. The Oregon State Game Commission sent data from one large hatchery which showed an average loss of only 4.14 percent for this category. In the absence of further information, the above three figures were used to compute the mean loss. The result is a mortality figure of 34.7 percent.

As was the case with the two salmon species, there was no information available on the number of eggs lost (through natural spawning attempts) by females being retained.

As was mentioned previously, a significant portion of the eggs are usually left in the female trout after the egg-taking process because the spawn is removed from the live fish by pressure instead of through the killing and incision method used for the salmon species. Taft and Shapovalov (1945) selected 12 manually spawned fish at random and found that about 10 percent of the total egg complement was left in each female. Hobbs (1948) remarked: ". . . there is no evidence that trout attempt to spawn these residual eggs." Therefore, this 10.0 percent must be recorded as a loss until such a time that it can be shown otherwise.

Fortunately, there were more data available on hatchery mortality with this species than were found for the salmon. Taft and Shapovalov (*loc. cit.*) observed that the hatchery loss in this species was between 10 and 20 percent. Fish (1940), in his paper giving an evaluation of trout culture, listed information on steelhead which resulted from analyses of the progress of over 6,000,000 eggs in 12 lots in six western hatcheries. The average egg loss was 18.2 percent, and the fry loss was an additional 1.94 percent. An average from several Washington state hatcheries gave an 18.2 percent mortality, and information from one Oregon state hatchery indicated that the usual loss was about 17.70 percent. The average from the figures taken from the above sources is 18.7 percent.

The crude average survival, for the portion of the life cycle under consideration, was computed as follows: 100—34.7=65.3; 10.0 percent of 65.3=6.5; 65.3—6.5=58.8; 18.7 percent of 58.8=11.0; 58.8—11.0= 47.8 percent.

ASPECTS OF LOSSES IN NATURAL PROPAGATION

The average redd mortality in Prairie Creek during the two seasons has been calculated by means of redd samples for three native salmonid species. In addition to redd mortalities, there are other factors which might possibly cause a reduction in the potential number of young fish. Many of the early writers were convinced that large numbers of the adults died before reaching the spawning area, due to injuries received on the journey. This belief has generally been refuted wherever spawning ground studies have been made, for, in these cases, the new arrivals almost always have been found in good condition, with no injuries to suggest that the migration had been especially hazardous. Therefore, there is no reason to believe that the procedure of trapping adults at some distance below their spawning grounds will provide substantially more females for artificial propagation than would survive to spawn naturally. A few streams in Alaska, in areas where there are large bear or seal populations, may prove to be exceptions. The effects of fishing mortality are not included.

A second factor which merits consideration is the possibility that some eggs might be retained by the female after completion of the spawning process. Chamberlain (1907) examined 636 spent red salmon females and found 80.0 percent with no eggs remaining and 20.0 percent with an average of 97 eggs. Hobbs (1937) discovered that 22 spent king salmon contained an average of only eight eggs and the same author (1948) found that 14 brown trout averaged only seven eggs for each fish. During the Prairie Creek study, 16 king salmon averaged less than seven retained eggs and eight silver salmon yielded an average of slightly less than four eggs. In Prairie Creek, and probably most other areas as well, the number of eggs eliminated in this manner is so small that no adjustment in the calculation of the natural spawning mortality need be made.

Undoubtedly a few eggs are lost during the spawning process, but this mortality (previously discussed on page 20) also seems normally to be so small (at least in smaller streams) that it can have no significant effect upon the number of young eventually produced. The only remaining conceivable causes of pre-emergence loss are the possible disruption of true redds by superimposition or through flood-caused erosion. Insofar as Prairie Creek is concerned, neither of these causes was found to be of great importance. The spawning grounds were not utilized to the extent that the first redds were dug up by later arrivals, and it has been shown (page 46) that, in the two seasons of this study, no flood damage was evident.

Since no significant losses can be ascribed to the above causes in Prairie Creek, it may be assumed that the average redd mortality figure for each species (as previously determined) also can be used to represent the average natural mortality for the entire portion of the life cycle up to the emergence stage.

COMPARISON OF NATURAL AND ARTIFICIAL PROPAGATION

The silver salmon of Prairie Creek, during the two seasons of the study, proved capable of producing emergent fry from about 74.3 percent of the eggs that were carried upstream by the female. In comparison, the small amount of available information crudely indicates that about 58.5 percent of such eggs are reared to the same stage by hatchery methods now employed on the Pacific Coast. The king salmon of Prairie Creek over the same period showed the ability to produce emergent fry from 86.0 percent of the eggs so transported by the female, while only an approximate 65.1 percent survival was calculated for the artificial propagation of this species. Finally, the steelhead trout, of the study area, evidently produced 64.9 percent free-swimming fry from all the

TABLE 8

Natural and Artificial Propagation

Species	Percent of emergent fry produced from naturally spawned eggs in Prairie Creek	Percent of emergent fry produced by artificial methods
Silver salmon	74.3	58.5
King salmon	86.0	65.1
Steelhead trout	64.9	47.8

eggs of the mature females. In comparison, such evidence as was available indicated that only 47.8 percent of these eggs survived under artificial conditions. The above information is summarized in Table 8.

SUMMARY OF PART II

The natural redds of three salmonid species, silver salmon, king salmon, and steelhead trout, were sampled at the eyed and/or larval stage of development. Samples from 15 silver salmon nests indicated a redd mortality of 25.7 percent, data from seven king salmon redds gave a mortality figure of 14.0 percent, and information from 13 steelhead nests showed a 35.1 percent loss.

Some of the silver salmon and steelhead redds were found to be infested with an unidentified species of oligochaete worm. This annelid had a pronounced detrimental effect upon the developing eggs. In the four silver salmon redds so affected the average mortality was 55.8 percent compared to a 14.8 percent average loss for the remaining 11. Seven steelhead redds were infested with an average mortality of 55.4 percent compared to an average loss of only 13.7 percent in the six clean redds. It was concluded that almost all of the variation previously shown in the average redd mortality among the three species was caused by the actions of this animal. The results of controlled experiments on the effect of the worm on the king salmon and steelhead eggs tended to demonstrate further the lethal nature of this type of infestation.

The only thorough redd sampling program in the past was carried on by Hobbs (1937, 1940) in New Zealand. The results of the Prairie Creek study, together with the small amount of previous work done in North America, offer a decided contrast to Hobbs' figures and it appears that fewer young fish are added to the salmonid populations via natural reproduction in their native North American range than in New Zealand.

The degree of natural fertilization, calculated from samples from eight silver salmon, six king salmon, and three steelhead trout redds, showed that 93.4, 92.4, and 96.2 percent, respectively, of these ova had been fertilized. The average from all 17 redds was 94.0 percent.

It was possible to obtain some indications of the efficiency of artificial propagation through information supplied by state and federal agencies engaged in fish cultural operations in the three Pacific coast states and in New Zealand. For the portion of the life cycle up to the free-swimming fry stage, the survival of individuals was computed, beginning with the eggs which were brought upstream by the mature females. Utilizing the small amount of information available, a crude percentage survival was calculated as follows: Silver salmon, 58.5; king salmon, 65.1, and steelhead trout, 47.8 percent. These percentages may be compared to the survival data for the same three species under natural conditions in Prairie Creek: Silver salmon, 74.3; king salmon, 86.0, and steelhead trout, 64.9 percent. Therefore, there is no doubt that, during the period of study, substantially more young fish were introduced as fry into Prairie Creek via natural propagation than could be supplied through standard hatchery methods utilizing the entire run in the creek.

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