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DEPARTMENT OF FISH AND GAME

FISH BULLETIN No. 98

The Life Histories of the
Steelhead Rainbow Trout
(*Salmo gairdneri gairdneri*)

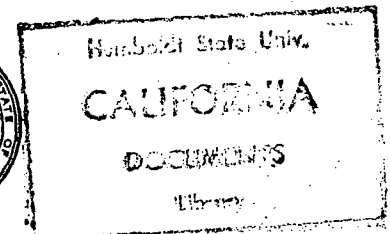
and

Silver Salmon
(*Oncorhynchus kisutch*)

With

Special Reference to Waddell Creek, California, and
Recommendations Regarding Their Management

By LEO SHAPOVALOV and ALAN C. TAFT



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FOREWORD

The California Department of Fish and Game has received a continuing stream of requests from administrators, legislators, biologists, and sportsmen for basic, quantitative information on the life histories of the steelhead and silver salmon. This bulletin has been prepared in response to these requests.

As additional information about the steelhead and silver salmon is gathered the concepts regarding their management will be broadened and in some instances changed to meet new situations. However, the fundamental facts about the life histories of these fishes will remain unchanged and from this viewpoint this bulletin will have lasting value.

LEO SHAPOVALOV and ALAN C. TAFT

May, 1954

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May, 1954

The Life Histories of the Steelhead Rainbow Trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*)

With

Special Reference to Waddell Creek, California, and
Recommendations Regarding Their Management

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and
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INTRODUCTION

The Steelhead Rainbow Trout, *Salmo gairdneri gairdneri* Richardson, and Silver Salmon, *Oncorhynchus kisutch* (Walbaum), are two of the most important fishes found along the Pacific Coast of North America. A considerable amount of published material regarding their biology, distribution, systematic status, propagation, and management already exists. However, up to the present time, and especially to the start of the experiments described in the present paper, there has been a notable lack of quantitative data regarding both species, particularly with regard to their life histories.

Because of this lack of quantitative data, so necessary for sound regulatory, stocking, and other management programs, the California Trout Investigations, a cooperative unit of the California Division of Fish and Game (now the California Department of Fish and Game) and the U. S. Bureau of Fisheries (now a part of the U. S. Fish and Wildlife Service) in 1932 initiated a program of study at Waddell Creek, a typical coastal stream in Santa Cruz County, California. Upon the termination of the formal cooperative agreement in 1937, these studies were conducted independently by the California Division of Fish and Game.

The plan of the experiment was to study the steelhead and the silver salmon in their natural habitat. Since both fishes are anadromous, the logical approach was to construct a dam or weir at which both the upstream and downstream migrants could be counted. In the process of counting, observations could be made on the migrants (measurements, scale samples, sexual maturity, parasites, etc.), fluctuations of popula-

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tions determined from the counts, and the counts complemented by observations made on the fishes in the stream (spawning activities, feeding habits, etc.).

Waddell Creek was chosen for the following reasons: It was a stream under as nearly natural conditions as could be found in California at the present time and was still reasonably accessible; it was large enough to possess a full biota and small enough to be dammed at reasonable cost and to permit complete counts of at least all upstream migrants, and thus avoid errors that might result from sampling; it was so situated that it could be kept under observational and legal control as a unit, with the general public excluded.

Waddell Creek in its general characteristics is typical of the great majority of California coastal streams of like size. Moreover, in miniature it is almost a replica of the larger stream systems, such as the Klamath and the Eel. This fact is of great importance in that the habits and ecology of the trout and salmon in the small streams and the large



FIGURE 1. Steelhead and salmon streams of the California coast.

ones are similar. Consequently, the conclusions regarding the proper management of these fishes derived from the present study are applicable, at least in the broader aspects, to the coastal streams in general.

Obviously, certain limitations are imposed by a program that consists of studying the natural fluctuations of a population in a limited area. Large-scale sampling involving the killing of specimens cannot be carried on without danger of disturbing the natural balance. Thus, it is not possible to make various measurements such as egg counts and pyloric caeca counts, stomach analyses, etc. The very great advantage of Waddell Creek in this respect was that its drainage basin is adjacent to that of Scott Creek, a stream of comparable size, with comparable environmental conditions and a similar fauna, in which the lacking data could be gathered. Scott Creek had the advantage of being the location of a State egg collecting station and a State hatchery (the latter situated on a tributary, Big Creek) and of being set aside as a State Fish Refuge. Consequently, it was possible not only to gather data on egg production and to secure measurements but also, through marking of the naturally-spawned fish in Waddell Creek and the artificially-spawned and hatchery-reared fish in Scott Creek, to carry out a comparative study of two adjacent streams, one under natural conditions and the other under artificial management, and to study the amount of "homing" and "straying" between the two streams.

As will be discussed further in this paper, certain conditions already existed or were created by the experiment which altered natural conditions to varying degrees, especially in the direction of making difficult a true evaluation of population fluctuations under natural conditions, but the essential quantitative picture of the life histories of the species concerned has remained a correct one.

DESCRIPTION OF THE EXPERIMENTAL PLAN

The basic physical portion of the Waddell Creek experiments consisted of a dam and a two-way trap for counting upstream and downstream migrants (Figure 2). This trap was designed by Taft, who has presented accounts of its operation in two papers (1934, 1936). A detailed description and illustrations of the physical plan are contained in the latter publication. This detailed description will not be repeated in the present paper, but a general explanation of the nature and operation of the dam and trap is in order.

The dam and trap were constructed during the summer of 1933, approximately 7,250 to 9,250 feet above the mouth of the stream (the distance depending upon the varying location of the mouth) and 3,300 feet above the uppermost limit of tidewater. The location of the dam (elevation about 25 feet) was the point farthest downstream at which it was believed that a dam could be constructed without danger of flood-water washing around it.

The dam acted as a barrier which the fish could not pass on their migration upstream. As a result they sought the "fish ladder" which led into a tank, where they were trapped. Downstream migrants were brought into another compartment of the same tank by way of a short flume leading from the stream above the dam. They were separated from the upstream fish and were prevented from passing downstream by a double set of screens, the finest of which was of quarter-inch mesh.

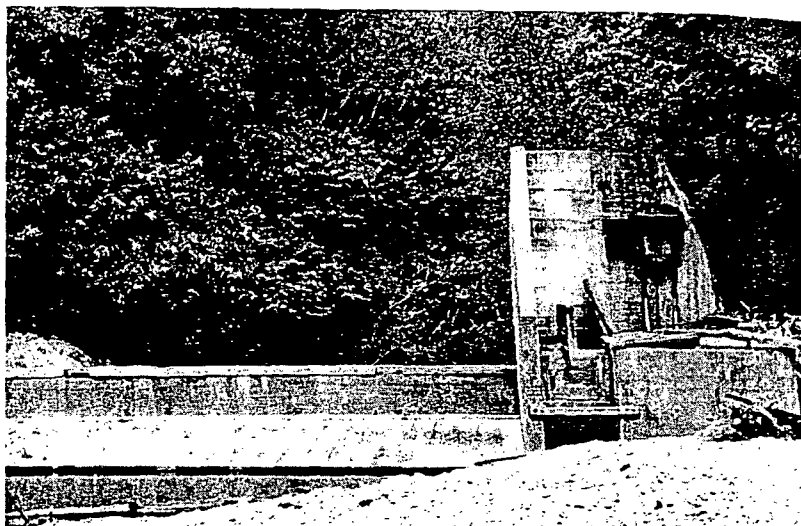


FIGURE 2. Waddell Creek dam and trap at low water, showing apron to prevent upstream fish from jumping over dam. *California Department of Fish and Game photograph.*

All of the adult fish coming to the dam were taken in the trap and were counted and scale samples taken for purposes of life history determination. The number of adults of each life history category in each season² was thus determined. This was the first and most important step in determining the population fluctuations from season to season. (During extreme flood water in some seasons a certain number jumped upstream over the dam and in each season some fish spawned below the dam. The numbers of such fish and their effects on the experiment will be discussed further in this paper.)

The second and more difficult step was the determination of the number of juvenile fish of each age moving from the stream to the ocean in each season. It was possible to strain only a small portion of the water passing downstream during high water (Figure 3) and it therefore follows that only a portion of the total number of fish migrating could be trapped. However, the calculation of the percentage of fish taken in the trap was possible through the marking of the migrants caught in the trap. Alternate pectoral fins and the adipose were removed in each season during the seasons 1933-1934 to 1937-1938, inclusive, so that the fish migrating downstream in each season could be recognized when they returned as adults. The total number of migrants

² At Waddell Creek, the yearly period chosen for the purpose of the studies was that included from October 1st of a given year to September 30th of the following year. To avoid confusion with calendar years, such a period is called a "season." Thus, the season of 1937-1938 comprised the period from October 1, 1937, to September 30, 1938, inclusive. This season also coincides with the U. S. Geological Survey water year. The rainy season in California, which, together with its direct effect (water flows, etc.), under natural conditions is the dominating factor in the life history of the Pacific salmon and the steelhead, normally lasts from November into April, and so also falls within the season chosen. Thus, at Waddell Creek and in neighboring streams the spawning seasons, hatching seasons, periods of emergence from gravel, and principal upstream and downstream migrations of both juveniles and adults of the steelhead and silver salmon are completed within the period from October 1st of one year through September 30th of the next.

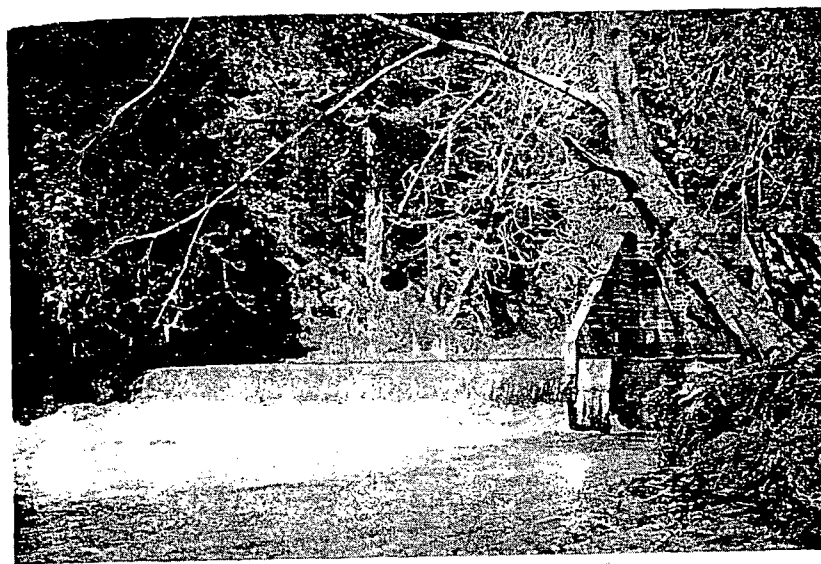


FIGURE 3. Waddell Creek dam and trap at high water; apron submerged. *Photograph by Leo Shapovalov.*

in any one year was then calculated in accordance with the proportion of marked to unmarked fish of the same life history. During the seasons 1938-1939 to 1941-1942 the downstream migrants taken in the traps were not marked, but were counted and measured.

DESCRIPTION OF WADDELL CREEK

Waddell Creek is located in central California, approximately two-thirds of the way from San Francisco to Monterey Bay. It enters the Pacific Ocean approximately 17 air-line miles and 20 miles by coast northwest of the northern end of Monterey Bay and three air-line miles southwest of Año Nuevo Point, on the coast of Santa Cruz County, at lat. 37° 6' N., long. 122° 17' W. The location of the stream and its relation to nearby features of interest in connection with the present study are shown in Figure 4.

The area is near the southern border of the humid coast belt. The headwaters of most of the streams in this belt are subject to a great deal of precipitation during the winter months. The headwaters portion of Waddell Creek has a mean annual rainfall of between 55 and 60 inches. The lower portion of the watershed receives much less rainfall, averaging in the neighborhood of 30 inches near the coast. More than one-half of the rain falls during December, January, and February.

Because of the distinct wet and dry seasons, there are tremendous fluctuations in the flow of most of the coastal streams. The extent of these fluctuations in Waddell Creek may be gathered from Table 1, which shows the peak floods and low points in each year during the period 1934-1942.

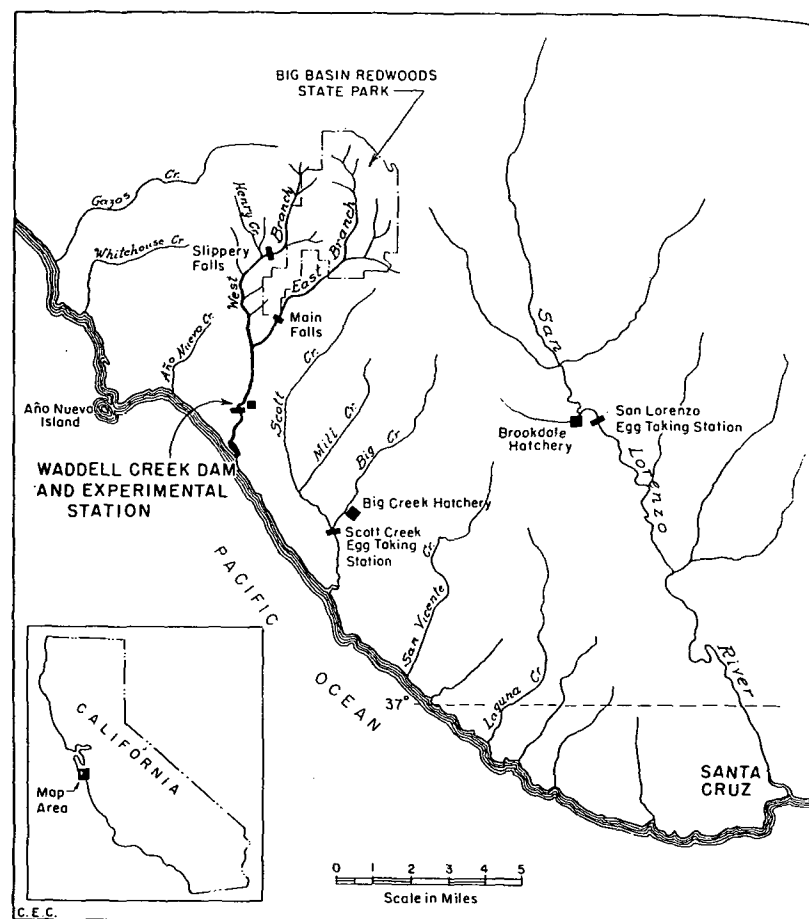


FIGURE 4. Waddell Creek and nearby streams.

During a portion of the year, which may be spring or summer or both, dense fogs roll in from the ocean and blanket the lower portion of the stream. These cool the water and even temporarily increase the flow to a slight extent.

Like nearly all California coastal streams, small or large, Waddell Creek terminates in a drowned mouth or lagoon, which is subject to tidal action during those portions of the year when it is not closed by a sand bar. The mouths of only a few of the larger California streams (Klamath River, Eel River, Noyo River) regularly stay open throughout the summer months. Depending upon stream flows, tides, and wind and wave action, from approximately April to July or August sand bars intermittently open and close the mouths even of such streams as the Russian River and the San Lorenzo River. During July or August

the bars usually form to remain until they are broken (October-November) by the first heavy rains of the wet season. Following this there may again be a period of intermittent closings, until the bars finally break out (usually December) to remain open until the following spring or summer. Table 2 shows the openings and closings of the mouth of

TABLE 1
Waddell Creek: Yearly Maximum and Minimum Flows *

Year	Maximum flow		Minimum flow	
	Date	Second-feet	Date	Second-feet
1934	February 26	278	September 8	0.7
1935	April 3	625	September 19	2
1936	February 22	1,390	October 3	1
1937	March 21	1,390	November 7	3
1938	January 31	1,540	September 27	2
1939	March 9	114	September 28	4
1940	March 30	6,460	November 15, 16, 22	5
1941	February 9	2,065	October 15	4
1942	January 24	1,800		

* Measurements made at the dam.

Waddell Creek. The mouth of Scott Creek has usually opened and closed on the same dates.

The lagoons of the different California streams are not all of a size proportionate to the size of the stream. Some streams have characteristically "large" lagoons, while others have "small" lagoons. In a given stream, too, the size and shape is not constant from year to year, especially in those cases in which man-made construction (bridges, jetties, etc.) has affected the lower end of the stream or caused abnormal fluctuations of flow. The mouth of Waddell Creek has shifted over a distance of 2,500 feet during the course of these experiments and the depth of the lagoon has varied from only a few inches of running water to over eight feet. The area of the lagoon has also varied widely. In 1933 it was subject to tidal action for about one mile from the ocean.

TABLE 2
Waddell Creek: Openings and Closings of Mouth

Year	First closing date	Permanent closing date	First opening date	Permanent opening date
1933			October 31	December 28
1934	April 21	May 11	November 18	December 13
1935	May 30	July 19	October 11	December 29
1936	June 19	July 3	November 19	December 26
1937	August 24	August 24	October 26	December 8
1938	October 25	October 25	October 27	October 27
1939	June 29	July 9	November 24	December 7
1940	July 26	August 14	September 13	December 16
1941	July 24	September 14	October 9	December 9
1942	September 25			



FIGURE 5. Lower Waddell Creek in late summer, showing the dry (right). Photograph by Leo Shapovalov, August 31, 1939.

Waddell Creek has its source in the Redwood belt of the Santa Cruz Mountains, at an altitude of 1,500 to 2,300 feet, in the form of half a dozen or so small tributary streams located in the California Redwood State Park (Big Basin). These small tributaries unite to form two larger streams, the East Branch and the West Branch, which in turn join to form the main branch of Waddell Creek. The length from mouth to source is approximately 12 miles. The hydrographic basin of Waddell Creek has an area of 26 square miles.

The distance from the uppermost limit of tidewater to the junction of the East Branch with the West Branch (called "The Forks") is 14,500 feet. The distance from The Forks (elevation about 90 feet) to Slippery Falls (elevation about 185 feet) on the West Branch, usually the uppermost limit to which upstream migrants can ascend on the West Branch, is 14,000 feet. The distance from The Forks to the Main Falls on the East Branch (elevation about 210 feet), the uppermost limit to which upstream migrants can ascend the East Branch, is almost exactly one mile.

The current of Waddell Creek is rapid to moderate throughout its course. The small headwater tributaries of Waddell Creek first meander over sandy bottoms or tumble through ravines among the virgin redwoods of Big Basin. As they become larger and unite to form the East and West branches, they cascade and fall over boulders and bedrock and cut through steep-walled, fern-covered gorges. Especially the East Branch has many deep pools (up to 15 feet), which are separated by short stretches of stream flowing over large rubble and boulders and bedrock and culminating in falls up to five feet in vertical drop. These upper reaches of stream flow through the Transition Life Zone, characterized here by a forest of Redwood (*Sequoia sempervirens*) and Douglas Fir (*Pseudotsuga taxifolia*).³

³ The major plant associations of the region have been discussed by Orr (1942).



The lower portion of the West Branch (from Henry Creek to The Forks) and the main stream (below The Forks) are broader and contain fewer deep pools. Here there are abundant gravel and small rubble beds, interspersed with stretches of sandy bottom or coarse rubble. The stream banks are lined by Red Alder (*Alnus rubra*), Big-leaf Maple (*Acer macrophyllum*), Buckeye (*Aesculus californica*), Madrono (*Arbutus menziesii*), California Laurel (*Umbellularia californica*), and, in the lowermost portion, by willows (*Salix* spp.). Also encountered occasionally are Tan Oak (*Lithocarpus densiflora*), Box Elder (*Acer negundo*), White Alder (*Alnus rhombifolia*), Black Cottonwood (*Populus trichocarpa*), California Nutmeg (*Torreya californica*), Redwood, and Douglas Fir.

The redwoods extend to within about a mile of the coast at this point and the lowermost portion of the stream flows through the Upper Sonoran Life Zone. Here several patches of cultivated grassland and crop fields are scattered through a valley, which is about 2,000 feet wide at its broadest point and extends inland about 6,000 feet. The hill-slopes are populated mostly by chaparral, pines, and Douglas fir. The predominant sandstone formation is covered with a loose, whitish, diatomaceous shale.

Immediately above the lagoon the stream flows through a small area of marshland. The lagoon is bordered by shifting sand dunes.

Some changes from the primitive condition of the area have taken place as a result of human usage. The redwood forest of the watershed below Big Basin was logged off by 1870 and is now covered by a second growth. The early lumbering operations have resulted in the creation of several semipermanent log jams and temporary accumulations of logs, which have hastened erosion of the stream banks, with consequent increase in silting during flood stage.

OUTLINE OF THE LIFE HISTORIES OF THE SILVER SALMON AND STEELHEAD RAINBOW TROUT

In order that those not fully acquainted with the silver salmon and steelhead might have a better understanding of the purposes and character of the experiments, a brief outline of the life histories of these species is here presented.

Both the silver salmon and the steelhead are members of the family Salmonidae, which includes such groups as the trouts, salmon, char, and whitefishes.

Generally, the salmonids are inhabitants of cool, clear waters in the temperate and boreal regions of the world. A good, readily understandable description of the distribution and relationships of the salmonids, particularly the trouts, and the species present in California is given by Snyder (1940).

In appearance, the steelhead and the silver salmon, although belonging to different genera, are very similar. The outstanding difference between the two and also the genera that they represent is not a morphological, but a biological one. The several species of the genus *Oncorhynchus*, commonly called the Pacific salmon, all die after spawning once, whereas the numerous species of the genus *Salmo*, which includes not only all of the true trouts but also the Atlantic Salmon (*Salmo salar*), are biologically capable of spawning more than once.

Under the proper environmental conditions both the steelhead and silver salmon are anadromous, i.e., they spend a portion of their lives, during which they put on the greater part of their growth and attain sexual maturity, in the ocean and then ascend streams for spawning purposes. The eggs are deposited in pits, known as redds or nests, dug in the gravel of the stream bottom by the female fish. Immediately after deposition and simultaneous fertilization by the male fish, the eggs are covered with gravel by the females. After a certain period in the gravel, the length of which depends upon temperature, oxygen, and other factors, as well as the species involved, the young fish hatch from the gravel and gradually work their way to the surface of the stream bed. After emergence from the gravel, the young fish spend a certain time in the stream, which is usually a year or longer but depends primarily upon the species and secondly upon various environmental factors, and then descend to the ocean. In the case of the silver salmon, some of the males mature and return to spawn after one summer in the ocean, while the females and the remaining males return to spawn after two summers in the ocean. In the case of the steelhead, some of both males and females mature and return to spawn after one summer in the ocean, and practically all of the remaining fish return after the second summer. It must be pointed out that a certain proportion, in some cases perhaps a considerable proportion, of the steelhead may remain in the stream, attain sexual maturity, and spawn without descending to the ocean. Silver salmon do not spawn until they have spent some time in the ocean.⁴

⁴A few males may attain precocious sexual maturity prior to their entry into the ocean, but such fish do not participate in the spawning.

From the foregoing account it is seen that the life histories of the steelhead and silver salmon are in general quite similar, except in that all of the silver salmon die after spawning once and do not spawn without a period in the ocean. This brief account of the life histories of the two fishes will suffice for the present, but more detailed descriptions of the various life history phases will be presented further on in this paper, along with references to the published literature. It should be kept in mind that there are certain exceptions to most of the above general statements.

The general distribution of the steelhead is in the coastal streams of the Pacific Coast of North America, from the United States-Mexico boundary or possibly even Baja California northward to and including Alaska. The general distribution of the silver salmon is from some of the streams entering Monterey Bay, California, to the Amur River in Asia. Again, it must be kept in mind that certain exceptions occur. A discussion of the geographic distribution of the Pacific salmon is given by Davidson and Hutchinson (1938).

To a varying but in each case marked extent, both the steelhead and silver salmon exhibit a "homing instinct," i.e., the young fish which descend from fresh water to the ocean return to their "parent stream" for spawning purposes (young fish artificially hatched and liberated return to the stream in which they were liberated, not to the stream to which their parents returned or in which they were hatched). Some of the experiments on which these conclusions are based are described by Taft and Shapovalov (1938), and the whole subject of a homing instinct in trout and salmon is reviewed and discussed by Shapovalov (1941b).

In California, the steelhead (as well as all other trout) are barred to commercial fishermen, but are taken in very large numbers by sports anglers, both as adult and as immature fish, at sea and in fresh or brackish water. The silver salmon is of both commercial and game importance, being taken in the mature form by commercial fishermen at sea, and by sports anglers both as adult and as immature fish at sea and in fresh or brackish water.

A biological and economic comparison of the two species is given in Table 3.

TERMINOLOGY

In order that further portions of this paper may be better understood, the writers believe that it is well at this point to define the terminology that will be used.

Common and Scientific Names

First the use of common names should be clarified. In this paper, the common name Silver Salmon will apply to the species *Oncorhynchus kisutch*. One popular misconception that has existed along various parts of the Pacific Coast is that the hook-nosed salmon, called "dog salmon" by local residents, form a distinct species. Such fish are simply males whose snouts have become hooked and elongated during the spawning season. This phenomenon takes place to a greater or less extent in all of the species of Pacific salmon and to some extent in the steelhead. A

TABLE 3

Steelhead and Silver Salmon: Biological and Economic Comparison

	Steelhead	Silver salmon
Die after first spawning?	No	Yes
Sometimes spawn without some time spent in the ocean?	Yes	No
Females dig spawning nests in gravel?	Yes	Yes
Some males return to spawn after one summer in ocean?	Yes	Yes
Some females return to spawn after one summer in ocean?	Yes	No
Remaining males and females return to spawn after two summers in ocean?	Yes*	Yes*
Spawning range	U. S.-Mexico boundary to and including Alaska	Monterey Bay to Amur River, Siberia
Exhibit homing instinct?	Yes	Yes
Caught commercially in California?	No	Yes
Caught as game fish in California?	Yes	Yes

* A few fish, probably less than 1 percent in most streams, may return to spawn after three summers in ocean.

distinct species of salmon, the Chum Salmon (*Oncorhynchus keta*), is sometimes also known as dog salmon, but it occurs comparatively infrequently in California. Common names applied to the silver salmon are jack salmon (applied especially to young males), dog salmon or hookbill (applied to males with hooked snouts and red sides), coho, and silversides.

In this paper, the common name Steelhead Rainbow Trout will apply to the subspecies *Salmo gairdneri gairdneri*, irrespective of the habitat, size, or sexual condition of the individuals concerned, but for the sake of brevity the unofficial common name "steelhead" will be used. When individuals of this subspecies remain in a stream throughout their lifetime they grow at a much slower rate than those individuals which have entered the ocean, and take on the typical bright coloration of "stream trout" or "rainbow trout."

Some writers fully recognize that the small coastal trout and the adult spawning fish form a single species or subspecies, but prefer to use the term "steelhead" not as the common name of a distinct species or subspecies but as a term designating any species of trout that has been in salt water. According to this system of nomenclature, there are both "rainbow steelhead" and "cutthroat steelhead." In the east there would then be "eastern brook steelhead." This terminology has certain merits, but its chief fault is that it has not "stuck" in the popular usage of the vast army of anglers.

There has also been some difference of opinion as to which scientific name should be applied to the steelhead, *Salmo gairdneri* or *Salmo irideus*. This is a technical point, depending upon the date and validity of the original descriptions which first used these names. Inasmuch as the great majority of scientists up and down the Pacific Coast now use the name *Salmo gairdneri* and because the writers have satisfied themselves that the description of the fish which accompanied the first use of this name could apply only to the form herein called steelhead, this name will be used in this paper. A discussion of the scientific name that should be applied to this species is given by Shapovalov (1941a).

Among common names that are applied to the steelhead are the following: rainbow (applied to individuals that color up and/or mature

in fresh water), half-pounder (applied to small sea-run individuals or large, silvery individuals that have remained in fresh or brackish water, weighing usually from one pound to two and one-half pounds; term used particularly on the Eel River system of California), summer salmon (applied to green spring-run fish, especially in the Middle Fork of Eel River), and sea-run rainbow.

Terms Applied to Various Life History Stages

The following list is one of terms applied in this paper to various stages in the life histories of the steelhead and silver salmon.

Juvenile. Fish which is sexually immature.

Adult. Fish which has matured sexually in one or more summers of sea life. This term includes grilse.

Grilse. Fish which has matured sexually in only one summer of sea life.

Resident fish. Fish which is an offspring of parents that spawned without having been to sea and which itself has not been to sea.

Sea-run fish. Fish which has entered a stream to spawn after one or more summers of sea life.⁵

Stream fish. Fish which has not been to sea, irrespective of its parentage or sexual maturity.

Ripening fish. Fish whose sexual products are developing preparatory to spawning.

Spent fish. Fish which has not yet recovered from the effects of spawning.

Fall-run fish. Fish which enters a stream at any time from the late summer through the following spring and will spawn sometime during that same period.⁶

Spring-run fish. Fish which enters a stream in the spring or early summer, but which will not spawn until the following fall, winter, or spring.

Maiden fish. Fish, whether male or female, which has not spawned.

Ripe fish. Fish which is ready for spawning.

Most of the terms in the above list are in general use, but some often have been used dissimilarly in different publications or have not been sharply defined. The term "grilse" has sometimes been used to designate not only those fish which have matured after only one summer of sea life, but also those which have matured prior to the modal year of maturity for the species. Sometimes the term "mature fish" has been used as a synonym for what in this publication is called "sea-run fish." Pautzke and Meigs (1940) apply the term "immature" to steelhead prior to their initial entrance into salt water and "mature" to

⁵ In the Eel River and in some other streams, especially the larger ones, some steelhead apparently return to fresh water after a brief sojourn (less than one summer) at sea without having attained sexual maturity. Some of the "half-pounders" fall in this category. Such fish are not "sea-run fish" within the meaning of the definition used herein.

⁶ The term "winter-run" is sometimes applied, especially in the case of the steelhead, to fish entering fresh water during the winter months, but fundamentally such fish are part of the "fall-run," in that they will not "summer over" before spawning. In the past, the terms "fall-run" and "spring-run" have been applied mainly to the King Salmon (*Oncorhynchus tshawytscha*), but they have application to other species as well.

fish which are returning from salt water to fresh water for the purpose of spawning. Since steelhead often become sexually mature without entering salt water, the writers believe that the terms used in the present paper are more applicable. The term "trout" has not infrequently been applied, especially in the parlance of the angler, to those steelhead which in the present paper are defined as "stream fish" and the term "steelhead" to what are here called "adult." Such usage has been based on misconception.

Terminology of "Scale Reading"

As has long been known, the determination of the life histories of salmonids is possible from a microscopic examination of the scales. The developed scale shows ridges which appear as concentric rings, and are termed *circuli*. In general, the scales start to register the growth of the fish immediately after their formation, the *circuli* being more widely spaced during rapid growth and more narrowly spaced during slow growth. A prolonged cessation, brief interruption, or disturbance of growth is reflected by notably closer spacing and usually by irregularities and anastomosis of the *circuli*. In the present paper any such closely spaced and irregular group of *circuli* will be termed a *check*. One that forms between annual growing seasons will be termed an *annulus* or *year check*, while one that forms as a result of some disturbance during the course of the growing season will be termed a *false annulus* or *false check*. Over the range of salmonids as a whole the *annulus* forms during the winter, but in Waddell Creek and other California coastal waters with mild winters and dry summers such growth cessation or slowing-down often takes place in the autumn or even in the late summer, as will be discussed more fully further in this paper. *Freshwater growth* will be used to denote that part of the scale which had formed during residence in fresh water, and *sea growth* or *saltwater growth* to designate the part formed at sea. *Intermediate growth* will indicate the portion of the scale formed during the season of migration to the sea, prior to entry into salt water. *New growth* will be used to designate that part of the scale which had formed during the growing season in which the scale was collected. Spawning is reflected in the scale by a more or less marked *erosion* or *absorption* of the edge of scale. Since spawning usually takes place at the time of formation of the *annulus*, this erosion usually replaces or obliterates the *annulus* that has just formed or is forming. Since the silver salmon spawns but once, the spawning erosion is found only at the edge of a scale. In the case of the steelhead, however, spawning is normally followed by a growing period, so that in following years the erosion of the spawning season is reflected in the scale as a jagged scar or line typically cutting across a number of *circuli*. Such a formation is known as a *spawning mark*. *Regenerated scales* are those which have replaced lost scales. In regenerated scales the portion represented by the lost scale is "blank," i.e., without *circuli*, and so such scales are generally of little use in scale reading.

Designation and Recording of Age

Standard methods of (1) designating and (2) recording the age of fishes, and even of salmonids as a group, have never been adopted and are very difficult to compose. Some of the difficulties encountered in attempting to designate age are posed by the following questions: Should the *beginning of life* be computed from the time of fertilization of eggs or time of hatching of eggs? Should the *end of a year of life* be computed as the end of a calendar year, the anniversary of the date of fertilization or hatching, or the end of a growing period?

In the case of human beings, the exact date of birth of an individual is ordinarily known, and so it is an easy matter to mark age by birthday anniversaries. This method of age designation for human beings is satisfactory because it is accurate and because we are often interested in human beings as individuals. In the case of fish under natural conditions, however, it is impossible in practice to determine from scale reading the exact time of either fertilization or hatching. Furthermore, from the viewpoint of fisheries management and especially in the case of salmonids, the thing that we are interested in and around which the biological work centers is not individuals as such but *brood years*, and individuals only as units of the *year classes* that result from the brood years.

In the present paper the year in which the fish *hatched* is considered as the *brood year* of a fish and the *end of a growing period* as the *end of a year of life*.

The year in which a fish *hatched* rather than the one in which the egg was fertilized is chosen as the brood year for the following reasons.

(1) Although in some waters the calendar year in which the fish *hatched* and in which the egg was fertilized are the same, in many others the beginning of a calendar year comes in the middle of the spawning season for various salmonids, while the hatch from a given spawning run always or practically always takes place within a calendar year. (2) The time of hatching places the beginning of life in salmonids on a comparable basis with the beginning of life for human beings, while the time of fertilization would not for purposes of age designation. The time of hatching also makes this system of age designation more readily applicable to viviparous fishes, while the time of fertilization would not. (3) The time of hatching marks the beginning of growth of the fish in its approximate final form. (4) The time of hatching in all fishes is ordinarily followed by a growing period within the same calendar year, while the time of fertilization often is not.

Salmonids spawn only once a year and, although in some cases they have a prolonged spawning season, a definite growing period normally intervenes between the spawning seasons. Thus, it is logical to use growing periods as indexes of years of life and the end of a growing period to mark the end of a "year" of life. From scale examination it is usually impossible to mark exactly the *beginning* of the formation of the *annulus* for the reason that this is not a clearly marked point but appears as a *gradual* narrowing of the *circuli*. (This is particularly true of waters in which there is no season of markedly low temperatures.) On the other hand, the *end* of the formation of the *annulus*, which is also the *beginning of new growth*, is nearly always quite

clearly marked. In this paper, then, the end of the annulus and the beginning of new growth have been chosen as the point marking the completion of one year of life and the beginning of another. In the case of fish that spawn at the end of a growing season an annulus often is not formed, so the beginning of new growth following the spawning mark is used as the point marking the completion of that year of life.⁷

The computation of the end of a year of life on the basis of anniversary of date of fertilization or hatching would both be unsatisfactory, if only from the point of view that these dates cannot be determined in scale reading. The basis of the end of a calendar year would also be unsatisfactory, for the reason that the fish of a given age group would change their age with the end of that year without any biological basis. Confusion in recording age would be apt to result in the case of a species whose spawning season extended from one calendar year into the next, as in the case of both steelhead and silver salmon at Waddell Creek.

The procedure herein outlined places the age of the fish on a biological basis and thus makes possible the comparison of the age and growth of the same species from different waters, even when the spawning and hatching times are quite different for such waters.

In accordance with the system outlined above, a fish is in its first year of life from the time that it hatches until the beginning of formation of new growth following completion of the first annulus. The age group of such a fish is recorded by the sign "+." (Some writers, e.g., Hile (1941) record fish which have not yet formed their first annulus as members of the "O" group.) From the time that new growth begins following completion of formation of the first annulus until completion of the second annulus or formation of a spawning mark and the beginning of new growth, the fish is in its second year and its age is recorded by the numeral "1," and so on. In other words, the numerals used to show the age of the fish also show the number of annuli and spawning marks. If the annulus is thought of as the birthday anniversary of the fish, this system places the age on the same basis as that for human beings and becomes understandable to the layman as well as the biologist.

The procedure outlined in the preceding paragraph is adequate when the discussion is concerned only with *total age*. It is sometimes also desirable to record the details of the life histories of individuals or groups, and for this purpose the following system is proposed and used in the present paper. The sign "/" is used to separate life in fresh water (*stream life*) from that in salt water (*sea life*). Thus, a fish which had spent two growing seasons in fresh water only would be represented by the formula 2/ and one that had migrated to sea in its first year and had spent its first two years at sea would be represented by the formula +/2. Continuing, the formula 2/1 represents a fish that had spent two years (growing seasons) of stream life and one year of sea life. In the case of steelhead, a capital "S" is used to indicate a

⁷In comparatively rare instances it happens that a fish makes no growth during a normal growing season or for other reasons fails to form an annulus. This may occur during the first normal growing season or in later seasons. In such cases the end of a year of life must be judged by the normal time of annulus formation or other criteria of the end of the growing season for the species in the particular locality.

spawning, normally represented on the scales by a spawning mark. The S is not added until a fish has completed spawning. Thus, if a fish had spent two years of stream life and one year of sea life and had then entered fresh water and spawned it would be represented by the formula 2/1S. A period is used to separate years (growing seasons) followed by a spawning from years not followed by a spawning. Consequently, if the same fish had not entered fresh water and spawned until the end of a second year of sea life it would be represented by the formula 2/1.1S. If instead the fish had spawned at the end of both its first and second years of sea life it would be represented by the formula 2/2S. If the same fish began another year of sea life it would be represented by the formula 2/2S.1 until it had again entered fresh water and spawned, when it would be represented by the formula 2/3S. By this system, the total age of the fish may easily be computed by adding the numerals in the formula.

This system for recording life histories is easily understood and has the advantage over some other systems that have been used in that it is readily reproduced on a typewriter. It has been described in further detail by Shapovalov (1947); the system used for recording measurements is also described in this paper.

TECHNIQUES AND METHODS OF MEASUREMENT

Scales were removed from the side of the body in the region between the lateral line and the anterior portion of the dorsal fin and stored for mounting in scale books. Scale samples from juveniles, resident fish, and stream fish were taken from the right side of the body and those from adults from the left side of the body. This system was followed in order to avoid taking regenerated scales in sea-run fish that had been sampled as juveniles.

All fish were measured according to *fork length*, which is here defined as the distance from the tip of the snout to the fork of the caudal fin, and hereafter references to "length" will mean such length. It was not practicable to take the standard length (distance from tip of snout to end of hypural fan) with live fish. The measurement used was also deemed more accurate than a total length based on distance from tip of snout to end of the caudal fin, for the reason that the tips of the caudal fin are often frayed or worn off, especially in spawning trout and salmon. In both sea-run steelhead and silver salmon the relation of the standard length to the fork length appears to be fairly constant, the standard length varying from 88.4 to 90.1 percent of the fork length in seven specimens from Waddell and Scott creeks. All measurements were made in a straight line between the points indicated with the fish placed on a rule and were recorded to the following unit of measurement. Fish 300 mm. or under in length were measured to the following millimeter and those over 300 mm. to the following centimeter. In practically all cases sea-run fish are more than 300 mm. in length and juveniles, stream fish, and resident fish are less than 300 mm. in length.

Preparation and Examination of Scale Samples

The scales were soaked in water and cleaned with a small brush, or merely by rubbing between the fingers. They were mounted "dry" (in air), with the edges of the cover glass glued down with "Duco Household Cement," in some cases and in white "Karo Syrup" in others. Each form of mounting produces a permanent slide. Two or three scales were mounted in the case of sea-run fish and from that number to a dozen in the case of the smaller fish. Care was taken to avoid scales with regenerated centers or of highly asymmetrical or otherwise irregular form.

All measurements were made along the anterior radius of the scale, using a microscope and a mechanical stage, with attached micrometer which recorded in hundredths of a millimeter.

The following procedure generally was used to gage the validity of scale interpretations. The investigator recorded his measurements and immediately denoted doubtful features. He then re-examined the doubtful scales only, without reference to his initial interpretation. If a doubtful but probable feature was interpreted the same way on each occasion, the interpretation was listed as "certain." In a few instances the other investigator checked the doubtful scales, again without reference to the initial interpretation.

FISH FAUNA OF WADDELL CREEK

In common with the other coastal streams from the Golden Gate to Monterey Bay, Waddell Creek contains no strictly fluvial fishes. As Snyder (1914) has pointed out, the San Lorenzo, Pajaro, and Salinas rivers, farther to the south, possess a fluvial fish fauna whose affinities are with that of the Sacramento River system.

The species regularly found in flowing (fresh) water in Waddell Creek, besides the steelhead and silver salmon, are the Prickly Sculpin (*Cottus asper*), the Aleutian Sculpin (*C. aleuticus*), the Three-spined Stickleback (*Gasterosteus aculeatus*), and the Tidewater Goby (*Eucyclogobius newberryi*).

Other native species that are found only in the brackish water of the lagoon or only occasionally enter the fresh water of the stream are the following: Starry Flounder (*Platichthys stellatus*), Staghorn Sculpin (*Leptocottus armatus*), and Top Smelt (*Atherinops affinis*).

The only introduced species in Waddell Creek is the Striped Bass (*Morone saxatilis*), which in some years enters the lagoon from the ocean, but insofar as the writers have been able to ascertain, does not spawn in the Waddell Creek drainage.

Lampreys, so common in many of the larger California coastal streams, and usually called "eels" by local residents, do not enter Waddell Creek nor Scott Creek. They are, however, found in the San Lorenzo River.

A number of facts concerning the habits and ecology of the various non-salmonid species mentioned have been discovered in the course of the studies, but these will be discussed in the present paper only in part and only as they concern the steelhead and/or silver salmon. However, just enough facts regarding the local distribution and breed-

ing habitat of these species will be stated at this time to orient the reader for further discussion of their interrelationships with the trout and salmon.

Cottus asper is the larger and by far the more abundant of the two species of sculpins present. Although at times occurring farther upstream, both species apparently breed within 3,300 feet above the uppermost limit of tidewater. Both species make regular upstream and downstream migrations. The downstream migrations apparently are for spawning purposes.

The Three-spined Stickleback is found in fresh water, brackish water, and in the salt water of the ocean and apparently breeds in all three habitats. At times there is a marked downstream migration of this species in Waddell Creek.

The Tidewater Goby has been found only in the brackish portion of the upper part of the lagoon and in the lower half-mile of flowing water. No intrastream migrations have been observed.

The Starry Flounder, Top Smelt, and Staghorn Sculpin are normally saltwater forms and only occasionally enter the lagoon. However, apparently the same individuals may remain in the lagoon for days and even weeks. In nearby Pescadero Creek, the Starry Flounder has been caught by angling with salmon eggs several hundred yards above the lower end of the flowing water of the stream.

The Striped Bass enters the lagoon only occasionally, but at such times may remain for over a month. In former years this species was reported by local residents on occasion to have ascended about a mile into the flowing water of the stream, but since the start of the experiments, in 1933, no individuals of this species have been seen above the limits of tidewater. No evidence has been gathered to show that the species spawns in Waddell Creek.

WADDELL CREEK VERTEBRATES OTHER THAN FISHES

Amphibians

The amphibians which regularly enter the stream are the following: California Newt (*Triturus t. torosus*), Pacific Giant Salamander (*Dicamptodon ensatus*), California Yellow-legged Frog (*Rana boylei boylei*), and California Red-legged Frog (*Rana aurora draytoni*). The Pacific Giant Salamander has been seen but infrequently in Waddell Creek. The other species are more or less common and make regular downstream migrations.

Reptiles

The reptiles which regularly enter the stream are the following: Pacific Pond Turtle (*Clemmys m. marmorata*) and one or two species of garter snake (*Thamnophis*). Some of the garter snakes make regular downstream migrations.

Birds

Several species of aquatic or semiaquatic birds are regularly associated with the stream, as follows: California Heron (*Ardea herodias hyperonca*), American Egret (*Casmerodius albus egretta*), Black-crowned Night Heron (*Nycticorax nycticorax hoactli*), American Bittern (*Botaurus lentiginosus*), Wood Duck (*Aix sponsa*), American

Coot (*Fulica americana americana*), Western Belted Kingfisher (*Megasceryle alcyon caurina*), and Dipper (*Cinclus mexicanus unicolor*). Several other birds, such as loons, grebes, ducks, various shore birds, gulls, and terns are occasional visitors to the lagoon or lower stream, but in all probability do not affect their economy to a marked extent. None of the species present are to be found in great abundance. Over the entire drainage of Waddell Creek, probably no species is represented by more than a dozen or at the most several dozen individuals. Both the Golden Eagle (*Aquila chrysaetos canadensis*) and the Southern Bald Eagle (*Haliaeetus leucocephalus leucocephalus*) are represented by a few individuals, and at least the latter species feeds on the carcasses of spent salmon, but they do not play an important role in the economy of the stream. The American Merganser, often called "fish duck," which in other California streams appears to eat appreciable numbers of trout and salmon and trout and salmon eggs, and the American Osprey are absent from the area or are rare visitors.

Mammals

The only mammal that is known to have a direct relationship to the salmon and trout in Waddell Creek is the California Coon (*Procyon lotor psora*), which eats dead or weakened adult steelhead and salmon. No beaver or mink are present.

WADDELL CREEK INVERTEBRATES

The assemblage of native aquatic invertebrates in Waddell Creek is quite varied, with numerous genera represented, and is rather typical of the invertebrate life in other coastal streams. Nearly all of the aquatic invertebrates have some relation to the trout and salmon and most of them are eaten by these fishes to a greater or less extent. The importance of the various groups as trout and salmon food will be discussed further in the paper.

The largest mollusk present in the stream is the freshwater mussel *Margaritifera margaritifera falcata*. During the course of the experiments it has not been observed in abundance anywhere in the stream. Several other mollusks, consisting mainly of several species of small snails, are present.

The introduced (?) crayfish *Pacifastacus klamathensis* apparently increased greatly in abundance during the last three years of the experiments (1940-42). It is the largest and most conspicuous crustacean. Several other crustaceans are present. *Corophium*, *Gammarus*, *Neomysis*, and *Exosphaeroma* are abundant in the lagoon.

The aquatic insects are strongly represented by the orders Trichoptera, Ephemera, Diptera, Plecoptera, and Neuroptera. The order Coleoptera is represented chiefly by the Parnidae (riffle beetles).

Several references to aquatic invertebrates in Waddell Creek and its lagoon have appeared in the literature, as follows: Needham (1934a, 1934b, 1935, 1938, 1940), Shapovalov (1936), and Shepherd (1928).

A list of the aquatic invertebrates recorded from Waddell Creek and its lagoon, which undoubtedly is not a complete list of the invertebrate fauna of the stream, is given below. Terrestrial forms eaten by trout

or salmon have been included. Symbols used have the following meanings: l = larvae; p = pupae; n = nymphs; a = adults; A = typically aquatic; T = typically terrestrial; T/ = semiaquatic, inhabiting shores of streams, etc. The symbol (X) under the column heading "Stream" means that the organism has been found under freshwater conditions, but in an area covered at times by brackish water.

Scientific name	Common name	Literature reference	Habitat	Stream	Lagoon	Eaten by steelhead	Eaten by silver salmon
PROTOZOA							
Class Ciliata							
<i>Spirostomus</i>		Needham 1940	A		X		
<i>Euplotes</i>		Needham 1940	A		X		
<i>Pleuronema</i>		Needham 1940	A		X		
<i>Colpidium</i>		Needham 1940	A		X		
<i>Prorodon</i>		Needham 1940	A		X		
<i>Oxytricha</i>		Needham 1940	A		X		
ROTIFERA							
		Needham 1940	A		X		
ANNELIDA							
Class Chaetopoda							
Order Oligochaeta							
		Needham 1940			X		
		Shepherd 1928		X		X	
ARTHROPODA							
Class Crustacea							
Order Ostracoda							
		Needham 1940	A		X		
Order Isopoda							
<i>Exosphaeroma oregonensis</i> (Dana)							
		Needham 1940	A	(X)	X	X	
		Shapovalov MS	T	X		X	
	"Pill bugs"	Shepherd 1928		X		X	
		Needham 1940	A		X		
Order Copepoda							
<i>Salmincola californiensis</i> Dana							
		Shapovalov MS	A	X			
Order Amphipoda							
<i>Gammarus confervicolis</i> (Stimpson)							
	Scud	Needham 1940	A	(X)	X	X	
<i>Corophium spirocorne</i> Stimpson							
		Needham 1940	A		X		
Order Mysidacea							
<i>Neomysis mercedis</i> Holmes							
		Needham 1940	A		X		
Order Decapoda							
<i>Crago</i> sp.							
	Shrimp	Shapovalov MS	A		X		
<i>Pacifastacus klamathensis</i>							
	Crayfish	Shapovalov MS	A	X			
Class Diplopoda							
Class Insecta							
Order Corrodentia							
Psocids, bark lice, etc.							
	Fam. Psocidae n.	Shepherd 1928	T	X		X	
Order Ephemera							
Mayflies							
	Fam. Ephemera n.	Shapovalov MS	A	X		X	
	Fam. Heptageniidae n.	Shepherd 1928	A	X		X	
	Fam. Baetidae n.	Shepherd 1928	A	X		X	
	<i>Baetis</i> sp. n.	Shapovalov MS	A	X		X	
	<i>Paraleptophlebia</i> sp. n.	Shapovalov MS	A	X		X	
Order Odonata							
Dragonflies							
Damsel flies							
	Damsel fly n.	Shepherd 1928	A	X		X	
Order Neuroptera							
Dobson flies, ant lions, etc.							
	Fam. Myrmeleonidae l.	Shapovalov	A	X			
	Fam. Sialidae	Shepherd 1928	T	X		X	
	<i>Sialis</i> sp.	Shapovalov MS	A	X		X	

Scientific name	Common name	Literature reference	Habitat	Stream	Lagoon	Eaten by steel-head	Eaten by silver salmon
ARTHROPODA—Continued							
Class Insecta—Continued							
Order Plecoptera							
Fam. Perlidae n	Stoneflies	Shepherd 1928	A	X		X	
<i>Alloperla</i> sp.		Shapovalov MS.	A	X		X	
Order Trichoptera l, p, a							
Fam. Rhyacophilidae	Caddisflies	Shepherd 1928	A	X		X	
<i>Glossosoma</i> sp. l		Shepherd 1928	A	X		X	
<i>Agapetus</i> sp. l		Shepherd 1928	A	X		X	
Fam. Hydropsychidae		Shepherd 1928	A	X		X	
<i>Hydropsyche</i> sp. l		Shepherd 1928	A	X		X	
Fam. Philopotamidae		Shepherd 1928	A	X		X	
<i>Chimarra</i> sp.		Shepherd 1928	A	X		X	
Fam. Odontoceridae		Shepherd 1928	A	X		X	
<i>Nerophilus californicus</i>							
Hagen l		Shepherd 1928	A	X		X	
<i>Psilotreta</i> sp. l		Shapovalov MS.	A	X		X	
Fam. Hydropsychidae		Shepherd 1928	A	X		X	
<i>Hydropsyche</i> sp. l		Shepherd 1928	A	X		X	
Fam. Sericostomatidae l, p		Shepherd 1928	A	X		X	
<i>Brachycentrus</i> sp.		Shepherd 1928	A	X		X	
<i>Lepidostoma zineureum</i>							
Banks l		Shepherd 1928	A	X		X	
<i>Atomyia unicolor</i> Banks (?)		Shepherd 1928	A	X		X	
<i>Notidobia nigricula</i>							
McLachlan (?) l		Shepherd 1928	A	X		X	
<i>Notidobia</i> sp.		Shapovalov MS.	A	X		X	
Fam. Limnophilidae l		Shepherd 1928	A	X		X	
<i>Limnophilus</i> sp. l		Shapovalov MS.	A	X		X	
<i>Halesus</i> sp.		Shepherd 1928	A	X		X	
Genus l sp.		Shepherd 1928	A	X		X	
<i>Glyptopsyche</i> sp. (?) l		Shepherd 1928	A	X		X	
<i>Apatania</i> sp.		Shepherd 1928	A	X		X	
Order Homoptera							
	Leafhoppers, aphids, etc.						
Fam. Cercopidae a		Shepherd 1928	T	X		X	
Fam. Jassidae a		Shepherd 1928	T	X		X	
Fam. Chermidae a		Shepherd 1928	T	X		X	
Order Hemiptera							
	True bugs						
Fam. Coreidae a		Shepherd 1928	A	X		X	
Fam. Notonectidae a		Shepherd 1928	A	X		X	
Fam. Reduviidae a		Shepherd 1928	T	X		X	
Fam. Coreidae a		Shepherd 1928	T	X		X	
Fam. Saldidae a		Shepherd 1928	T	X		X	
Fam. Gerridae		Needham 1935	A	X		X	
Fam. Belostomatidae	Water striders						
	Giant water bugs						
<i>Lethocerus americanus</i> (Leidy)		Shapovalov MS.	A	X			
<i>Abedus hungerfordi</i>							
De Carlo		Shapovalov MS.	A	X			
Order Coleoptera							
	Beetles						
Fam. Pyrochoridae a		Shepherd 1928	T	X		X	
Fam. Carabidae a		Shepherd 1928	T	X		X	
Fam. Histeridae a		Shepherd 1928	T	X		X	
Fam. Dytiscidae a		Shepherd 1928	A	X		X	
Fam. Cryptophagidae a		Shepherd 1928	T	X		X	
Fam. Staphylinidae a		Shepherd 1928	T	X		X	
Fam. Scolytidae a		Shepherd 1928	T	X		X	
Fam. Curculionidae a		Shepherd 1928	T	X		X	
Fam. Paridae l, a		Shapovalov MS.	A	X		X	
Order Diptera							
	True flies	Needham 1940			X		
Fam. Cecidomyiidae l		Shepherd 1928	T	X		X	
Fam. Scatophagidae a		Shepherd 1928	T	X		X	
Fam. Muscidae a		Shepherd 1928	T	X		X	

Scientific name	Common name	Literature reference	Habitat	Stream	Lagoon	Eaten by steel-head	Eaten by silver salmon
ARTHROPODA—Continued							
Class Insecta—Continued							
Order Diptera—Continued							
Fam. Phoridae a		Shepherd 1928	T	X		X	
Fam. Chironomidae l, p		Shepherd 1928	A	X		X	
l, a		Shapovalov MS.	A	X		X	
Fam. Mycetophilidae a		Shepherd 1928	T	X		X	
Fam. Syrphidae l, a		Shepherd 1928	T	X		X	
Fam. Simuliidae l, p, a		Shepherd 1928	A	X		X	
l		Shapovalov MS.	A	X		X	
<i>Simulium</i> sp.		Needham 1934b	A	X		X	
		Needham 1940	A	X		X	
Fam. Tipulidae l		Shepherd 1928	T	X		X	
Fam. Tabanidae l		Shepherd 1928	T	X		X	
Fam. Dixidae							
<i>Dixa</i> sp. l		Shapovalov MS.		X		X	
Order Lepidoptera l							
Order Hymenoptera							
Fam. Chalcididae a		Shepherd 1928	T	X		X	
Fam. Vespidae a		Shepherd 1928	T	X		X	
Fam. Apidae a		Shepherd 1928	T	X		X	
Fam. Bombidae a		Shepherd 1928	T	X		X	
Class Arachnida							
Order Acarina							
Fam. Hydrachnidae	Water mites	Needham 1940	A		X		
MOLLUSCA							
Class Pelecypoda							
Order Eulamellibranchia							
<i>Margaritifera margaritifera</i>							
<i>falcata</i> (Gould)	Freshwater mussel	Shapovalov MS.	A	X			

LIFE HISTORIES OF THE SILVER SALMON AND STEELHEAD

In the following pages for the sake of clarity the life histories of the silver salmon and of the steelhead will be treated separately. That of the silver salmon will be treated first because in nearly all of its aspects it is the simpler, for the following reasons: (1) all of the adults die after spawning once, (2) all of the juveniles migrate to sea and reach sexual maturity there, (3) all of the adults return to spawn either in their second or third year, (4) practically all of the juveniles migrate to sea in their second year.

Before the separate life histories are considered, however, it is felt apropos to make some general remarks in connection with them. First, we must constantly keep in mind that variation, i.e., deviation from the norm, is one of the most marked characteristics of animal life. And of the vertebrates, the trouts are among the most variable of all. Further, of the trouts the steelhead is one of the most variable forms. Variation is also often encountered among the silver salmon, but to a lesser extent. Such variation applies not so much to the essential biology of the two species as to their habits, form, and behavior. This does not mean that on a mass basis we cannot predict what each species will do in a given environment, but it does mean that a departure from the

norm, often a wide departure, may be expected among individuals. As an example, in the coastal streams *most* of the juvenile steelhead migrate to sea in their second year, but *some* fish migrate in their first, third, fourth, or fifth years, or do not migrate at all.

This factor of variation is of considerable importance in planning a management program for the species involved.

Secondly, we must constantly keep in mind the factor of compensation. Thus, if environmental factors act to interfere with the normal course of the life history of an individual trout or salmon or a certain year class, that individual or year class attempts to overcome the obstacle in its path toward the normal completion of its life cycle. For example, if a barrier is placed in a stream the fish will either try to ascend the barrier or drop down and spawn below it; if the best spawning beds are crowded a fish will either try to drive off the other fish or will select a less favorable site, which it would not use if the crowding did not exist; if a certain type of food is scarce or not available, the fish will switch to some other type of food.

Under natural conditions, then, with no control of environmental conditions, it is extremely difficult to analyze the individual influence of the many factors affecting the life history of an individual or a year class. This does not mean that each of these factors is not exercising an influence, but that it is very difficult or impossible to analyze the quantitative amount of the influence of a particular factor. To illustrate, an unsuccessful attempt was made (Frances Felin, unpublished MS) to establish a correlation between water volume and temperature and the spawning migration of silver salmon at Waddell Creek. Yet poachers and other interested local residents and biologists who have an intimate field acquaintance with the various species of anadromous salmonids usually know rather definitely at what times a particular species is going to enter and ascend a particular stream. Certainly, water volume and temperature (there is a general correlation between the two, since rainfall creates a water temperature of approximately 50 to 55 degrees F.) do exercise an influence on the spawning migration, but the extent of their influence is greatly altered by other complicating factors (variables), such as the time of year, the number of fish that have already entered and ascended the stream, the length of time that it has been raining and consequently the length of time that the stream has been high, the condition of the tides, etc. The existence of homing, which has been briefly mentioned on page 19 and will be discussed in greater detail further in this paper, limits the potential total number of fish that may enter the stream. Obviously, if most of this number have already entered the stream, comparatively few more will enter even with optimal physical conditions of water height, temperatures, tides, etc. This approach seems so obvious that it would not be necessary to mention it, except for the fact that biologists so often have tended to disregard it, by ignoring influencing factors if they could not be graphed to show correlation, or conversely, by considering their graphs in error if exceptions occurred. Actually, graphs suitable for a given set of conditions could be made, but the trouble often has been that no graph showing a correlation could be prepared when all of the variables that enter into the problem exerted their influences.

LIFE HISTORY OF THE SILVER SALMON

Spawning Migration

There may be some question as to what is the proper point in the life cycle of the silver salmon to begin a discussion of its life history, but the writers believe that the clearest presentation can be obtained by starting with the adults that are about to enter the stream for spawning purposes.

Time and Size of the Spawning Migration

Over the range of the species, spawning runs of silver salmon enter streams, move upstream, and spawn within the period September through March. The major spawning takes place during the period November through January. In most streams entry, upstream migration, and spawning take place within the confines of a more limited season characteristic of the particular stream or area. Spring-run silver salmon are not known.

As has been noted earlier in this paper, Waddell Creek and most other California streams are closed by sand bars at their mouths during a portion of the annual dry season. Obviously, under such conditions no fish can enter the stream until the bar breaks open. The permanent breaking of the bar occurs with the first heavy rains of the wet season, or after a series of light rains sufficient to increase the discharge of the stream to an appreciable extent. On occasion the bar will open with early rains or high tides and winds and will then again close the stream for a period of days or weeks, before it finally breaks out to remain open until the following spring or summer.



FIGURE 6. Waddell lagoon at low water, showing tenuous connection with the ocean. Photograph by Leo Shapovalov, December 11, 1939.

At Waddell Creek (and Scott Creek) some silver salmon have entered the stream whenever the first opening of the bar has been of sufficient extent to enable them to do so. The dates of openings of the bar and those on which the first silver salmon have been taken in the trap are shown in Table 4. This implies that the fish are "waiting" at or very near the mouth of the stream for the bar to open, or make a rapid journey to the mouth of the stream with the approaching storm.

TABLE 4

Waddell Creek, Silver Salmon: Time of Initial Capture in Trap, in Relation to Opening of the Bar

Year	First opening of bar	First silver salmon taken in trap	Permanent opening of bar
1933.....	October 31	December 8	December 28
1934.....	November 19	November 21	December 13
1935.....	October 11	December 29	December 29
1936.....	November 19	December 25	December 26
1937.....	October 26	December 12	December 8
1938.....	October 27	December 2	October 27
1939.....	November 24	December 11	December 7
1940.....	September 13	December 17	December 16
1941.....	October 9	November 30	December 9

However, all or even the majority of the seasonal "run" has never entered the stream at one time, i.e., during one storm or within a period of a week. On the contrary, each succeeding storm results in the entry of a fresh run of fish, until the whole season's run has entered the stream.

The entry of the fish into the stream is not dependent on their sexual maturity, for examinations made at the mouth have revealed that some of the fish are sexually immature, or "green," while others are completely sexually mature, or "ripe." It may be further pointed out that at various egg collecting stations in California, both green and ripe silver salmon have been taken in the traps.

In streams the mouths of which remain permanently open, the same pattern of migration occurs, i.e., fresh runs keep entering and ascending the stream, with the difference that the initial entry is not regulated by the opening of a bar.

The question might be raised whether any salmon would enter Waddell Creek if unseasonal heavy rains occurred in September or October. Since such rains did not occur during the course of the experiments, a direct answer was not obtained. However, an indirect or partial answer may be obtained from an examination of what occurs in streams the mouths of which are open permanently. We find that in such streams silver salmon do not enter throughout the year, but within the general confines of a season characteristic of that particular stream. For example, in the lower portion of the Eel River of Northern California the first silver salmon of the season are regularly caught each year in September, and this is probably close to the date of their initial entry into the stream. (The actual spawning of silver salmon in the Eel River takes place later, mainly in December and January.)

In Northern California the rainy season begins earlier than at Waddell Creek and the runs of silver salmon also occur earlier. For example, at Redwood Creek the first fish usually enter the stream in September and complete their spawning by the time the first fish are entering Waddell Creek (November-December).

Over their range, silver salmon spawn mostly within the period November-January. In southeastern Alaska (Prince of Wales Island) silver salmon have been reported (Chamberlain, 1907) sometimes to spawn in small numbers throughout the winter, even as late as March. The latest that an unspawned adult was taken in the upstream trap at Waddell Creek is March 21st.

Most of the earlier studies on silver salmon and other anadromous salmonids on the Pacific Coast have been made in large streams. Perhaps as a result of this there has existed the impression among some workers that the different runs of fish in a stream constitute different "races." The writers do not wish to dispute the existence of different biological or morphological races within large stream systems, and in fact are inclined to believe that such races do exist, but they do wish to point out that the existence of races probably does not explain entirely the different runs of the same species during a season. There is no evidence to support the belief, and it is hardly to be expected, that different races would exist in a stream as small as Waddell Creek.

Just what is the explanation of the different runs—why the fish do not all enter the stream at one time—is not known, but the reason is probably determined by the habits and migrations of the fish in the ocean. The ocean life history of the silver salmon is still much of a mystery. We do know that the fish make very rapid growth in the ocean, that they are powerful and rapid swimmers, and that they make long journeys.

During the nine seasons of operation of the upstream trap, 1933-34 through 1941-42, 2,218 adult silver salmon were taken. The numbers of fish taken during each season, arranged by sexes and weekly periods, are shown in Table 5 and Figure 7.

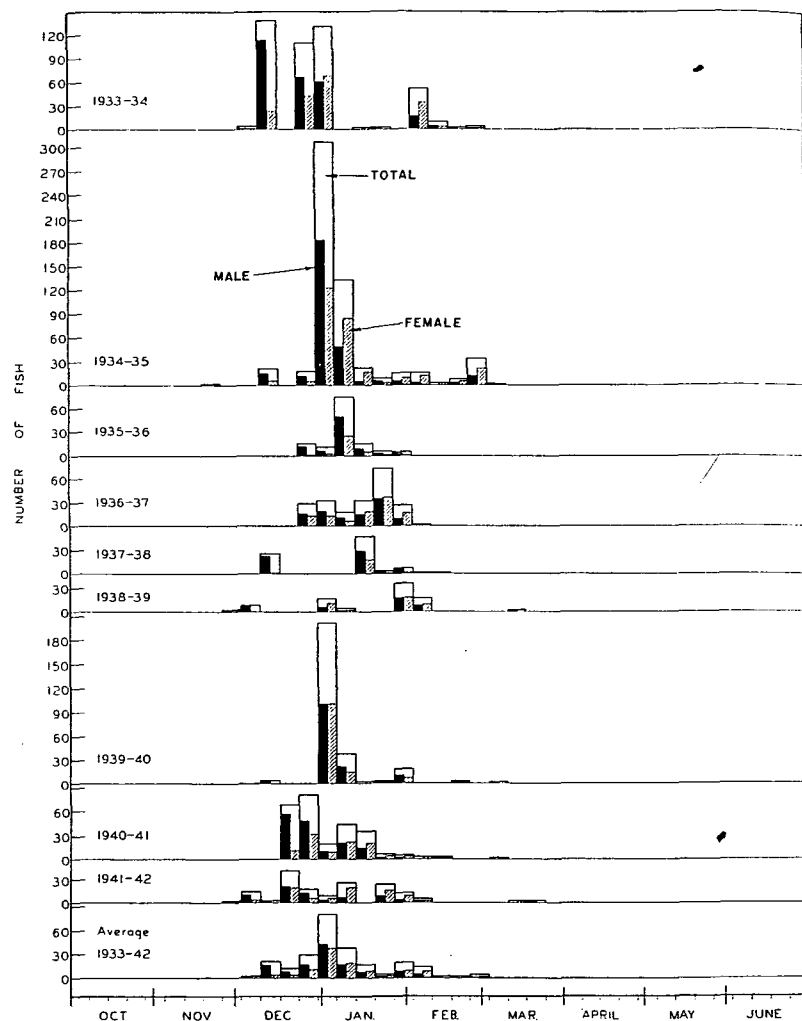


FIGURE 7. Adult silver salmon checked through the upstream trap at Waddell Creek, by weekly periods.

From the above table and graph, it will be seen that the earliest fish was taken during the week ending November 25, and the latest, during the week ending March 24. Despite this long spread, it will be noted that 33 percent of all fish were taken during the weekly period December 31-January 6, 81 percent were taken during the six weeks December 10-January 20, and 96 percent during the nine weeks December 10-February 10. It is thus evident that the run is quite concentrated from point of view of time.

At Benbow Dam on the South Fork of the Eel River and Sweasey Dam on the Mad River the runs are equally concentrated, although slightly earlier than at Waddell Creek (Figure 8). At Benbow Dam 83

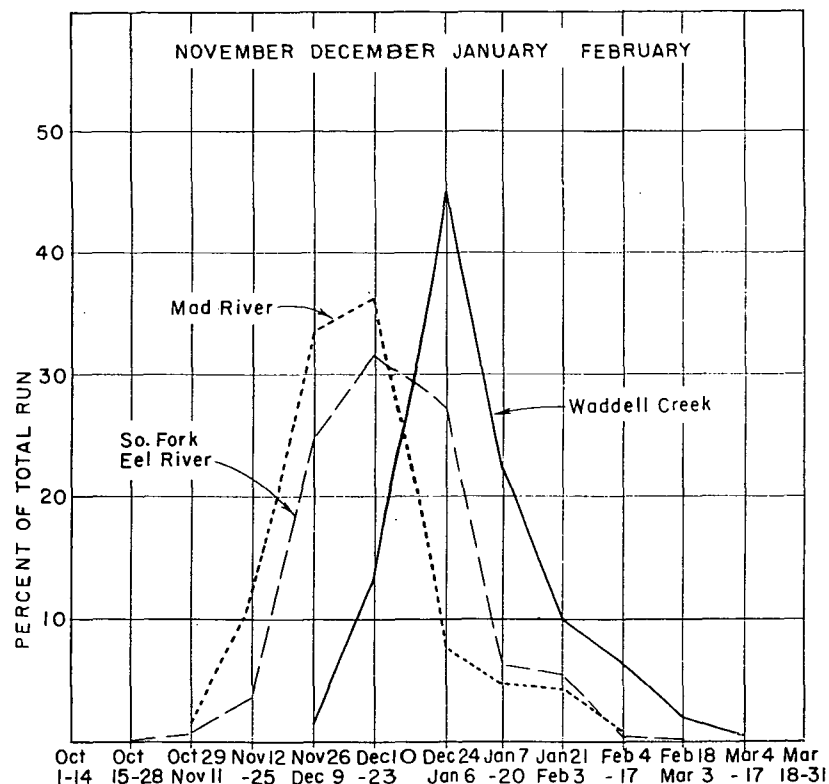


FIGURE 8. Seasonal distribution of the silver salmon spawning runs in Waddell Creek, South Fork of the Eel River, and Mad River.

percent of all silver salmon during six seasons passed upstream in the six weeks November 26-January 6, and at Sweasey Dam 81 percent during nine seasons passed upstream in the six weeks November 12-December 23 (Tables 6 and 7).

In other streams as well, the bulk of the upstream migration and the spawning appear to cover a fairly short period. Foerster (1944)

TABLE 6

South Fork of the Eel River (at Benbow Dam), Silver Salmon: Adults Counted Upstream Through Fishway, by Two-week Periods

Period	1938-39	1939-40	1940-41	1941-42	1942-43	1943-44	Total	Percentage of total run
Oct. 1-14							1	
Oct. 15-28					1		1	
Oct. 29-Nov. 11			386	29	3		418	0.6
Nov. 12-25			26	185	1,766	630	2,607	3.8
Nov. 26-Dec. 9	2,919		101	8,152	4,808	818	16,798	24.4
Dec. 10-23	518	7,291	3,370	2,741	1,943	5,742	21,605	31.4
Dec. 24-Jan. 6	1,983	744	7,007	1,926	4,199	3,029	18,888	27.4
Jan. 7-20	1,279	391	183	564		1,958	4,375	6.4
Jan. 21-Feb. 3	460	203		86	2,269	789	3,807	5.5
Feb. 4-17	206				48	64	318	0.5
Feb. 18-Mar. 3				11			11	
Mar. 4-17	5						5	
Mar. 18-Sept. 30								
Totals	7,370	8,629	11,073	13,694	15,037	13,030	68,833	

reports that the spawning run of 1942 in the Cowichan River, British Columbia, "reached the spawning grounds in 20-30 days (one to two months in 1941) and were spawned-out in 30 to 60 days."

There has been considerable fluctuation in the size of the seasonal runs at Waddell Creek. The largest number taken in the trap was 583, during the season of 1934-35, and the smallest number 84, during the season of 1937-38. Possible reasons for these fluctuations will be discussed in the sections on survival and pathology (pages 95-104).

Age and Size of the Fish

Waddell Creek scale examinations and marked fish returns indicate that all adults return either as males in the season following downstream migration (age 1/1, one growing season in ocean) or as males and females in the second season following downstream migration (age 1/2, two growing seasons in ocean).

Table 8 shows the numbers of silver salmon taken in each season in the upstream trap at Waddell Creek, arranged by age-sex categories and size.

Scale examinations and returns of marked fish at Scott Creek during several seasons are in entire agreement with the above findings.

Other workers have reported that the great majority of silver salmon adults fall into the above age categories, but have noted some exceptions. For example, Marr (1943) recorded that of 885 silver salmon taken in the commercial gill net fishery of the lower Columbia River in 1914, 1/2 fish comprised 83.9 percent of the total sample and 1/1 fish 6.1 percent.⁸ Thus, the two categories represented at Waddell Creek

⁸ Marr concludes that "the samples are representative of that part of the commercial catch from which they were drawn, but are not truly representative of the total run, inasmuch as there will be a tendency for the smaller and larger sizes to be inadequately represented, because of the selective action of the gill nets by which the fish were taken."

TABLE 7
Mad River (at Sweasey Dam), Silver Salmon: Adults Counted Upstream Through Fishway, by Two-week Periods

Period	1941-42	1942-43	1946-47	1947-48	1948-49	1949-50	1950-51	1951-52	1952-53	Total	Percentage of total run
Oct. 1-28										46	1.4
Oct. 29-Nov. 11	4			32	94	8	83	84	6	377	11.5
Nov. 12-25	189	48	18	72	176	274	110	110	9	1,104	33.6
Nov. 26-Dec. 9	24	62	105	137	137	131	23	188	51	1,190	36.2
Dec. 10-23	56	197	64	375	44	51	5	22	2	257	7.8
Dec. 24-Jan. 6	28	54	28	42	12	48		6		155	4.7
Jan. 7-20	7	10	108	5	7				2	134	4.1
Jan. 21-Feb. 3					24				2	26	0.8
Feb. 4-17											
Feb. 18-Sept. 30											
Totals	308	378	415	530	515	512	149	410	72	3,289	

TABLE 8

Waddell Creek, Silver Salmon: Adults Checked Through Upstream Trap; Length-frequency Distributions, by Seasons

Length in cm.	1933-34			1934-35			1935-36			1936-37			1937-38		
	1/1		1/2	1/1		1/2	1/1		1/2	1/1		1/2	1/1		1/2
	♂	♂	♀	♂	♂	♀	♂	♂	♀	♂	♂	♀	♂	♂	♀
30	--	--	--	--	--	--	(3)*	--	--	--	--	--	--	--	--
31	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
32	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--
33	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--
34	1	--	--	--	--	--	2	--	--	--	--	--	1	--	--
35	6	--	--	--	--	--	1	--	--	--	--	--	1	--	--
36	10	--	--	--	--	--	1	--	--	--	--	--	--	--	--
37	4	--	--	1	--	--	--	--	--	--	--	--	2	--	--
38	8	--	--	--	1	--	6	--	--	--	--	--	2	--	--
39	12	--	--	3	--	--	8	--	--	--	--	--	3	--	--
40	14	--	--	3	--	--	7	--	--	--	--	--	3	--	--
41	13	--	--	3	1	--	2	--	--	--	--	--	3	--	--
42	14	--	--	3	--	--	2	--	--	--	--	--	--	--	--
43	13	--	--	4	--	--	8	--	--	3	--	--	2	--	--
44	6	--	--	1	--	--	7	--	--	--	--	--	1	--	--
45	5	--	--	1	2	--	4	--	--	--	--	--	--	--	--
46	4	--	--	2	1	--	2	--	--	--	--	--	1	--	--
47	2	--	--	--	--	1	2	--	--	--	--	--	1	--	--
48	2	1	--	--	2	--	--	--	--	--	--	--	--	--	--
49	--	--	--	--	1	1	--	--	--	--	--	1	--	--	--
50	--	--	--	--	2	2	--	--	--	--	--	--	--	--	--
51	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--
52	--	--	1	--	1	1	--	--	--	--	--	--	--	--	--
53	--	3	1	--	3	2	--	3	--	--	--	--	--	--	--
54	--	2	1	--	1	2	--	--	1	--	--	--	--	--	--
55	--	--	1	--	2	6	--	1	1	--	--	--	--	--	--
56	--	2	--	--	7	5	--	--	--	--	2	1	--	--	1
57	--	2	--	--	3	6	--	--	--	--	2	1	--	1	--
58	--	6	4	--	7	3	--	--	--	--	2	4	--	--	--
59	--	2	6	--	9	9	--	--	2	--	3	5	--	1	--
60	--	6	8	--	7	14	--	1	2	--	2	7	--	1	--

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61	--	3	11	--	9	17	--	2	3	--	4	9	--	4	--			
62	--	9	10	--	13	24	--	1	2	--	5	4	--	--	--			
63	--	8	11	--	26	36	--	1	2	--	7	7	--	2	1			
64	--	13	12	--	26	17	--	2	4	--	10	8	--	4	--			
65	--	7	7	--	21	36	--	2	--	--	10	13	--	3	2			
66	--	12	20	--	27	29	--	3	3	--	5	10	--	6	2			
67	--	10	21	--	20	26	--	2	4	--	8	4	--	2	5			
68	--	10	12	--	19	25	--	3	3	--	12	11	--	4	3			
69	--	8	17	--	13	13	--	1	4	--	8	6	--	1	2			
70	--	10	11	--	12	7	--	2	3	--	4	7	--	4	2			
71	--	9	12	--	14	2	--	3	2	--	6	3	--	3	--			
72	--	9	5	--	7	3	--	1	1	--	3	2	--	2	1			
73	--	8	4	--	9	--	--	--	--	--	8	3	--	3	2			
74	--	9	2	--	3	--	--	3	--	--	1	--	--	--	1			
75	--	2	--	--	2	--	--	--	1	--	--	1	--	1	--			
76	--	--	--	--	2	--	--	--	1	--	--	--	--	--	--			
77	--	1	--	--	--	--	--	--	--	--	1	--	--	--	--			
78	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--			
79	--	--	--	--	--	--	--	2	--	--	--	--	--	--	--			
80	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--			
Mean length.....	{	cm.		39.8	65.7	65.2	41.2	64.0	63.2	41.0	65.8	63.9	42.5	65.8	64.3	39.6	66.1	67.2
		inches		15.7	25.9	25.7	16.2	25.2	24.9	16.1	25.9	25.2	16.7	25.9	25.3	15.6	26.0	26.5
Number.....		118	152	177	21	275	287	56	33	39	3	104	107	20	42	22		
Percentage in each age group.....		26.4	34.0	39.6	3.6	47.2	49.2	43.7	25.8	30.5	1.4	48.6	50.0	23.8	50.0	26.2		

SPRUEHEAD AND SILVER SALMON LIFE HISTORIES

TABLE 8—Continued

Waddell Creek, Silver Salmon: Adults Checked Through Upstream Trap; Length-frequency Distributions, by Seasons

Length in cm.	1938-39			1939-40			1940-41			1941-42			Total		
	1/1		1/2	1/1		1/2	1/1		1/2	1/1		1/2	1/1		1/2
	♂	♂	♀	♂	♂	♀	♂	♂	♀	♂	♂	♀	♂	♂	♀
30	--	--	--	--	--	--	--	--	--	--	--	--	(3)*	--	--
31	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
32	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--
33	--	--	--	--	--	--	--	--	--	--	--	--	3	--	--
34	1	--	--	--	--	--	--	--	--	--	--	--	5	--	--
35	--	--	--	--	--	--	--	--	--	--	--	--	8	--	--
36	2	--	--	--	--	--	2	--	--	--	--	--	15	--	--
37	1	--	--	1	--	--	2	--	--	--	--	--	11	--	--
38	1	--	--	4	--	--	5	--	--	2	--	--	28	1	--
39	2	--	--	5	--	--	2	--	--	--	--	--	35	--	--
40	2	--	--	5	--	--	10	--	--	--	--	--	44	--	--
41	3	--	--	5	--	--	2	--	--	--	--	--	31	1	--
42	2	--	--	7	--	--	8	--	--	1	--	--	37	--	--
43	1	--	--	12	--	--	3	--	--	1	--	--	47	--	--
44	1	--	--	3	--	--	6	--	--	1	--	--	25	1	--
45	--	--	--	1	--	--	6	--	1	--	--	--	17	2	1
46	--	--	--	2	--	--	9	--	--	1	--	--	20	2	--
47	1	--	--	3	--	--	3	--	1	--	--	1	12	--	3
48	--	--	--	3	--	--	4	--	--	1	--	--	9	4	--
49	--	--	--	1	--	--	3	--	--	2	--	--	4	3	2
50	--	--	--	--	--	--	--	--	--	--	--	1	--	2	3
51	--	--	--	--	--	--	--	--	1	--	--	--	--	1	1
52	--	--	1	--	1	--	--	--	1	3	2	--	--	5	6
53	--	--	--	--	--	2	--	--	--	2	4	--	--	11	9
54	--	1	--	--	--	--	--	--	2	2	2	--	--	6	8
55	--	2	--	--	--	--	1	2	--	1	3	--	--	7	13
56	--	--	--	--	--	2	--	2	--	4	3	--	--	15	14
57	--	--	2	--	2	--	1	2	--	5	1	--	--	16	12
58	--	--	--	--	2	--	3	3	--	1	9	--	--	19	25
59	--	--	--	--	2	5	3	6	--	4	10	--	--	24	43
60	--	3	2	--	1	--	--	5	3	--	1	14	--	27	50

61	--	2	4	--	2	2	--	4	5	--	8	5	--	38	56	
62	--	1	3	--	6	6	--	9	7	--	7	8	--	45	64	
63	--	3	5	--	3	9	--	10	13	--	6	2	--	66	86	
64	--	1	7	--	2	10	--	8	10	--	2	3	--	68	71	
65	--	6	2	--	7	8	--	6	14	--	8	5	--	70	87	
66	--	3	2	--	5	10	--	7	10	--	4	2	--	72	88	
67	--	1	4	--	8	17	--	8	9	--	1	--	--	60	90	
68	--	4	3	--	9	15	--	13	5	--	--	1	--	74	68	
69	--	1	1	--	8	7	--	6	4	--	1	1	--	47	55	
70	--	1	3	--	11	10	--	1	3	--	1	--	--	46	46	
71	--	--	1	--	5	13	--	3	1	--	--	--	--	43	34	
72	--	--	--	--	8	2	--	2	--	--	--	--	--	32	14	
73	--	--	--	--	6	3	--	2	--	--	--	--	--	36	12	
74	--	--	--	--	3	2	--	--	--	--	--	--	--	19	5	
75	--	--	--	--	3	--	--	--	--	--	--	--	--	8	2	
76	--	--	--	--	1	1	--	--	--	--	--	--	--	3	2	
77	--	--	--	--	1	--	--	--	--	--	--	--	--	3	--	
78	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	
79	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	
80	--	--	--	--	--	--	--	(1)†	--	--	--	--	--	(1)†	1	
Mean length.....	{ cm. inches	39.5	63.2	63.6	41.9	67.8	65.9	42.4	64.3	62.5	40.3	59.2	58.9	40.9	64.7	63.8
		15.6	24.9	25.0	16.5	26.7	26.0	16.7	25.3	24.6	15.9	23.3	23.2	16.1	25.5	25.1
Number.....		17	29	40	52	88	126	65	93	105	4	66	77	356	882	980
Percentage in each age group.....		19.8	33.7	46.5	19.5	33.1	47.4	24.7	35.4	39.9	2.7	44.9	52.4	10.1	39.8	44.2

* Lengths for these three fish not recorded.

† Length for this fish not recorded.

TABLE 11
Waddell Creek, Scott Creek, and Benbow Dam, Silver Salmon: Comparison of Sex-age Categories by Brood Seasons

Brood season	Number of fish			Percentage 1/1 ♂			Percentage 1/2 ♂			Percentage 1/2 ♀		
	Waddell Creek	Scott Creek	Benbow Dam	Waddell Creek	Scott Creek	Benbow Dam	Waddell Creek	Scott Creek	Benbow Dam	Waddell Creek	Scott Creek	Benbow Dam
1931-32	748			18.3			40.4			41.3		
1932-33	131			16.8			38.2			45.0		
1933-34	395			21.5			38.7			39.8		
1934-35	111			3.6			63.1			33.3		
1935-36	130			26.2			30.8			43.0		
1936-37	279	513	6,765	8.6	22.0	19.7	37.6	33.2	38.0	53.8	44.8	42.3
1937-38	279	681	11,434	22.2	23.1	28.0	36.6	29.1	31.0	41.2	47.8	41.1
1938-39	324	374	12,087	21.9	7.8	23.5	38.3	43.0	33.7	39.8	49.2	42.9
1939-40			15,531			28.6			28.4			43.0
1940-41			14,662			26.9			29.7			43.4
Totals	2,397	1,568	60,479									
Averages*	300	523	12,096	17.4	17.6	25.3	40.5	35.1	32.2	42.1	47.3	42.5

* Average percentages are means of seasonal percentages.

In Table 11, for purposes of comparison, the sex-age categories of silver salmon counted at Scott Creek and at Benbow Dam on the South Fork of Eel River are also shown. It should be noted that at the latter station determinations of both sex and age category were made as the fish passed over a counting board, without handling of the fish. Determinations of age category were based on the approximate size of the fish.¹¹ The essential agreement of the Benbow Dam and Scott Creek data with those from Waddell Creek strengthens the significance of each. The Benbow Dam data have the advantage of large numbers, while the Waddell and Scott Creek data have the advantage of individual measurements of fish.

At all three localities the total number of males resulting from any given brood season considered as a percentage of that brood season's total run is quite stable (Waddell Creek, eight seasons, 46.2 to 66.7 percent, average 57.9 percent; Benbow Dam, five seasons, 56.6 to 59.0 percent, average 57.5 percent; Scott Creek, three seasons, 50.8 to 55.2 percent, average 52.7 percent), while the ratio of the grilse to the two-year-ocean males resulting from a given brood season varies within much wider limits. It necessarily follows that the number of fish which return as two-year-ocean males is strongly influenced by the number which have returned as grilse and that the mortality rate of two-year-ocean males during their second year at sea is much the same from season to season, in other words, that the bulk of the ocean mortality occurs during the brood's first year at sea. The number of fish which return as two-year-ocean males in a given season is therefore largely dependent upon (1) mortality to the time that some of the males return as grilse, and (2) the proportion of males which return as grilse. It is lack of knowledge of the second factor that prevents an accurate prediction of the size of the run of two-year-ocean males in a given season. The reliability of our predictions then, is determined by the variation from season to season in the proportion of the brood that returns as grilse.

Changes in Sex-Age Composition During the Run

The age and sex composition of the fish is not the same throughout the run. Males predominate in the early portions of the run, while females predominate in the latter portion. Other workers have noted the predominance of males in the early portions of the runs for the Pacific salmon. This change in sex ratio may be noted in Figure 7 and Table 5.

Since the sexes and age categories are associated, it follows that changes in the representation of the age categories also occur throughout the run. These changes are shown in Table 12 and Figure 9.

Factors Influencing the Time of Upstream Migration

It has already been noted that in certain streams entry and upstream migration may necessarily be delayed by physical conditions. Studies by the writers at Waddell and Scott creeks and at Benbow Dam on the South Fork of Eel River, and by workers in other areas (e.g.,

¹¹ The dividing line between silver salmon grilse and older fish was set at 24 inches (60.96 cm.). This limit is too high and if followed exactly would have included approximately 10 percent of two-year-ocean fish with the grilse. However, in practice the field observers were guided by the relative differences in size between grilse and two-year-ocean fish as much or more than by the actual lengths.

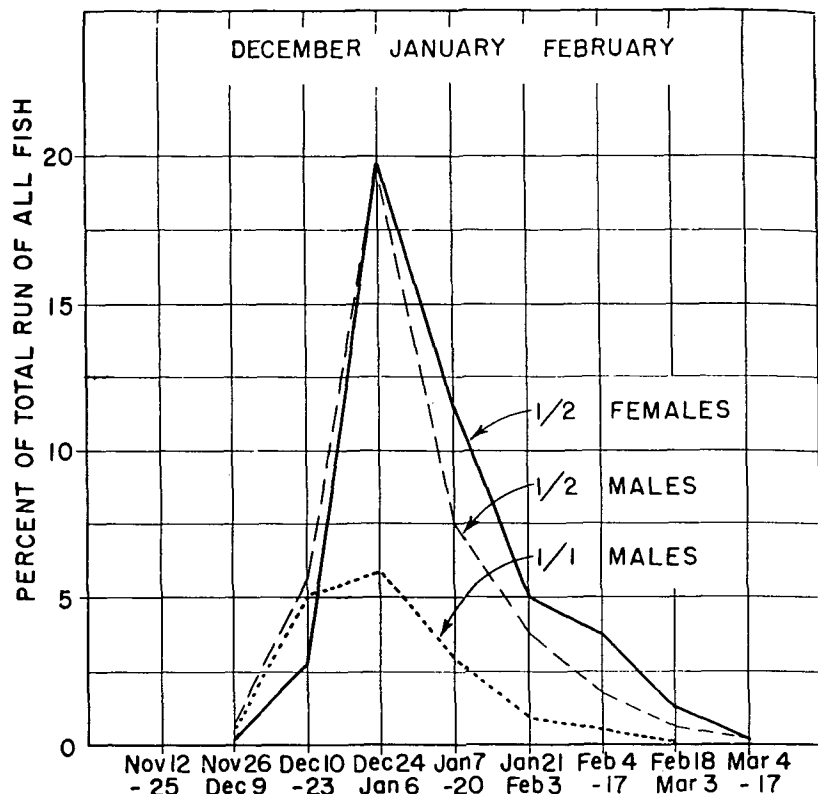


FIGURE 9. Seasonal distribution of sex-age categories in the Waddell Creek silver salmon spawning run.

Neave (1943) for Cowichan River, British Columbia) show that the first heavy upstream migrations coincide with large increases in stream flow, especially in streams which attain low summer levels.

It was seen that at Waddell Creek 96 percent of the fish were taken during the period December 10-February 10. Since this is also the time of heaviest precipitation, there is a correlation between the general period of the spawning run and the general period of rainfall. The writers believe that there is also a definite relationship between ascension of the stream by spawning fish and stream flow, but so far it has proved impossible to show this quantitatively. The relationship between ascension of the stream by spawning fish and stream flow is neither one of positive correlation nor of negative correlation. Salmon (and steelhead) ascend both on rising and falling stream levels, but cease movement during peak floods. However, the number of fish taken during any given water height is not approximately the same, but depends upon the proportion of the run that has already ascended the stream during the storm and during the season, upon preceding flows and climatic conditions, and possibly upon other factors, such as sexual ripeness of the fish and turbidity of water. For example, on more than

TABLE 12
Waddell Creek, Silver Salmon: Seasonal Changes in Sex-age Composition of the Spawning Run; Fish Checked Through Upstream Trap, by Two-week Periods

Season	Category	Nov. 26-Dec. 9	Dec. 10-23	Dec. 24-Jan. 6	Jan. 7-20	Jan. 21-Feb. 3
1933-34	1/1 ♂ 1/2 ♂ 1/2 ♀	1	60	48	1	1
1934-35	1/1 ♂ 1/2 ♂ 1/2 ♀	1	2	14	4	13
1935-36	1/1 ♂ 1/2 ♂ 1/2 ♀	1	1	15	36	2
1936-37	1/1 ♂ 1/2 ♂ 1/2 ♀	1	1	1	1	1
1937-38	1/1 ♂ 1/2 ♂ 1/2 ♀	1	15	1	4	1
1938-39	1/1 ♂ 1/2 ♂ 1/2 ♀	8	2	6	1	2
1939-40	1/1 ♂ 1/2 ♂ 1/2 ♀	2	1	27	10	11
1940-41	1/1 ♂ 1/2 ♂ 1/2 ♀	31	26	19	11	3
1941-42	1/1 ♂ 1/2 ♂ 1/2 ♀	1	21	1	6	12
Totals	1/1 ♂ 1/2 ♂ 1/2 ♀	10	112	180	67	21
Percentage of total run of all fish	All fish	28	296	996	492	218
	1/1 ♂	0.5	5.1	5.9	3.0	0.9
	1/2 ♂	0.6	5.6	19.3	7.6	3.9
	1/2 ♀	0.2	2.8	19.6	11.5	5.0
	All fish	1.2	13.4	45.0	22.2	9.8

TABLE 12—Continued
Waddell Creek, Silver Salmon: Seasonal Changes in Sex-age Composition of the Spawning Run;
Fish Checked Through Upstream Trap, by Two-week Periods

Season	Category	Feb. 4-17	Feb. 18-Mar. 3	Mar. 4-17	Totals	Total all fish
1933-34	1/1 ♂ 1/2 ♀	7	1	---	152	447
1934-35	1/1 ♂ 1/2 ♀	---	1	---	177	---
1935-36	1/1 ♂ 1/2 ♀	3	13	1	275	583
1936-37	1/1 ♂ 1/2 ♀	---	---	---	33	128
1937-38	1/1 ♂ 1/2 ♀	10	---	---	104	214
1938-39	1/1 ♂ 1/2 ♀	2	---	---	42	84
1939-40	1/1 ♂ 1/2 ♀	1	---	---	29	86
1940-41	1/1 ♂ 1/2 ♀	---	---	---	88	266
1941-42	1/1 ♂ 1/2 ♀	2	---	---	93	263
Totals	1/1 ♂ 1/2 ♀	12	3	3	882	2,218
Percentage of total run of all fish	All fish	137	44	7	2,218	---
	1/1 ♂	0.5	0.1	0.1	39.8	---
	1/2 ♀	1.8	0.6	0.1	44.2	---
	All fish	6.2	2.0	0.3	---	---

one occasion a number of salmon have entered Waddell Creek during a storm or series of storms, but have "holed up" in pools in the lower portion of the stream, below the trap, as a result of sudden cessation of the storm and lowering of flow. Such fish will not move up so long as the fair weather continues, even though they be sexually ripe and begin to deteriorate in physical condition and even die. Following such a period, even a light rain and small rise in stream level will cause a large number of these fish to ascend through the trap or spawn below the trap. We may now turn to a consideration of diurnal fluctuations in migration.

Counts of silver salmon, king salmon, and steelhead at the Benbow Dam station of the California Department of Fish and Game and of silver salmon and steelhead at Waddell and Scott creeks indicate that as a rule these fishes move upstream mainly in the daytime. Studies of various workers in other areas generally are in agreement with these findings.

Neave (1943) found that silver salmon (and king salmon) at Skutz Falls, Cowichan River, B. C., migrated mainly during daylight hours, but found no correlation between diurnal fluctuations in number of migrants and water temperature or stream discharge. Within the daylight period, either one or two peaks of major activity were observed. Artificial light, as used, had no effect on night migratory movements.

Chapman (1941), studying steelhead, king salmon, and red (sock-eye) salmon (*Oncorhynchus nerka*) passing through the fishways at Rock Island Dam on the upper Columbia River, concluded that the red salmon as a whole "showed a preference for running in the early morning, the number decreasing as the day progressed, but those going through the middle ladder acted in a directly opposite manner, running predominantly in the late afternoon." He found that the king salmon and steelhead ran heavily through the middle of the day. Chapman states that he "was never able to arrive at a conclusion as to the factors influencing the movements of the fish through the ladder (probably multiple with complex inter-relationships). . . ." (Night counts were not made at Rock Island Dam.)

Neave (1943) and others have noted the occasional occurrence of periods of relative inactivity in upstream movement of various salmonids within the daylight hours. No correlations between such fluctuations in movement during the daytime and environmental factors have been demonstrated. Such fluctuations have been noted at Benbow Dam for silver salmon, king salmon, and steelhead and at Scott and Waddell creeks for silver salmon and steelhead, but to date it has not been possible to form definite conclusions regarding the factors creating them. As Chapman (*loc. cit.*) pointed out, they are "probably multiple with complex inter-relationships." Ripeness of fish, size of run at the immediate locality, and water and climatic conditions may all play a part in determining the pattern of the fluctuations under discussion. It may be noted that particularly at Scott Creek two daily peaks of migration among the steelhead have been noted by the writers on successive days, without any marked changes in stream discharge, turbidity of water, or general weather conditions (other than light and temperature).

Changes in Body Form and Coloration Associated With Maturation

The changes in body form and coloration which are associated with maturation in the different species of the Pacific salmon are well known and have been described elsewhere (e.g., Chamberlain, 1907). Consequently, only a brief résumé will be presented at this time.

The changes which take place vary with species, sex, and size, and also with individual fish. In the males, the changes in form are characterized by the elongation of the jaws, the growth of canine-like teeth, and the increase in depth of body by the ridging of the back. (The latter character has given rise to the term "razor-back.") These changes are most pronounced in the larger fish. (They are seen also in the steelhead, but usually to a lesser extent.) (Juvenile salmon which mature prior to entry into salt water show no evident change in bones or teeth.)

In the male silver salmon, the upper jaw elongates and often becomes quite hooked. Individuals in which this process has been extensive are often known as "hook-bills" or "dog salmon." Sometimes the hooking and knobbing are so great as to prevent closure of the mouth. The lower jaw also elongates, but more often becomes knobbed than hooked. The jaws of the female elongate only slightly and rarely become hooked. With a little experience, these differences between males and females enable the observer to determine the sex of the fish at a glance.¹²

In the sea, all species of the Pacific salmon are quite silvery. In fresh water, the changes in body coloration soon take place. These vary with the species. The larger male silver salmon often acquire a red on the sides which is sometimes quite bright. The grilse and females are usually not nearly so brilliantly colored. The females most often assume a brassy greenish color.

The scales, which are loosely attached in individuals in salt water and in recent arrivals from the sea, become firmly imbedded with the approach of spawning, particularly in the males.

Spawning Beds

Silver salmon ascend practically all accessible streams within their range flowing into the Pacific Ocean, from the largest to the very smallest. This statement is borne out by the observations of other writers. For example, Chamberlain (1907) wrote in regard to choice of spawning streams by silver salmon in southeastern Alaska:

"The coho is probably less particular (in comparison with the other Pacific salmon) in its requirements. The fry were found, without exception, in every stream and brook examined; even a tiny seepage rill entering Naha Bay which would become dry with the first week of fair summer weather contained its little school of coho fry."

Females choose the redd sites, as is the case with other species of salmon and trout. Examination of many redds shows that the site selected is typically near the head of a riffle (which is also the lower end

¹² While some bones increase their size and acquire new material, parts of others and of the scales are absorbed. The changes which take place in the skulls of breeding salmonids have been described in a series of papers by Tchernavin (1918, 1921, 1937a, 1937b, 1938a, 1938b, 1938c, 1938d).

of a pool) composed of medium and small gravel. Usually the site is close to the point where the smooth surface water "breaks" into the riffle.

No differences could be found between the individual sites chosen by silver salmon and steelhead at Waddell Creek. Occasionally fish of the two species spawned at the same time on the same riffle, while in other instances fish of one species spawned in the exact spot used by earlier spawners of the other species. If the runs are considered as a whole, the silver salmon consistently spawn lower in Waddell Creek than do the steelhead. The spawning beds of the lower portion of the stream are composed of gravel not so coarse as that found in the upper stream, but whether or not this is the factor that causes the silver salmon to spawn lower down than the steelhead is not known.

The silver salmon do not ascend streams for as great distances as do the king salmon, red salmon, or steelhead, usually not proceeding upstream in large numbers more than 150 miles even in the larger rivers. This characteristic has been noted by other writers, e.g., Chamberlain (1907), who said: "... long journeys do not find favor with it. Wallowa (northeastern Oregon) and Baker (northern Washington, tributary to the Skagit River) lakes seem to be about the limit to which it travels."

The nature of the redd site insures a good supply of oxygen for the eggs, since in streams a considerable portion of the water flowing through a swift riffle flows below the surface. The circulation of the water through the gravel no doubt also is of considerable aid to the fry in making their way to the surface.

Silver salmon often spawn in very shallow water, but so choose their redds that they are rarely exposed by naturally falling stream levels, in either Waddell Creek or other California streams.

Spawning

Insofar as the writers know, there is no published account of the spawning of silver salmon, but in its general features it is similar to that of other species of salmon and of trout. A generalized account is here presented.

The female may select and abandon several trial sites. Having chosen a satisfactory site, she begins digging. One or more males may accompany the female, but the males do not participate in the digging. Usually one male becomes the mate; the other males, although sometimes persistent in approaching the female, seem to sense this and usually yield to the dominant male when he makes a rush at them. Probably more often than not the mate is a larger fish than the "accessory" attendant males, but even if smaller, his "right" to the female is usually recognized. The fighting and digging often result in a great deal of commotion, especially when several males are in attendance. Occasionally a male, usually a grilse, becomes hurt so badly in the fighting that he dies without spawning.

While the female is digging the nest, the mate assumes a position slightly behind (downstream) and to one side of her. At frequent intervals this male approaches the side of the female closely and the two fish quiver, together or separately. This quivering has often been

mistaken for the emission of the sexual products, but the behavior accompanying the latter action is quite different. Fish of both sexes face upstream during the spawning activities.

In digging the nest the female turns partly on her side and with powerful and rapid movements of the tail disturbs the bottom materials, which are then carried a short distance downstream by the current. As this process is repeated the nest takes form and finally results in an oval or roundish pit or depression, at least as deep and as long as the fish.

The writers have not witnessed the actual deposition of the sexual products, but it is probably very similar to that of the steelhead, described in the comparable section of this paper (pages 144-148). Since the site of the redd, the construction of the pit, and the behavior of the spawning fish are so similar in silver salmon and steelhead, it may be confidently expected that the efficiency of fertilization and covering of eggs will also be much alike.

For many years the view was generally held that natural reproduction of salmonids is a rather ineffective process, but various studies contradict this opinion.

Probably at least 97 percent of the eggs spawned lodge in the pit and are properly buried. Apparently both the eggs and milt are held in the pit by current eddies below the normal level of the stream bed. This view has been advanced for the spawning of various salmonids by Peart (1920) and others. In the spawning of steelhead witnessed by P. R. Needham, A. C. Taft, and Leo Shapovalov and recorded by Needham and Taft (1934) and in the observations of Greeley (1932) on Eastern Brook Trout (*Salvelinus fontinalis*), Brown Trout (*Salmo trutta*), and "rainbow trout" very few eggs were swept out of the pit. Hobbs (1937), in his studies in New Zealand, concluded that at least 97.5 percent of the brown trout eggs lodged in the redds at the time of spawning. His data did not admit of the quantitative expression of the non-lodgment loss in the case of king salmon and "rainbow trout", but his observations suggest that, as was the case with brown trout, the great majority of the eggs produced by them lodged in the places prepared for them by the parent fish, unless interfered with.

On the basis of observations on numbers of silver salmon redds, it is known that the female may dig several pits to complete spawning. The pits are arranged progressively upstream, in chronological order. Probably normally a few hundred eggs are deposited in each pit.

To complete spawning may take a week or more. The length of time probably depends upon the ripeness of the fish, water and atmospheric conditions (especially temperature and volume of water), and the extent to which the mating fish are interrupted by intruders (human beings, stream-side mammals, birds, and other fish).

No quantitative estimate can be made of the amount of damage done to redds by subsequent spawners, which may be steelhead or other silver salmon. It is probable that although the losses from this cause may be severe in individual nests, the percentage loss for all eggs deposited in the stream is not large. Superimposition probably causes more damage to silver salmon than to steelhead redds, since most of the steelhead in California streams spawn after the salmon.

Egg-eating species of fishes present on salmonid spawning grounds often contain eggs in their stomachs. In Waddell Creek such fish are stream steelhead and silver salmon and sculpins (*Cottus*). Such eggs are probably occasional ones shed by fish on their way upstream or in the course of nest digging, disturbed by superimposition of nests on nests prepared by previous fish, or swept out of the spawning pits before they were covered. Hobbs (1937) records brown trout and king salmon eggs in the stomachs of brown trout, and king salmon eggs in the stomachs of rainbow trout, and is also of the opinion that such eggs are occasional ones made available in some of the ways cited above. Greeley (1932) expressed a similar view. The rapid burial of eggs precludes any but an insignificant proportion of eggs being eaten.

All silver salmon, both males and females, die after first spawning. Degeneration of the gonads and certain other physiological changes take place, even before the death of the fish. The occurrence of such changes in a stream such as Waddell Creek, where many of the fish spawn within two miles of the stream mouth, shows conclusively that death is not caused by the rigors of a long journey, but results from independent physiological changes.

Egg Production

The calculation of numbers of eggs produced by Waddell Creek silver salmon is based on the numbers produced by Scott Creek silver salmon, since collection of eggs from Waddell fish would have destroyed the experimental plan. There is no evidence to indicate that the Scott Creek salmon produce a different average number of eggs for a given size of fish from Waddell salmon.

Correlation of Number of Eggs With Size of Fish

The relationship between the length of the fish and the number of eggs produced is shown in Figure 10. This relationship was determined from 29 actual counts of eggs plus 36 measurements of the amount (volume) of eggs and the size (volume) of individual eggs from fish of known lengths.¹³

Measurements of the eggs were carried out according to a method originated by Taft. This, in essence, consists of dividing the actual total volume of eggs from one fish by the average measured volume per egg for that fish. In practice, the eggs from one fish are placed in a graduated glass cylinder, with sufficient water to cover them, and a reading is taken of the volume occupied by the total egg mass. The volume of individual eggs is obtained by taking the average of a series of eggs (usually 10 at Scott Creek) measured in a burette. The measured volume occupied by the total egg mass is then multiplied by a predetermined factor (F) which reduces it to the actual volume of the eggs. The actual volume is then divided by the volume per egg, which gives the calculated number of eggs produced by that fish.

¹³ Counts of eggs were obtained from one Waddell Creek fish taken during the 1933-34 season, four Scott Creek fish spawned during the 1935-36 season, and 24 Scott Creek fish spawned during the 1937-38 season. Measurements of eggs were obtained from 36 fish spawned at Scott Creek in 1935-36. The spawning was done by the incision method (in which the fish is cut open and the eggs removed) by experienced hatchery personnel. The measurements of fish and eggs were made by the writers and various assistants. After the eggs were fertilized they were placed in two-quart glass jars.

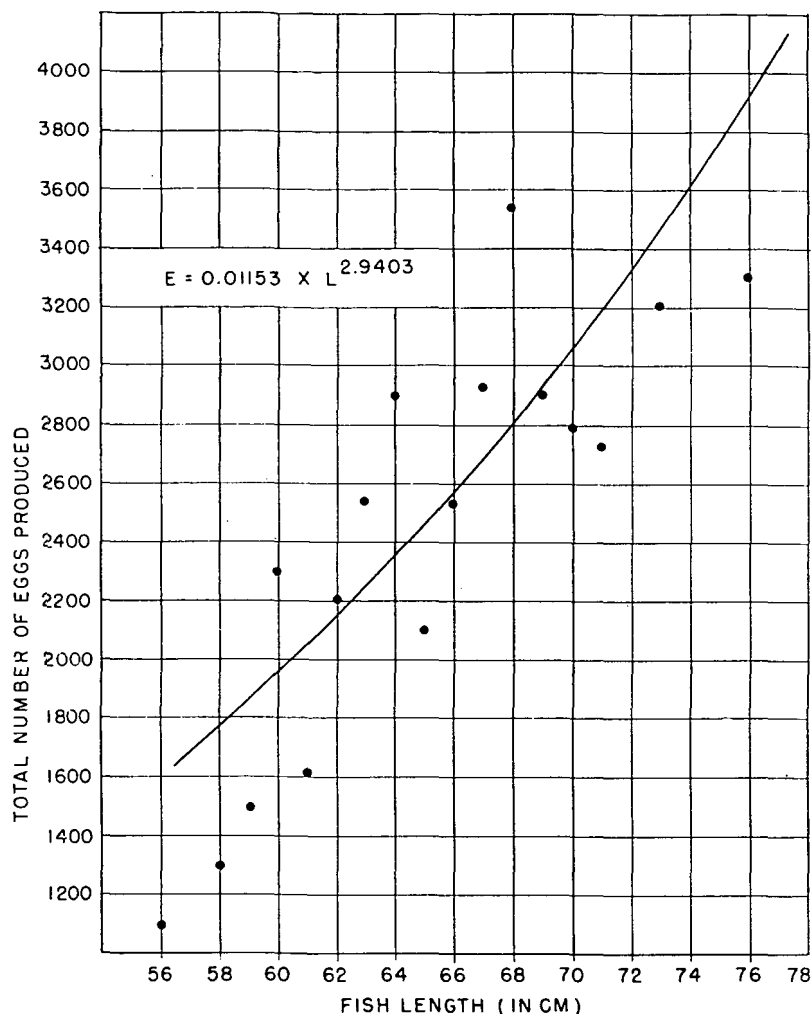


FIGURE 10. Egg production of Scott Creek silver salmon.

F, the reduction factor, or volume factor, as it will be called henceforth in this paper, is calculated according to the following procedure: (1) the volume of the total egg mass and the volume per egg for one fish are measured in the manner outlined, (2) an actual count of the number of eggs is made, (3) the counted number of eggs is multiplied by the volume per egg to give the actual volume occupied by the eggs, (4) the actual volume occupied by the eggs is divided by the graduate reading (volume of total egg mass) to give the volume factor (F). The calculation of the volume factor may be represented by the following formula:

Counted number of eggs (N) \times volume of individual egg (v) = Actual volume of eggs (V)

Actual volume of eggs (V)

Then: $\frac{\text{Actual volume of eggs (V)}}{\text{Measured volume of eggs (M)}} = \text{Volume factor, or portion of measured egg volume occupied by eggs (F)}$

In calculating the volume factor for Scott Creek silver salmon, actual counts of eggs and measurements of total volume from two fish were used. For each of the two fish selected, the volume in c.c. of individual eggs was obtained by averaging the volume of 50 eggs measured in lots of 10 in a burette. Total volume of eggs was measured in water in a 1,000 c.c. glass graduate. From these values a volume factor of 0.680 was obtained. The data used in obtaining F are shown in Table A-2 of the Appendix. The frequency distribution of quantity of eggs (in c.c.) obtained from Scott Creek silver salmon is given in Table A-3 of the Appendix.¹⁴

Using the volume factor of 0.680, the calculated number of eggs was obtained for each of the 36 fish for which egg volumes had been measured. To it was added the number of eggs remaining in the fish to obtain the total number of eggs.

The total number of eggs contained in the above 36 fish and in the 29 for which actual total egg counts had been made was plotted in 200-egg intervals against fish length in 1-cm. intervals and a regression line was fitted to the points. This line was fitted by the method of least squares and, since the relationship is curvilinear, the regression line was determined on a logarithmic scale and later transposed to a linear scale. This regression line is not as accurate as one determined from the original paired variates, but is close enough to the true one to be used here, considering all possible sources of error. Its equation is Number of Eggs = $0.01153 \times \text{Length}^{2.9403}$. The correlation ratio, γ , for the relationship between eggs produced and fish length is 0.682.

Other workers have found a correlation between number of eggs and size of fish for various species of salmonids, including other species of Pacific salmon. For example, Foerster and Pritchard (1941) found a positive significant correlation between the number of eggs contained in the ovaries and both length and weight of individuals in the red salmon (*Oncorhynchus nerka*) and the pink salmon (*O. gorbuscha*). Weights of the Scott Creek silver salmon were not obtained.

As Foerster and Pritchard (*loc. cit.*) have pointed out for the red salmon and pink salmon, the existence of a definite positive correlation between size of females and egg content suggests two important implications, namely, (1) "... any fishing effort which tends to remove the larger fish will proportionately reduce the extent of the egg deposition

¹⁴ The volume factor will vary with (1) size and shape of graduate used, (2) amount of eggs in the graduate, (3) average size of eggs, (4) amount of water over the eggs, and (5) amount of shaking of eggs to settle them in the graduate. All Scott Creek silver salmon and steelhead eggs were measured in a 1,000 c.c. graduate and the eggs were shaken down. Inaccuracies resulting from the "packing effect," which increased with increasing volume of eggs, and the change in the relative amount of the loose "floating layer" of eggs on top with changes in the total volume, are not believed to be large enough to affect the results seriously. For Golden Trout (*Salmo gairdneri*) eggs measured in a 100 c.c. graduate and not shaken down, Curtis (1934) obtained a volume factor of 0.59.

of the spawning escapement and militate against the normal conservation of the species" and (2) "... due caution must be observed in using data pertaining to egg content to indicate racial differences between populations . . . in different rivers."

Published studies of egg production by silver salmon are quite limited. Foerster (1944), summarizing studies in two small streams tributary to the Cowichan River in British Columbia, reported that 88 females in Oliver Creek presumably deposited 199,500 eggs (an average of 2,267) and that 28 in Beadnell Creek deposited 78,100 (average 2,789).

Percentage of Eggs Deposited

The average total number of eggs *produced* was discussed in the preceding section. To calculate the total number of eggs *deposited* in Waddell Creek in each season it was necessary to know the average number of eggs left in the fish after spawning.

The silver salmon that spawn do so quite completely. Actual counts of eggs remaining were recorded for only five fish, as follows: 20, 35, 47, 100, 100 (average 60). However, a number of others were found to have spawned quite completely, the average number of eggs remaining in the fish being well under 100 and probably under 50. It is likely that the number of eggs left in the fish after natural spawning bears little or no relation to the size of the fish (and consequently the number of eggs produced).

The small number of eggs remaining after natural spawning is in agreement with the findings of other workers for various species of salmon and trout. Hobbs (1937) found an average retention of eight eggs per female (range 0 to 53 for 22 fish) in the case of king salmon and 6.7 eggs per female (14 fish) in the case of brown trout. Foerster (1929) found that over 75 percent of 57 dead red salmon examined at Cultus Lake, British Columbia, contained 20 or fewer eggs. (Only three of these salmon, or 5 percent of the total, were found unspawned. Several others had apparently died before completing spawning.)

On the basis of these various observations, it was decided not to subtract any number in calculating the eggs deposited by Waddell Creek silver salmon *which are believed to have completed spawning*, but to use the *total egg production* figures obtained for Scott Creek silver salmon of the same lengths and expressed by the regression line in Figure 10. However, allowance was made for fish which died without completing spawning in each season. The figures previously cited are for eggs remaining in fish that had *completed* spawning. In most streams a certain (usually small) percentage of fish dies without completing spawning. Such fish die from (a) disease, (b) injuries caused by predators, fishermen, fighting, and stream obstacles, and (c) old age, and the numbers dying from such causes depend upon local conditions. The number of eggs remaining after completion of spawning is largely independent of local conditions.

Percentage of Eggs Fertilized

Although quantitative data for Waddell Creek silver salmon are not available, there is every indication that the percentage of eggs fertilized is very high and rather constant.

Extensive spawning work done by personnel of the Department of Fish and Game has shown that the percentage of fertilization of silver salmon eggs *can* be quite high under the close to ideal conditions existing in artificial fertilization. But the only data available to show what happens in Waddell Creek and other coastal streams under natural conditions are the extensive investigations of Hobbs (1937) in New Zealand, the observations of other workers, and general observations (not strictly quantitative) on the emergence of fish from the gravel in Waddell Creek.

It is true that the observations of other workers have been made on other species of salmonids, but the conclusions reached by them fit in so well with the observations of the writers that it appears legitimate to apply them in the present studies, especially since the spawning of the various salmon and trouts follows essentially the same pattern and local conditions usually play a more important role than the factors peculiar to the species involved.

Hobbs found that his material, taken as a whole, indicated a uniformly high efficiency of fertilization in the eggs of all three species which he observed, king salmon, brown trout, and "rainbow trout": over 99 percent. In 32 brown trout redds in 10 different streams the average fertility was 99.17 percent, with a range of from 96.73 to 100 percent.

Hazzard (1932) examined an average sample of 201 eggs in the eyed stage from each of 21 eastern brook trout nests in New York streams. He found that 27 to 98.5 percent, with an average of 79.8, of the eggs contained embryos. In all but one nest more than 69 percent of the eggs were found to be alive.

The observations of the writers and the various seasonal observers consistently indicated a tremendous emergence from the gravel in most seasons; during the few weeks following peak emergence the shallows of the stream seemed alive with fry, which of course could not occur if a high percentage of the eggs had not been fertilized.

Embryology and Hatching of Eggs

The embryology of the silver salmon is in general similar to that of the other Pacific salmon and of trout. The length of time for the eggs to develop to various stages and to hatch is in general dependent upon average temperature of the water, but for a given temperature the average hatching time may vary several days between egg lots taken from different fish and even between eggs taken from the same fish.

The number of days required for silver salmon eggs to hatch varies from about 38 at an average temperature of 51.3 degrees F. to about 48 at an average temperature of 48.0 degrees F. At the temperatures prevailing in Waddell Creek, the usual hatching time is from 35 to 50 days.

Chemical conditions (oxygen, pH, etc.) have some effect on the rate of development of salmon and trout eggs, but probably do not play a significant role within the limits found in Waddell Creek and in the great majority of other coastal streams. Cheyne (1941) found that chum salmon eggs developed at approximately the same rate and pro-

duced healthy fry in waters with dissolved oxygen levels lying between 3.55 and 7.84 p.p.m., although the eggs held at the highest oxygen level produced the largest fry.

Most experiments dealing with the rate of development of salmon and trout eggs have been conducted with uncovered eggs placed in hatchery baskets or incubators. Shapovalov (1937) showed that steelhead eggs in gravel hatch at approximately the same time as those in hatchery baskets.

The percentage of silver salmon eggs which hatch probably varies widely under natural conditions, and in Waddell Creek and other coastal streams free from mining is likely dependent principally upon the amount and character of silting caused by floods occurring between fertilization and hatching. Such silting smothers the eggs, i.e., deprives them of the oxygen necessary for development. Mining silt has a similar effect.

The adverse effect of silting on the development of silver salmon eggs is indicated by the experiments of Shapovalov and Berrian (1940) and Shaw and Maga (1943). The latter authors conclude that "mine silt deposited on gravel spawning beds during either the early or later stages of incubation results in negligible yields of fry and is therefore a serious menace to natural propagation." Hobbs (1937) found that in New Zealand streams the mortality of salmon and trout eggs was greatest in redds containing the largest proportion of fine materials (under 0.03 inch in diameter). Harrison (1923) cites a series of experiments with the eggs of red salmon to determine which of a number of kinds of bottom material was most suitable for the artificial planting of eggs. They show that the finer the material is the heavier is the loss.

Under normal hatchery conditions the hatch is between 80 and 90 percent of silver salmon eggs taken.

Hobbs (1937, 1940) conducted an extensive series of investigations on the natural reproduction of salmonids in New Zealand streams. A large proportion of his studies was concerned with the extent of losses occurring at different stages while the eggs and larval fish were in the gravel.

Hobbs (1937) found that in one stream, Winding Creek, a hatch of over 97 percent of king salmon eggs lodged in redds sampled was indicated in 1933. For brown trout he found that in Black Creek, where losses (of unmeasured extent) occur through the disturbance of earlier redds by later spawners, a hatch in undisturbed redds or portions of redds of over 95 percent of eggs lodged was indicated. In the Selwyn River, where it was not known if later spawners disturbed the contents of early redds, in undisturbed redds or portions of redds a hatch of over 97 percent of brown trout eggs was indicated. In a third stream (Slovens Creek), however, in which redds were not disturbed by subsequent spawners, a loss of something over 25 percent of the eggs of brown trout lodged was indicated. For the streams examined, Hobbs concluded that heavy losses of fertilized eggs are the outcome of adverse environmental conditions and not of inherent weakness, that the extent of losses of fertilized eggs in undisturbed redds depends primarily on the amount of very fine material in the redds during the development of eggs before eyeing, that losses, of unmeasured extent, of the eggs of brown trout occur through the superimposition of redds of later

spawners, that all floods tend to be harmful in that they increase the deposition of fine material in redds, and that although floods rarely effect substantial modification of the contours of redds, they may cause losses considerable enough to account for the partial failure of a year class when they do so.

In further studies, based on 529 samples consisting of 422,841 specimens from natural redds of brown trout and "rainbow trout" in nine New Zealand river systems, Hobbs (1940) estimated survival to time of hatching among eggs of both brown trout and "rainbow" trout to have been approximately as follows: 96.80, 95.36, 94.50, 93.92, 93.15, 90.64, 88.62, 87.14, and 70.71 percent, giving an average of 90.1 percent. In commenting on these figures, an editorial in *The Salmon and Trout Magazine*, No. 101, January, 1941, states: "This last district, however, must be exceptional, as the next highest [loss] is only 12.86 percent, and if this particularly bad one is omitted the average loss is less than 7½ percent." However, the unusually heavy losses appear to be characteristic of that particular river system, since in 18 of 28 samples dead eggs exceeded 10 percent, and in 10 of the 18 were in excess of 20 percent, so probably should be included in arriving at an average. The problem of the treatment of exceptional cases is one that often confronts the biologist, and one that cannot always be solved by statistical analysis. In the case under discussion, for example, Hobbs stated that the heavy losses "reflect unsatisfactory features of the spawning medium." These features consist of the presence of clay and swamp detritus in the gravel in excessive quantities, and the inimical conditions were aggravated by the massing of redds, so that material disturbed by late spawners had frequently settled in redds immediately below. Any investigator, in attempting to apply some average from data obtained by another investigator to his own studies, must decide whether or not the unusual cases of the other investigator are also unusual in his data, or entirely absent, or characteristic. Thus, if spawning grounds in some area are uniformly of high quality, we have some justification for using the figure of 7.5 percent as probable pre-hatching loss; if poor spawning areas occur in the approximate ratio of 1:8, we should expect to be more nearly correct if we use the figure of 9.1; while if the spawning grounds are uniformly poor we should probably use the pre-hatching loss figure of 29 percent.

Some criticism has been made of Hobbs' method of calculating losses in the gravel, which consists of digging up the natural redds and determining the proportional numbers of dead and live eggs and larvae in different stages. Some workers believe that Hobbs' survival figures may be too high, because of irrecoverable eggs (eggs not recovered because of decomposition, crushing in digging up the redds, or through oversight in digging up the redds). It is true that in egg burial experiments with known numbers of eggs, in which dead eggs and larvae have been dug up, there has been an unaccounted for loss. Carl (1940), in an experiment directed toward determining the possibility of the production of differences in eye diameter by incubation in gravel and in open hatchery troughs, planted 2,000 silver salmon eggs from several females in gravel (taken from an area normally used for spawning) to a depth

of 6 to 8 inches in a hatchery trough screened at both ends and obtained a survival of 53.7 percent, with 160 eggs (8 percent) unaccounted for. The same number of control eggs in a standard hatchery basket yielded a hatch of 87.9 percent. Carl states: "The high losses were probably the result of the extra handling during the intermingling of the eggs of different fish and during the subsequent counting." And, in regard to the unaccounted for eggs, "A similar disintegration in nature may explain in part the high rates of efficiency obtained by basing the estimated loss in eggs in the redd only upon the number of 'blank' eggs found in the gravel." If in the same experiment a calculation had been based on the number of fry produced as compared with the number of dead eggs recovered, the survival figure obtained would have been 58.5 percent, a difference of only 4.8 percent from the true figure. With the higher survival figures obtained by Hobbs (about 90 percent in his 1940 paper), the percentage difference would also be somewhat higher. Assuming a total deposition of 2,000 eggs and an unaccounted for loss of 8 percent, or 160 eggs, the calculated survival would be 1,656 eggs (90 percent of 2,000 — 160 = 1,840) and the number of dead eggs found would be 184 (10 percent of 2,000 — 160 = 1,840). The true loss would then be $184 + 160 = 344$, or 17 percent, a difference of only 7 percent.

In experiments described by Shaw and Maga (1943) both the mortality and unaccounted for loss were much higher than in the experiment of Carl (*loc. cit.*). In these experiments 21 lots of 500 silver salmon eggs each (altogether from 17 females) were buried in gravel to a depth of 3 or 4 inches. Since mining silt was artificially introduced into some of the lots, only the seven gravel control lots will be considered at this time. From Table 13 it is seen that the average survival to time of emergence was 16.2 percent, with a maximum of 25.4 percent, that the average recovery of dead eggs and fry from the gravel was

TABLE 13

Silver Salmon: Yield and Recoveries of Fry and Eggs From Gravel in Hatchery Troughs

Nest*	Yield of fry		Fry and eggs recovered from gravel			Fry and eggs unrecovered from gravel	
	Number of fry	Percent-age yield	Number of fry	Number of eggs	Percent-age fry and eggs	Number	Percent-age
1.....	30	6.0	36	4	8.0	430	86.0
2.....	8	1.6	3	4	1.4	485	97.0
3.....	64	12.8	5	9	2.8	422	84.4
4.....	127	25.4	24	1	5.0	348	69.6
5.....	106	21.2	12	11	4.6	371	74.2
6.....	111	22.2	7	14	4.2	368	73.6
7.....	120	24.0	35	3	7.6	342	68.4
Totals.....	566		122	46		2,766	
Averages.....	81	16.2	17	7	4.8	395	79.0

* Five hundred eggs buried in each nest.

4.8 percent, and that the average unaccounted for loss was 79.0 percent. As Shaw and Maga (*loc. cit.*) point out, while the eggs and fry were in the gravel "several storms brought in natural sediment which tended to settle in the upper nests of the trough." And: "Visual observation indicated that most of this sediment . . . settled on the first three nests while the last four were relatively free from silt." The authors go on to say "The higher and fairly constant yield of live fry from the last four nests is therefore representative of development without appreciable silting, while the lower values from nests 1-3 represent yield of fry for gravel beds that were subject to natural silting." In regard to the survival to emergence, the present writers agree that the differences between the first three and the last four nests reflect relative differences in the amount of silting, but it also seems quite possible that there was sufficient silting in the case of the last four nests to make it a factor of some consequence in the yield.

An experiment on the survival of silver salmon eggs in gravel conducted by Shapovalov and Berrian (1940) resulted in the low emergence of 10.2 percent, which was attributed to silting from severe storms. In the control, 65.9 percent of the eggs hatched and 48.2 percent survived to the time that the experimental fish had finished emerging from the gravel.

In justification of the figures obtained by Hobbs: (1) He considered the possibilities of dead eggs and fry having decomposed to stages which would not permit of their recovery by the methods employed (1937, pages 32-33), and carried out tests on the rate of decomposition of freshly killed eggs artificially buried in the gravel at various temperatures. Hobbs concluded (1940, page 43): "Generally, data available do not suggest that failure to take decomposition of dead ova into account will cause errors comparable in extent to any resulting from the exigencies of sampling." (2) Many of Hobbs' samples were collected at early stages of development, while in the burial experiments cited by Carl (1940) and Shaw and Maga (1943) the dead eggs and fry were not dug up until the live fry had finished emerging from the gravel. The time between burial and removal of eggs was not recorded by Carl, but it was 98 days in the experiments cited by Shaw and Maga. From the viewpoint of the time element alone, then, one would expect an unaccounted for loss to be much less in the case of Hobbs.

In view of the low survival figures obtained in the different egg burial experiments, compared to Hobbs' figures, one might be led to ask, "What accounts for the difference, if not an unaccounted for loss?" In reply, the following facts might be pointed out. (1) In at least two of the experiments cited (Shapovalov and Berrian, 1940; Shaw and Maga, 1943) varying quantities of silt were brought into the water by storms. Conditions in this respect in the experiments of Carl (1940) are not known. (2) It seems likely that the same amount of silt carried in water in a hatchery trough would settle in greater quantities and cause greater mortality than in natural stream water, which would have a higher velocity. (3) Losses in experiments may be increased by (a) handling of the eggs in counting and burial, (b) introduction of *Saprolegnia* (fungus) and its greater development than would occur under natural conditions, (c) improper reproduction of natural conditions

(kind and size of gravel, depth and manner of burial, flow of water through the gravel). In regard to fungussing, Hobbs (1937) says that "*Saprolegnia* appeared to be the only important factor in the reduction of dead ova from a recoverable to an irrecoverable state" and that it was clear in the case of trout redds "that the cleaner the redd was the more rapid was the infection of the dead ova with fungus."

Less complete studies made by other workers do not disagree materially with the findings of Hobbs. For example, White (1930) obtained a hatch of 77 percent (342 of 452) eastern brook trout eggs dug from a redd on Prince Edward Island immediately after spawning. The losses included eggs that died from injuries received when they were removed from the gravel. In another test naturally fertilized eggs placed on a screen filled with gravel and buried in a redd yielded a hatch of 66 percent.

In conclusion, it appears to the present writers that if Hobbs' survival figures are too high because of unaccounted for loss, the error is probably not more than 10 percent of the total; in other words, if this error exists, Hobbs' 1940 previously cited average of 90 percent may actually be between 80 and 90 percent, which would still make natural reproduction under normal conditions quite an efficient process.

The losses computed by Hobbs (*loc. cit.*) necessarily did not include those that occurred through removal of eggs from the redds, which is caused principally by floods and superimposition. Losses resulting from these two factors will vary tremendously from stream to stream and from season to season. Hobbs concludes that the general tenor of such information as is available regarding the extent of losses caused by direct flood action "is to suggest that in many streams the chances of flood loss are very remote, while in others, while losses occur, they do so only at irregular intervals." In Waddell Creek, serious losses probably occur only in the case of exceptional floods. Hobbs found superimposition to be general in the streams which he studied, but was unable to measure the extent of losses resulting from displacement of eggs. In Waddell Creek, utilization of areas used by earlier spawners has been noted on various occasions, but no quantitative estimate of the amount of loss can be made, although it is not believed to form a large percentage of all the eggs deposited.

Emergence From the Gravel

Silting, which has been pointed out in the preceding section as the principal factor determining the survival rate from deposition and fertilization of eggs to hatching, is also probably the principal factor determining the survival rate from hatching to emergence from the gravel.

In various experiments with burial of silver salmon eggs in gravel, it has been impossible to segregate survival from time of burial to hatching from survival from hatching to emergence, but the following percentage survivals to time of emergence have been obtained: Harrison (1923) 75; Carl (1940) 53.7; Shapovalov and Berrian (1940) 10.2 (heavy silting); Shaw and Maga (1943) 16.2 average (some silting), 1.16 average (artificially introduced mining silt).

From the above figures it is evident that the percentage emerging may vary widely and that it probably depends upon the amount and

character of silting. In the presence of silting the heaviest losses probably occur in pre-hatching stages. Shaw and Maga (1943) found that the artificial introduction of mining silt only during the time that the fish had hatched but were still in the gravel results in less severe losses (13.4 percent survival) than when the silt is introduced at earlier stages. Hobbs (1940) found it to be generally true for the various species of salmonids which he studied that the loss between hatching and time of emergence was extremely light, exceeding 1 percent in only one river system.

In the various experiments cited the water in the hatchery troughs had a considerably lower velocity than would water in a natural stream laden with an equal amount of silt and so it may be that under natural conditions the percentage of emergence is rarely as low as was the case in some of the experiments.

Foerster (1944), summarizing studies in two small streams tributary to the Cowichan River in British Columbia, reported that the records of percentage efficiency of natural propagation in terms of counted fry were: Oliver Creek, 14.4, 11.8, 30.4, 26.0, and 25.6 percent during five years, and Beadnell Creek, 40.0, 30.1, and 16.3 percent during three years.

Again, there is no quantitative basis for estimating the average percentage of silver salmon emerging from the gravel in Waddell Creek, but the writers believe that under favorable conditions (principally absence of heavy silting) it is high, probably between 65 and 85 percent of the eggs deposited. There is, of course, no stage in hatchery operations directly comparable to the period from time of hatching to time of emergence under natural conditions, but under hatchery conditions the losses during the equivalent period of time normally are light, so that hatchery survival to time that silver salmon finish emerging from the gravel under natural conditions is still between 80 and 90 percent of the eggs taken.

The experiments conducted by Shapovalov and Berrian (1940) and Shaw and Maga (1943) indicate that the silver salmon fry start emerging from the gravel two to three weeks after hatching and require in addition two to seven weeks to complete emergence, with peak emergence occurring within three weeks of hatching. This is probably what happens under normal conditions in California coastal streams. Shallow burial, loose gravel, absence of silt, and high temperatures may all be expected to speed emergence, while the opposite conditions may be expected to retard it.

Under normal conditions the fry rarely emerge from the gravel before the yolk sac is absorbed. Shallow burial results in premature emergence, a fact noted by Babcock (1911). The time of peak emergence from the gravel approximately coincides with the beginning of feeding in the hatcheries.

Because of the normal long period of emergence, the first fish to emerge have usually put on considerable growth by the time the last fish emerge, despite the fact that the eggs were deposited at the same time.

In the experiments cited by Shapovalov and Berrian (1940) apparently most of the fish emerged at night. It is probable that a similar emergence in nature provides the young fish considerable protection from enemies.

**Stream Life Prior to Seaward Migration
(General Features)**

At Waddell Creek the only quantitative data regarding numbers of fish were obtained at times of migration through the trap, so the following account will necessarily be based on general observations.

As the young fish emerge from the gravel they seek out and take up residence in the shallow gravel areas, especially at the sides of the stream. At first they tend to congregate in schools, but as time passes and the fish grow these schools break up and the fish spread up and down the stream. Individuals tend to take up niches, and to drive out other fish of approximately the same size from their selected "territories." As in the case of the adults at spawning time, individuals seem to recognize the "right" of possession, and it is not uncommon to see a fish that has taken up residence in a particular spot dart at and drive away a larger individual of the same age class without much opposition from the intruder.

The fry in the shallows feed avidly and grow rapidly (Table 14). They rise to nearly every small object drifting downstream or falling into the water, selecting those that are suitable and rejecting those that are not wanted. Following the rise, they return to the original position.

It is obvious from general observations that following the peak of emergence there is a marked decline in the numbers of fry in the stream. It will be seen from the following section that very few fish of the season migrate to sea, so the losses must occur in the stream.

Possible causes of losses at Waddell Creek are the following: (1) predators, (2) drying stream channels, and (3) disease.¹⁵ The proportionate losses from these different causes during the first growing season are not known, but through a process of elimination one is led to the conclusion that predatory fishes make the greatest inroads. Other predators on fish of such small size are limited in Waddell Creek and most other California streams to garter snakes and the Dipper. These are not present in sufficient numbers to be the principal cause of loss at this stage. Many, if not most, of the fish taken by garter snakes are those from drying portions of the stream. The fry persist in hugging the shallows even when such areas are likely to go dry because of dropping stream levels. In some California streams, especially in their lower portions, appreciable losses occur in drying side pools and even main stream channels, but in Waddell Creek such losses are not of major proportions. Disease is the third possible cause of losses at this stage. Normally disease among salmon and trout in natural surroundings is not prevalent. It is possible that in 1933-34 furunculosis took a certain toll, but disease is not believed to be a principal cause of loss of fry in Waddell Creek.

As the fish grow, they gradually move into deeper water and eat coarser food. Around July or August they move into the deeper pools,

¹⁵ In other California streams high temperatures, pollution, and lack of suitable food at times also cause losses, but may be eliminated from consideration in the case of Waddell Creek.

TABLE 14
Waddell Creek, Silver Salmon: Growth During First Year of Life, by Two-week Periods

Source	Item	Downstream migrants		Seined in stream		Upstream migrants	
		Number	Mean length (mm.)	Number	Mean length (mm.)	Number	Mean length (mm.)
	Apr. 1-14	10	12	35	38	8	33
	Apr. 15-28	12	12	38	38	1	33
	Apr. 29-May 12	2	12	39	39	1	33
	May 13-26	12	12	51	51	1	33
	May 27-June 9	6	13	45	56	1	33
	June 10-23	13	25	58	58	1	33
	June 24-July 7	16	16	59	59	1	33
	July 8-21	2	16	58	58	1	33
	July 22-Aug. 4	2	16	58	58	1	33
	Aug. 5-18	2	16	65	65	1	33
	Aug. 19-Sept. 1	2	16	78	78	1	33
	Sept. 2-15	1	16	64	64	1	33
	Sept. 16-30	1	16	64	64	1	33
	Oct. 1-14	1	16	62	62	1	33
	Oct. 15-28	1	16	62	62	1	33
	Oct. 29-Nov. 11	1	16	79	79	1	33
	Nov. 12-25	1	16	80	80	1	33
	Nov. 26-Dec. 9	1	16	80	80	1	33
	Dec. 10-23	1	16	80	80	1	33
	Dec. 24-Jan. 6	1	16	80	80	1	33
	Jan. 7-20	1	16	82	82	1	33
	Jan. 21-Feb. 3	1	16	81	81	1	33
	Feb. 4-17	1	16	86	86	1	33
	Feb. 18-Mar. 3	1	16	93	93	1	33
	Mar. 4-17	1	16	89	89	1	33
	Mar. 18-31	1	16	101	101	1	33

TABLE 15

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap, by Seasons and Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record										
Oct. 8-14		4	1							5	1
Oct. 15-21		2								2	+
Oct. 22-28											
Oct. 29-Nov. 4											
Nov. 5-11		1								1	+
Nov. 12-18		10	39				4			53	7
Nov. 19-25			378							378	47
Nov. 26-Dec. 2			81							81	10
Dec. 3-9			6							6	1
Dec. 10-16	1									1	+
Dec. 17-23							1			1	+
Dec. 24-30		1	5	2					2	10	1
Dec. 31-Jan. 6			17	2			5			24	3
Jan. 7-13		2	8	2						12	1
Jan. 14-20			17	2						19	2
Jan. 21-27			8							8	1
Jan. 28-Feb. 3											
Feb. 4-10	2			3			1			6	1
Feb. 11-17			1	3	1	1				6	1
Feb. 18-24				1						1	+
Feb. 25-Mar. 3		2	1							3	+
Mar. 4-10		1	4				2			7	1
Mar. 11-17	4		8				1			13	1
Mar. 18-24	3		2				6			11	1
Mar. 25-31	15	1	1				3			20	2
Apr. 1-7	52	21		1	1	6				81	9
Apr. 8-14	239	6	2		1	26	2		2	278	31
Apr. 15-21	606	49	16	24	5	143	51	2	1	897	99
Apr. 22-28	910	200	120	16	4	316	102	2	1	1,671	186
Apr. 29-May 5	909	755	1,086	142	19	163	72	15	49	3,210	357
May 6-12	415	881	1,327	329	104	157	300	60	149	3,722	414
May 13-19	143	555	1,278	307	679	24	262	33	161	3,442	382
May 20-26	61	624	343	132	781	9	425	29	139	2,543	283
May 27-June 2	27	271	109	87	261	1	366	6	32	1,160	129
June 3-9	39	131	39	8	48	2	113	1	112	493	55
June 10-16		21	11	4	5	2	18		32	93	10
June 17-23		13	1	2	16		4	2	8	46	5
June 24-30		8	2		1			2	6	19	2
July 1-7	1	5					1		5	12	1
July 8-14		6				2			5	13	1
July 15-21									4	4	+
July 22-28	1								2	3	+
July 29-Aug. 4											
Aug. 5-11											+
Aug. 12-18						1			1	2	+
Aug. 19-25											
Aug. 26-Sept. 1		2								2	+
Sept. 2-8											
Sept. 9-15	1									1	+
Sept. 16-22	1									1	+
Sept. 23-30		1								1	+
Totals	3,430	3,573	4,911	1,067	1,926	852	1,740	152	711	18,362	--

often those with overhanging logs. It appears that about this time the fish cease feeding or at least greatly diminish it, since the growth rate slows down. Movement of the fish into the holes and cessation of feeding and growth are associated with the period of maximum stream temperatures and minimum flow. It is of interest that silver salmon in hatchery ponds, in which the water volume is constant, also take a greatly diminished amount of food beginning about July. This indicates that stream temperatures may be the influencing factor in the cessation of feeding in late summer. In this connection it may be pointed out that rate of increase or relative increase in temperatures, as well as absolute temperatures reached, may determine the time and extent of cessation of feeding.

During the period of heavy rainfall and lowest temperatures, December through February, feeding continues to be light and growth negligible, according to measurements and scale reading. The stream is often at flood stage and turbid during this period. It is therefore difficult to make observations in the stream, but judging by counts of fish taken in the traps at the dam and such general observations as have been possible, it appears that the fish are not swept downstream¹⁶ and do not move downstream voluntarily in large numbers.

Following the period of maximum precipitation the fish start making extremely rapid growth (March). Rising temperatures at this time of year, coupled with an abundance of aquatic food organisms, likely influence the fish to resume heavy feeding. The resumption of feeding and growth is reflected in the rapid increase in average size of fish, and consequently in the structure of the scales.

Toward the end of March or sometime in April, approximately a year following their emergence from the gravel, the fish begin to migrate to the ocean.

Data to be presented in a subsequent section (page 101) indicate that there is an inverse correlation between average amount of growth made to time of migration and the number of migrants (= total stream population of age 1 fish).

Seaward Migration of Juveniles

During the nine seasons of operation of the trap¹⁷, 18,362 juvenile silver salmon were checked on their downstream migration. The number taken during each weekly period in each season is shown in Table 15.

Table 16 shows the sizes of the juvenile silver salmon migrating downstream, grouped by 5 mm. intervals and two-week periods for the nine seasons combined. The same data for the individual seasons are given in Tables A-4 to A-12 of the Appendix. The length of these fish from tip of snout to fork of caudal fin was recorded in mm., measurement being made to the next highest mm.¹⁸

¹⁶ The fish probably make use of backwater and eddies in maintaining their position in the stream. Even after the greatest floods, practically no fish have been found in the areas from which the water has receded.

¹⁷ In 1933-34, the first season, the trap was not put into operation until the week of December 3-9.

¹⁸ From May 29th through September 30th of the 1933-34 season and from October 1st through November 20th of the 1934-35 season the fish were measured only as three inches and under or over three inches (approximately 76 mm. and under or over 76 mm.). This system was in effect during a period when a regular observer was not available and the fish were checked by hatchery personnel. The demarcation line of three inches was chosen as the approximate line between fish of the season and older fish.

TABLE 16

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap; Length-frequency Distribution by Two-week Periods, All Seasons Combined

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29-Nov. 11	Nov. 12-25	Nov. 26-Dec. 9	Dec. 10-23	Dec. 24-Jan. 6	Jan. 7-20	Jan. 21-Feb. 3	Feb. 4-17	Feb. 18-Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25	*4	*2		*6										
30														
35														5
40														5
45														
50														
55														
60				1				2						
65	1			4	1		2							
70				33	5		4	1						
75				94	18	1	6	4	2	2		1		
80				125	26	1	8	2	2	2	1	2	3	1
85				98	20		6	12	1	1	1	3	3	5
90				44	10		3	5	3	3		7	3	6
95				18	3		2	5		3		6	3	5
100				3	1		3					2		16
105				1	2					1	1		4	25
110					1						1		2	45
115													2	57
120													6	87
125														65
130													1	20
135														5
140													1	5
145														1
150														
155														
160														1
165														
			†1	†4										
Totals	Age +													10
	Age 1	5	2	1	431	87	2	34	31	8	12	4	20	349

* Recorded only as 3 inches or under.

† Recorded only as over 3 inches.

NOTE: In this and other length-frequency tables, the central figure of the three consecutive length frequencies representing the greatest total number of fish is printed in bold face type.

Scale samples were taken from the great majority of the fish during the first six seasons of operation, i.e., 1933-34 through 1938-39. Although time permitted reading of only a small portion of them, it is evident from Table 16 that all of the fish fall into two groups, representing a very few fish of the season and a large number of age 1 fish. Examination of scale samples of the largest fish taken and also of fish taken at abnormal migration periods confirms this view. Of the 18,362 fish taken in the downstream trap, 18,256 were age 1 fish and only 106 age + fish.

All scales of *adult* silver salmon taken at Waddell Creek show the fish to have migrated to the ocean at age 1. From this and general observations we know that the juveniles go to sea in the same season in which they migrate downstream. It is therefore proper to speak of the downstream migration as a seaward migration. Whether the very few age + fish occurring in the migration remain in fresh water until the following season or go to sea and perish is not known, but their

TABLE 16—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap; Length-frequency Distribution by Two-week Periods, All Seasons Combined

Length in mm.	Apr. 15- 28	Apr. 29- May 12	May 13- 26	May 27- June 9	June 10- 23	June 24- July 7	July 8- 21	July 22- Aug. 4	Aug. 5- 18	Aug. 19- Sept. 1	Sept. 2- 15	Sept. 16- 30	Tot- al	
21-25	--	--	--	--	--	*1	--	--	--	--	*1	--	*14	
30	--	--	--	1	--	--	--	--	--	--	--	--	1	
35	1	--	--	2	--	--	--	--	--	--	--	--	8	
40	10	2	1	--	2	--	--	--	--	--	--	--	20	
45	1	--	2	--	1	--	--	--	--	--	--	--	4	
50	--	--	2	--	1	5	1	--	AGE +				9	
55	--	--	3	2	1	6	5	1	--	--	--	--	18	
60	--	--	4	--	4	5	5	--	--	--	--	--	21	
65	--	--	--	1	1	4	3	1	2	--	--	1	21	
70	--	--	--	--	1	1	1	--	--	--	--	--	46	
75	--	1	--	--	1	2	1	--	--	1	--	--	134	
80	2	--	--	--	1	2	--	--	--	--	--	--	178	
85	4	5	4	4	--	--	--	--	--	1	--	--	168	
90	9	20	29	7	3	1	--	--	--	--	--	1	154	
95	43	105	114	43	9	--	--	--	--	--	--	--	359	
100	136	328	373	126	25	1	--	--	--	--	--	--	1,016	
105	306	757	765	248	30	1	--	--	--	--	--	--	2,141	
110	489	1,371	1,163	334	20	--	--	--	--	--	--	--	3,426	
115	548	1,562	1,277	361	16	1	--	--	AGE 1				3,824	
120	453	1,372	1,190	255	10	--	--	--	--	--	--	--	3,373	
125	293	781	613	152	4	1	1	--	--	--	--	--	1,910	
130	131	388	298	54	6	--	--	--	--	--	--	--	898	
135	83	159	105	16	1	--	--	--	--	--	--	--	369	
140	30	51	20	4	1	--	--	--	--	--	--	--	112	
145	21	18	13	3	--	--	--	--	--	--	--	--	60	
150	6	6	5	--	--	--	--	--	--	--	--	--	18	
155	1	4	3	--	1	--	--	--	--	--	--	--	9	
160	1	1	1	1	--	--	--	--	--	--	--	--	5	
165	--	1	--	--	--	--	--	--	--	--	--	--	1	
				†39				†1					†45	
Totals	Age +	12	2	12	6	13	26	16	2	2	2	1	2	106
	Age 1	2,556	6,930	5,973	1,647	126	5	1	1	--	--	--	--	18,256

numbers are so small that it is a matter of little consequence. Therefore, this section of the paper will deal only with the age 1 migrants.

An examination of Table 16 reveals that there is a distinct increase in length of the fish from the time that they are taken during the fall and winter as atypical migrants to the time of the beginning of the spring migration. Scale reading shows that the great majority of the fish in the spring migration have started growth of the new season, even in the early part of the migration. This fact indicates that the difference in size between the abnormally early migrants and those of the regular spring migration represents growth taking place in the year class as a whole. The early start of the growing season at Waddell Creek holds good for the steelhead as well (pages 160-163). Mean lengths of age + and age 1 seaward migrant silver salmon by two-week periods for each season are given in Tables A-13 and A-14 of the Appendix.

The question now arises to what extent the migration through the trap is representative of the total downstream migration (i.e., migration through the trap plus the uncounted migration over the dam and migration of fish produced below the dam), as regards time of migration.

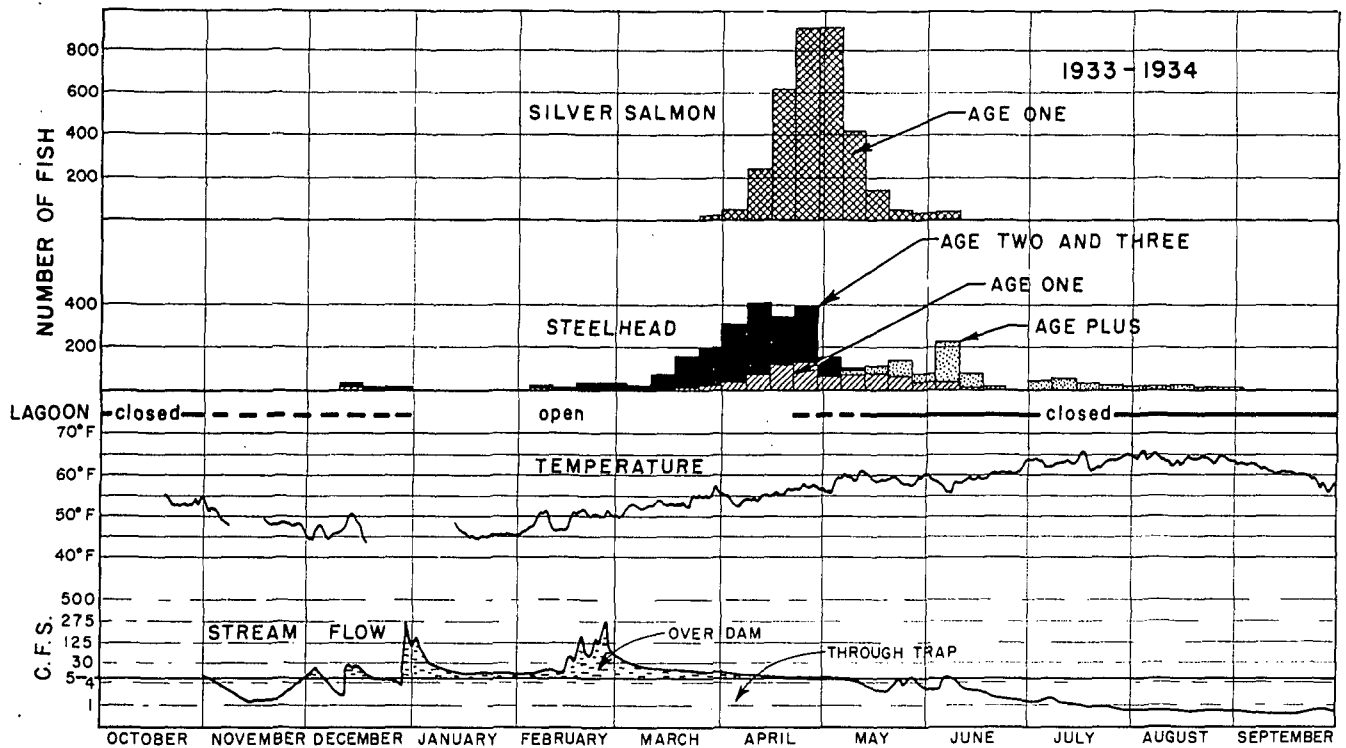


FIGURE 11. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1933-34 season.

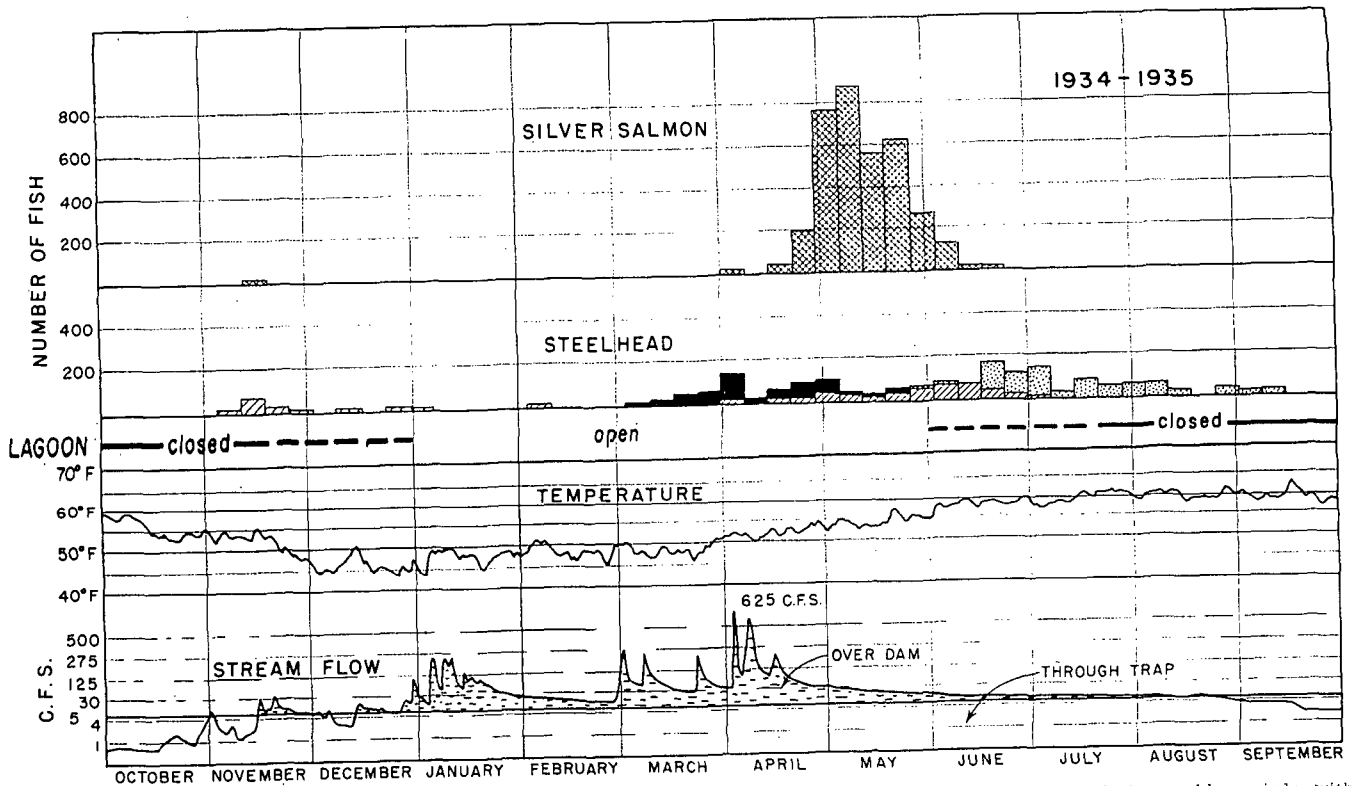


FIGURE 12. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1934-35 season.

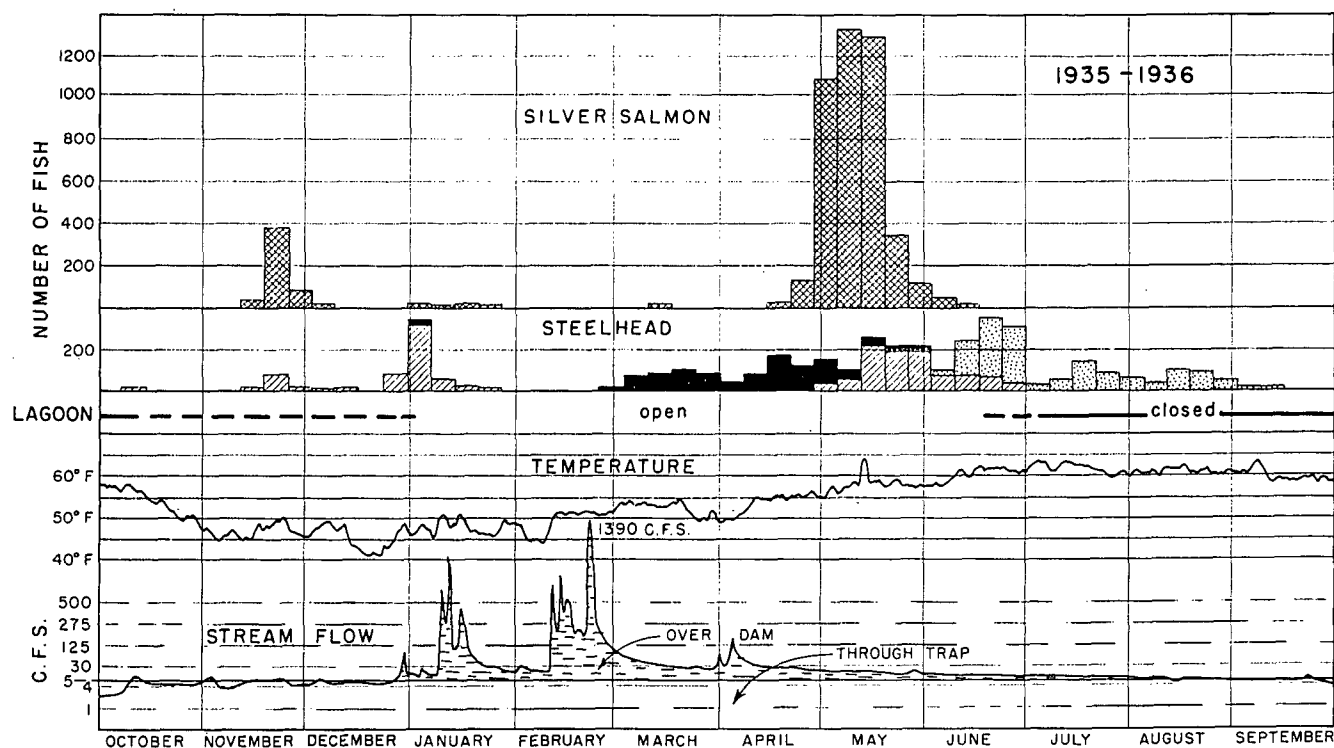


FIGURE 13. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1935-36 season.

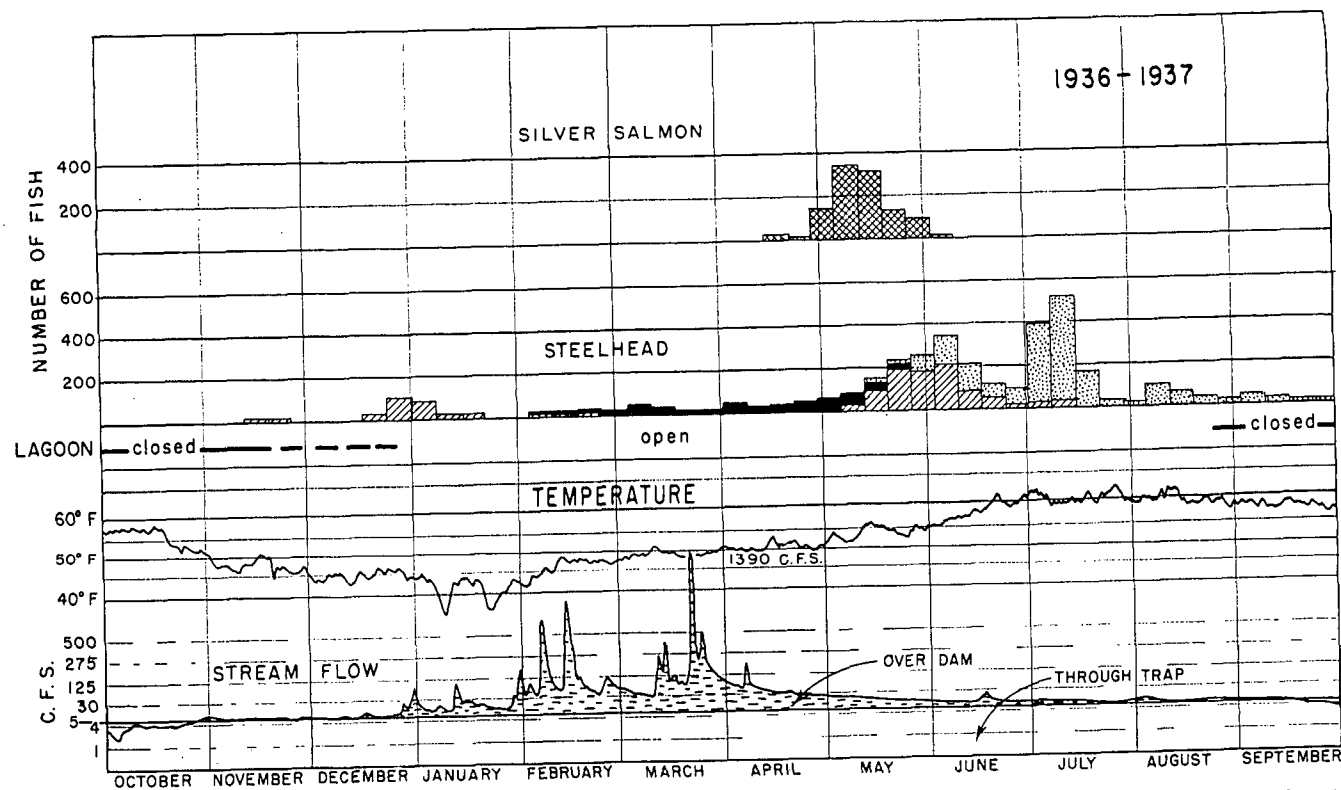


FIGURE 14. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1936-37 season.

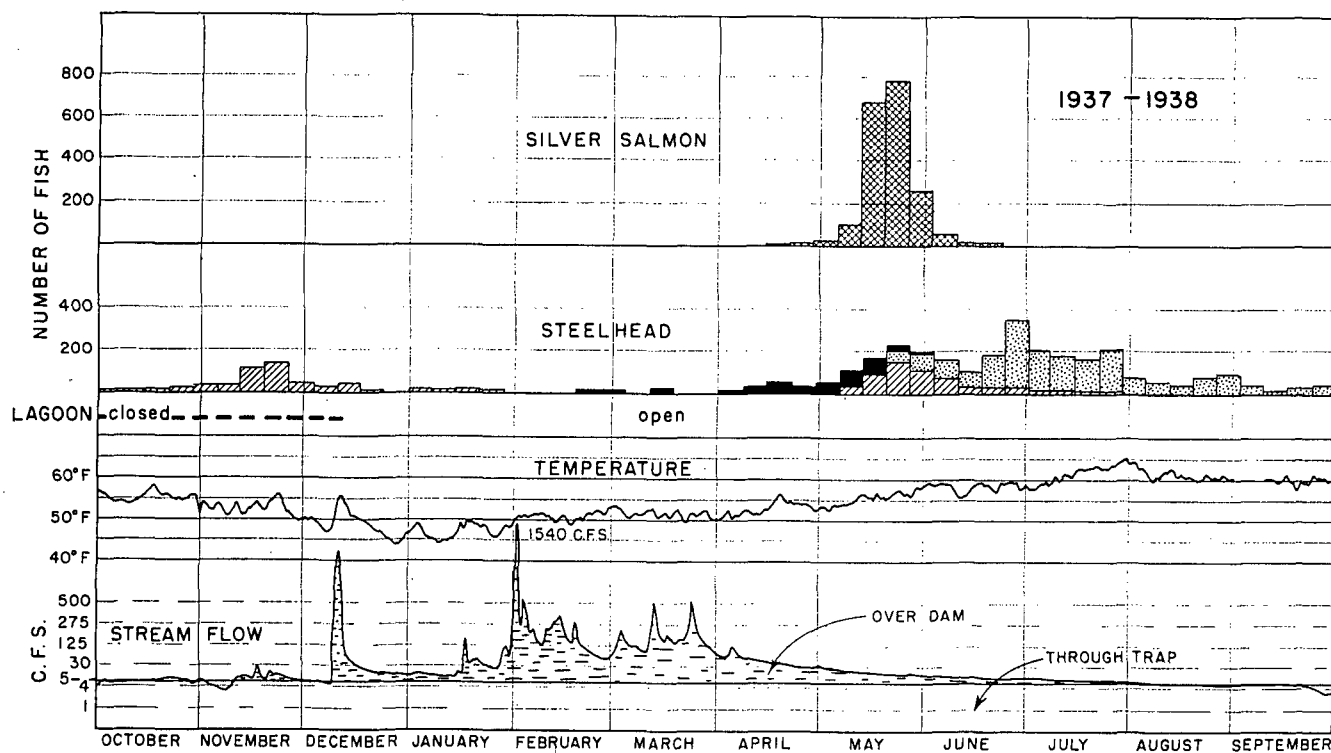


FIGURE 15. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1937-38 season.

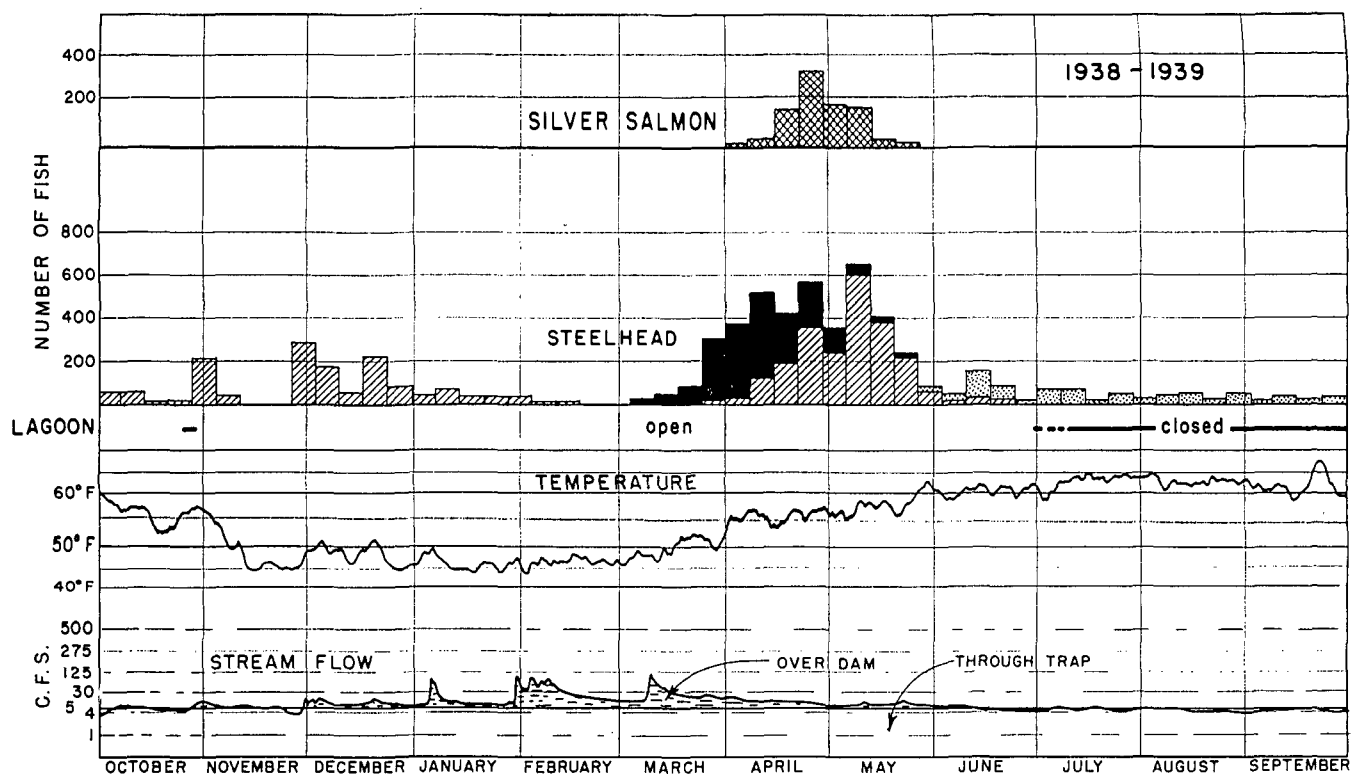


FIGURE 16. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1938-39 season.

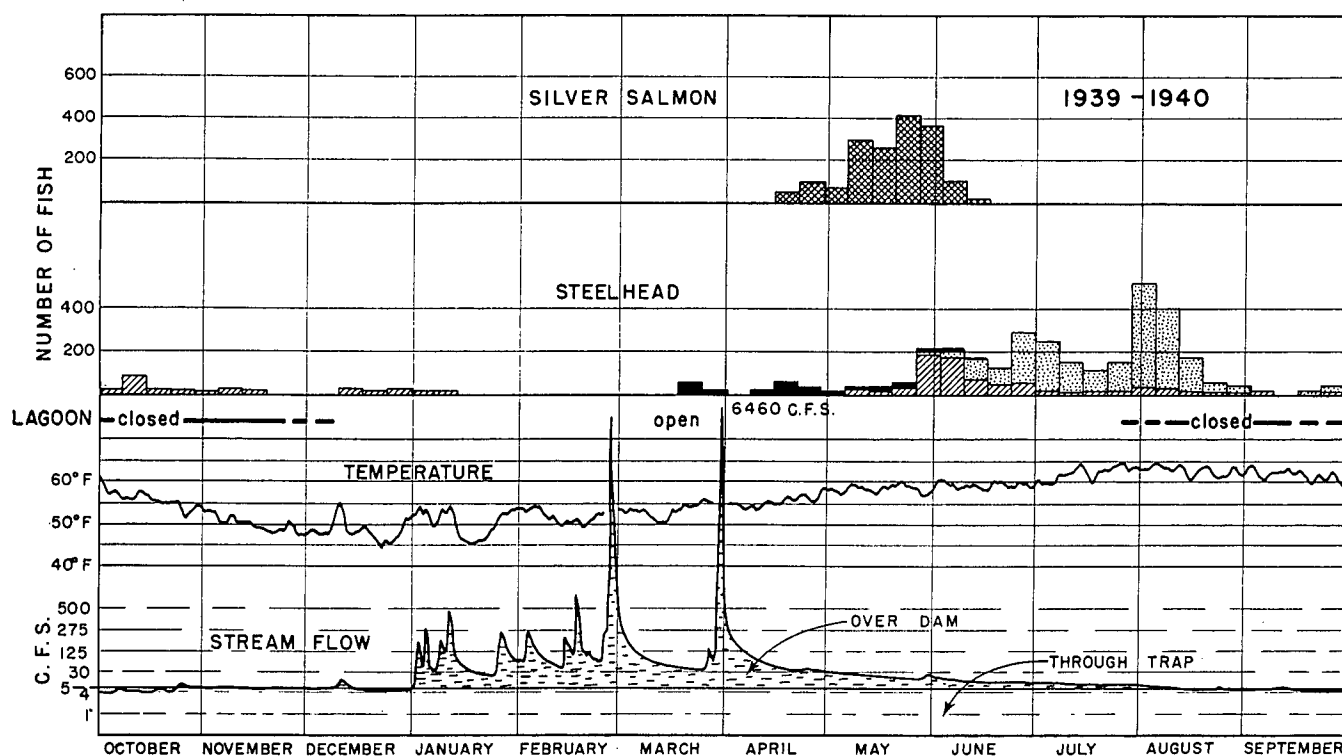


FIGURE 17. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1939-40 season.

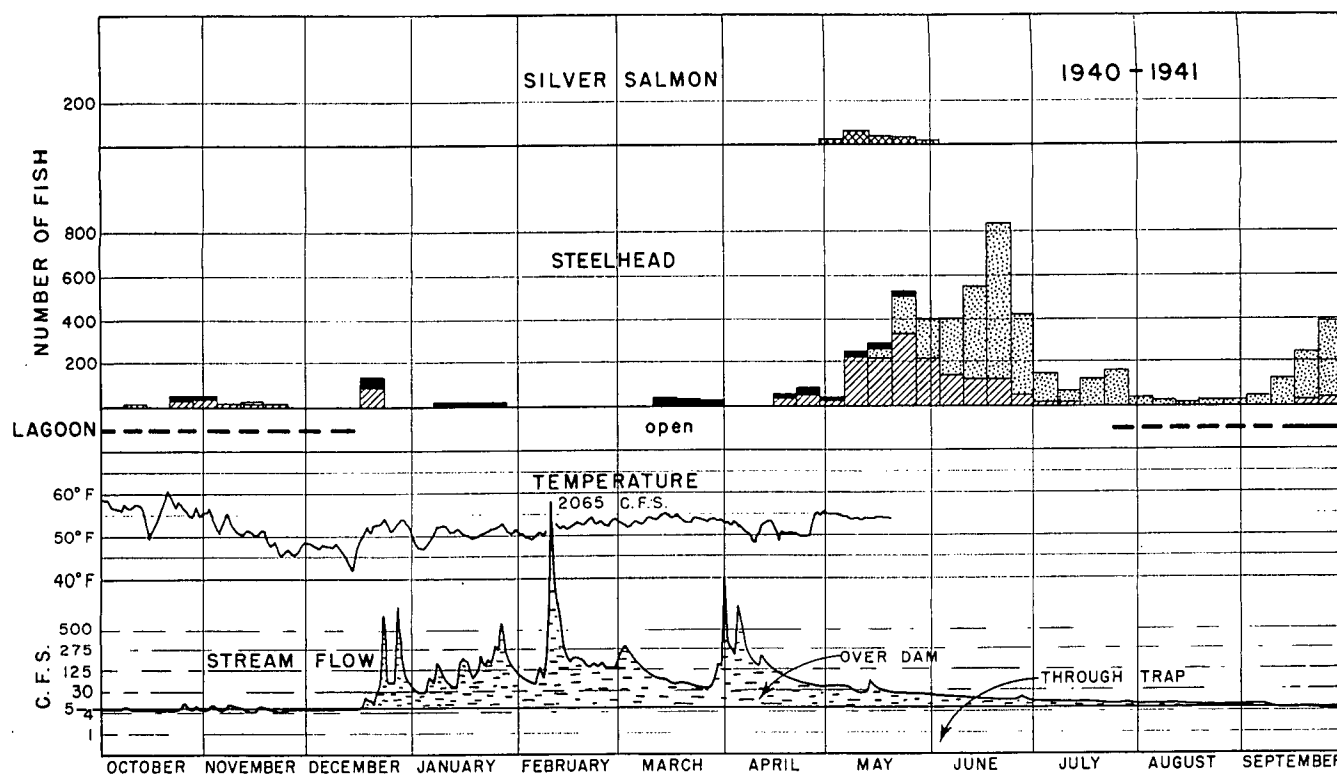


FIGURE 18. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1940-41 season.

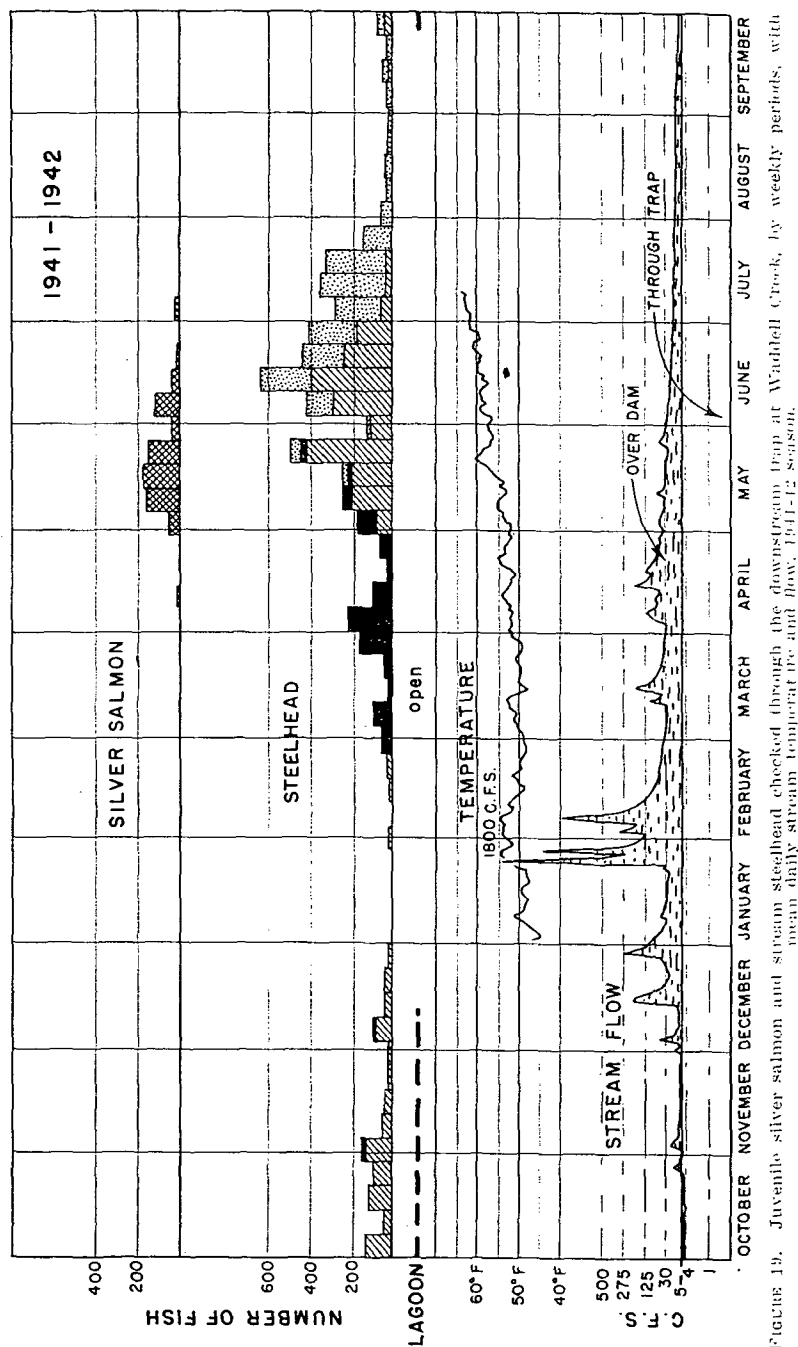


FIGURE 19. Juvenile silver salmon and stream steelhead checked through the downstream trap at Waddell Creek, by weekly periods, with mean daily stream temperature and flow, 1941-42 season.

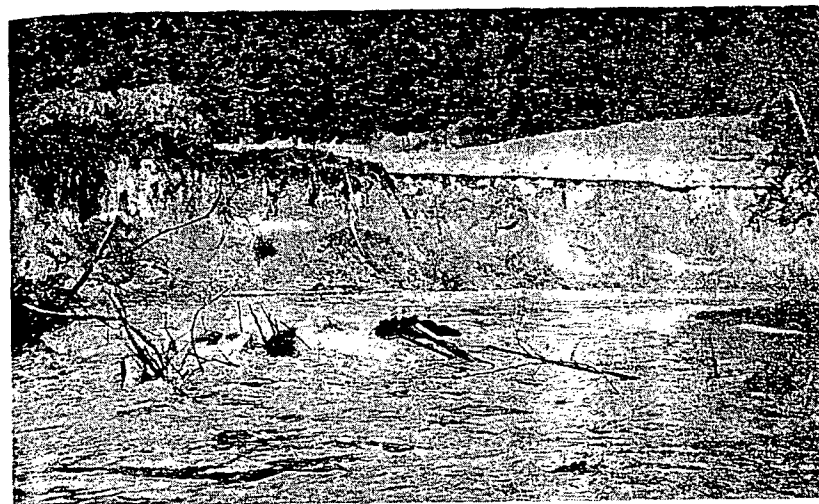


FIGURE 20. Waddell Creek in flood, about one-half mile above the dam. Photograph by Paul R. Needham.

Nearly all of the downstream migrants passing through the trap were taken during April and May, when there was generally about three times as much water flowing over the dam as through the trap (Figures 11-19). Thus one would expect that about three-quarters of the downstream migrants went over the dam (and escaped marking). The numbers of unmarked and marked returning adults indicate that in normal seasons somewhat more than two-thirds of the downstream migrants went over the dam.

There is no way of knowing if many fish migrated downstream over the dam during the period of heavy rainfall (December through March) when the stream was often at flood stage and turbid (Figure 20), but general observations at Waddell and Scott creeks and data obtained from other streams strongly indicate that there is little downstream migration of silver salmon during this period. Part-season counts made at the California Department of Fish and Game's Benbow Dam Station show that the migration there takes place at approximately the same time of year as in Waddell Creek. Studies conducted in 1935 by Taft in a diversion ditch from Beaver Creek, a tributary of the Klamath River 160 miles above the mouth, indicate that a downstream migration of age 1 silver salmon also takes place there during approximately the same period. Catches made in a trap at the head of Naha Bay, Revillagigedo Island, southeastern Alaska, in 1903 and 1904 (Chamberlain, 1907) indicated a heavy migration of silver salmon yearlings into salt water in May.¹⁹

¹⁹ Chamberlain nevertheless believed that "the greater part seek the sea as soon as they become free-swimming", evidently basing his statement at least in part on a heavy migration of fry in Steelhead Creek on Naha Bay in 1904. Chamberlain reports over 1,100 fry taken on May 19, water temperature 48 degrees F., with the run reaching its maximum 10 days later, when over 3,000 fry were taken in a single night, and continuing "until sometime in July." Chamberlain reports that the fry taken in the trap from May to July 9 averaged between 37 and 40 mm. in length, with no appreciable increase in size. "The main movement was early in the evening, the lifting of the trap at 1.30 a.m. and 9.30 a.m. of the same day showing a catch of 2,015 between dusk (about 10 p.m.) and 1.30 a.m. and 50 during the morning twilight."

Probably the general period of migration is shown quite accurately in Figures 11-19, but it is to be expected that proportionately larger numbers than are shown on the graphs migrate downstream in the early stages of the migration, when more water is passing over the dam. As the flow decreases and the proportion of water passing through the trap increases, probably the proportion of fish passing through the trap also increases.

Variations from the basic pattern as regards time of migration are infrequent. The great majority of juvenile silver salmon migrate downstream within a very limited portion of the season, over 95 percent coming during the nine-week period April 8-June 9. In all seasons the peak of the migration is reached not earlier than the week of April 22-28 and not later than the week of May 20-26.

Factors Influencing the Time of Migration and Size at Migration

In discussing possible factors influencing the time of migration and the size of migrants it will simplify our analysis to assume that we have a homogeneous population of potential downstream migrants, i.e., that racial characteristics or inherent factors such as *inherent* growth rate are not playing a part. In fact, there is no evidence to indicate that different "races" of silver salmon are present in Waddell Creek.

Environmental factors which may influence both the time of migration and the size of the fish are (a) flow (relative or absolute), (b) temperature, (c) chemical factors (e.g., oxygen), (d) light, and (e) food.

Time of migration may also be influenced by size of fish, while the size of the fish, conversely, may depend upon the time of migration. Most of the environmental factors are related to both time of migration and size of fish and also to each other.

Any of the factors mentioned may be an influencing factor (the one which *as such* impels the fish to migrate) or simply an incidental factor, correlated with the time of migration but not influencing it. For example, temperature and flow are correlated with each other, but it may be that only one is an influencing factor and the other merely an incidental factor. Actually, it is likely that more than one factor exercises an influence during the migration period. One factor may be governing or dominating at one time, and another at another time.

Also, it should be noted that the factors mentioned are not of equal magnitude in all portions of the stream at the same time. For example, in Waddell Creek and in other California streams in general, proceeding upstream we find progressively lower temperatures and a progressively smaller but more constant flow.

In regard to size of fish and the factors influencing it, the discussion will deal with the size distribution within a season, rather than with the size fluctuations occurring from season to season in comparable fish.

From Table 15 we see that the migration as a whole occurs later or earlier in some seasons than in others. An examination of Figures 11-19 reveals that the "early" seasons (notably 1933-34 and 1938-39) are those with generally low stream levels during the migration period for

the same dates on which in late seasons (notably 1934-35, 1937-38, 1939-40, and 1940-41) stream levels were generally high. The effects of the absolute stream levels on the time of migration are probably modified by rate of drop in stream level, sudden spring freshets, etc. It may be noted that there is a similar association between spring water levels and time of migration among the steelhead (Figures 11-19).

It will also be seen from an examination of Table 16 that there is a gradual decrease in the average size of the age 1 fish migrating in the spring. (The same phenomenon occurs among the steelhead of a given age class; see page 179.) What actually happens is not known, but the same result could be achieved by (1) the larger fish from all portions of the stream migrating first, (2) the fish from the lower portions of the stream (on the whole, larger than the fish from the upper portions, because of more favorable growing conditions) migrating first, or (3) the fish from all portions of the stream starting migration at the same time. For the Atlantic Salmon (*Salmo salar*) British investigators (e.g., Went, 1942) believe that what they call the law of "growth for age" at migration is generally operative: that the quick growers migrate first, but that the later migrants are always a little bigger when they go to sea than the quicker growers which migrated earlier. It is not evident that such a law operates in the case of the Waddell Creek silver salmon (or steelhead), since the later migrants are usually smaller than the earlier migrants.

It should also be noted that speed of migration may influence the size composition of migrants past a fixed point. For example, if fish from the same point in the upper reaches of a stream start their migration at different times, as they reach a certain size, but those which migrate later travel at a greater speed than those migrating earlier, the later migrants will be smaller when they reach a fixed point than were the earlier migrants, providing that the same growth rate has prevailed during the time. No evidence is at hand to indicate that speed of migration increases within a season in the case of juvenile salmon, but various authors have pointed out that in large rivers adult salmonids which enter late in the season ascend at a faster rate than do those entering early. Speed probably plays a minor role in Waddell Creek and other short streams, but may be of importance in the longer ones.

In some seasons at Waddell Creek a gradual increase in average size of downstream migrants precedes the typical gradual decrease, which has already been discussed. The initial increase in size is probably due to a rapid growth rate outbalancing the conditions which create a decrease.

The various possible factors influencing time of migration and size at migration have been discussed at length in order to emphasize the point that even when the downstream migration takes place in a small stream and involves a single age class, various fluctuations may be expected. Although supporting data are incomplete, it may now be useful to develop the following hypothetical picture of the downstream migration as regards time of migration and size of fish, and to use this picture until such time as portions of it may be proved erroneous.

The fish are influenced in starting their downstream migration by both size and environmental factors. Even if an individual has reached

the size at which the group migration begins, that individual tends not to migrate downstream unless the proper environmental factors have also been reached. Conversely, the fish as a group tend not to start their migration, even if the proper environmental factors have been reached, unless the proper size has also been reached. Now, as the approximate proper size and general, more or less fixed environmental conditions (probably principally light) are reached the fish start migrating downstream, with the migration somewhat retarded or advanced by local, fluctuating environmental conditions, principally flow and temperatures. Lower flow and higher temperatures advance the time of migration. The larger fish from all portions of the stream start migrating first. If size is an influencing factor, this happens because these fish have reached the approximate "migration size." If environmental factors dominate, this happens because the larger fish in each pool are the first to be affected by the diminishing volume. Also, proportionately more fish from the lower portions of the stream, with the more favorable growing conditions, have reached the approximate migration size, and so are more heavily represented in the early part of the migration than those from the upper portions. Decreasing average size at a fixed point, such as the dam, results both because the larger fish from all portions of the stream migrate first and because the fish from the lower portions of the stream migrate first. Fluctuations in growing conditions both before and after the start of migration further vary the pattern of the size composition of the migrants through the period of migration, in proportion to their magnitude. Despite variations caused by seasonal conditions, *within any season* 95 percent of the migrants passed the dam during the nine-week period April 8 to June 9 at age 1 and at an average size of from 103.11 to 116.61 mm.

The significance of the time of migration in regard to management will be discussed on pages 266-267.

Characteristics of the Migration

The migrating fish move downstream in schools. The size limits of these schools have not been determined, but those seen were composed of some 10 to 50 individuals. It is possible that their size is influenced by the size of the stream and the total population of migrants. It is likely that individuals of the same general size school together.

Quantitative observations were not made in regard to diurnal distribution of the migration. General observations indicate that most fish move downstream in the night or twilight, although some may move down during the day.

In approaching irregularities in the stream, such as falls or barriers, that break up the regular pattern of flow, the schools "play around," often spurting upstream from the falls several times before being carried over them as a group.

Sufficient numbers of downstream migrants have not been sexed to determine quantitatively the representation of sexes, but the sex ratio among the returning adults indicates that approximately a 1:1 sex ratio exists among the downstream migrants.

General color notes were taken for a number of the 1933-34 season migrants. They indicate that the parr marks were prominent in the

earliest migrants of the spring migration (March). As the season progressed, the fish became more "silvery," with parr marks barely visible. Forty-three fish taken April 4-7, inclusive, ranging in length from 102 to 128 mm., were recorded as being "silvery but with parr marks visible".

Sea Life

The extremely rapid growth made in the sea, as compared with that made in fresh water, is well known and has been directly observed at Waddell Creek by measurements of juveniles descending to the sea and of fish of the same year classes returning to spawn in the following and in the second seasons. Since the seaward migration consists almost entirely of one age class and since the periods covered by both the seaward and spawning migrations are fairly compact, each being concentrated in two months, it is possible to obtain an accurate picture of the growth made (Figure 21).

Little is known regarding the movements of silver salmon in the sea. Only a very few marked Waddell Creek fish have been reported caught at sea, by either commercial fishermen or sports anglers. Marked salmon from Waddell Creek have been caught off Fort Bragg, 200 miles to the north (Taft, 1937). A single marked salmon from Waddell Creek was taken by a sports angler at the mouth of the San Lorenzo River, 20 miles to the south. It is evident from these records that all fish do not simply remain near the mouth of the stream from which

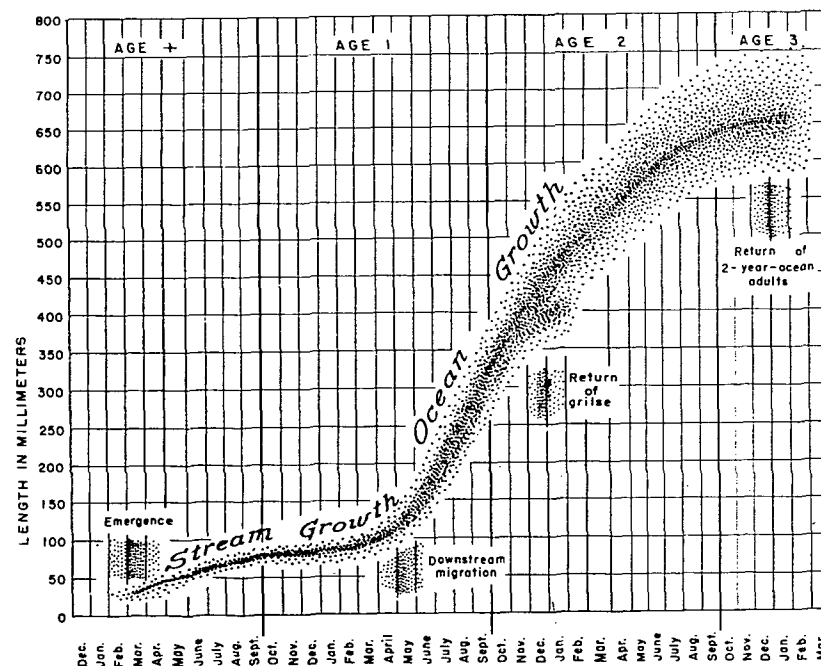


FIGURE 21. Growth of Waddell Creek silver salmon.

they migrated, but may travel considerable distances. To what extent fish as adults return to that stream or stray to other streams will be discussed in the following section of this paper.

Although it has been seen that silver salmon travel considerable distances along the coast, this does not mean that they travel equal distances directly away from the coast. Along the California coast the continental shelf extends approximately 100 miles from the shoreline, and there is some evidence to indicate that all of the anadromous salmonids remain within its limits.

Probably the young salmon, on first migrating to the sea, remain fairly close to the shoreline. Very little is known regarding how soon and to what extent they begin to spread out, but after a few months they begin to be taken at various points at sea, sometimes in large numbers away from the mouth of any stream possessing a run of consequence.

Considerable evidence gathered by various agencies indicates that the migrations of the various Pacific salmon take place in the form of mass movements. As one example, let us consider Monterey Bay, where for many years there has existed a considerable fishery for both king salmon and silver salmon. At times the ratio between these species changes rapidly and in orderly progression within a limited area, indicating the influx of one species and the departure of the other.

Also on the basis of the similar pattern of ocean growth reflected in the scales of king salmon marked and liberated in the Klamath River as a single lot but taken at widely scattered points in the ocean at different times, Snyder (1924) inferred that "king salmon after entering the ocean may remain together in the same locality or migrate in the same school for one or more years, possibly throughout life." It is not improbable that silver salmon exhibit similar behavior.

Little is known of the extent to which silver salmon from different streams mix while at sea. Marked king salmon from both the Klamath and the Sacramento river systems, hundreds of miles apart, have been caught off Fort Bragg, and also in Monterey Bay (Snyder 1921b, 1923, and 1924). It is fairly certain that masses of silver salmon from different streams visit some of the same areas at sea.

Basing his statements largely on collections of the ALBATROSS in Alaskan waters in various years, Chamberlain (1907) has the following to say regarding silver salmon upon entrance into salt water:

"From the above data it is seen that the cohos remain for some months about the shores near the streams whence they issue. They may be found about the mouths of the streams in brackish water perhaps soon after their descent of the stream. It may be they remain about the streams for a time to accustom themselves to the salt water, but this is not evident in case of the fry. The sea-run examples are readily distinguished by the silvery appearance and usually by the greater depth of body which follows habitual distension of the stomach. In some cases, while near in shore, insects appear to continue a staple article of diet, as in the fresh water. The cohos feed less on crustacea than the sockeyes, perhaps inhabiting slighter depths; correlated to this is the abundance of small fishes found in their stomachs—sticklebacks in brackish water and herring and sand launces in more open regions.

"From the catches at Naha and Yes bays it would seem that the cohos continue to school after reaching salt water. The results of the seine hauls indicate that the different species of salmon school together, or at least in the same waters."

Regarding the approach of silver salmon to land, on their way to the spawning grounds, Chamberlain (1907) states:

"The presence of salmon can be noted only by their habit of leaping from the water as they approach the land. It is often possible by this means not only to recognize the presence of a school, but also to distinguish the species. In jumping, salmon do not leave the water with their ventral surface downward, as do flying-fishes. They always jump sideways with one side at an acute angle to the water surface. . . . Cohos usually leave the water entirely, falling back on the caudal peduncle held rigid with the fin directed upward. The tail may then drag through the water a short distance till the fish falls on its side and disappears."

Homing and Straying

Considerable discussion exists in the literature regarding "homing" among anadromous members of the salmon family—its existence, significance, and causes. It is the opinion of the present writers that evidence obtained through marking experiments carried out by scientific workers in this and other countries has established as a fact the existence of such homing. Briefly, young salmonids which descend from fresh water to the sea return to their "parent stream" for spawning purposes. (Young fish artificially hatched and liberated return to the stream in which they were liberated, not to the stream to which their parents returned or in which they were hatched.) For a review of the subject of homing in trout and salmon and the important literature concerning it, the reader is referred to a paper by Shapovalov (1941b).

Taft and Shapovalov (1938) presented preliminary data for the extent of homing and straying among silver salmon between Waddell Creek and Scott Creek, $4\frac{1}{2}$ miles apart. Table 17 shows the complete figures for the six seasons of marking (1933-34 through 1938-39) and the seven seasons for which returns were possible (1934-35 through 1940-41).²⁰

Fish listed as returning include only those taken at the traps in each stream, to obtain as nearly comparable a basis as possible. Males and females have been grouped together in the table, since no significant sexual differentiation has been revealed in the straying fish as compared with those of the same year class returning to their parent stream. It should be kept in mind that the fish marked and liberated in Scott Creek were hatchery-reared.

From Table 17 it is seen that during the entire period 314²¹ (85.1 percent) of the fish marked at Waddell Creek returned there and 55 (14.9 percent) strayed to Scott Creek. Of those marked at Scott Creek, 41 (73.2 percent) returned there and 15 (26.8 percent) strayed to Waddell Creek. The percentage of straying is considerably larger than

²⁰ Returns for marking done at Waddell Creek in 1931 and at Scott Creek during the 1932-33 season are omitted, because of incomplete records at Scott Creek in 1933-34 and 1934-35.

²¹ Excluding seven fish returning to Waddell Creek during the 1934-35 season, since strays to Scott Creek for that season were not available for comparison.

Other marked Waddell silver salmon have been reported caught by anglers in the surf or offshore along the Santa Cruz County coast, usually in November. For example, a fish of the 1933-34 year class (marked Ad-LP at Waddell Creek) was taken in the surf at the mouth of Soquel Creek in November, 1936, and "quite a few" were reported being caught in that vicinity at the same time. Without further evidence, these fish cannot be treated as strays.

Between Scott Creek and the San Lorenzo River are several small streams, namely, San Vicente, Liddell, Respini, Laguna, Coja, Baldwin, and Medler creeks; these streams support few, if any, salmon. No marked fish have been reported from any of these streams, although no facilities to secure returns were in operation and any reports would have resulted from chance catches made by anglers.

To the north of Waddell are three small streams, Finny, Año Nuevo, and Whitehouse creeks, which probably do not have salmon runs. Gazos Creek, $6\frac{1}{2}$ miles north of Waddell, and Pescadero Creek, 14 $\frac{1}{2}$ miles north, both have salmon runs, but again, no marked Waddell fish have been reported from these two localities, where no special facilities to secure returns were in operation.

In the preceding discussion we saw that apparently the rate of straying is fairly constant for fish returning in different seasons but resulting from a single year class. From this it appears that by the time adults first start returning (as 1/1 males) the amount of straying that will result has already been determined and is more dependent upon conditions existing up to that time than on conditions existing at the time of entry into the streams for spawning. Until contradictory evidence is presented, it appears satisfactory to set up the hypothesis that conditions existing at the time of the migration to the ocean determine the amount of straying that will take place one and two seasons later. What these conditions are, it has not been found possible to state definitely on the basis of the data which are available and have been analyzed, but it appears worthwhile to call attention to certain possibilities. (1) There is a tendency toward a positive correlation between size of downstream migration and rate of straying. (2) There is a tendency toward a negative correlation between average size of fish at downstream migration and rate of straying. In other words, the greater the number of downstream migrants and the smaller the size of downstream migrants, the greater is the amount of straying. Possible explanations for these correlations may be advanced. One is that an unusually large number of downstream migrants attracts predators out of proportion to the average, with the result that the fish entering the ocean are rapidly scattered or in some other way affected so they do not return to their home stream in average numbers. Another is that unfavorable growing conditions (resulting in small size of fish) in some way affect the fish so they do not return to their home stream in average numbers. It must be emphasized that the significance of these tendencies has not been established; it would be of interest and profitable to carry out marking experiments planned to test the indicated tendencies.

It was pointed out in the previous section that upon descending to the ocean the young fish do not simply remain near the mouth of the

stream of liberation, but may wander great distances. In answer to the view that such fish are "lost" and will not return to the parent stream, and that only fish which remain under the influence of water from the parent stream will return to it, it is pointed out that the mouths of most California silver salmon streams are closed by sand bars during the summer months and that in some cases the lower courses of the streams are entirely dry, so that no fresh water reaches the ocean.

One other phase of homing remains to be considered, and that is the extent to which fish returning to the parent stream return to the same portion of the stream. For Waddell Creek, an attempt to determine this matter was made on the basis of the distribution of marked and unmarked adults within the stream. The problem was made difficult by the fact that only fish which had completed spawning could be used with certainty, with the result that the numbers available for comparison in any one season were too small to obtain conclusive evidence. In view of this and the fact that some spent marked fish were found below the dam, for the purposes of the present studies the proportion of marked to unmarked fish has been considered to be the same above and below the dam.

Survival

Since nearly all of the silver salmon migrate downstream at age 1 and go to sea in the same season, and since they spawn only once, it is relatively simple to calculate survival to maturity at Waddell Creek either from eggs produced (over-all survival) or from downstream migration (secondary survival).

Over-all survival, without a breakdown into survival at intervening stages, is shown in Table 18. It is seen that the survival varies from 0.02 to 0.30 percent for the six seasons for which complete returns were possible, with a mean of 0.13 percent.²³

²³ In Table 18 and subsequent tables dealing with survival of both silver salmon and steelhead, calculations have been made of (1) the total percentage of survival, and (2) the mean of seasonal percentages of survivals. The former is based on total numbers for all seasons, with the survivors under discussion considered as a percentage of the fish or eggs from which they originated. In each instance only the mean percentage of survival is noted in the text. This figure is probably the more significant one, the assumption being that the seasonal percentage survivals are representative for the individual seasons.

TABLE 18
Waddell Creek, Silver Salmon: Over-all Survival

Season	Spawning females	Total egg production	Returned as adults				Percent survival
			1/1 ♂	1/2 ♂	1/2 ♀	Total	
1933-34.....	222	560,690	85	153	157	395	0.07
1934-35.....	309	725,014	4	70	37	111	0.02
1935-36.....	59	141,233	34	40	56	130	0.09
1936-37.....	157	377,352	24	105	150	279	0.07
1937-38.....	37	91,728	62	102	115	279	0.30
1938-39.....	56	130,074	71	124	129	324	0.25
Totals.....	840	2,026,091	280	594	644	1,518	0.07
Mean*.....							0.13

* Mean of seasonal percentages.

One of the striking features to be noted in Table 18 is the inverse correlation between the total egg production and the survival percentage. The fact that the same phenomenon is encountered for steelhead (pages 204-205 and Table 58) indicates strongly that the correlation is not due to chance but is real.

In Table 18, the numbers of spawning females are the estimated total numbers in Waddell Creek in each season, including those checked upstream through the trap, the dam jumpers, and those spawning below the dam. It was necessary to include all three groups for the reason that in calculating survival from eggs deposited it was impossible to recognize the fish produced by one group from those produced by another group. Survival may also be calculated on the basis of marked fish, and this is done on pages 97-101, but such survival dates from time of downstream migration (i.e., time of marking) and not from time of egg production.

In calculating the number of eggs deposited by each spawning run, the number of eggs produced by each fish was calculated on the basis of the egg number-fish length relationship previously established (pages 59-62) and shown in Figure 10. The lengths of all fish checked upstream were, of course, known. Egg production estimates for fish jumping upstream over the dam and for those spawning below the dam were based on fish lengths when known. For the remaining fish they were based on the *average* egg production for fish checked upstream through the trap. This is shown in Table 19.

For purposes of estimating survival, fish straying from other streams to Waddell Creek were included, i.e., it was assumed that the straying of surviving fish to and from Waddell Creek had been equal.

TABLE 19

Waddell Creek, Silver Salmon: Estimate of Total Egg Production, by Seasons

Season	Females checked through upstream trap		Females jumped over dam		Total egg production above dam	Females spawning below dam		Total Waddell Creek egg production
	Number	Egg production	Number	Egg production		Number	Egg production	
1933-34	177	449,675	25	61,675	511,350	20	49,340	560,690
1934-35	287	675,492	2	4,502	679,994	20	45,020	725,014
1935-36	39	94,053	0	-----	94,053	20	47,180	141,233
1936-37	107	259,350	0	-----	259,350	50	118,002	377,352
1937-38	22	51,243	0	-----	51,243	15	40,485	91,728
1938-39	40	95,271	0	-----	95,271	16	34,803	130,074
1939-40	126	334,353	0	-----	334,353	24	61,968	396,321
1940-41	105	236,406	0	-----	236,406	10	21,480	257,886
1941-42	77	147,945	2	3,714	151,659	50	92,850	244,509
Totals	980	2,343,788	29	69,891	2,413,679	225	511,128	2,924,807
Seasonal means	109	260,421	3	7,766	268,187	25	56,792	324,979

The previous discussion of survival and the accompanying tables have included both marked and unmarked fish. Now considering survival among marked fish, we are able to increase our insight into the processes that take place, since possible errors resulting from straying are eliminated.

Survival of Marked Waddell Creek Silver Salmon

Table 20 shows the number of downstream juveniles marked (as age 1 fish) in each season, and the number of these marked fish that returned to the trap as adults. Marked Scott Creek strays, fish marked in Waddell Creek in 1931-32, and all unmarked fish have been excluded, since none of them is comparable to those marked on a downstream migration.

From Table 20 it is seen that the percentage of survival from time of downstream migration varies from 0.6 to 5.4, with a mean of 2.3. It must be noted that these figures are based only on marked adults returning to the trap, and that some additional marked adults returned to the stream but spawned below the dam. It is of interest that there is a tendency toward an inverse correlation between the number marked and the percentage of returning adults, with the lowest survival rate resulting from the greatest number marked and the highest survival rate resulting from the smallest number marked. The significance of this phenomenon will be discussed later in this section.

A comparison of Table 20 with Table 76 for the steelhead indicates basic similarities as regards survival. The average return to the trap from the number marked at the same age (1) is much the same for both species (2.3 percent for silver salmon and 2.4 percent for steelhead). There is also a rough correlation between the season of marking and the survival, when salmon and steelhead of the same age (1) are compared. However, survival does not appear to be correlated with the mark given, as such. The same mark used on silver salmon in different seasons (Ad-RP) resulted in both a survival much above average and one much below average.

In the preceding pages we have determined the survivals from eggs deposited to returning adults for the stream as a whole and from downstream migrants to adults returning to the trap for marked fish. In order also to determine the survival from eggs deposited to downstream migrants (primary survival) it is necessary to know the total number of downstream migrants, including those that went over the dam uncounted and those that were produced below the dam. The total number of downstream migrants was calculated by applying the ratio of marked to unmarked fish among the adults of a given brood year (returning during the course of two seasons) to the marked downstream migrants of the same brood year.²⁴ The total downstream migrants were then expressed as a percentage of the eggs deposited for each brood year.

Table 21 shows the ratio of marked to unmarked adults among the age 1/1 and 1/2 fish, respectively, resulting from each brood season and the division according to this ratio of the fish of the same life history categories estimated to have spawned below the dam.

²⁴ "Unmarked" fish include marked strays from Scott Creek.

TABLE 20
Waddell Creek, Silver Salmon: Secondary Survival of Marked Fish

Brood season	Season of marking	Mark	Number of juveniles marked	Marked fish returning to trap as adults									Percentage survival
				First season			Second season			Total			
				♂	♀	♂ + ♀	♂	♀	♂ + ♀	♂	♀	♂ + ♀	
1932-33-----	1933-34----	Ad-RP----	3,202	7	--	7	11	9	20	18	9	27	0.8
1933-34-----	1934-35----	Ad-LP----	3,481	15	--	15	52	44	96	67	44	111	3.2
1934-35-----	1935-36----	Both P----	4,392	0	--	0	20	6	26	20	6	26	0.6
1935-36-----	1936-37----	Ad-RP----	1,059	9	--	9	19	29	48	28	29	57	5.4
1936-37-----	1937-38----	Ad-LP----	1,895	10	--	10	40	50	90	50	50	100	5.3
Totals-----			14,029	41	--	41	142	138	280	183	138	321	3.1
Mean-----													2.3

TABLE 21
Waddell Creek, Silver Salmon: Entire Spawning Runs From Five Brood Seasons, Ratio of Marked to Unmarked Fish *

Brood season	1/1 ♂						1/2 ♂ + ♀						All returning adults		
	Checked through upstream trap			Run below dam			Checked through upstream trap			Run below dam					
	Marked	Un-marked	Ratio	Total	Marked	Un-marked	Marked	Un-marked	Ratio	Total	Marked	Un-marked	Marked	Un-marked	Total
1932-33.....	7	14	33.3:66.7	1	0	1	20	52	27.8:72.2	37	10	27	37	94	131
1933-34.....	15	41	26.8:73.2	29	8	21	96	115	45.5:54.5	99	45	54	164	231	395
1934-35.....	0	3	0:3	1	0	1	26	38	40.6:59.4	43	17	26	43	68	111
1935-36.....	9	11	45.0:55.0	14	6	8	48	21	69.6:30.4	27	19	8	82	48	130
1936-37.....	10	7	58.8:41.2	7	4	3	90	124	42.1:57.9	41	17	24	121	158	279
Totals.....	41	76		52	18	34	280	350		247	108	139	447	599	1,046

* No salmon from these five brood seasons jumped over the dam.

TABLE 22
Waddell Creek, Silver Salmon: Primary, Secondary, and Over-all Survival

Brood season	Total egg production	Returning adults			Downstream migrants		Percentage survival		
		Total	Marked	Unmarked	Ratio marked to unmarked	Marked	Estimated total	Primary	Secondary
								(Eggs to downstream migrants to adults)	(Downstream migrants to adults)
1933-34.....	560,600	305	164	231	1:1.41	3,481	8,389	1.50	4.71
1934-35.....	725,014	111	43	68	1:1.58	4,392	11,331	1.50	0.98
1935-36.....	141,233	130	82	48	1:0.59	1,056	1,684	1.19	7.72
1936-37.....	377,352	279	121	158	1:1.31	1,895	4,377	1.16	6.37
Totals.....	1,804,280	915	410	505	1:1.23	10,827	25,781	1.43	3.55
Seasonal means.....	451,072	220	103	126	1:1.22	2,707	6,445	1.35	4.95

From Table 22 it is seen that for the four brood seasons (1933-34 through 1936-37) for which figures are possible the percentage of survival from eggs deposited to downstream migrants is fairly constant, varying from 1.16 to 1.56, with a mean of 1.35. These figures indicate that *within the limits of conditions encountered during the above four seasons* the number of downstream migrants is approximately proportional to the number of eggs deposited.

From Table 22 it is also seen that the estimated percentage of survival from downstream migrants to returning adults for the stream as a whole varied markedly, from 0.98 to 7.72, with a mean of 4.95. It will be noted that there is an inverse correlation between the number of downstream migrants and the percentage of return as adults. If this inverse correlation is generally representative and not due to chance conditions occurring during the seasons under discussion, it appears that the most plausible explanation for the phenomenon is that the greater the concentration of fish, the more likely are predators to be attracted to them, and the proportionately greater are the in-reads made on the fish. The tendency toward an inverse correlation between the number of fish marked and number surviving (page 97) probably resulted only because the number of fish marked also was roughly proportional to the number of fish in the total downstream migration.

From data presented in the section on "Homing and Straying" (page 93) it was seen that it appears likely that the *rate* of straying from Waddell Creek to Scott Creek and *vice versa* may vary to some extent with each year class. If this is the case the various calculated survivals which are based partly on unmarked fish of unknown origin are affected. The year class at Waddell Creek which resulted in the *most straying* to Scott Creek also resulted in the *lowest survival* at Waddell Creek (brood season 1934-35), while the two year classes which resulted in the *least straying* to Scott Creek also resulted in the two *highest survivals* at Waddell Creek (brood seasons 1935-36 and 1936-37). Calculated survivals are probably also affected to some extent by differences in numbers of strays contributed by each stream resulting from different numbers of returning adults of a given year class produced by each stream, irrespective of *rate* of straying.

One other interesting fact may be derived from Table 22. A comparison of the total numbers of downstream migrants with the average size of downstream migrants (Appendix, Table A-14) indicates that an inverse correlation exists between the two.

Pathology

Diseases

As a rule disease is not prevalent among trout and salmon in their natural environment. Occasionally epidemics occur, often in the presence of unusual environmental conditions, such as abnormally high water temperatures. Under such conditions one or more disease organisms, most frequently protozoa or bacteria, which probably have been present in small numbers, may flourish and cause considerable mortality.

High temperatures and adverse chemical conditions may in themselves cause loss of vitality and mortality, but strictly speaking are not

diseases, and generally speaking do not occur in the natural environment of trout and salmon. Such conditions are more apt to occur in impounded and polluted waters.

In hatcheries and rearing ponds, in which the fish are concentrated to a far greater extent than in their natural environment, diseases are much more common.

At Waddell Creek there has been no known loss of silver salmon because of high temperatures or lack of oxygen, and very little evidence of disease causing mortality.

A disease believed to be furunculosis caused some mortality among unspawned steelhead at Waddell Creek during the course of the experiments (see pages 239-241). However, practically all of the silver salmon females are believed to have succeeded in spawning more or less completely before dying, so if this disease has been present among the adults it has not materially affected deposition of eggs.

The extent of losses from this disease among the juvenile salmon is not known exactly, but observations on the downstream migrants in the tanks have revealed very little evidence of this disease, and observations on the stream have not shown large numbers dead at any time.

In 1933-34 abnormally large numbers of dead fish, including juvenile silver salmon, adult and stream steelhead, sculpins, and sticklebacks, were found in the trap and in the stream both above and below the dam. Some of the salmonids had red spots on the body, particularly at the bases of the fins, and were believed to be infected with furunculosis. However, many of the salmonids and nearly all of the sculpins and sticklebacks found dead showed no external signs of disease or injury, so it is very difficult to assess even the proportionate mortality from different causes. There is also no way of determining the total number that died, since we do not know what percentage of the fish that died in the stream was found. It is of interest that during the same season abnormally large numbers of other animals, mostly rodents (rats, gophers, etc.) were found dead in the streams. The relation to the dead fish is not known. In any case, however, it seems evident that some condition in the stream, either a disease organism or organisms or some condition of the water, caused abnormal mortality among the juvenile silver salmon and other fishes.

During the 1933-34 season the trap itself was apparently a source of mortality. In that season 171 dead juvenile silver salmon were removed from the trap and an additional 67 dead marked juveniles were found below the dam. Most of these were probably killed or injured by the buffeting they received in the trap. Yearling silver salmon were found to be helpless in turbulent water in which steelhead of the same size could easily maintain themselves. When this was discovered the downstream trap was modified to reduce turbulence. In the succeeding eight years only 60 juvenile silver salmon were found dead in the trap.

Fungus (*Saprolegnia parasitica*) is present in all or practically all trout and salmon streams; it is a secondary infection which gains a foothold on breaks in the skin caused by mechanical injury or disease. It is very common in the form of white patches on spawning and spent adult Pacific salmon. Under normal conditions it does not cause much damage to salmonids in their natural environment.

As a rule many of the downstream migrant yearlings possess from a few to many cysts under the skin on the sides of the body, but otherwise appear to be in good condition. These cysts, which appear in the form of black spots, are formed by encysted strigeid larvae (*Trematoda*).

Freshwater copepods are found attached to some of the downstream migrants, but apparently cause no serious damage. Apparently these copepods are specific, being found much less frequently on the salmon than on the steelhead migrating downstream at the same time. The species found in Waddell Creek has been identified as *Salmincola californiensis* Dana by Charles B. Wilson. In the juvenile fish it is found most commonly attached to the bases of the fins, especially the pectorals and dorsal. Usually not more than one or two are found on a fish. Circumstantial evidence is strong that these copepods die in salt water, since they were not found on any adult silver salmon (or steelhead) returning from the ocean.

Marine copepods ("sea lice") occur on adult fish entering the stream, but have never been found on any of the fish by the time that they have reached the dam. Three marine copepods taken from a silver salmon stranded on the beach in attempting to enter Waddell Creek were identified by Charles B. Wilson as *Lepeophtheirus salmonis* Kröyer. Apparently this species had not previously been recorded from silver salmon, but since it has been found on various species of salmonids (Wilson, 1908), its occurrence on silver salmon is not surprising.

At least one other species of marine copepod (*Argulus pugettensis* Dana) has been recorded from silver salmon (Wilson, *loc. cit.*).

Lampreys, which sometimes cause damage when they attach themselves to fish, do not occur in Waddell Creek.

During the 1933-34 season the field observer, F. H. Sumner, recorded two downstream migrants lacking pigment, as follows:

April 19, 102 mm., "lacking pigment, whitish".

April 23, 115 mm., "partly albino (whitish)".

No other such records appear among the field notes.

On occasion downstream migrants with one or both opercles turned under have been taken. In 1933-34, during the period April 29-June 2, the following such fish were recorded: right opercle turned under, 8; left opercle, 5; both opercles, 2. During this period 1,535 yearlings were handled, but it is not known whether or not all of them were examined for this feature. The cause of this abnormality is not known. In hatcheries opercles that do not fully cover the gills result from a variety of causes, usually associated with the diet of the fish.

Fish that were blind or partially blind in one or both eyes, as evidenced by opaqueness of the eye, were fairly common among the adults but were met with only rarely among the juveniles. Consideration is here given only to fish in which no mechanical injury to the eye was apparent. The writers believe that such opaqueness often, if not usually, is the result of fish scraping the eye after it has entered fresh water, e.g., in leaping falls, passing through log jams, spawning, or being handled in nets at traps. This condition has been noted frequently at various egg collecting stations, especially when the fish had been handled in dip nets made of seine material with prominent knots.

The records at Waddell Creek indicate that the diseases encountered, including the external parasites, have not been associated with size of fish, within a year class.

Teratology

Deformities are rare among salmon and trout in their natural environment, and this general rule has held good at Waddell Creek. Of particular interest are abnormalities of the fins, because of their relation to marking programs.

Although abnormal or naturally missing fins were watched for in all seasons among the downstream migrants, it is possible that a few were missed. An especially careful watch was kept during the 1934-35 season and the record for the 3,532 yearling migrants is as follows: Left pectoral fin naturally missing (scar present), three fish; adipose very small, three fish; "practically no adipose fin," one fish. The fact that a scar was present in the case of the missing pectoral fins indicates that the fins were lost through injury or disease. Occasionally salmonids with fins missing from birth are encountered in nature. On several occasions the writers have encountered salmonids with the adipose fin completely absent, and on one occasion one of them (Shapovalov) examined an adult king salmon with both ventral fins and the supporting bone structure (pelvic girdle) completely missing. Migrants with a part of the caudal fin missing or with deformed fin rays have also been taken on rare occasions.

The record for 1934-35 and the discussion of the preceding paragraph show that although missing fins are not common, they do occur and may influence the apparent returns of a marking program if *only one fin is clipped*. Such naturally missing fins are not to be expected to interfere with a program in which mass returns for a given locality are expected, but may prove a serious hindrance in those cases in which reliance is placed upon small returns, as in the cases of straying or individual fish taken at sea. In any case, the extra labor involved in marking two separate fins is well worth while in terms of reliability of results.

The frequency with which a given fin is missing may vary with the population under consideration, and also from season to season. In one case the writers encountered approximately 17 fish with three ventral fins out of a lot of approximately 10,000 trout being marked. Almost certainly these abnormal fish were the product of a single female. In the same way, a number of fish with similar abnormalities may be produced in nature by a single female. Probably the fin most commonly completely absent from birth is the adipose, but the fins most commonly missing as a result of injury are the pectorals or ventrals. Among hatchery fish the fins most commonly missing or deformed are the pectorals or ventrals, due to biting by other fish, and the dorsal, due to disease (fin rot or *Gyrodactylus*). Almost no fish with fins missing because of these diseases were encountered at Waddell Creek, except in adults straying from Scott Creek.

The occurrence of missing and deformed fins among adult fish is perhaps somewhat greater than among juveniles, principally due to injuries to these fins that have taken place at sea.

Deformities of the body, like abnormalities in the fins, are rare among salmonids in their natural environment. Occasionally silver salmon with twisted snouts or deformed upper or lower jaws have been taken both among the juveniles and the adults. Even more rarely so-called "S" fish, with a curvature of the spine, have been taken among the juveniles and adults. Similarly, rare specimens of "stubby" fish, i.e., fish which are abnormally short for their depth and age, have been taken. The various deformities listed are much more common among hatchery fish, but such fish rarely survive to return as sea-run spawners.

Food

It is evident from the accumulating literature on the food of young salmonids that there is considerable variation in the food of a given species, depending upon locality, time of year, size of fish, and the relative abundance of the various food items. The greater the variations in these factors, the greater is the variation in food likely to be, but especially in trout there is sometimes even a marked variation in the food of individuals of the same size taken at the same time and in the same place.

In California, the streams inhabited by silver salmon are generally similar, and so the food of the young fish is probably similar at a given time of year and for the same size of fish. It is not unlikely that in most California streams the food of the young silver salmon is similar to that of steelhead of the same size.

Almost nothing is known of the food of juvenile silver salmon at Waddell Creek on the basis of stomach examinations. The only stomach examined was that of a juvenile upstream female 100 mm. long, taken on January 30, 1935; this stomach contained only "a little debris."

In the section on "Predators" (page 253) it will be seen that Pritchard (1936b) had found that during the seaward migration of various species of Pacific salmon in the spring of the year at McClinton Creek, British Columbia, yearling silver salmon had consumed large quantities of pink salmon fry, and small numbers of chum salmon fry and silver salmon fry and fingerlings. In the same section it will also be noted that in California silver salmon probably do not consume large numbers of steelhead and silver salmon because of the fact that the latter two species emerge from the gravel after the seaward migration of the yearling silver salmon, but that they may eat larger numbers of king salmon, which generally hatch earlier and many of which migrate as fry.

Chamberlain (1907) reported that in Alaska silver salmon fish of the season, taken from May through July (lengths 33 to 43 mm.), had fed mainly on insects. Larger fish, taken in night hauls in August and September, had eaten most terrestrial insects, and also aquatic insect larvae (principally caddisflies), snails, and sticklebacks, with a scattering of miscellaneous items. The data for the August-September fish have been gathered into Table 23.

Chamberlain adds: "The yearling cohos taken in the Naha were found to eat the young salmon fry whenever taken with them in the nets. That they sometimes were able to prey upon them in a natural state was evidenced by the presence of digested fry in some examples that were seined in Roosevelt Lagoon in May."

TABLE 23

Alaska, Silver Salmon: Foods of Young Fish

Class of food	Percentage of fish eating class of food listed		
	Aug. 22—15 fish, av. length 95 mm., range 63-122 mm.	Aug. 24—55 fish, av. length 85.6 mm., range 53-130 mm.	Sept. 10—88 fish, av. length 83 mm., range 51-120 mm.
Winged insects (flies, ants, etc.)	66	91	44
Beetles	13	42	20
Caddisfly larvae	13	5	44
Other larvae	13	—	7
Snails	26	7	5
Sticklebacks	13	7	2
Mites, eggs, etc.	—	14	11

The general feeding habits and growth of silver salmon at Waddell Creek have already been described in the section on "Stream Life Prior to Seaward Migration (General Features)" (pages 70-73).

Bradley (1908) recorded the tube-dwelling amphipod, *Corophium salmonis*, from many stomachs of young silver salmon 71 to 79 mm. in length taken at Karluk Beach and in the estuary of Karluk River, Alaska, June 8 and July 24, 1903. A closely related species, *C. spinicorne*, is one of the most abundant organisms in Waddell Creek lagoon.

Chamberlain records that young silver salmon taken with a hook in brackish water at the Klawak cannery wharf contained insects and a few beach crustaceans.

In regard to the food of small silver salmon in salt water, Chamberlain has the following to say:

"The young coho in salt water is more easily observed than the other species. It readily takes the hook, and apparently is less timid than the others in approaching surface and shore. In 1904, 45 were taken at the Loring cannery wharf August 2. They averaged 190 mm. (158-226). On July 10 at the same place about 30 were taken. No measurements were made except of the largest, which was 138 mm. On August 2, 1905, a scattered school came about the ALBATROSS while anchored at the extreme head of Yes Bay; 26, averaging 202 mm. (152-237), were taken with a hook over the ship's side. Only a few, 6 or 8, would appear at once, and they took the hook baited with bits of meat, etc., very shyly in the perfectly clear water. Most of the stomachs contained offal from the ship's messes; 5 contained fishes up to 65 mm. in length, all that could be identified being sand launces; 2 contained young sticklebacks, one of them 10 individuals; 2 had isopods, and only 3 had taken insects from the surface. Another example taken later, a male of 265 mm., contained 4 small herring.

"At Karluk young cohos are occasionally taken in the cannery seines; two, 180 mm. long, preserved from the catch of June 8, contained 2 species of amphipods and one a young cottoid; one, 158 mm., preserved from the seine July 3, was an empty female; July 24, another, 175 mm. long, contained *Ammodytes*. As will be seen, these records indicate the presence of very few young cohos about Karluk Beach.

"The general collections of the ALBATROSS afford the following data:

"A number of cohos were taken at Karta Bay with larger sockeyes and smaller dog salmon on June 26, 1897. Of the specimens preserved 8 males average about 80 mm. (56-100), and 14 females average nearly 100 mm. (80-140). They were feeding mainly on insects and crustacea.

"At Thorne Bay, July 5, of a number of small cohos together with a few dog salmon, seined probably at the mouth of the river, 24 males averaged about 55 mm. and 50 females about 56 mm., the high average of the latter being due to the presence of a few slightly larger individuals (extremes, males 45-65 mm., females 45-78 mm.). The stomachs examined contained insects for the most part; a few had small crustaceans and 2 had flatfishes.

"At Port Alexander, July 3, 1903, many young cohos were taken in the seine; 4 males and 2 females were preserved; average about 150 mm. They were feeding on young herring and sand launces, also larval crabs and amphipods.

"Of the specimens saved from Uganuk, June 5, 1903, 5 are males, averaging 138 mm., and 8 females, 130 mm. All but 3, which were empty, were feeding on young herring, each containing from 1 to 5 individuals. . . .

"At Unalaska 6 examples, taken July 23, 1888, average 148 mm., contained insects, crustaceans, grubs, and in one case a small fish like a salmon fry. One humpback fingerling was in this lot.

"Twelve examples, taken at Sumner Harbor July 2, 1896, averaged about 60 mm. and were feeding on insects and crustacea. They were in company with the smaller sockeyes. . . ."

Pritchard and Tester (1944), in a study directed toward shedding light on possible conflict between salmon and herring fisheries, presented an account of the food of silver salmon along the coast of British Columbia and summarized the results of some studies for other areas. The investigations probably give an indication of the types of food eaten elsewhere at sea, although the authors emphasize that there was a marked variation between areas and years in the kind and quantity of the organisms forming the major food items during the three years of their studies. Examinations of 257 silver salmon stomachs indicated the food of this species to be similar to that of king salmon in that herring and sand launces were the two most important items, but the silver salmon appeared to feed somewhat more extensively on other fish and invertebrates than the king salmon. The silver salmon also had a greater range of diet than the king salmon, since more types of food organisms were found in the smaller number of stomachs examined. The authors believe it to be probable that there was no active selection of the kind of food eaten by either species and that both fed on whatever food of suitable size was present in sufficient quantity to repay them for the effort. Certain types of organisms, namely, herring, sand lance, amphipods, euphausiids (red feed), and crab larvae, were found in all three years; others, namely, sardines, anchovies, capelin, rockfish, black cod, and isopods, were found in two of the three years; still others, namely, silver salmon, lanternfish, Pacific saury, hake, whiting, sculpin, squid, goose barnacles, and jellyfish, were found in one year only. The authors believe that "this variation is doubtless related, in

part at least, to variation in the number of stomachs examined in each of the three years. . . ."

Chapman (1936) found the food of 400 silver salmon from the Neah Bay, Washington, region to consist of euphasiids, sardines, and herring, in the order named, to the practical exclusion of all other organisms. Both in numbers and weight the euphasiids were the most important single item of food. Black cod and squid were only incidental. Twenty-five stomachs were empty.

In the same paper, Chapman notes that the data on 85 silver salmon from Westport differed considerably from those for Neah Bay: (1) a much higher percentage of the stomachs was empty (Westport 39 percent, Neah Bay 6 percent), (2) euphasiids were completely absent, and (3) sardines were of greater importance in comparison with herring than they were at Neah Bay. The Neah Bay fish were purse-seine-caught fish, while the Westport fish were caught by troll.

Chamberlain (1907) lists the food of only four adult silver salmon taken at sea in Alaskan waters. Two individuals seen at Karta Bay the first of August were filled with sand lance; another contained a herring. A female taken at Quadra early in August was filled with crab larvae.

Apparently, seasonal studies of the food of silver salmon in the sea have not yet been conducted.

Summing up, it appears that young silver salmon in fresh water live very largely upon insects, both aquatic and terrestrial, that smaller individuals in salt water depend heavily upon marine invertebrates, and that the larger fish in salt water are chiefly piscivorous.

LIFE HISTORY OF THE STEELHEAD

Spawning Migration

As with the silver salmon, the discussion of the life history of the steelhead is begun with the adults that are about to enter the stream for spawning purposes.

Time and Size of the Spawning Migration

Both over its range as a whole and in individual streams, the spawning season of the steelhead extends over a much longer period of time than does that of the silver salmon. In general, the bulk of the fish enter the streams and spawn in the winter and spring, but it is probable that in the larger rivers, such as the Sacramento, Eel, Klamath, and Columbia, some steelhead enter from the sea in all or nearly all months.

Roughly, steelhead may be divided into those of the spring run (fish in general entering and migrating upstream on dropping stream levels, while quite green, and spawning in the following season) and those of the fall run (fish in general entering on rising stream levels, with sexual products in various stages of development, but spawning within the same season). With local variations, the spring-run fish enter the streams in April and May and reach the pools in which they "summer over" in June and July. Such fish generally do not feed in fresh water, but remain fat and in good condition until they spawn, usually in November and December. Spring-run steelhead do not occur in most California streams, ascending probably only those that are snow-fed and possess deep pools. Fall-run fish may enter from salt water

throughout the year, from August (early fish) through July (late fish), but spawn within about four months of their entry. The late-running fish generally spawn within a month or so.

Several specific instances of the occurrence of spring-run steelhead in California may be cited. In 1938 the attention of one of the writers (Shapovalov) was called to the presence of "summer salmon" in the Middle Fork of Eel River. These fish were found to constitute a true spring run of steelhead, entering the main Eel River probably mostly in May and migrating upstream (Shapovalov, 1939b). They usually make their appearance in the Middle Fork in July, and ascend to the section from its confluence with Black Butte River to Asa Bean Falls. Here they rest in deep pools, gradually "ripening" until the following October, November, or December, when they spawn. Like the fall-run steelhead, they do not feed in fresh water, with possible rare exceptions, but remain in good condition throughout the summer. At times they refuse to strike at a lure, while at other times they avidly seize a spinner or grasshopper. The fish often run from 7 to 12 pounds in weight.

The only other portion of the Eel River in which their presence is known to the writers is the section of the Van Duzen River known as Eaton Roughs, above Bridgeville. Here they are reported to be already present when the water levels drop and the water clears enough to see into these "salmon holes"; this is probably usually in June. Runs that are probably comparable ascend certain of the snow-fed tributaries of the Klamath River. For example, steelhead of average size, which were green and would not spawn until the following winter, were ascending Elk Creek, tributary to the Klamath 100 miles above its mouth, on June 3, 1934 (Taft and Shapovalov, 1935, page 66).

In the comparable section on silver salmon it was pointed out that Waddell Creek and most other California streams are closed by sand bars at their mouths during a portion of the annual dry season, as a result of which the entry of the first fish of the spawning run is dependent upon the breaking of the bar with the start of the rainy season. The same consideration, of course, applies to the steelhead.

As with the silver salmon, at Waddell Creek (and Scott Creek) some steelhead have entered the stream with the first opening of the bar, whenever that has occurred, as shown in Table 24. This implies that

TABLE 24

Waddell Creek, Steelhead: Time of Initial Capture in Trap, in Relation to Opening of the Bar

Year	First opening of bar	First steelhead taken in trap	Permanent opening of bar
1933	October 31	December 14	December 28
1934	November 18	November 21	December 13
1935	October 11	December 29	December 29
1936	November 19	December 30	December 26
1937	October 26	December 12	December 8
1938	October 27	December 2	October 27
1939	November 24	December 11	December 7
1940	September 13	October 27	December 16
1941	October 9	October 31	December 9

the fish are "waiting" very near the mouth of the stream for the bar to open, or make a rapid journey to the mouth of the stream with the approaching storm.

Again as in the case of the silver salmon, only a portion of the seasonal "run" enters Waddell Creek with the first storm and with each succeeding storm. In the case of the steelhead, however, a smaller proportion of the total run enters the stream with the first storms, especially if these occur early, and the run stretches out past the salmon spawning season.

The entry of the fish into the stream is not determined entirely by their sexual maturity, for examinations made at the very mouth have revealed that some of the fish are sexually immature, or "green," while others are completely sexually mature, or "ripe." There is a greater tendency for the early steelhead, in comparison with the silver salmon, to be green. Such a situation is to be expected in view of the fact that although the spawning seasons of the two species overlap, the bulk of the steelhead spawning takes place later than that of the silver salmon in Waddell Creek and most other California streams.

The increasing earliness of the runs and the spawning season with progression to the north, which was noted for the silver salmon, is not apparent in the steelhead. It is true that some steelhead enter the streams of northern California earlier than do any of those running into Waddell Creek and its neighbors, but even in those streams the spawning season takes place about the same time as in the southern streams. Although steelhead enter the mouth of the Eel River in considerable numbers as early as August, they do not ascend the South Fork until about the time of the Waddell Creek and Mad River runs

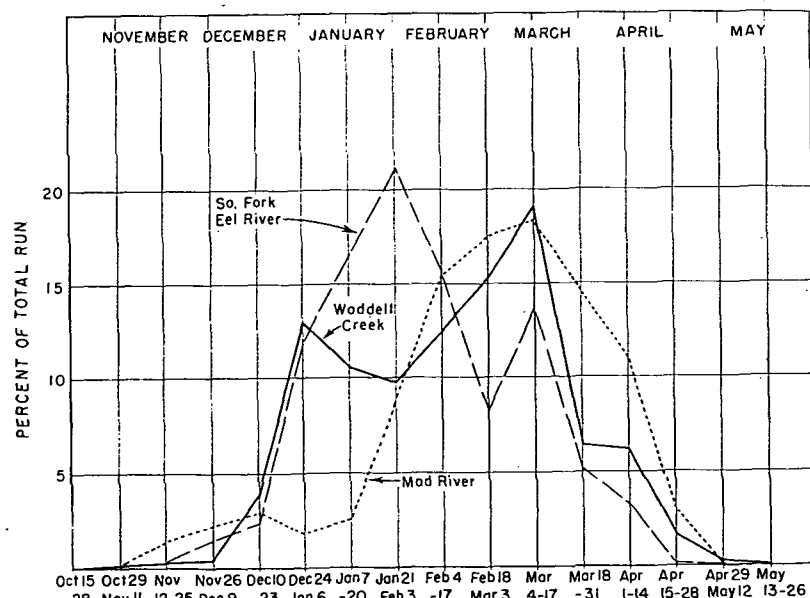


FIGURE 22. Seasonal distribution of the steelhead runs in Waddell Creek, South Fork of the Eel River, and Mad River.

(Figure 22). Table 25 shows the runs in the South Fork of the Eel River by two-week periods for six seasons, and Table 26 shows the Mad River runs for nine seasons.

As in the case of the silver salmon, the writers have wondered if any steelhead would enter Waddell Creek if unseasonal rains occurred in

TABLE 25

South Fork of Eel River, Steelhead: Adults Counted Upstream Through Fishway at Benbow Dam, by Two-week Periods

Period	1938-39	1939-40	1940-41	1941-42	1942-43	1943-44	Total	Percentage of total run
Oct. 1-14.....			1		3		4	+
Oct. 15-28.....			17	9	9		38	+
Oct. 29-Nov. 11.....	3		2	19	139	26	186	0.2
Nov. 12-25.....			16	76	694	43	1,520	1.4
Nov. 26-Dec. 9.....	691		47	62	1,394	215	2,710	2.4
Dec. 10-23.....	208	784	1,126	1,515	3,484	1,690	13,445	12.0
Dec. 24-Jan. 6.....	507	1,202	4,498	4,491	221	4,622	18,448	16.5
Jan. 7-20.....	3,414	5,526	2,799	2,130	7,517	4,165	23,616	21.2
Jan. 21-Feb. 3.....	1,479	1,572	2,708	985	5,525	3,892	17,583	15.7
Feb. 4-17.....	2,901	1,765	1,147	1,820	2,047	2,103	9,306	8.3
Feb. 18-Mar. 3.....	424	1,141	872	3,775	2,900	4,251	15,329	13.7
Mar. 4-17.....	2,390	645	809	1,643	649	1,339	5,831	5.2
Mar. 18-31.....	746	609	194	771	436	1,099	3,297	3.3
Apr. 1-14.....	188	33	44	36	14		169	0.2
Apr. 15-28.....	42	73	21	24			120	0.1
Apr. 29-May 12.....	2		10				10	+
May 13-26.....								
May 27-Sept. 30.....								
Totals.....	12,995	14,476	18,308	17,356	25,032	23,445	111,612	

TABLE 26

Mad River, Steelhead: Adults Counted Upstream Through Fishway at Sweasey Dam, by Two-week Periods

Period	1941-42	1942-43	1946-47	1947-48	1948-49	1949-50	1950-51	1951-52	1952-53	Total	Percentage of total run	
Oct. 1-28.....		6			6	1	50	1		64	0.1	
Oct. 29-Nov. 11.....					30	10	78	83	3	621	1.4	
Nov. 12-25.....	4	376	15	22		64	47	58	4	955	2.2	
Nov. 26-Dec. 9.....	180	120	475		7	21	403	79	229	1,253	2.9	
Dec. 10-23.....	30	276	86		129	31	15	268	67	50	782	1.8
Dec. 24-Jan. 6.....	25	31	6	289		9	109	8	62	1,113	2.6	
Jan. 7-20.....	116	279	6	524		54	52	413	1,565	3,802	8.9	
Jan. 21-Feb. 3.....	523	205	908	81	1	1,108	675	306	215	6,607	15.4	
Feb. 4-17.....	246	2,140	1,171	417	329	1,359	65	949	362	7,499	17.5	
Feb. 18-Mar. 3.....	267	1,242	983	1,534	738	1,097	1,186	648	2,078	7,884	18.4	
Mar. 4-17.....	765	995	732	363	830	287	1,097	1,186	259	6,263	14.6	
Mar. 18-31.....	1,075	910	525	249	322	640	1,531	526	4,790	11.1		
Apr. 1-14.....	1,180	60	108	103	678	287	317	1,531	526	4,790	11.1	
Apr. 15-28.....	172		95		38	219	281	222	257	1,284	3.0	
Apr. 29-May 12.....							3	33		36	0.1	
May 13-Sept. 30.....												
Totals.....	4,583	6,640	5,110	3,582	3,139	4,074	4,631	5,584	5,610	42,953		

September. Since such rains have not occurred during the course of the experiments, a direct answer has not been obtained.

The occurrence of different runs or "waves" of migrating fish brings up the question of "races." It is possible that different biological or morphological races exist within large stream systems, but the occurrence of fresh runs with each succeeding storm in Waddell Creek and other small streams indicates that different runs during a season are not necessarily the result of different races. There is no evidence to indicate that different races exist in Waddell Creek and one would hardly expect

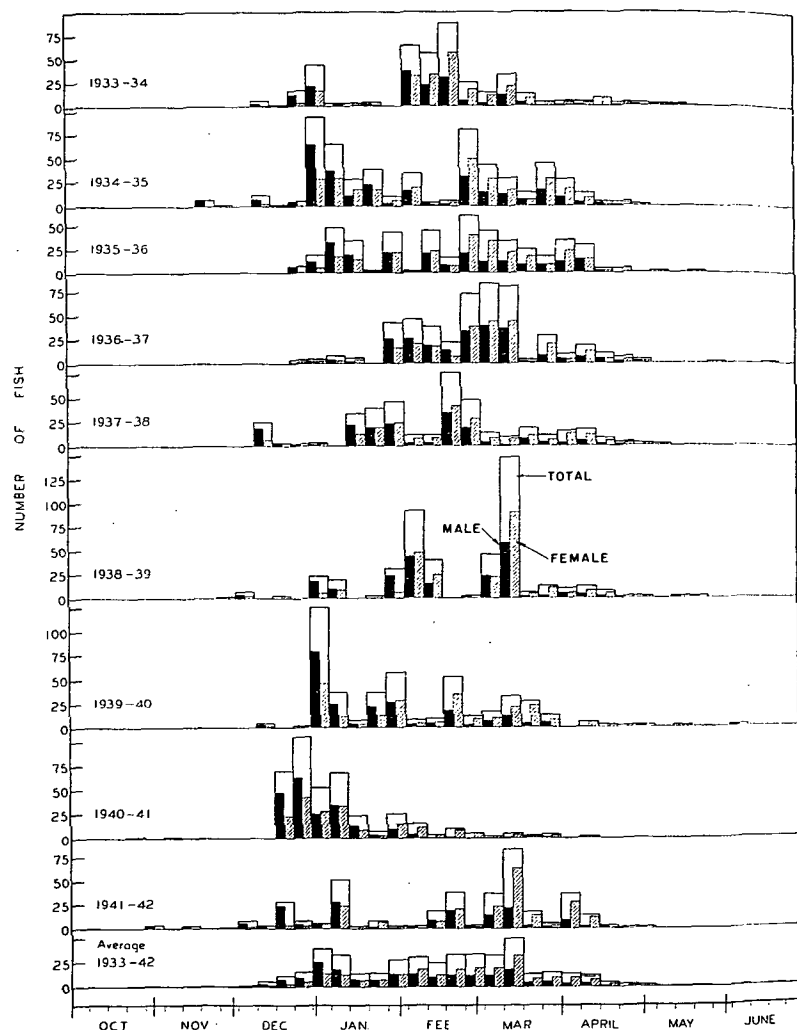


FIGURE 23. Adult steelhead checked through the upstream trap at Waddell Creek, by weekly periods.



FIGURE 24. Slippery Falls, barrier to upstream migrants, on the West Branch of Waddell Creek. Photograph by Paul R. Needham.

different *sea-run* races to occur in a stream so small and in which the entry of the fish was restricted to a portion of the season.

Just what is the explanation of the different runs—why the fish do not enter the stream at one time—is not known, but the reason is probably tied up with the habits and migrations of the fish in the ocean. The life history of the steelhead at sea is even more of a mystery than that of the silver salmon. Some of those facts that we do know will be presented in the section on "Sea Life" (pages 191-197).

During the nine seasons of operation of the upstream trap, 1933-34 through 1941-42, 3,888 adult steelhead were taken. The numbers of fish taken during each season, arranged by sexes and weekly periods, are shown in Table 27 and Figure 23.

From the above table and graph, it will be seen that the earliest fish was taken during the week ending October 28, and the latest fish

TABLE 27

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Seasons and Weekly Periods

Period	1933-34			1934-35			1935-36			1936-37		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
Oct. 1-7
Oct. 8-14
Oct. 15-21
Oct. 22-28
Oct. 29-Nov. 4
Nov. 5-11
Nov. 12-18
Nov. 19-25	6	..	6
Nov. 26-Dec. 2	1	..	1
Dec. 3-9
Dec. 10-16	3	2	5	7	3	10
Dec. 17-23	1	..	1	1	..	1
Dec. 24-30	13	3	16	4	..	4	6	..	6	1	..	1
Dec. 31-Jan. 6	27	16	43	64	27	91	11	6	17	2	2	4
Jan. 7-13	..	2	2	35	27	62	31	16	47	4	3	7
Jan. 14-20	..	2	2	10	16	26	19	13	32	2	3	5
Jan. 21-27	2	1	3	21	16	37	1	1	2
Jan. 28-Feb. 3	3	6	9	21	21	42	25	16	41
Feb. 4-10	36	32	68	15	18	33	..	1	1	23	20	43
Feb. 11-17	22	33	55	2	1	3	20	23	43	19	18	37
Feb. 18-24	32	55	87	2	3	5	8	7	15	14	7	21
Feb. 25-Mar. 3	6	18	24	30	49	79	20	39	59	34	37	71
Mar. 4-10	3	11	14	13	28	41	11	33	44	39	44	83
Mar. 11-17	12	21	33	12	16	28	11	21	32	36	44	80
Mar. 18-24	4	8	12	6	12	18	8	16	24	2	1	3
Mar. 25-31	..	3	3	16	28	44	8	16	24	8	20	28
Apr. 1-7	1	3	4	9	17	26	11	22	33	5	4	9
Apr. 8-14	1	3	4	4	8	12	14	14	28	6	12	18
Apr. 15-21	..	8	8	3	1	4	2	2	4	5	5	10
Apr. 22-28	1	2	3	1	3	4	..	4	4	2	4	6
Apr. 29-May 5	1	..	1	..	1	1	2	2	4
May 6-12	1	..	1
May 13-19
May 20-26	1	1
May 27-June 2
June 3-9
June 10-16
June 17-23	1	1	2
June 24-30
July 1-7
July 8-14
July 15-21
July 22-28
July 29-Aug. 4
Aug. 5-11
Aug. 12-18
Aug. 19-25
Aug. 26-Sept. 1
Sept. 2-8
Sept. 9-15
Sept. 16-22
Sept. 23-30
Totals	166	223	389	265	274	539	202	248	450	228	245	473

TABLE 27—Continued

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Seasons and Weekly Periods

Period	1937-38			1938-39			1939-40			1940-1941		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
Oct. 1-7
Oct. 8-14
Oct. 15-21	1	..	1
Oct. 22-28
Oct. 29-Nov. 4	1	..	1
Nov. 5-11
Nov. 12-18
Nov. 19-25	1	..	1
Nov. 26-Dec. 2	3	2	5
Dec. 3-9	3	1	4
Dec. 10-16	18	6	24	47	22	69
Dec. 17-23	2	..	2	..	2	2	1	62	104
Dec. 24-30	1	..	1
Dec. 31-Jan. 6	1	2	3	18	5	23	79	46	125	25	27	52
Jan. 7-13	10	9	19	24	12	36	34	28	62
Jan. 14-20	20	11	31	4	3	7	14	9	23
Jan. 21-27	19	19	38	..	2	2	22	14	36	4	3	7
Jan. 28-Feb. 3	22	23	45	24	5	29	27	29	56	10	14	24
Feb. 4-10	3	7	10	43	48	91	3	4	7	4	11	15
Feb. 11-17	2	8	10	15	24	39	4	5	9	..	3	3
Feb. 18-24	32	38	70	18	35	53	1	9	10
Feb. 25-Mar. 3	18	28	46	1	..	1	2	9	11	..	2	2
Mar. 4-10	4	8	12	22	22	44	6	10	16	..	5	5
Mar. 11-17	1	8	9	58	90	148	12	21	33	1	4	5
Mar. 18-24	7	10	17	1	4	5	4	23	27	1	1	2
Mar. 25-31	4	6	10	2	11	13	5	7	12	..	4	4
Apr. 1-7	3	12	15	5	8	10	..	5
Apr. 8-14	5	11	16	4	8	12	..	1	1
Apr. 15-21	2	5	7	2	5	7	..	1	1
Apr. 22-28	1	3	4	1	..	1	..	1	1
Apr. 29-May 5	..	2	2	..	1	1	1	..	1
May 6-12	..	1	1
May 13-19	1	..	1	..	1	1
May 20-26
May 27-June 2
June 3-9
June 10-16
June 17-23
June 24-30
July 1-7
July 8-14
July 15-21
July 22-28
July 29-Aug. 4
Aug. 5-11
Aug. 12-18
Aug. 19-25
Aug. 26-Sept. 1
Sept. 2-8
Sept. 9-15
Sept. 16-22
Sept. 23-30
Totals	165	208	373	212	243	455	214	228	442	205	185	390

TABLE 27—Continued

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Seasons and Weekly Periods

Period	1941-42			Total			Average		
	♂	♀	Total	♂	♀	Total	♂	♀	Total
Oct. 1-7	--	--	--	--	--	--	--	--	--
Oct. 8-14	--	--	--	--	--	--	--	--	--
Oct. 15-21	--	--	--	--	--	--	--	--	--
Oct. 22-28	--	--	--	1	--	1	+	--	+
Oct. 29-Nov. 4	3	--	3	3	--	3	+	--	+
Nov. 5-11	--	--	--	1	--	1	+	--	+
Nov. 12-18	2	--	2	2	--	2	+	--	+
Nov. 19-25	--	--	--	6	--	6	1	--	1
Nov. 26-Dec. 2	1	--	1	3	--	3	+	--	+
Dec. 3-9	6	2	8	9	4	13	1	+	1
Dec. 10-16	3	--	3	34	12	46	4	1	5
Dec. 17-23	24	4	28	75	28	103	8	3	11
Dec. 24-30	5	3	8	91	50	141	10	6	16
Dec. 31-Jan. 6	5	--	5	232	131	363	26	15	40
Jan. 7-13	28	23	51	166	120	286	18	13	32
Jan. 14-20	--	2	2	69	59	128	8	7	14
Jan. 21-27	1	7	8	70	63	133	8	7	15
Jan. 28-Feb. 3	1	2	3	133	116	249	15	13	28
Feb. 4-10	2	--	2	129	141	270	14	16	30
Feb. 11-17	9	8	17	93	123	216	10	14	24
Feb. 18-24	18	20	38	125	174	299	14	19	33
Feb. 25-Mar. 3	2	1	3	113	186	299	13	21	33
Mar. 4-10	14	23	37	112	181	293	12	20	33
Mar. 11-17	21	62	83	164	287	451	18	32	50
Mar. 18-24	3	12	15	36	81	117	4	9	13
Mar. 25-31	2	3	5	45	90	135	5	10	15
Apr. 1-7	9	28	37	43	91	134	5	10	15
Apr. 8-14	2	12	13	36	73	109	4	8	12
Apr. 15-21	2	1	3	16	28	44	2	3	5
Apr. 22-28	1	--	1	7	17	24	1	2	3
Apr. 29-May 5	1	--	1	5	6	11	1	1	1
May 6-12	--	--	--	1	1	2	+	+	+
May 13-19	--	--	--	1	1	2	+	+	+
May 20-26	--	--	--	1	1	2	+	+	+
May 27-June 2	--	--	--	--	--	--	--	--	--
June 3-9	--	--	--	--	--	--	--	--	--
June 10-16	--	--	--	--	--	--	--	--	--
June 17-23	--	--	--	--	1	1	--	+	+
June 24-30	--	--	--	--	--	--	--	--	--
July 1-7	--	--	--	--	--	--	--	--	--
July 8-14	--	--	--	--	--	--	--	--	--
July 15-21	--	--	--	--	1	1	--	+	+
July 22-28	--	--	--	--	--	--	--	--	--
July 29-Aug. 4	--	--	--	--	--	--	--	--	--
Aug. 5-11	--	--	--	--	--	--	--	--	--
Aug. 12-18	--	--	--	--	--	--	--	--	--
Aug. 19-25	--	--	--	--	--	--	--	--	--
Aug. 26-Sept. 1	--	--	--	--	--	--	--	--	--
Sept. 2-8	--	--	--	--	--	--	--	--	--
Sept. 9-15	--	--	--	--	--	--	--	--	--
Sept. 16-22	--	--	--	--	--	--	--	--	--
Sept. 23-30	--	--	--	--	--	--	--	--	--
Totals	165	212	377	1,822	2,066	3,888	202	230	432

was taken during the week ending July 21. Despite this long spread, 3,864 (96 percent) of all fish were taken during the 22 weeks December 3-May 5. Within any of these 22 weeks steelhead may be expected in most California steelhead streams, depending upon seasonal weather and water conditions. It will be noted from the nine-year averages for Waddell Creek that there are two peaks, occurring during the weeks ending January 6 and March 17, respectively. The occurrence of these two peaks so far apart is not a matter of chance, but is the result of the tendency of fish of different sex-life history categories to run at different times of the season.

It is of interest that 38.7 percent of all fish have been taken after February 28, the usual closing date of the winter steelhead season in California. At Benbow Dam 24.2 percent have been taken after the end of February, and at Sweasey Dam, 53.1 percent. The significance of these facts will be discussed in the section on "Recommendations for Management" (pages 267-268).

From Table 27 and Figure 23 it will also be seen that there has not been nearly so much fluctuation in the size of the seasonal runs as in the case of the silver salmon. The reason for the lesser fluctuation, and possible causes of the fluctuations which do occur, will be discussed in the sections on "Survival" and "Pathology" (pages 204-243). The largest number taken in the trap was 539 (265 males, 274 females), during the season of 1934-35, and the smallest number 373 (165 males, 208 females), during the season of 1937-38. (These are the same seasons in which the largest and smallest numbers of salmon were taken in the trap.)

Age and Size of the Fish

Steelhead of many life history categories make up the runs in Waddell Creek. Unlike silver salmon, steelhead migrate to sea at various ages and over a long period within a season, spend varying amounts of time in the ocean and return over a fairly long period within a season, are capable of spawning more than once, sometimes spawn before their first journey to sea, and may even remain in fresh water for their entire lives. This combination of possible life histories makes steelhead scale reading laborious and subject to some error.

The writers believe, however, that the great majority of the scale readings are unquestionably accurate. At Waddell Creek interpretation of the scales was facilitated by the fact that (1) an entire population was being studied over a considerable period of time, (2) fish length and time of migration were known, (3) returning marked and tagged fish with known ocean histories were available in large numbers for comparison, and (4) all scale readings were made by the same person (Shapovalov), with occasional corroborative readings by others.

Scales from all adult steelhead taken in the upstream trap were examined. The assignment to life history category was considered definitely correct for 86 percent of these fish, and probably correct, but somewhat doubtful, for 8 percent. For 2 percent, stream history was unknown (although ocean history could be calculated) because all scales had regenerated centers, and for 4 percent, stream history was

doubtful (with a possible error of one year). All of the doubtful fish were assigned to the various possible groups in the same proportions as the fish of more certain history.

The present discussion of age and size at maturity will be confined to sea-run fish. Also, any spawnings prior to initial migration to sea will be disregarded, since such spawnings are often very difficult to recognize in scale examinations. In other words, fish listed as "first spawners" are those spawning for the first time after one or more seasons at sea, irrespective of possible spawnings prior to initial migration to sea. Fish that have spawned prior to their initial migration to sea are believed to be in the great minority, and confined largely to the comparatively few fish that go to sea for the first time after three or four years in fresh water.

In Table 28 the adult steelhead taken in the upstream trap in each season have been divided according to number of spawnings, life history category, and sex. A number of interesting points are revealed by a study of this table.

First, we see that 82.8 percent (range 70.0-96.1 percent) of all adults had entered the stream for their first spawning. Although first spawners are in the great majority, repeat spawners are sufficiently numerous (17.2 percent) to be given serious consideration in a study of the biology of the species and in a management program. As is to be expected, among the repeat spawners the representation of each group declines as the number of spawnings increases. There is a sharp decline in numbers from second spawners (15.0 percent) to third spawners (2.1 percent). Fish spawning for the fourth time form a negligible proportion of the run (0.1 percent), and none spawning more than a fourth time was encountered. However, at Scott Creek two fish spawning for the fifth time (both females, season 1931-32) have been recorded. These fish add two additional life history categories to the 32 shown in Table 28: 1/4S.1 and 2/4S.1.

It is believed that this general picture in regard to composition of the runs is representative of California steelhead streams *where more or less natural conditions exist*. It is evident that unfavorable factors (physical conditions hampering return of fish to the ocean, holding of fish in tanks at spawning stations, and fishing) tend to diminish the number of repeat spawners. This phase of the subject will be discussed in greater detail in the section on "Recommendations for Management."

A further examination of Table 28 shows that, despite the great number of life history categories, on the average only four of them are of sufficient importance to exceed 5 percent of the run, as follows: 2/1 (29.8 percent), 2/2 (26.5 percent), 3/1 (10.5 percent), and 2/1S.1 (8.1 percent). Together, these four categories form 75 percent of the run.

Obviously, all second spawners are derived from first spawners, all third spawners from second spawners, and all fourth spawners from third spawners. An examination of the table shows that the life history categories represented most heavily among each group of the repeat spawners are derived from categories most strongly represented among the preceding group. This is strikingly shown in Table 29.

TABLE 28

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Sex and Life History Category (Percentages)

Season	Sex	Fish spawning for first time											
		1/1	2/1	3/1	4/1	1/2	2/2	3/2	4/2	1/3	2/3	3/3	4/3
1933-34	♂	3.9	15.2	3.6	---	0.5	11.3	1.0	---	---	---	---	---
	♀	0.8	6.4	3.3	0.3	3.9	30.6	2.8	---	---	---	---	---
	Total	4.6	21.6	6.9	0.3	4.4	41.9	3.9	---	---	---	---	---
1934-35	♂	0.9	20.0	13.7	0.2	2.4	7.6	2.6	---	---	0.4	---	---
	♀	0.7	8.0	16.5	0.6	6.1	13.2	3.0	---	---	0.2	---	---
	Total	1.7	28.0	30.2	0.7	8.5	20.8	5.6	---	---	0.6	---	---
1935-36	♂	1.6	16.7	2.7	0.7	0.2	12.2	1.6	---	---	0.2	---	---
	♀	1.1	8.2	4.5	0.4	0.7	22.0	7.6	0.4	---	---	---	---
	Total	2.7	24.9	7.1	1.1	0.9	34.2	9.1	0.4	---	0.2	---	---
1936-37	♂	---	11.6	14.4	2.1	1.7	9.5	1.1	---	---	0.2	---	---
	♀	0.6	11.0	14.2	3.0	1.7	10.4	1.7	---	---	---	---	---
	Total	0.6	22.6	28.6	5.1	3.4	19.9	2.7	---	---	0.2	---	---
1937-38	♂	---	12.9	1.9	---	0.5	12.9	4.6	0.3	---	0.3	---	---
	♀	0.8	13.1	1.6	---	1.9	11.8	6.2	1.3	---	---	---	---
	Total	0.8	26.0	3.5	---	2.4	24.7	10.7	1.6	---	0.3	---	---
1938-39	♂	1.3	21.8	2.9	0.2	0.7	12.7	0.4	0.2	0.2	0.2	0.2	---
	♀	0.4	17.4	0.9	0.2	1.3	18.5	2.2	---	---	---	---	---
	Total	1.8	39.2	3.7	0.4	2.0	31.2	2.6	0.2	0.2	0.2	0.2	---
1939-40	♂	7.5	28.7	1.4	---	1.6	5.9	0.7	---	---	---	---	---
	♀	4.1	22.4	0.9	---	2.0	17.0	0.5	---	---	---	---	---
	Total	11.5	51.1	2.3	---	3.6	22.8	1.2	---	---	---	---	---
1940-41	♂	6.9	27.4	---	---	2.3	8.2	---	0.3	0.3	---	---	---
	♀	2.3	10.0	0.8	---	4.9	14.9	1.5	---	0.3	---	---	---
	Total	9.2	37.4	0.8	---	7.2	23.1	1.5	0.3	0.5	---	---	---
1941-42	♂	9.0	13.8	5.0	0.3	0.5	4.8	0.5	---	---	---	---	---
	♀	2.4	4.0	6.1	2.7	4.8	14.8	1.3	---	---	0.5	---	0.3
	Total	11.4	17.8	11.1	2.9	5.3	19.6	1.9	---	---	0.5	---	0.3
Averages*	♂	3.3	18.8	5.5	0.4	1.2	9.4	1.4	0.1	0.1	0.2	+	---
	♀	1.4	11.3	5.9	0.8	3.0	16.8	3.0	0.2	+	0.1	---	+
	Total	4.7	30.0	11.4	1.2	4.2	26.3	4.3	0.3	0.1	0.2	+	+
Averages†	♂	3.5	18.6	5.1	0.4	1.2	9.5	1.4	0.1	0.1	0.1	+	---
	♀	1.5	11.2	5.4	0.8	3.0	17.0	3.0	0.2	+	0.1	---	+
	Total	4.9	29.8	10.5	1.2	4.2	26.5	4.4	0.3	0.1	0.2	+	+
Totals	♂	127	730	213	16	47	367	54	3	2	6	1	---
	♀	56	438	229	31	118	655	115	7	1	3	---	1
	Total	183	1,168	442	47	165	1,022	169	10	3	9	1	1
Grand totals	♂	1,566 (40.3%)											
	♀	1,654 (42.5%)											
	Total	3,220 (82.8%)											

All first spawners

TABLE 28—Continued

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Sex and Life History Category
(Percentages)

Season	Sex	Fish spawning for second time									
		1/1 S.1	1/1 S.1	2/1 S.1	3/1 S.1	4/1 S.1	1/1.1 S.1	2/1.1 S.1	3/1.1 S.1	4/1.1 S.1	2/1 S.2
1933-34	♂	---	---	5.9	0.5	---	---	0.3	---	---	---
	♀	0.3	---	3.3	---	---	0.3	3.1	0.3	---	---
	Total	0.3	---	9.3	0.5	---	0.3	3.3	0.3	---	---
1934-35	♂	0.4	---	0.6	0.2	---	---	---	---	---	0.2
	♀	---	---	---	0.4	---	---	2.0	---	---	---
	Total	0.4	---	0.6	0.6	---	---	2.0	---	---	0.2
1935-36	♂	---	---	6.9	1.8	---	---	0.4	---	---	---
	♀	---	---	2.0	4.0	0.4	---	3.3	---	---	---
	Total	---	---	8.9	5.8	0.4	---	3.8	---	---	---
1936-37	♂	---	0.2	4.7	0.8	0.2	---	---	---	---	0.6
	♀	---	---	2.1	0.8	---	0.2	2.7	1.5	---	---
	Total	---	0.2	6.8	1.7	0.2	0.2	2.7	1.5	---	0.6
1937-38	♂	0.5	---	5.9	3.5	---	0.3	0.5	---	---	---
	♀	---	---	5.6	4.3	1.3	0.8	4.6	0.3	---	---
	Total	0.5	---	11.5	7.8	1.3	1.1	5.1	0.3	---	---
1938-39	♂	---	---	4.2	0.7	---	---	0.4	---	---	---
	♀	---	---	4.4	0.4	---	---	2.9	1.5	0.2	---
	Total	---	---	8.6	1.1	---	---	3.3	1.5	0.2	---
1939-40	♂	0.5	---	1.8	---	---	0.2	0.2	---	---	---
	♀	0.2	---	2.9	---	---	---	0.7	---	---	---
	Total	0.7	---	4.8	---	---	0.2	0.9	---	---	---
1940-41	♂	1.3	---	5.6	0.3	---	---	---	---	---	---
	♀	1.5	---	6.2	1.3	---	2.1	1.3	---	---	---
	Total	2.8	---	11.8	1.5	---	2.1	1.3	---	---	---
1941-42	♂	1.6	---	5.8	0.3	---	---	0.3	---	---	---
	♀	0.5	---	5.0	0.5	---	1.6	5.8	0.5	---	---
	Total	2.1	---	10.9	0.8	---	1.6	6.1	0.5	---	---
Averages*	♂	0.4	+	4.4	0.8	+	0.1	0.2	---	---	0.1
	♀	0.3	---	3.3	1.3	0.2	0.5	2.8	0.5	+	---
	Total	0.7	+	7.7	2.1	0.2	0.5	3.1	0.5	+	0.1
Averages†	♂	0.5	+	4.6	0.9	+	0.1	0.2	---	---	0.1
	♀	0.3	---	3.5	1.3	0.2	0.6	3.2	0.5	+	---
	Total	0.8	+	8.1	2.2	0.2	0.6	3.4	0.5	+	0.1
Totals	♂	17	1	172	33	1	2	9	---	---	4
	♀	10	---	129	49	7	19	111	18	1	---
	Total	27	1	301	82	8	21	120	18	1	4
Grand totals	♂	---	---	239	(6.2%)	All second spawners					
	♀	---	---	344	(8.8%)						
	Total	---	---	583	(15.0%)						

TABLE 28—Continued

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Sex and Life History Category
(Percentages)

Season	Sex	Fish spawning for third time						
		1/2 S.1	2/2 S.1	3/2 S.1	4/2 S.1	1/1.2 S.1	2/1.2 S.1	3/1.2 S.1
1933-34	♂	0.5	---	---	---	---	---	---
	♀	---	0.3	0.3	---	0.3	0.5	0.5
	Total	0.5	0.3	0.3	---	0.3	0.5	0.5
1934-35	♂	---	---	---	---	---	---	---
	♀	---	---	---	---	---	---	---
	Total	---	---	---	---	---	---	---
1935-36	♂	---	---	---	---	---	0.4	---
	♀	---	---	---	---	---	0.4	---
	Total	---	---	---	---	---	0.4	---
1936-37	♂	---	0.8	0.2	---	---	---	---
	♀	---	0.4	1.1	---	0.2	---	0.2
	Total	---	1.3	1.3	---	0.2	---	0.2
1937-38	♂	---	0.3	---	---	---	---	---
	♀	0.3	0.8	---	---	---	0.3	0.5
	Total	0.3	1.1	---	---	---	0.3	0.5
1938-39	♂	---	0.4	---	---	---	0.4	---
	♀	---	1.8	0.4	---	0.2	0.4	---
	Total	---	2.2	0.4	---	0.2	0.4	---
1939-40	♂	---	---	---	---	---	0.2	---
	♀	---	0.5	---	---	0.2	0.2	---
	Total	---	0.5	---	---	0.2	0.2	---
1940-41	♂	---	---	---	---	---	---	---
	♀	---	0.5	---	---	---	---	---
	Total	---	0.5	---	---	---	---	---
1941-42	♂	---	1.6	0.3	---	---	---	---
	♀	0.5	2.4	0.3	0.3	---	1.6	0.3
	Total	0.5	4.0	0.5	0.3	---	1.6	0.3
Averages*	♂	0.1	0.3	0.1	---	---	0.1	0.2
	♀	0.1	0.7	0.2	+	0.1	0.4	0.2
	Total	0.1	1.0	0.3	+	0.1	0.4	0.2
Averages†	♂	0.1	0.3	0.1	---	---	0.1	0.2
	♀	0.1	0.7	0.2	+	0.1	0.4	0.2
	Total	0.1	1.1	0.3	+	0.1	0.4	0.2
Totals	♂	2	13	2	---	---	4	6
	♀	2	27	9	1	4	14	6
	Total	4	40	11	1	4	14	6
Grand totals	♂	---	17	(0.4%)	All third spawners			
	♀	---	63	(1.6%)				
	Total	---	80	(2.1%)				

TABLE 28—Continued

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Sex and Life History Category (Percentages)

Season	Sex	Fish spawning for fourth time			Total number
		1/3S.1	2/3S.1	2/1.3S.1	
1933-34	♂	---	---	---	166
	♀	---	---	0.3	223
	Total	---	---	0.3	389
1934-35	♂	---	---	---	265
	♀	---	0.2	---	274
	Total	---	0.2	---	539
1935-36	♂	---	---	---	202
	♀	---	---	---	248
	Total	---	---	---	450
1936-37	♂	---	---	---	228
	♀	---	---	---	215
	Total	---	---	---	473
1937-38	♂	---	---	---	165
	♀	0.3	---	---	208
	Total	0.3	---	---	373
1938-39	♂	---	---	---	212
	♀	---	0.2	---	243
	Total	---	0.2	---	455
1939-40	♂	---	---	---	214
	♀	---	---	---	228
	Total	---	---	---	442
1940-41	♂	---	---	---	205
	♀	---	---	---	185
	Total	---	---	---	390
1941-42	♂	---	---	---	165
	♀	---	0.3	---	212
	Total	---	0.3	---	377
Averages*	♂	+	---	---	
	♀	+	0.1	+	
	Total	+	0.1	+	
Averages†	♂	---	---	---	
	♀	+	0.1	+	
	Total	+	0.1	+	
Totals	♂	---	---	---	1,822
	♀	1	3	1	2,066
	Total	1	3	1	3,888
Grand totals	♂	---	0 (0.0%)	---	
	♀	---	5 (0.1%)	---	
	Total	---	5 (0.1%)	---	

* Means of totals.

† Means of seasonal percentages.

From Table 29 it will be seen that the representation of the different life history categories among the second spawners is not directly proportional to the representation of the life history categories from which they were derived among the first spawners. For example, among the first spawners the 2/2 fish are represented almost as strongly (26.5 percent) as the 2/1 fish (29.8 percent), while among the second spawners the 2/1.1S.1 fish, derived from the former, form only 3.4 percent of all fish, while the 2/1S.1 and 2/1S.2 fish, derived from the

TABLE 29

Waddell Creek, Steelhead: Derivation of Repeat Spawners From Previous Groups

Sex	First spawners		Second spawners		Third spawners		Fourth spawners	
	Category	Percentage of all fish	Category	Percentage of all fish	Category	Percentage of all fish	Category	Percentage of all fish
♂	2/1	18.6	2/1S.1	4.7	2/2S.1	0.3	2/3S.1	---
		11.2		3.5		0.7		0.1
		29.8		8.2		1.1		0.1
♀	2/2	9.5	2/1.1S.1	0.2	2/1.2S.1	---	2/1.3S.1	---
		17.0		3.2		0.4		+
		26.5		3.4		0.4		+
♂	3/1	5.1	3/1S.1	0.9	3/2S.1	0.1	3/3S.1	0.0
		5.4		1.3		0.2		
		10.5		2.2		0.3		
♀	1/1	3.5	1/1S.1	0.5	1/2S.1	0.1	1/3S.1	---
		1.5		0.3		0.1		+
		4.9		0.8		0.1		+
♂	3/2	1.4	3/1.1S.1	---	3/1.2S.1	---	3/1.3S.1	0.0
		3.0		0.5		0.2		
		4.4		0.5		0.2		
♀	1/2	1.2	1/1.1S.1	0.1	1/1.2S.1	---	1/1.3S.1	0.0
		3.0		0.6		0.1		
		4.2		0.6		0.1		
♂	4/1	0.4	4/1S.1	+	4/2S.1	---	4/3S.1	0.0
		0.8		0.2		+		
		1.2		0.2		+		
♀	4/2	0.1	4/1.1S.1	---	4/1.2S.1	0.0	4/1.3S.1	0.0
		0.2		+				
		0.3		+				
♂	2/3	0.1	2/2.1S.1	0.0	2/2.2S.1	0.0	2/2.3S.1	0.0
		0.1						
		0.2						
♀	1/3	0.1	1/2.1S.1	0.0	1/2.2S.1	0.0	1/2.3S.1	0.0
		+						
		0.1						
♂	4/3	---	4/2.1S.1	0.0	4/2.2S.1	0.0	4/2.3S.1	0.0
		+						
		+						
♀	3/3	+	3/2.1S.1	0.0	3/2.2S.1	0.0	3/2.3S.1	0.0

		+						

TABLE 30

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Spawning Experience and Total Age

Season	Fish spawning for first time							Fish spawning for second time						
	Total age	2	3	4	5	6	7	2	3	4	5	6	7	
1933-34.....	♂	15	61	58	4	---	---	---	---	23	3	---	---	
	♀	3	40	132	12	---	---	---	1	14	12	1	---	
	Total	18	101	190	16	---	---	---	1	37	15	1	---	
1934-35.....	♂	5	121	115	17	---	---	---	2	3	2	---	---	
	♀	4	76	160	20	---	---	---	---	---	13	---	---	
	Total	9	197	275	37	---	---	---	2	3	15	---	---	
1935-36.....	♂	7	76	67	11	---	---	---	---	31	10	---	---	
	♀	5	40	119	36	2	---	---	---	9	33	2	---	
	Total	12	116	186	47	2	---	---	---	40	43	2	---	
1936-37.....	♂	---	63	113	16	---	---	---	1	22	7	1	---	
	♀	3	60	116	22	---	---	---	---	11	17	7	---	
	Total	3	123	229	38	---	---	---	1	33	24	8	---	
1937-38.....	♂	---	50	55	18	1	---	---	2	23	15	---	---	
	♀	3	56	50	23	5	---	---	---	24	33	6	---	
	Total	3	106	105	41	6	---	---	2	47	48	6	---	
1938-39.....	♂	6	102	72	4	2	---	---	---	19	5	---	---	
	♀	2	85	88	11	---	---	---	---	20	15	7	---	
	Total	8	187	160	15	2	---	---	---	39	20	7	---	
1939-40.....	♂	33	134	32	3	---	---	---	2	9	1	---	---	
	♀	18	108	79	2	---	---	---	1	13	3	---	---	
	Total	51	242	111	5	---	---	---	3	22	4	---	---	
1940-41.....	♂	27	116	33	---	1	---	---	5	22	1	---	---	
	♀	9	58	62	6	---	---	---	6	32	10	---	---	
	Total	36	174	95	6	1	---	---	11	54	11	---	---	

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STEELHEAD AND SILVER SALMON LIFE HISTORIES

1941-42.....	♂	34	54	37	3	---	---	---	6	22	2	---	---
	♀	9	33	79	17	---	1	---	2	25	24	2	---
	Total	43	87	116	20	---	1	---	8	47	26	2	---
Totals.....	♂	127	777	582	76	4	---	---	18	174	46	1	---
	♀	56	556	885	149	7	1	---	10	148	160	25	1
	Total	183	1,333	1,467	225	11	1	---	28	322	206	26	1
Totals in percentages.....	♂	3.3	20.0	15.0	2.0	0.1	---	---	0.5	4.5	1.2	+	---
	♀	1.4	14.3	22.8	3.8	0.2	+	---	0.3	3.8	4.1	0.6	+
	Total	4.7	34.4	37.9	5.8	0.3	+	---	0.7	8.3	5.3	0.7	+

TABLE 30—Continued

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Spawning Experience and Total Age

Season	Fish spawning for third time							Fish spawning for fourth time							Total
	Total age	2	3	4	5	6	7	2	3	4	5	6	7		
1933-34	♂	---	---	2	---	---	---	---	---	---	---	---	---	166	
	♀	---	---	---	2	3	2	---	---	---	---	---	1	223	
	Total	---	---	2	2	3	2	---	---	---	---	---	1	389	
1934-35	♂	---	---	---	---	---	---	---	---	---	---	---	---	265	
	♀	---	---	---	---	---	---	---	---	---	---	1	---	274	
	Total	---	---	---	---	---	---	---	---	---	---	1	---	539	
1935-36	♂	---	---	---	---	---	---	---	---	---	---	---	---	202	
	♀	---	---	---	---	2	---	---	---	---	---	---	---	248	
	Total	---	---	---	---	2	---	---	---	---	---	---	---	450	
1936-37	♂	---	---	---	4	1	---	---	---	---	---	---	---	228	
	♀	---	---	---	3	5	1	---	---	---	---	---	---	245	
	Total	---	---	---	7	6	1	---	---	---	---	---	---	473	
1937-38	♂	---	---	---	1	---	---	---	---	---	---	---	---	165	
	♀	---	---	1	3	1	2	---	---	---	1	---	---	208	
	Total	---	---	1	4	1	2	---	---	---	1	---	---	373	
1938-39	♂	---	---	---	2	---	---	---	---	---	---	---	---	212	
	♀	---	---	---	9	4	---	---	---	---	---	1	---	243	
	Total	---	---	---	11	4	---	---	---	---	---	1	---	455	
1939-40	♂	---	---	---	---	---	---	---	---	---	---	---	---	214	
	♀	---	---	---	3	1	---	---	---	---	---	---	---	228	
	Total	---	---	---	3	1	---	---	---	---	---	---	---	442	
1940-41	♂	---	---	---	---	---	---	---	---	---	---	---	---	205	
	♀	---	---	---	2	---	---	---	---	---	---	---	---	185	
	Total	---	---	---	2	---	---	---	---	---	---	---	---	390	

1941-42	♂	---	---	---	6	1	---	---	---	---	---	1	---	165
	♀	---	---	1	9	7	2	---	---	---	---	1	---	212
	Total	---	---	1	15	8	2	---	---	---	---	1	---	377
Totals	♂	---	---	2	13	2	---	---	---	---	1	---	---	1,822
	♀	---	---	2	31	23	7	---	---	---	1	3	1	2,066
	Total	---	---	4	44	25	7	---	---	---	1	3	1	3,888
Totals in percentages	♂	---	---	0.1	0.3	0.1	---	---	---	---	+	0.1	+	---
	♀	---	---	0.1	0.8	0.6	0.2	---	---	---	+	0.1	+	---
	Total	---	---	0.1	1.1	0.6	0.2	---	---	---	+	0.1	+	---

2/1 group, form 8.2 percent of all fish. Therefore, it appears that survival beyond first spawning is a function of total age, as well as of number of spawnings.

In Table 30 the fish discussed previously are grouped according to total age.

It is believed that the general composition of the runs in Waddell Creek is representative of the composition of the runs in many other Pacific Coast streams under natural conditions. Comparisons are almost impossible to make, however, because the few published or otherwise available data are either (1) not representative of the entire runs for the localities in question or (2) not taken from localities in which normal conditions prevail. Even numerically adequate samples of the run in a given locality are apt not to be representative of the composition of the run, for the reason that the composition of the run changes markedly during a season, as will be shown on pages 141-142. Abnormal conditions are apt to alter the normal composition of a run in the following and other ways: (1) traps at egg taking stations often permit the escape of steelhead of small size; (2) the longer holding of males at egg taking stations is apt to diminish the percentage of repeat spawners among the males of the run; (3) the selection of parts of the run at an egg taking station for stripping of eggs is apt to diminish the number of repeat spawners among the fish selected for stripping, which are apt to represent certain life history categories more strongly than others; (4) a heavy fishery is apt to draw on certain life history categories more strongly than on others. An attempt at comparison with other localities is further complicated by the fact that some published material has combined first spawners with repeat spawners. As we have seen from the preceding tables, the sex ratios within the life history categories and total age groups and the proportions of the total run formed by the various life history categories and total age groups must be considered separately for first spawners and the various repeat spawners.

An analysis of the complete run at Scott Creek during the 1932-33 season is available, but it is doubtful that this run is representative of normal conditions, as evidenced by the fact that the males formed only 26 percent of the total run, while females formed 74 percent of the run. Of the total run of 377 fish, 59 percent had entered to spawn for the first time, 36 percent for the second time, 4 percent for the third time, and 1 percent for the fourth time. Although the proportion of repeat spawners was greater than the *average* for Waddell Creek, it may be pointed out that in individual seasons the various groups of repeat spawners at Waddell Creek have approached or exceeded those from Scott Creek cited above. In 1937-38 the second spawners formed 27.6 percent of the run at Waddell Creek, while in 1941-42 the third spawners formed 7.2 percent of the run there.

Pautzke and Meigs (1940) reported that of a sample of 99 sea-run Puget Sound steelhead, only five fish (5.1 percent) had spawned previously.²⁵ Of these, two fish (2.0 percent), one male and one female, were spawning for the second time and three fish (3.0 percent), all females, were spawning for the third time. Total ages of the 99 fish were as follows: three years, 13 percent; four years, 60 percent; five years, 23 percent; six years, 4 percent. At Waddell Creek, the total ages of the

²⁵ Two other fish, both males, had spawned prior to initial entry into salt water.

TABLE 31

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Spawning Experience and Total Age (Summary)

Spawning experience	Total age						Totals
	2	3	4	5	6	7	
1st spawners	183	1,333	1,467	225	11	1	3,220
2d spawners		28	322	206	26	1	583
3d spawners			4	44	25	7	80
4th spawners				1	3	1	5
Totals	183	1,361	1,793	476	65	10	3,888
Percentages	4.7	35.0	46.1	12.2	1.7	0.3	100.0

3,888 fish checked through the upstream trap have been as follows: two years, 4.7 percent; three years, 35.0 percent; four years, 46.1 percent; five years, 12.2 percent; six years, 1.7 percent; seven years, 0.3 percent. These figures are presented in tabular form in Table 31.

In summing up the results from the available data, we may state that for steelhead runs the following facts exist: (1) at least 59 percent of the fish (at Waddell, at least 70 percent) are spawning for the first time (excluding fish that have spawned prior to initial entry into salt water); (2) fish spawning for a second time *may* form an important contribution, constituting as high as 36 percent of the total run; (3) fish spawning for the third time form a very minor part of the total run; (4) fish spawning for the fourth and fifth times form a negligible portion of the run; (5) fish of a total age of over six years form a negligible portion of the run; (6) no fish more than seven years old have been encountered. Fluctuations in the representation of the various life history categories and inadequate data prevent definite statements regarding the representation of the various categories beyond the one that it is probable that 2/1 and 2/2 fish form the most important contributions among normal populations, with 3/1, 1/1, 3/2, and 2/1S.1 occasionally contributing to an appreciable extent. No other categories have formed as much as 10 percent of the total run in any season at Waddell Creek, and also do not appear to be of importance in other streams.

We may now turn to a discussion of size. In Table 32 the seasonal average lengths of adults checked through the upstream trap have been arranged in the same manner as were percentages in Table 28. In preparing Table 32, however, all fish for which there was any question regarding sex or scale interpretation of age, and also all known hatchery fish, have been eliminated, since in the present case it was necessary only to obtain sufficient numbers to show representative lengths for the fish of each sex, by life history categories, in each season.

The rate of growth is so much greater in the ocean than in fresh water that it is obvious the ocean growth in general determines the size

TABLE 32
Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Life History Category and Sex
Mean Length (in cm.)

Season	Sex	Fish spawning for first time											
		1/1	2/1	3/1	4/1	1/2	2/2	3/2	4/2	1/3	2/3	3/3	4/3
1933-34	♂	38.3 (13)	44.8 (43)	48.3 (4)	-----	67.0 (2)	71.0 (39)	77.0 (2)	-----	-----	-----	---	---
	♀	38.0 (2)	49.9 (18)	49.3 (4)	-----	64.3 (12)	67.0 (108)	67.9 (7)	-----	-----	-----	---	---
	Total	38.3 (15)	46.3 (61)	48.8 (8)	-----	64.7 (14)	68.0 (147)	69.9 (9)	-----	-----	-----	---	---
1934-35	♂	38.1 (5)	43.6 (100)	56.9 (69)	55.5 (1)	63.9 (13)	71.1 (38)	75.9 (10)	-----	-----	77.0 (2)	---	---
	♀	41.3 (4)	44.4 (41)	56.2 (83)	55.5 (1)	65.8 (32)	67.6 (66)	68.5 (12)	-----	-----	70.5 (1)	---	---
	Total	39.5 (9)	43.9 (141)	56.5 (152)	55.5 (1)	65.3 (45)	68.9 (104)	71.9 (22)	-----	-----	74.8 (3)	---	---
1935-36	♂	39.6 (6)	42.8 (67)	48.8 (11)	53.5 (2)	68.5 (1)	67.8 (40)	70.2 (6)	-----	-----	79.5 (1)	---	---
	♀	39.1 (5)	43.4 (32)	49.4 (18)	53.5 (2)	62.0 (2)	65.1 (92)	70.0 (29)	73.0 (2)	-----	79.5 (1)	---	---
	Total	39.4 (11)	43.0 (99)	49.2 (29)	53.5 (2)	64.2 (3)	66.0 (141)	70.0 (35)	73.0 (2)	-----	79.5 (1)	---	---
1936-37	♂	37.5 (1)	51.3 (37)	57.7 (49)	58.7 (5)	68.3 (4)	70.9 (36)	69.2 (3)	-----	-----	71.5 (1)	---	---
	♀	37.5 (1)	53.3 (29)	55.7 (41)	57.3 (6)	66.5 (5)	67.0 (41)	68.5 (5)	-----	-----	71.5 (1)	---	---
	Total	37.5 (1)	52.2 (66)	56.8 (90)	58.0 (11)	67.3 (9)	68.8 (77)	69.3 (8)	-----	-----	71.5 (1)	---	---
1937-38	♂	40.2 (3)	46.5 (43)	51.3 (5)	-----	71.5 (2)	70.0 (42)	72.7 (13)	-----	-----	-----	---	---
	♀	40.2 (3)	51.3 (48)	51.5 (3)	-----	64.1 (5)	67.4 (39)	69.7 (17)	70.5 (2)	-----	-----	---	---
	Total	40.2 (3)	49.1 (91)	51.4 (8)	-----	66.2 (7)	68.8 (81)	71.0 (30)	70.5 (2)	-----	-----	---	---
1938-39	♂	36.3 (6)	49.0 (93)	53.8 (11)	55.5 (1)	66.0 (2)	72.4 (47)	-----	79.5 (1)	77.5 (1)	73.5 (1)	---	---
	♀	45.5 (2)	51.8 (70)	53.8 (3)	55.5 (1)	68.0 (6)	69.2 (81)	69.6 (8)	79.5 (1)	77.5 (1)	73.5 (1)	---	---
	Total	38.6 (8)	50.2 (163)	53.8 (14)	55.5 (1)	67.5 (8)	70.4 (128)	69.6 (8)	79.5 (1)	77.5 (1)	73.5 (1)	---	---
1939-40	♂	41.0 (23)	45.9 (114)	52.5 (2)	-----	64.6 (6)	70.0 (22)	73.0 (2)	-----	-----	-----	---	---
	♀	42.1 (14)	50.0 (90)	55.5 (4)	-----	64.5 (8)	65.4 (69)	68.5 (1)	-----	-----	-----	---	---
	Total	41.4 (37)	47.7 (204)	54.5 (6)	-----	64.6 (14)	66.5 (91)	70.8 (3)	-----	-----	-----	---	---
1940-41	♂	38.5 (23)	43.7 (96)	52.5 (1)	-----	69.0 (2)	71.2 (28)	-----	79.5 (1)	-----	-----	---	---
	♀	38.8 (6)	45.5 (37)	52.5 (1)	-----	67.9 (12)	66.8 (51)	70.6 (6)	79.5 (1)	-----	-----	---	---
	Total	38.6 (29)	44.2 (133)	52.5 (1)	-----	68.1 (14)	68.3 (70)	70.6 (6)	79.5 (1)	-----	-----	---	---
1941-42	♂	37.0 (30)	42.1 (48)	52.8 (12)	59.5 (1)	58.0 (2)	68.2 (15)	64.5 (1)	-----	-----	69.5 (1)	---	---
	♀	38.1 (9)	44.3 (12)	54.6 (7)	55.5 (2)	60.9 (16)	65.1 (50)	66.5 (1)	-----	-----	69.5 (1)	---	---
	Total	37.3 (39)	42.0 (60)	53.4 (19)	56.8 (3)	60.6 (18)	65.5 (65)	65.5 (2)	-----	-----	69.5 (1)	---	---
Averages*	♂	38.5 (100)	45.3 (641)	55.6 (163)	57.3 (9)	65.4 (34)	70.4 (316)	72.9 (37)	79.5 (2)	77.5 (1)	75.7 (5)	---	---
	♀	40.2 (46)	49.0 (377)	54.9 (164)	56.7 (9)	65.0 (98)	66.7 (597)	69.4 (86)	71.8 (4)	79.5 (1)	70.0 (2)	---	---
	Total	39.1 (152)	46.7 (1018)	55.3 (327)	57.0 (18)	65.1 (132)	68.0 (913)	69.5 (123)	74.3 (6)	78.5 (2)	74.1 (7)	---	---
Averages†	♂	38.4	45.5	52.8	56.8	66.3	70.3	71.8	79.5	77.5	75.4	---	---
	♀	40.1	48.2	53.2	56.1	64.9	66.7	71.8	79.5	79.5	70.0	---	---
	Total	40.0	46.6	53.0	55.9	65.4	67.0	69.8	75.6	78.5	73.8	---	---

TABLE 32—Continued
Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Life History Category and Sex
Mean Length (in cm.)

Season	Sex	Fish spawning for second time									
		1/1S.1	1/1S.1	2/1S.1	3/1S.1	4/1S.1	1/1.1S.1	2/1.1S.1	3/1.1S.1	4/1.1S.1	2/1S.2
1933-34	♂	52.5 (1)	-----	61.1 (22)	60.0 (2)	-----	69.5 (1)	67.5 (1)	-----	-----	-----
	♀	52.5 (1)	-----	62.0 (11)	60.0 (2)	-----	69.5 (1)	75.2 (12)	-----	-----	-----
	Total	52.5 (1)	-----	61.4 (33)	60.0 (2)	-----	69.5 (1)	74.6 (13)	-----	-----	-----
1934-35	♂	57.0 (2)	-----	57.2 (3)	69.0 (2)	-----	-----	74.7 (11)	-----	-----	78.5 (1)
	♀	57.0 (2)	-----	57.2 (3)	69.0 (2)	-----	-----	74.7 (11)	-----	-----	78.5 (1)
	Total	57.0 (2)	-----	57.2 (3)	69.0 (2)	-----	-----	74.7 (11)	-----	-----	78.5 (1)
1935-36	♂	-----	-----	58.6 (26)	66.6 (6)	-----	-----	74.0 (2)	-----	-----	-----
	♀	-----	-----	59.4 (8)	64.3 (16)	68.5 (1)	-----	73.2 (13)	-----	-----	-----
	Total	-----	-----	58.8 (34)	65.0 (22)	68.5 (1)	-----	73.3 (15)	-----	-----	-----
1936-37	♂	-----	-----	63.0 (17)	65.0 (2)	64.5 (1)	-----	74.2 (9)	78.5 (7)	-----	74.5 (2)
	♀	-----	-----	62.6 (9)	65.2 (3)	-----	-----	74.2 (9)	78.5 (7)	-----	74.5 (2)
	Total	-----	-----	63.3 (26)	65.1 (5)	64.5 (1)	-----	74.2 (9)	78.5 (7)	-----	74.5 (2)
1937-38	♂	39.5 (1)	-----	63.6 (19)	66.8 (12)	-----	73.5 (1)	66.0 (2)	-----	-----	-----
	♀	39.5 (1)	-----	66.5 (20)	65.7 (14)	69.0 (2)	69.2 (3)	71.6 (15)	-----	-----	-----
	Total	39.5 (1)	-----	64.8 (39)	66.2 (26)	69.0 (2)	70.3 (4)	71.0 (17)	-----	-----	-----
1938-39	♂	-----	-----	63.7 (15)	66.5 (1)	-----	-----	77.0 (2)	-----	-----	-----
	♀	-----	-----	67.0 (19)	66.5 (2)	-----	-----	75.1 (11)	74.3 (4)	75.5 (1)	-----
	Total	-----	-----	65.5 (34)	66.5 (3)	-----	-----	75.4 (13)	74.3 (4)	75.5 (1)	-----
1939-40	♂	59.0 (2)	-----	60.2 (6)	-----	-----	67.5 (1)	-----	-----	-----	-----
	♀	54.5 (1)	-----	63.0 (11)	-----	-----	67.5 (1)	75.5 (3)	-----	-----	-----
	Total	57.5 (3)	-----	62.0 (17)	-----	-----	67.5 (1)	75.5 (3)	-----	-----	-----
1940-41	♂	60.5 (4)	-----	59.8 (20)	64.8 (3)	-----	69.0 (6)	69.5 (5)	-----	-----	-----
	♀	62.3 (4)	-----	61.9 (20)	64.8 (3)	-----	69.0 (6)	69.5 (5)	-----	-----	-----
	Total	61.4 (8)	-----	60.8 (40)	64.8 (3)	-----	69.0 (6)	69.5 (5)	-----	-----	-----
1941-42	♂	57.7 (5)	-----	59.3 (21)	55.5 (1)	-----	69.5 (5)	74.5 (1)	-----	-----	-----
	♀	56.0 (2)	-----	59.6 (18)	63.5 (1)	-----	69.5 (5)	72.5 (19)	75.0 (2)	-----	-----
	Total	57.2 (7)	-----	59.4 (39)	59.5 (2)	-----	69.5 (5)	72.6 (20)	75.0 (2)	-----	-----
Averages*	♂	57.3 (14)	-----	60.8 (149)	65.5 (24)	64.5 (1)	70.5 (2)	72.0 (8)	76.7 (13)	75.5 (1)	75.8 (3)
	♀	58.5 (8)	-----	63.1 (116)	65.2 (41)	68.8 (3)	69.2 (15)	73.4 (98)	76.7 (13)	75.5 (1)	75.8 (3)
	Total	57.7 (22)	-----	61.8 (265)	65.3 (65)	67.8 (4)	69.4 (17)	73.3 (106)	76.7 (13)	75.5 (1)	75.8 (3)
Averages†	♂	54.7	-----	60.7	63.4	64.5	70.5	71.8	75.9	75.5	76.5
	♀	56.3	-----	62.8	65.6	68.8	69.3	73.5	75.9	75.5	76.5
	Total	54.2	-----	61.5	64.5	67.3	69.2	73.4	75.9	75.5	76.5

TABLE 32—Continued
Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, by Life History Category and Sex
Mean Length (in cm.)

Season	Sex	Fish spawning for third time						Fish spawning for fourth time			Total number	
		1/2S.1	2/2S.1	3/2S.1	4/2S.1	1/1.2S.1	2/1.2S.1	3/1.2S.1	1/3S.1	2/3S.1		2/1.3S.1
1933-34	♂	71.0 (2)	63.5 (1)	74.5 (1)				81.5 (2)	79.5 (1)		80.5 (1)	166
	Total	71.0 (2)	63.5 (1)	74.5 (1)				81.5 (2)	79.5 (1)		80.5 (1)	223
1934-35	♂									76.5 (1)		265
	Total									76.5 (1)		274
1935-36	♂							76.5 (2)				539
	Total							76.5 (2)				202
1936-37	♂		69.5 (3)	70.7 (5)		75.5 (1)						248
	Total		69.5 (3)	70.7 (5)		75.5 (1)						450
1937-38	♂	76.5 (1)	63.5 (1)						67.5 (1)			228
	Total	76.5 (1)	63.5 (1)						67.5 (1)			245
1938-39	♂		72.5 (2)	74.0 (2)				82.5 (1)				473
	Total		72.5 (2)	74.0 (2)				82.5 (1)				165
1939-40	♂		73.5 (1)									298
	Total		73.5 (1)									373
1940-41	♂		67.0 (2)									214
	Total		67.0 (2)									228
1941-42	♂	70.5 (1)	65.7 (5)	71.5 (1)				75.0 (6)	70.5 (1)			442
	Total	70.5 (1)	65.7 (5)	71.5 (1)				75.0 (6)	70.5 (1)			205
Averages*	♂	71.0 (2)	68.2 (10)	71.9 (9)		75.5 (1)	77.1 (11)	74.2 (3)	67.5 (1)	76.5 (1)	80.5 (1)	165
	Total	73.5 (2)	69.0 (30)	71.9 (9)		75.5 (1)	77.1 (11)	74.2 (3)	67.5 (1)	76.5 (1)	80.5 (1)	212
Averages†	♂	71.0	69.2	72.7		75.5	78.9	74.2	67.5	76.5	80.5	377
	Total	73.5	68.2	72.7		75.5	78.9	74.2	67.5	76.5	80.5	---

* Means of totals.
† Means of seasonal averages.

attained by the fish of a given sex and life history category in a given season. Certain exceptions to this rule will be discussed further in this section.

In the case of the silver salmon (page 46 and Table 8) we saw that there was a tendency for males to attain a larger size than females. A careful study of the data in Table 32 reveals some very interesting facts in this regard for the steelhead. Taking up the first spawners, we find that among the fish that have spent two or more years at sea prior to return to fresh water, the males on the average attain a larger size than do females. This is shown most clearly for those categories for which the numbers of fish (shown in parentheses in Table 32) are the largest, large enough to be significant. In the case of the 2/2 fish, which are by far the most numerous in this group and the scales of which are the easiest to interpret, the males average larger than the females in each season.

Among the fish that returned to spawn after only one year at sea, among the most numerous group (2/1) the females attain a larger size than do the males. This is true in every season. In the case of the 1/1 fish, the average size of females is greater than that of males for all seasons combined, and also in five of the seven seasons for which both males and females were available.

In the case of the 3/1 fish, the females are larger than the males if the average for all seasons combined is calculated as means of seasonal averages (assumption that the seasonal averages are representative of the particular season), but the males are larger than the females if the averages are based on total numbers. A very interesting fact is revealed by an examination of the situation in individual seasons. It is seen that in those seasons in which the fish of this category were the largest (especially 1936-37 and 1934-35, with the largest numbers of fish) the males averaged larger than the females, while in those seasons in which the fish were markedly below average in size (1933-34 and 1935-36) the females averaged larger than the males.

In the case of the 4/1 fish, the numbers are probably too small to reach valid conclusions.

What is the explanation for the general tendency of males to reach a larger size than females among the fish spending two years at sea before returning to fresh water, and females to reach a larger size than males among the fish spending one year at sea before returning to fresh water? The most plausible explanation which occurs to the writers is that a greater proportion of males than of females has attained sexual maturity in fresh water prior to initial entry into the ocean among the fish returning to fresh water after one year at sea than among those returning after two years at sea. We know that among various species, including the Pacific salmon, males often mature precociously. Why the relative percentage of males attaining such precociousness should be greater among the fish returning after one year at sea than among those returning after two years at sea is not known, but may be dependent upon size attained in fresh water by grilse in comparison with size attained in the same length of time by fish which return after two years at sea, or may be dependent upon some other phase of the biology of the fish.

It appears that the reason why among the 3/1 fish the males average larger than the females in those seasons in which the fish of this category are larger than average, while the females average larger than the males in those seasons in which the fish are smaller than average, may be bound up with the proportionate numbers of fish of each sex reaching precocious sexual maturity under conditions producing larger than average fish and smaller than average fish. It will be noticed that among both the 3/1 and 2/1 fish there is proportionately more fluctuation in size from season to season than among other life history categories. The reason for this lies partly in growth conditions at sea, but is probably even more dependent upon the proportion which have spent a growing season in the lagoon. The proportion which does this is determined not only by the biology of the fish but also by fluctuating physical conditions. In some seasons a deep and large lagoon has persisted through the summer, while in other seasons there has been hardly any lagoon. In those seasons in which a large proportion of the fish had spent a summer in the lagoon, the average size is larger, while in those seasons in which a small proportion had spent a summer in the lagoon, the average size is smaller. The presence of fish of both types in the same season results in bimodal length-frequency distributions for fish of the same life history category.

It is possible that secondary sexual characters, especially the elongated snout of males, play some part in determining the relative size of males and females among the different life history categories, but that these are not of primary importance is indicated by the fact that among the various categories of fish spawning for a second or third time we find that the same size relationships persist: among the repeat spawners derived from first spawners which had returned to fresh water after one year at sea the females are larger than the males. This is clearly brought out in Table 33. Numbers of repeat spawners derived from first spawners which had returned to fresh water after two or more years at sea are so small that the probable reverse tendency among them is not clearly marked.

The data in Table 33 also indicate that growth is resumed following spawning among all life history categories. The only exceptions occur among two minor groups, 3/1.1S.1 and 1/2S.1; small numbers of fish may well be the cause of the apparent lack of growth in these cases.

From Table 33 it is also seen that the greatest increase in growth following first spawning, both absolute and relative, is made by the 1/1 group (males 18.8 cm., 49 percent; females 18.3 cm., 46 percent; total 18.6 cm., 48 percent), followed by the 2/1 fish (males 15.5 cm., 34 percent; females 14.1 cm., 29 percent; total 15.1 cm., 32 percent). Thus, it is evident that the greatest increase is made by the smallest fish. That increase is dependent upon size and not age may be seen from a comparison of the growth made by the 1/2 fish (males 5.1 cm., 8 percent; females 4.2 cm., 6 percent; total 4.3 cm., 7 percent), with that made by the 2/1 fish, which are of the same age.

That relative size attained by males and females is not a function of age alone is shown by the fact that among 2/1 fish females consistently attain a larger average size than do males, while among 1/2 fish males consistently attain a larger average size than do females.

An extremely interesting and important fact to be noted from Table 32 is that, as in the case of the silver salmon, the size attained in a given season by one sex of a given life history category is paralleled by the size attained by the other sex, with due allowance in those cases in which numbers of fish are small. This coupled with the facts (1) that significant differences exist in average size attained by fish of the same life history category in different seasons and (2) that there appears to be a lack of correlation between the average size

TABLE 33

Waddell Creek, Steelhead: Adults Checked Through Upstream Trap, Arranged to Show Growth of Repeat Spawners Derived From Various Life History Categories

Sex	First spawners		Second spawners		Third spawners		Fourth spawners	
	Category	Mean length in cm.*	Category	Mean length in cm.*	Category	Mean length in cm.*	Category	Mean length in cm.*
♂	2/1	45.3 (641)	2/1S.1	60.8 (149)	2/2S.1	68.2 (10)	2/3S.1	76.5 (1)
♀		49.0 (377)		63.1 (116)		69.4 (20)		76.5 (1)
Total		46.7 (1018)		61.8 (265)		69.0 (30)		
♂	2/2	70.4 (316)	2/1.1S.1	72.0 (8)	2/1.2S.1	77.1 (11)	2/1.3S.1	80.5 (1)
♀		66.7 (597)		73.4 (98)		77.1 (11)		80.5 (1)
Total		68.0 (913)		73.3 (106)				
♂	3/1	55.6 (163)	3/1S.1	65.5 (24)	3/2S.1	71.9 (9)	3/3S.1	
♀		54.9 (164)		65.2 (41)		71.9 (9)		
Total		55.3 (327)		65.3 (65)				
♂	1/1	38.5 (106)	1/1S.1	57.3 (14)	1/2S.1	71.0 (2)	1/3S.1	67.5 (1)
♀		40.2 (46)		58.5 (8)		73.5 (2)		67.5 (1)
Total		39.1 (152)		57.7 (22)		72.3 (4)		
♂	3/2	72.9 (37)	3/1.1S.1	76.7 (13)	3/1.2S.1	74.2 (3)	3/1.3S.1	
♀		69.4 (86)		76.7 (13)		74.2 (3)		
Total		69.5 (123)						
♂	1/2	65.4 (34)	1/1.1S.1	70.5 (2)	1/1.2S.1	75.5 (1)	1/1.3S.1	
♀		65.0 (98)		69.2 (15)		75.5 (1)		
Total		65.1 (132)		69.4 (17)				
♂	4/1	57.3 (9)	4/1S.1	64.5 (1)	4/2S.1		4/3S.1	
♀		56.7 (9)		68.8 (3)				
Total		57.0 (18)		67.8 (4)				
♂	4/2	79.5 (2)	4/1.1S.1	75.5 (1)	4/1.2S.1		4/1.3S.1	
♀		71.8 (4)		75.5 (1)				
Total		74.3 (6)						
♂	2/3	75.7 (5)	2/2.1S.1		2/2.2S.1		2/2.3S.1	
♀		70.0 (2)						
Total		74.1 (7)						
♂	1/3	77.5 (1)	1/2.1S.1		1/2.2S.1		1/2.3S.1	
♀		79.5 (1)						
Total		78.5 (2)						
♂	4/3		4/2.1S.1		4/2.2S.1		4/2.3S.1	
♀								
Total								
♂	3/3		3/2.1S.1		3/2.2S.1		3/2.3S.1	
♀								
Total								

* Mean of totals.

TABLE 34

Waddell Creek, Steelhead: Mean Length (in cm.) of Comparable First Spawners and Repeat Spawners to Show Effect of Spawning on Growth

Season	Sex	One stream, two ocean		Two stream, two ocean		Three stream, two ocean		Four stream, two ocean	
		1/2	1/IS.1	2/2	2/IS.1	3/2	3/IS.1	4/2	4/IS.1
1933-34	♂	67.0 (2)	-----	71.0 (39)	61.1 (22)	77.0 (2)	60.0 (2)	-----	-----
	♀	64.3 (12)	52.5 (1)	67.0 (108)	62.0 (11)	67.9 (7)	-----	-----	-----
	Total	64.7 (14)	52.5 (1)	68.0 (147)	61.4 (33)	69.9 (9)	60.0 (2)	-----	-----
1934-35	♂	63.9 (13)	57.0 (2)	71.1 (38)	57.2 (3)	75.9 (10)	-----	-----	-----
	♀	65.8 (32)	-----	67.6 (66)	-----	68.5 (12)	69.0 (2)	-----	-----
	Total	65.3 (45)	57.0 (2)	68.9 (104)	57.2 (3)	71.9 (22)	69.0 (2)	-----	-----
1935-36	♂	68.5 (1)	-----	67.8 (49)	58.6 (26)	70.2 (6)	66.6 (6)	73.0 (2)	68.5 (1)
	♀	62.0 (2)	-----	65.1 (92)	59.4 (8)	70.0 (29)	64.3 (16)	73.0 (2)	68.5 (1)
	Total	64.2 (3)	-----	66.0 (141)	58.8 (34)	70.0 (35)	65.0 (22)	-----	-----
1936-37	♂	68.3 (4)	-----	70.9 (36)	63.0 (17)	69.2 (3)	65.0 (2)	-----	64.5 (1)
	♀	66.5 (5)	-----	67.0 (41)	62.6 (9)	68.5 (5)	65.2 (3)	-----	64.5 (1)
	Total	67.3 (9)	-----	68.8 (77)	63.3 (26)	69.3 (8)	65.1 (5)	-----	-----
1937-38	♂	71.5 (2)	39.5 (1)	70.0 (42)	63.6 (19)	72.7 (13)	66.8 (12)	70.5 (2)	69.0 (2)
	♀	64.1 (5)	-----	67.4 (39)	66.5 (20)	69.7 (17)	65.7 (14)	70.5 (2)	69.0 (2)
	Total	66.2 (7)	39.5 (1)	68.8 (81)	64.8 (39)	71.0 (30)	66.2 (26)	-----	-----
1938-39	♂	66.0 (2)	-----	72.4 (47)	63.7 (15)	-----	66.5 (1)	79.5 (1)	-----
	♀	68.0 (6)	-----	69.2 (81)	67.0 (19)	69.6 (8)	66.5 (2)	79.5 (1)	-----
	Total	67.5 (8)	-----	70.4 (128)	65.5 (34)	69.6 (8)	66.5 (3)	-----	-----
1939-40	♂	64.6 (6)	59.0 (2)	70.0 (22)	60.2 (6)	73.0 (2)	-----	-----	-----
	♀	64.5 (8)	54.5 (1)	65.4 (69)	63.0 (11)	68.5 (1)	-----	-----	-----
	Total	64.6 (14)	57.5 (3)	66.5 (91)	62.0 (17)	70.8 (3)	-----	-----	-----
1940-41	♂	69.0 (2)	60.5 (4)	71.2 (28)	59.8 (20)	-----	-----	79.5 (1)	-----
	♀	67.9 (12)	62.3 (4)	66.8 (51)	61.9 (20)	70.6 (6)	64.8 (3)	79.5 (1)	-----
	Total	68.1 (14)	61.4 (8)	68.3 (79)	60.8 (40)	70.6 (6)	64.8 (3)	-----	-----
1941-42	♂	58.0 (2)	57.7 (5)	68.2 (15)	59.3 (21)	64.5 (1)	55.5 (1)	-----	-----
	♀	60.9 (16)	56.0 (2)	65.1 (50)	59.6 (18)	66.5 (1)	63.5 (1)	-----	-----
	Total	60.6 (18)	57.2 (7)	65.8 (65)	59.4 (39)	65.5 (2)	59.5 (2)	-----	-----
Averages*	♂	65.4 (34)	57.3 (14)	70.4 (316)	60.8 (149)	72.9 (37)	65.5 (24)	79.5 (2)	64.5 (1)
	♀	65.0 (98)	58.5 (8)	66.7 (597)	63.1 (116)	69.4 (86)	65.2 (41)	71.8 (4)	68.8 (3)
	Total	65.1 (132)	57.7 (22)	68.0 (913)	61.8 (265)	69.5 (123)	65.3 (65)	74.3 (6)	67.8 (4)
Averages†	♂	66.3	54.7	70.3	60.7	71.8	63.4	79.5	64.5
	♀	64.9	56.3	66.7	62.8	68.9	65.6	71.8	68.8
	Total	65.4	54.2	67.9	61.5	69.8	64.5	75.6	67.3

* Mean of totals.

† Mean of seasonal averages.

of the downstream migrants of a given age and year class and returning adults derived from them, indicates that conditions in the ocean may vary sufficiently from season to season to affect markedly the size of steelhead from a given stream.

Any attempt to determine the influence of a particular ocean year on the average size of the adults of a given life history category is obscured by many factors, including small numbers, precocious maturity and residence in the lagoon (particularly in the case of the grilse), different average lengths of time spent at sea during the same growth season by fish of different life history categories (because of different migration times both downstream and upstream), and different sex ratios among the different life history categories. However, there does appear to be a tendency for the 1/2, 2/2, and 3/2 groups, fish of different year classes and life history categories but the same ocean histories, to parallel each other in growth achieved in certain seasons. We may note that in the 1941-42 season the fish not only of these categories, but also of all the other more important categories, were of markedly below average size. It is of extreme interest that in the same season the silver salmon were also decidedly below average in size (Table 8). Thus, the ocean growth season of 1941-42 (i.e., principally summer of 1941) appears to have been a very poor one for both steelhead and silver salmon.

One other interesting fact may be demonstrated by the data in Table 32: the repeat spawners of a given life history category are markedly smaller than first spawners of the same year class which have spent the same number of seasons in fresh water and in the ocean. For example, the 1/2 fish may be compared with the 1/1S.1 fish, the 2/2 fish with the 2.1S.1 fish, etc. These data are singled out in Table 34, which shows clearly how spawning cuts down the subsequent size of the fish. Exceptions occur: individual fish complete their spawning and return to sea in short order, and so make rapid growth again.

TABLE 35

Waddell Creek, Steelhead: Spawning Runs, by Seasons

Season	Checked through upstream trap			Jumped over dam			Spawned below dam			Total run		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
1933-34	166	223	389	33	9	42	20	35	55	219	267	486
1934-35	265	274	539	3	--	3	7	5	12	275	279	554
1935-36	202	248	450	42	6	48	7	8	15	251	262	513
1936-37	228	245	473	10	--	10	11	10	21	249	255	504
1937-38	165	208	373	10	--	10	25	20	45	200	228	428
1938-39	212	243	455	--	--	--	5	6	11	217	249	466
1939-40	214	228	442	25	5	30	10	10	20	249	243	492
1940-41	205	185	390	25	5	30	10	10	20	240	200	440
1941-42	165	212	377	30	10	40	16	16	32	211	238	449
Totals	1,822	2,066	3,888	178	35	213	111	120	231	2,111	2,221	4,332
Averages	202	230	432	20	4	24	12	13	25	234	247	481

It is of interest that Waddell Creek steelhead achieve approximately the same length as silver salmon of the same life history categories, as follows:

	1/1 males	1/2 males	1/2 females
Steelhead	38.5	65.4	65.0
Silver salmon	40.6	64.7	63.9

Very few data on lengths of steelhead from other streams are available for comparison, but there is some unpublished evidence that steelhead (and silver salmon) from the Columbia River are larger, while those from the Klamath River are smaller, than comparable Waddell Creek fish. It appears, therefore, that the size of steelhead is not correlated with the size or latitude of the home stream.

The previous tables of this section have dealt with the fish which were checked through the upstream trap. In addition, in all seasons a number of fish spawned below the dam and in all seasons but one a comparatively small number of fish succeeded in jumping over the dam at extreme flood stage. Estimates of the numbers of such fish were made and are included in Table 35, which shows the estimated total made and are included in Table 35, which shows the estimated total runs into Waddell Creek.²⁶ It is assumed that the sex-life history composition of the fish spawning below the dam was essentially the same as that of those spawning above; field observations yielded no evidence to indicate that this assumption was not valid. From an examination of the figures in Table 35 it is obvious that among fish jumping over the dam males were in excess of females out of all proportion to the sex ratio among fish checked through the upstream trap. Examination of unclipped fish seen spawning or found dead above the dam and checked downstream after spawning, as well as general field observations, has shown that males are much more successful than females in jumping a fall such as that created by the dam. However, the numbers of fish which jumped over the dam are comparatively so small that they alter the general picture of the composition of the expected steelhead spawning run but little.

Sex Ratio

From Tables 28 and 29 it is seen that both among first spawners and second spawners, males characteristically predominate in certain categories, while females predominate in others. It will be found that among both first spawners and second spawners, males predominate in the life history categories forming the fish of the lesser total ages, while females predominate in those forming the fish of the greater total ages. This was shown clearly in Table 30, in which the fish discussed previously were grouped according to total age.

From this table it is seen that in considering sex ratios when the fish are grouped according to total age, the first, second, third, and fourth spawners must be considered separately. It will be noticed that

²⁶ Fish which had been checked through the upstream trap could be distinguished from unchecked fish, since in the former the anterior corner of the dorsal was clipped when the fish were checked. Estimates of the numbers of males and females, respectively, which jumped over the dam in each season were based on the proportions of clipped to unclipped fish seen spawning, found dead, and checked downstream after spawning and on other field observations. Estimates of the numbers of males and females which spawned below the dam in each season were based on the numbers seen spawning and on other field observations.

among the first spawners, females predominate among the four-year fish, while among the second spawners males predominate among the four-year fish.

Referring back to Table 29, we see that survival following spawning is higher among females than among males. Even in those groups in which males predominated when the fish entered as first spawners, the relatively higher survival among females persists through each successive spawning, until finally the females are numerically superior. As a result, there are very few males among the older groups of repeat spawners. One might expect that the spawning act would affect the females more than the males, especially since the females dig the nests, and so that a reverse phenomenon would be encountered. However, the lower survival among males probably results from the fact that males serve more than one female, and so are exposed not only to prolonged physical exertion, but also to the dangers of being stranded in the stream by lowering water levels and the closing of the bar at the mouth of the stream. It is possible that in large streams, the mouths of which remain permanently open, survival among males is somewhat higher than in the smaller streams, like Waddell Creek.

It is obvious from the preceding discussion that we cannot speak of the sex ratio of the steelhead run as a whole, without considering the ramifications and complexities created by the multiplicity of life history categories, and variations of behavior within certain life history categories. However, it may be of interest also to consider the end result as regards sex ratio, keeping in mind the various factors that create it. From Tables 28 and 35 we see that on the average the sex ratio for the run as a whole is one male to 1.13 females (47 percent to 53 percent) if only the fish checked upstream are considered, and one male to 1.05 females (49 percent to 51 percent) if the estimated total run is used. Among first spawners, the ratio is 1:1.05 (49:51 percent) for fish checked upstream, and 1.02:1 (50:50 percent) for those in the estimated total run.

Despite possible slight variations from the above figures in the ratios actually existing under natural conditions in various streams, it is evident that some unnatural factors are operating at egg collecting stations and other places where females are greatly in excess of males, sometimes as much as six females to one male.

An excess of females over males among the first spawners that have spent two years or more at sea prior to return to fresh water is theoretically to be expected, assuming a 1:1 sex ratio among juveniles and an equal mortality rate among males and females in the ocean, since males predominate among the grilse. The general picture for the steelhead first spawners is much the same as that for the silver salmon, although females are represented to some extent among all categories of steelhead grilse, while the silver salmon grilse are all males.

In the following subsection we shall consider another phase of this subject, the normally changing sex ratios during the course of a spawning run.

Changes in Sex-Life History Category Composition During the Run

The life history category and sex composition of the runs is not the same throughout the season. As in the case of the silver salmon, males predominate in the early portions of the runs, while females predominate in the latter portions. This change in sex ratio may be noted in Figure 23 and Table 27.

Since the sexes and life history categories are associated, it follows that changes in the representation of the life history categories also occur throughout the run. Of the principal categories, the 2/1 fish of smaller size predominate strongly in the early part of the run. There appears to be a general tendency for 2/2 fish to appear in increasing numbers as the season progresses, reaching a peak at midseason, and thereafter declining in numbers. The larger grilse, composed of the 3/1 fish and the larger 2/1 fish, do not appear in large numbers until March or the latter part of February, and thenceforth increase in relative abundance during the remainder of the season. Most of the other categories occur in numbers too small to note definite trends. Even in the case of the major categories, exceptions occur, but the generalizations stated probably represent the normal pattern. Seasonal changes in the runs of six of the most important life history categories of Waddell Creek steelhead are shown in Figure 25 (and Table A-15 of the Appendix).

Sportsmen and others have noted the variations in the composition of the steelhead runs in streams which have not been investigated from a biological viewpoint. They speak of the occurrence of small fish in the early part of the run, followed by the "large winter steelhead," in turn followed by fish of medium size, often known as "bluebacks".

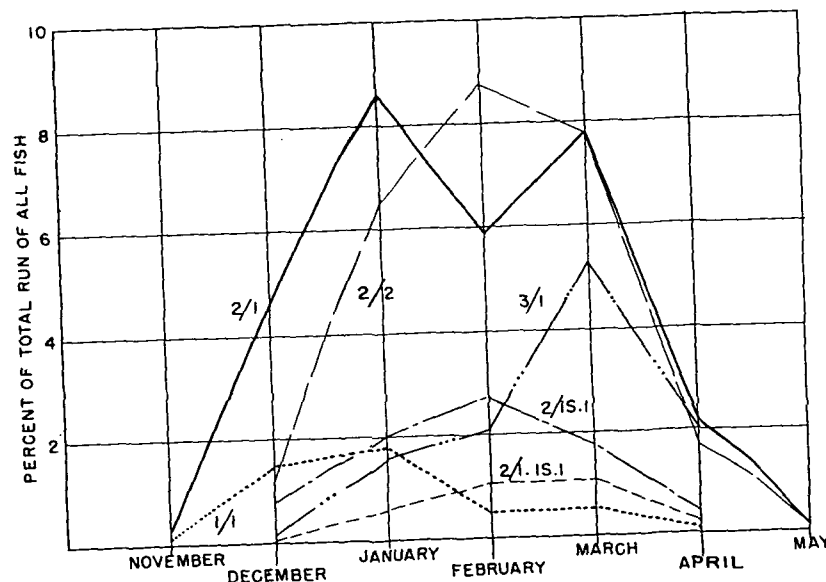


FIGURE 25. Seasonal distribution of life history categories in the Waddell Creek steelhead spawning run.

Deviations from the basic pattern are caused by abnormal environmental conditions, such as prolonged low stream flow, which delays the movement of some categories and the subsequent bunching of various categories when conditions again become suitable for upstream migration, and abnormal abundance or scarcity of certain life history categories.

The changing sex ratio in the steelhead run as a whole is accentuated by the fact that *within* certain life history categories the sex ratio changes in the same direction within the course of a season. Within the 2/1 group, males are greatly in excess at the beginning of the run, the sexes are approximately equally represented by the latter part of February or the early part of March, while females are usually somewhat in excess by the end of the run. Within the 2/2 group, there is some indication that males are more abundant in the early than in the late part of the run. Trends among the other categories are not evident.

Factors Influencing the Time of Upstream Migration

It has already been pointed out that in certain streams entry and upstream migration may necessarily be delayed by physical conditions. In many streams the first heavy upstream migrations coincide with large increases in stream flow, especially in streams which attain low summer levels, but such migrations often do not occur with the first large increases in stream flow.

As in the case of the silver salmon, the writers believe that in Waddell Creek and similar small streams there is also a definite relationship between ascension of the streams by spawning fish and flow of water, which so far it has proved impossible to show quantitatively, because of the existence of several variables. Steelhead, like silver salmon, ascend both on rising and falling stream levels, but cease movement during peak floods. However, the number of fish taken during any given water height is not approximately the same, but depends upon the proportion of the run that has already ascended the stream during the storm and during the season, upon preceding flows and climatic conditions, and possibly upon other factors, such as sexual ripeness of fish and turbidity of water. For example, on more than one occasion a number of steelhead have entered Waddell Creek during a storm or series of storms, but have "holed up" in pools in the lower portion of the stream, below the trap, as a result of sudden cessation of the storm and lowering of flow. These fish tend to remain "holed up" until a change of weather occurs, in which case even a light rain and small rise in stream level will cause a large number to ascend the stream or spawn below the pool in which they had waited. In this respect the steelhead appear to be less demanding than the silver salmon, sometimes ascending the stream or dropping below to spawn if the period of fair weather is quite prolonged. In general, the steelhead appear to be less exacting than silver salmon as regards the conditions under which they will spawn or ascend an obstacle in a stream, such as a fishway. Diurnal fluctuations in migration may now be considered.

Steelhead, silver salmon, and king salmon move upstream mainly in the daytime. Observations by Chapman (1941), Neave (1943), and the

writers which substantiate this statement were discussed in the comparable section for silver salmon (page 55). It was also pointed out that various workers have noted the occasional occurrence of periods of relative inactivity in upstream movement of various salmonids within the daylight hours, but that no correlations between such fluctuations in movement during the daytime and environmental factors have been demonstrated. As Chapman (1941) pointed out, they are "probably multiple with complex inter-relationships." It was noted that particularly at Scott Creek two daily peaks of migration among the steelhead have been observed by the writers on successive days, without any marked changes in stream discharge, turbidity of water, or general weather conditions (other than light and temperature).

Changes in Body Form and Coloration Associated With Maturation

The changes in body form and coloration which are associated with maturation in sea-run steelhead are of the same character as those in the silver salmon, but usually much less marked. In the males, these changes are characterized by elongation of the jaws, with knobbing but rarely with hooking, the growth of canine-like teeth, and the increase in depth of body by the ridging of the back. Among the larger fish, the extent of these changes is sufficiently greater in the males than in the females to enable the experienced observer to determine the sex by external examination. Among the smaller fish the sexual differences in these characters are sometimes so slight that considerable difficulty may be experienced in distinguishing between males and females, especially in fish which are not ripe. Following spawning these growths are partially resorbed, but the jaws never fully recover their original shape.²⁷

Like the Pacific salmon, steelhead at sea are quite silvery. In fresh water a pink or reddish lateral band, usually most prominent and brightest in males, develops along the body. The opercles (gill covers) become similarly colored.

As in the Pacific salmon, the scales, which are loosely attached in individuals in salt water and in those recently arrived from the sea, become firmly imbedded with the approach of spawning, particularly in the males.

Spawning Beds

Females choose the redd sites. Examination of many redds shows that the site selected is typically near the head of a riffle (which is also the lower end of a pool) composed of medium and small gravel. Usually the site is close to the point where the smooth surface water "breaks" into the riffle.

The nature of the redd site insures a good supply of oxygen for the eggs, since in streams a considerable portion of the water flowing through a swift riffle passes through the gravel.

Although steelhead ordinarily spawn in places that also look "good" to the experienced observer, and which he would have selected as

²⁷ While some bones increase their size and acquire new material, parts of others and of the scales are absorbed. The changes which take place in the skulls of breeding salmonids have been described in a series of papers by Tchernavin (1918, 1921, 1937a, 1937b, 1938a, 1938b, 1938c, 1938d).

probable spawning sites before the fish had arrived, occasional individuals pick sites which the observer would have picked as being unfavorable, either because of the composition or configuration of the bottom or the character of the flow. The power of the fish to dig a pit in apparently unfavorable bottom is illustrated by one example cited by Needham and Taft (1934). The female in question dug a nest in a hard, gravelly, semicemented mixture of decomposing rock forming a portion of a ford built for automobile passage in the East Branch of Waddell Creek just above The Forks. This ford had been constructed by piling up rocks which were held in place by wire poultry netting along the downstream margin. The female had crumbled this hardpan and worn away the edge of the outcrop so that it was evenly broken off near the edge of the ford. Fish select unusual and apparently unfavorable sites even when there is no overcrowding and apparently more favorable unused sites are available in readily accessible portions of the stream.

Steelhead so choose their redds that they are very rarely exposed by falling stream levels, in both Waddell Creek and other California coastal streams.

Spawning

The first complete, recorded observations on the spawning of sea-run steelhead were made during the spring of 1933 in Waddell Creek by P. R. Needham, A. C. Taft, and Leo Shapovalov and were described in detail by Needham and Taft (1934). Their account was confined largely to observations on three fish placed in a pen in the natural stream. A generalized account of the spawning of steelhead is here presented, as follows.

The female first selects a suitable spawning site. In this process several sites may be selected and abandoned. After a satisfactory site is finally chosen, the female begins nest digging. One or more males may accompany the female, but the males do not participate in the digging. Usually one male becomes the mate; the other males, although sometimes persistent in approaching the female, seem to sense this and usually yield to the dominant male when he makes a rush at them. Probably more often than not the mate is a larger fish than the attendant males, but even if smaller, his "right" to the female is usually recognized. On occasion the dominant males chase the accessory males viciously, even to the extent of driving them into the riffle above or below the nest. The fighting and digging often result in a great deal of commotion, especially when several males are in attendance, so that the resultant splashing may be heard several hundred feet from the stream.

While the female is digging the nest, the male assumes positions slightly behind (downstream) and to one side of her. The dominant male often changes his position from one side to the other, and apparently attempts to stimulate her. At frequent intervals he approaches the side of the female closely and the two fish quiver, together or separately. This quivering and also the nest digging have often been mistaken for the emission of the sexual products by different writers (e.g., Kendall and Dence (1929) for eastern brook trout), but the behavior accompanying the latter action is quite different. When several males accompany a female, the accessory males usually arrange themselves in an arc on the downstream side of the female. The distance that they

maintain depends upon the pugnacity of the dominant male. In the accompanying photograph (Figure 26) four males will be seen ranged about the mating pair and nest. Two other males, six to nine inches long (stream fish), participated but do not appear in the photograph. The dominant male then alternates between darts at these fish and courting of the female. Upon returning from an attack on other males, the dominant male often rubs his snout both over and under the tail of the female, probably either to stimulate her or as a sign of recognition. Fish of both sexes face upstream during the spawning activities.

In digging the nest the female turns on her side and with powerful and rapid movements of the tail disturbs the bottom materials, which are then carried a short distance downstream by the current. As this process is repeated the nest takes form and finally results in an oval or roundish pit or depression. Depending partly on the size of the fish, the pit is approximately from four inches to a foot in depth and 15 inches in diameter. After several vigorous digging operations the female usually drops back into the pit and may test its dimensions with her anal fin.

The length of time that elapses between the beginning of courting and nest building activities on the chosen redd and the deposition of the sexual products varies greatly. In the observations of 1933 the deposition of the eggs and milt took place four hours and twenty-five minutes after the fish were placed in the pen and one hour and twenty-five minutes after digging had been started.

At the moment of deposition, the female drops into the pit and lowers her vent and anal fin into the deepest part. The male instantly or simultaneously moves into a position parallel and next to her, so that the vents are opposite. Both fish open their mouths wide and arch their bodies so that they are rigid, with their backs concave (in the observations of 1933, the tip of the female's snout broke the surface of the water), and the eggs and milt are exuded simultaneously. The eggs drop into the bottom of the pit in a compact group and are enveloped by a cloud of milt. The whole process, from the time that the female drops into the pit until the synchronized orgasm resulting in the actual deposition of the eggs, takes only a few seconds.

For many years the view was generally held that natural reproduction of salmonids is a rather ineffective process, but various studies contradict this opinion. Probably rarely are any of the eggs swept out of the pit, even when the current is swift. Sometimes some of the milt may be swept downstream, but an ample amount settles with the eggs to insure thorough fertilization. Apparently both the eggs and the milt are held in the pit by current eddies below the normal level of the stream bed. This view has been advanced for the spawning of various salmonids by Peart (1920) and others.

Hobbs (1937), in his studies in New Zealand, concluded that at least 97.5 percent of the brown trout eggs lodged in the redds at the time of spawning. The present writers believe that 97.5 percent would express a minimum average for the number of eggs buried in the redds by steelhead.

Immediately upon deposition of the eggs and milt, the female, unaided by the male, begins to cover up the eggs. This she accomplishes in a few seconds by turning on her side and digging to each side and



FIGURE 26. A pair of Waddell Creek steelhead over spawning nest, with four smaller males ranged around the nest. Photograph by Paul H. Needham, April, 1943.

forward of the nest, the current sweeping the gravel into the pit. The eggs are well covered in a brief period of time. The males appear uninterested in this process.

When the eggs are well covered the female begins to dig another pit two or three feet directly upstream from the first. By working upstream in this manner the eggs of the first pit are buried deeper by materials washed downstream from the subsequent digging. This process is repeated as other pits are dug. In the 1933 observations the eggs were deposited in the second pit one hour and forty minutes after initial deposition, and digging of the third pit was started shortly. Apparently the fish in question completed spawning during the night, since by morning she had left the redd and retired to the adjoining pool. When she was killed for examination in the early afternoon it was found that only seven eggs remained.

Judging by the separately raised piles of gravel, which were in a straight line following the current, the 1933 fish dug six or seven pits to complete spawning. Since fish of similar size (60 cm. long) contain from 3,800 to 7,800 eggs, this female may have averaged a deposition of anywhere from 550 to 1,300 eggs at a time.

The completed redd was approximately 12 feet long and 5 feet wide (60 square feet). The depth of the water averaged about five inches over this area.

Although the 1933 fish completed spawning within 12 hours, it is believed that often the process takes a week or more. The length of time probably depends upon the ripeness of the fish, water and atmospheric conditions (especially temperature and height of water), and the extent to which the mating fish are interrupted by intruders (human beings, stream-side mammals, birds, and other fish).

Fish after natural spawning do not have much blood in the coelomic cavity, while in artificial spawning blood is often found in the coelomic cavity and is sometimes extruded with the last eggs, due to rupture of blood vessels. The amount of damage thus done to the fish depends principally upon (1) the skill of the spawner and (2) the extent to which he attempts to secure a high percentage of eggs contained.

No quantitative estimate can be made of the amount of damage done to redds by subsequent spawners, which may be silver salmon or other steelhead. It is probable that although the losses from this cause may be severe in individual nests, the percentage loss for all eggs deposited in the stream is small.

Spawning sea-run steelhead are very often accompanied by stream trout. Most of these are sexually mature males which act much like the smaller accessory sea-run males, darting in and out during the nest-building and courting process. Such fish are often called "egg-eaters" by anglers. However, their primary purpose in being present is probably to participate in the spawning activities. This is indicated by the fact that in occasional instances in which a single stream male has been seen to accompany a nest-building sea-run female unaccompanied by a sea-run male, the behavior of the stream male has been quite similar to that of a sea-run dominant male, the fish maintaining a position parallel to the female and slightly behind and to one side of her.

Accompanying stream fish often do contain a few eggs in their stomachs. Such eggs are probably occasional ones shed by fish on their way upstream or in the course of nest digging, disturbed by superimposition of nests on nests prepared by previous fish, or swept out of the spawning pits before they were covered. It is a general thing for trout of various species to contain eggs of whatever species of salmonids are spawning at the time. Some examples were cited in the comparable section on silver salmon spawning (page 59). Eggs eaten by sculpins (*Cottus*) are most likely occasional ones of the types described previously.

Egg Production

The calculations of numbers of eggs produced by Waddell Creek steelhead are based on the numbers produced by Scott Creek steelhead, since collection of eggs from Waddell fish would have destroyed the experimental plan. There is no evidence to indicate that the Scott Creek fish produce a different average number of eggs for a given size of fish from Waddell fish.

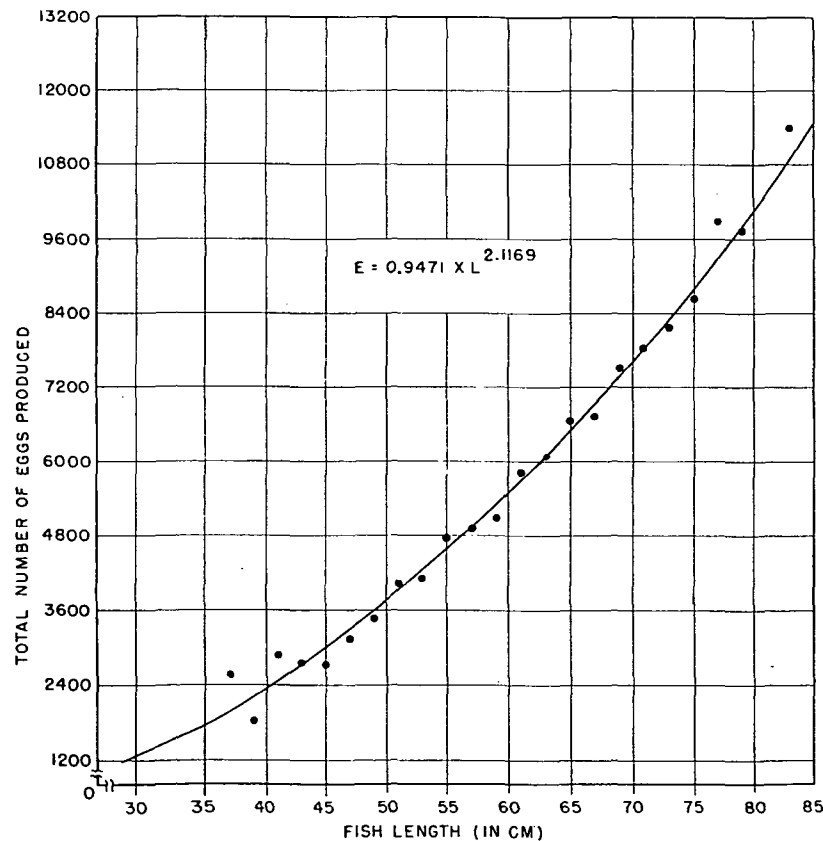


FIGURE 27. Egg production of Scott Creek steelhead.

Correlation of Number of Eggs With Size of Fish

The relationship between length of the fish and the number of eggs produced is shown in Figure 27. This relationship was determined from 562 measurements of the amount (volume) of eggs and the size (volume) of individual eggs obtained from manually spawned fish of known lengths, taken at Scott Creek during the 1931-32, 1932-33, and 1933-34 seasons.²⁸

Measurement of the eggs was carried out according to the Taft method, described in the comparable section for silver salmon (pages 59-61). This method is particularly valuable for securing data on trout egg production, since it permits the securing of the data without destroying either the fish or the eggs. As in the case of the salmon, total egg volume was measured in a 1,000 cc. glass graduate, and the volume of individual eggs by averaging the displacement of 10 eggs in a burette.

In calculating the volume factor (F) for Scott Creek steelhead, three egg counts and measurements from two fish were used. The volume in cc. of individual eggs was obtained from two of these measurements by averaging the volume of 110 eggs measured in lots of 10 and for the other by averaging the volume of 100 eggs measured in lots of 10. From these values a volume factor of 0.674 was obtained. The data used in obtaining F are shown in Table A-16 of the Appendix. The frequency distribution of quantity of eggs (in cc.) stripped from Scott Creek steelhead is given in Table A-17 of the Appendix.

Examination of 12 manually spawned fish taken at random during the seasons of 1931-32 and 1932-33 showed that in ordinary hatchery spawning only about 90 percent of the number of eggs contained in the fish is obtained, the remaining 10 percent being left in the ovaries (see Appendix, Table A-18). Therefore, to obtain the total number of eggs the calculated number was multiplied by 1.1.

Although the number of fish examined (12) to determine the percentage of eggs left in the fish in artificial spawning may not be large enough to give an exact figure, there is evidence to support the view that the percentage obtained is not far from the average. For 151 red salmon spawned by the expression method at Cultus Lake, British Columbia, in 1931 and 1932, Foerster (1936) records the average number of eggs left in the stripped fish as 14.5 percent of the total number of eggs. For 16 manually spawned golden trout (*Salmo gairdneri*), Curtis (1934) found the number of eggs left in the fish to be about 7 percent of the number contained. The percentage of eggs obtained in artificial spawning of steelhead probably depends principally upon (1) the skill of the spawner and (2) the ripeness of the fish. It does not appear to depend upon size or life history of the fish, or the number or size of eggs produced.

The total number of eggs was plotted in 400-egg intervals against fish length in 2-cm. intervals and a regression line was fitted to the points.

²⁸ Normal hatchery spawning procedure was followed in obtaining the eggs: in spawning steelhead the fish are not killed and cut open, as is often the case with Pacific salmon, but are "stripped" by means of manual pressure applied to the sides and belly of the fish. This is known as the "expression" method. The stripping was carried out by experienced hatchery personnel. The measurements of fish and eggs were made by A. C. Taft, J. H. Wales, Leo Shapovalov, and various assistants. After the eggs were stripped from the fish and fertilized they were placed in two-quart glass jars.

This line was fitted by the method of least squares and, since the relationship is curvilinear, the regression line was determined on a logarithmic scale and later transposed to a linear scale. This regression line is not as accurate as one determined from the original paired variates, but is close enough to the true one to be used here, considering all possible sources of error. Its equation is $\text{Number of Eggs} = 0.9471 \times \text{Length}^{2.1169}$. The correlation ratio, r , for the relationship between eggs produced and fish length is 0.838.

Before the factor used to obtain the calculated number of eggs (0.674) was chosen, a factor of 0.6888 had been used. Using this latter factor, and omitting the data for 1934-35, the regression of eggs produced on fish length had been calculated separately for first spawners, second spawners, and all fish combined. While these regressions are not believed to be as accurate as the present ones and therefore are not presented at this time, they do show that the differences between first and second spawners and between each of these categories and all fish combined are so slight that a single regression may be used.

Prior to the adoption of the method finally used, an attempt was made to calculate the number of eggs on the basis of the average diameter of 10 eggs rather than volume. This method was found to be unreliable.

In the corresponding section for silver salmon a correlation was shown to exist between number of eggs and length of fish, and it was pointed out that other workers had found a positive significant correlation between number of eggs and both length and weight in other species of salmonids. Weights of the Scott Creek steelhead were not obtained. The significance of such a correlation in the management and study of the species involved was also noted.

Percentage of Eggs Deposited

It was shown in the preceding section that in artificial stripping approximately 10 percent of the eggs are left in the fish. To calculate the total number of eggs deposited in Waddell Creek in each season it was necessary to know the average number of eggs left in the fish after spawning.

By the very nature of the plan of the experiments at Waddell Creek it was impossible to kill spent steelhead to determine the number of eggs left in the fish after spawning. Reliance therefore had to be placed on (1) chance dead spent steelhead found in Waddell Creek, (2) observations on other streams, and (3) observations on closely related adult salmonids of similar size and habits. There are only four records for counts of eggs in dead spent steelhead found in Waddell Creek. These fish contained 0, 3, 16, and 58 eggs, respectively. As noted in a previous section, the 60 cm. Scott Creek steelhead used in the 1933 spawning pen experiment at Waddell Creek contained only seven eggs after spawning. The average for the five fish for which definite counts are recorded is therefore only 16.8. This meager record is supported by a number of notes for dead steelhead at Waddell Creek made by different field observers to the effect that the fish were "completely spent". As stated in the corresponding section for silver salmon (page 62), these observations are in close agreement with the findings of the writers and other workers for other species of salmonids. Therefore,

it was decided not to subtract any eggs in calculating the number deposited by Waddell Creek steelhead, but to use the *total egg production* figures obtained for Scott Creek steelhead of the same lengths and expressed by the regression line in Figure 27. It is likely that the number of eggs left in the fish after natural spawning bears little or no relation to the size of the fish (and consequently the number of eggs produced).

Percentage of Eggs Fertilized

Although quantitative data for Waddell Creek steelhead are not available, there is every indication that the percentage of eggs fertilized is very high and rather constant. Extensive spawning work by personnel of the California Department of Fish and Game has shown that the percentage of steelhead eggs fertilized *can* be quite high under the close to ideal artificial conditions. In the corresponding section for silver salmon (page 63) it was noted that the observations of Hobbs (1937) indicated a uniformly high efficiency of fertilization (over 99 percent) for other species of salmonids, and that since the spawning of the various trouts and salmonids follows essentially the same pattern and local conditions usually play a more important role than the factors peculiar to the species involved, it appears legitimate to apply them in the present studies.

The previously cited observations on the spawning act of steelhead in Waddell Creek (pages 144-148) support the view that the percentage of fertilization is quite high. Besides, the observations of the writers and the various seasonal observers consistently indicate a tremendous emergence from the gravel.

Return of Adults to the Sea (Post-spawning Behavior)

After spawning the spent steelhead which have not succumbed to old age, disease, or predators descend to the sea. In the parlance of the angler, such fish are "downstreamers".

In certain streams, steelhead are reported to return to sea immediately after spawning, while in others they are known to delay their return, lingering in the larger pools for considerable periods of time.

In Waddell Creek, within the same season some fish have returned to sea almost immediately after spawning, while others have been taken as late as the week of December 10-16 of the following season. However, the bulk of the fish have been taken during the period April-June. The spent adults taken in the downstream trap at Waddell Creek during the nine seasons of operation are shown in Table 36. The figures do not represent total numbers, since a number of fish are known to have passed downstream over the dam, especially during the earlier portions of the migration, but do show the approximate period of migration.

The fish which do not proceed immediately to the sea gather in the larger pools, where they swim lazily about close to the surface. There is some tendency for the fish to gather in small groups, or for individuals to follow one another, but no real schooling takes place. In Waddell Creek, the same group of fish has been seen week after week in the pool above the dam. At times an individual will leave the pool and resume his downstream journey, or not uncommonly half-a-dozen or so may start toward the sea. The factors which influence the fish to resume

TABLE 36

Waddell Creek, Steelhead: Spent Adults Checked Through Downstream Trap, by Seasons and Weekly Periods

Period	1933-34			1934-35			1935-36			1936-37			1937-38		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
Oct. 1-7.....	--	--	--	--	--	--	--	--	--	†1	†1	--	--	--	--
Oct. 8-14.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Oct. 15-21.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Oct. 22-28.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4.....	†1	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 5-11.....	†1	--	†1	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 12-18.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 19-25.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 3-9.....	--	(*)1	(*)1	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 10-16.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 17-23.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 24-30.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 31-Jan. 6.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 7-13.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 14-20.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 21-27.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Feb. 4-10.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Feb. 11-17.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Feb. 18-24.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Feb. 25-Mar. 3.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Mar. 4-10.....	--	--	--	--	--	--	3	--	3	--	--	--	--	--	--
Mar. 11-17.....	--	--	--	--	--	--	1	--	1	--	--	--	--	--	--
Mar. 18-24.....	--	1	1	--	--	10	4	14	--	--	--	--	--	--	--
Mar. 25-31.....	--	--	--	2	--	2	6	3	9	--	--	--	--	--	--
Apr. 1-7.....	6	2	8	1	--	1	1	3	4	1	--	1	2	2	2
Apr. 8-14.....	--	1	1	--	--	--	2	--	2	1	--	1	--	1	1
Apr. 15-21.....	6	1	7	2	--	2	5	2	7	1	1	2	--	--	--
Apr. 22-28.....	13	7	20	--	1	1	3	1	4	1	2	3	1	2	3
Apr. 29-May 5.....	4	3	7	1	1	2	5	1	6	2	3	5	2	1	3
May 6-12.....	2	1	3	--	--	--	2	1	3	2	1	3	1	--	1
May 13-19.....	1	1	2	--	--	--	3	2	5	2	2	4	4	3	7
May 20-26.....	3	8	11	--	--	--	2	--	2	3	1	4	--	1	1
May 27-June 2.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
June 3-9.....	3	8	11	--	--	--	1	--	1	--	--	--	1	--	1
June 10-16.....	--	--	--	--	--	--	--	--	--	6	3	9	1	1	2
June 17-23.....	--	--	--	--	--	--	--	--	--	--	--	--	1	--	1
June 24-30.....	--	--	--	1	--	1	--	1	1	--	--	--	--	--	--
July 1-7.....	1	--	1	--	--	--	--	--	--	1	--	1	--	--	--
July 8-14.....	--	1	1	--	--	--	1	1	--	1	1	--	--	--	--
July 15-21.....	--	2	2	--	--	--	--	--	--	--	--	--	--	--	--
July 22-28.....	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--
July 29-Aug. 4.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Aug. 5-11.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Aug. 12-18.....	1	--	1	--	--	--	1	--	1	--	1	--	--	--	--
Aug. 19-25.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Aug. 26-Sept. 1.....	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 2-8.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 9-15.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 16-22.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 23-30.....	--	--	--	--	--	--	--	--	--	--	--	--	1	--	1
Totals.....	41	37	78	7	2	9	45	19	64	20	18	38	11	12	23

TABLE 36—Continued

Waddell Creek, Steelhead: Spent Adults Checked Through Downstream Trap, by Seasons and Weekly Periods

Period	1938-39			1939-40			1940-41			1941-42			Total			
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total	Average
Oct. 1-7.....	--	†1	†1	--	†1	†1	--	--	--	--	--	--	--	†3	†3	+
Oct. 8-14.....	--	†1	†1	--	--	--	--	--	--	--	--	--	--	†1	†1	+
Oct. 15-21.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Oct. 22-28.....	†1	†1	†2	--	--	--	--	†1	†1	--	--	--	†1	†2	†3	+
Oct. 29-Nov. 4.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 5-11.....	--	--	--	--	--	--	--	--	--	--	--	--	†1	--	†1	+
Nov. 12-18.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 19-25.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 3-9.....	--	--	--	--	--	--	--	--	--	--	--	--	2(†1)	--	2(†1)	+
Dec. 10-16.....	†1	--	†1	1	--	1	--	--	--	--	--	--	--	--	--	--
Dec. 17-23.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 24-30.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dec. 31-Jan. 6.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 7-13.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 14-20.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 21-27.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3.....	--	--	--	--	--	--	--	--	--	1	--	1	1	--	1	+
Feb. 4-10.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Feb. 11-17.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Feb. 18-24.....	--	--	--	--	--	--	--	1	1	--	--	--	1	--	1	+
Feb. 25-Mar. 3.....	--	--	--	--	--	--	--	--	--	1	--	1	1	--	1	+
Mar. 4-10.....	--	--	--	--	--	--	--	--	--	2	2	4	5	2	7	1
Mar. 11-17.....	--	--	--	--	--	--	--	--	--	1	1	1	1	1	2	+
Mar. 18-24.....	--	--	--	--	--	--	--	--	--	1	1	1	10	6	16	+
Mar. 25-31.....	4	5	9	--	--	--	7	--	7	2	1	3	21	9	30	3
Apr. 1-7.....	3	4	7	--	--	--	--	--	--	3	6	9	15	17	32	4
Apr. 8-14.....	6	21	27	--	--	--	--	--	--	--	--	--	9	23	32	4
Apr. 15-21.....	2	1	3	2	1	3	1	--	1	--	--	--	19	6	25	3
Apr. 22-28.....	3	6	9	--	--	--	--	--	--	2	1	3	23	20	43	5
Apr. 29-May 5.....	4	4	8	3	--	3	--	--	--	2	2	4	23	15	38	4
May 6-12.....	6	8	14	2	--	2	--	--	--	3	2	5	18	13	31	3
May 13-19.....	3	--	3	--	--	--	--	--	--	5	--	5	18	8	26	3
May 20-26.....	6	4	10	--	--	--	--	--	--	1	--	1	15	14	29	3
May 27-June 2.....	3	5	8	--	--	--	--	--	--	--	--	--	3	6	9	1
June 3-9.....	1	2	3	--	--	--	--	--	--	--	--	--	6	10	16	2
June 10-16.....	1	3	4	--	--	--	--	--	--	--	--	--	8	7	15	2
June 17-23.....	2	3	5	--	--	--	--	--	--	--	--	--	3	3	6	1
June 24-30.....	1	--	1	--	--	--	--	--	--	--	--	--	2	1	3	+
July 1-7.....	9	3	12	--	--	--	--	--	--	--	--	--	11	3	14	2
July 8-14.....	6	8	14	--	--	--	--	--	--	--	--	--	6	11	17	2
July 15-21.....	2	--	2	--	--	--	--	--	--	--	--	--	2	2	4	+
July 22-28.....	2	--	2	--	--	--	--	--	--	--	--	--	2	1	3	+
July 29-Aug. 4.....	--	2	2	--	--	--	--	--	--	--	--	--	--	2	2	+
Aug. 5-11.....	--	1	1	--	--	--	--	--	--	--	--	--	--	3	3	+
Aug. 12-18.....	--	--	--	--	--	--	--	--	--	--	--	--	--	3	3	+
Aug. 19-25.....	2	1	3	--	--	--	--	--	--	--	--	--	2	1	3	+
Aug. 26-Sept. 1.....	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	+
Sept. 2-8.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 9-15.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 16-22.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sept. 23-30.....	1	2	3	--	--	--	--	--	--	--	--	--	1	3	4	+
Totals.....	69	86	155	9	3	12	8	2	10	22	16	38	232	195	427	47

* From 1932-33 upstream migration.

† Taken during this week of following season.

the seaward journey following such prolonged interludes in pools are not yet fully known, although some such emigrations have followed light rains. In the larger streams much greater numbers of spent steelhead gather in the larger pools, especially behind dams. For example, hundreds of such fish have been observed in the extensive pool above Benbow Dam, on the South Fork of Eel River.

Spent adult steelhead typically do not resume feeding while in fresh water. As a result, those taken soon after spawning (unless weakened by disease or old age) are thin, but active and in good condition, while those taken several months after spawning are quite emaciated. Individuals captured in October-December of the following seasons apparently have not eaten following spawning; their stomachs are empty and shrunken and their mouths and gills are often covered by numerous parasitic copepods (*Salmincola*). The male taken during the week of December 10-16, 1939, must not have eaten for at least 34 weeks, since the last upstream male of the same size in the preceding season was taken during the week of April 15-21; it is remarkable that fish can remain alive and active following the rigors of spawning and such a prolonged fast. It is not known if individuals which have abstained from food for so long a period that their stomachs are shrunken are physiologically capable of resuming feeding.

Spent adults which have not resumed feeding will nevertheless strike at various objects, such as coins or pebbles thrown into the water. Fish in the pool back of Benbow Dam have been observed to rush at coins tossed in 10 or 12 feet away. In such cases one fish after another has been seen to seize and then "spit out" the coin in its descent to the bottom. A valid explanation of this interesting behavior seems to be lacking. It hardly seems likely that the fish see such an object as an enemy, yet we know that the fish are not seeking food. In any case, this behavior has resulted in the taking of spent steelhead on spinners, especially with a May 1 opening of the trout season.

Only a very few adults which have completed spawning have been taken again in the same season in the upstream trap at Waddell Creek. However, fish which have been artificially stripped, often return in large numbers to the upstream trap at spawning stations, usually within a few days of spawning. The incomplete removal of the sexual products under artificial conditions and the completeness of spawning under natural conditions may play a role in this difference in post-spawning behavior.

Following spawning, adult steelhead, which typically "color up" in fresh water before spawning, gradually assume a pale, "washed-out" appearance, although some of the redness may be retained. The scales remain firmly imbedded. Only following their re-entry into the sea does the silveriness typical of salmonids in salt water return.

Embryology and Hatching of Eggs

The best and only complete account of the development of steelhead eggs is that by Wales (1941). The embryology of the steelhead is in general similar to that of other trout and of salmon, and the details will not be presented in this paper.

The number of days required for steelhead eggs to hatch varies from about 19 at an average temperature of 60 degrees F. to about 80 at an

average temperature of 40 degrees F. At the temperatures prevailing in Waddell Creek, the usual hatching time is from 25 to 35 days.

Various exceptions and special considerations in regard to development and hatching have been cited and discussed under the comparable section for silver salmon and have general application to the steelhead. As in the case of the silver salmon, silting occurring between fertilization and hatching and caused by severe floods or mining is probably the principal cause of pre-hatching losses. Various experiments were cited to show this. Experiments conducted by Shapovalov (1937) on steelhead substantiate the results obtained with other species.

Under normal hatchery conditions the hatch is between 80 and 90 percent of steelhead eggs taken. There is no quantitative basis for estimating the average percentage of steelhead eggs hatching in Waddell Creek, but the writers believe that under favorable conditions (principally absence of heavy silting) it is comparable to that of hatchery eggs, or 80 to 90 percent of the eggs deposited. Even in periods of heavy floods, when the water is laden with silt, stream velocities in areas utilized for spawning by trout and salmon are probably sufficient to prevent excessive deposition of silt and thus damage to the eggs in the gravel.

At time of hatching steelhead are approximately 17 to 18 mm. (0.7 inch) long and weigh about 0.1 gram (270 fish per ounce).

Emergence From the Gravel

Silting is also probably the principal factor in determining the survival rate from time of hatching to emergence from the gravel.

In the experiments conducted by Shapovalov (1937) it was impossible to segregate the survival from time of burial to hatching from the survival from hatching to emergence, but the over-all survival to time of emergence was 29.8 percent in the presence of considerable silting and 79.9 percent in the absence of much silting. In the former instance the water flowing over the gravel had a considerably lower velocity than would water in a natural stream laden with an equal amount of silt and so it may be that under natural conditions the percentage of emergence is rarely as low as 29.8 percent. Again, there is no quantitative basis for estimating the average percentage of steelhead emerging from the gravel in Waddell Creek, but the writers believe that under favorable conditions (principally absence of heavy silting) it is high, probably between 70 and 85 percent of the eggs deposited. There is, of course, no stage in hatchery operations directly comparable to the period from time of hatching to time of emergence under natural conditions, but under hatchery conditions the losses during the equivalent period of time normally are light, so that hatchery survival to time that steelhead finish emerging from the gravel under natural conditions is still between 80 and 90 percent of the eggs taken.

For the areas which he examined, Hobbs (1937) concluded that (1) the incidence of loss subsequent to fertilization, where heavy loss occurs, is much greater in the pre-eyed than in the eyed eggs or in the hatched-fish-in-the-gravel stage, (2) heavy losses of fertilized eggs are the outcome of adverse environmental conditions and not of inherent weakness, (3) the extent of losses of fertilized eggs in undisturbed redds depends primarily on the amount of very fine material in the redds

during the development of eggs before eyeing, and (4) *Saprolegnia* (fungus) infection of dead pre-eyed eggs is responsible for losses of eggs at later stages.

Hobbs (1940) found the loss between hatching and the time of emergence to be extremely light, exceeding 1 percent in only one river system.

The experiments conducted by Shapovalov (1937) indicate that the steelhead fry start emerging from the gravel two to three weeks after hatching and require another two to three weeks to complete emergence. This is probably what happens under normal conditions existing in California coastal streams. Shallow burial, loose gravel, absence of silt, and high temperatures may all be expected to speed emergence, while the opposite conditions may be expected to retard emergence.

Under normal conditions the fry rarely emerge from the gravel before the yolk sac is absorbed. Shallow burial results in premature emergence. This was indicated by the experiments of Shapovalov (*loc. cit.*) and had previously been cited for Pacific salmon (*Oncorhynchus*) by Babcock (1911). The time of emergence from the gravel approximately coincides with the beginning of feeding in the hatcheries.

Because of the normal long period of emergence, at the time that the last fish emerge the first fish to have emerged are usually considerably larger than the former, despite the fact that the eggs were deposited at the same time.

At time of emergence from the gravel steelhead are approximately 23 to 26 mm. (0.95 inch) long and weigh about 0.16 gram (180 fish per ounce).

Stream Life Prior to Seaward Migration (General Features)

At Waddell Creek the only quantitative data regarding numbers of fish were obtained at times of migration through the traps, so the following account will necessarily be based on general observations.

The behavior of juvenile steelhead during their first year of life, especially during the first couple of months following emergence from the gravel, is generally similar to that of the silver salmon fry. The freshly-emerged fish first take up residence in the shallow gravel areas, especially at the sides of the stream. At first they tend to congregate in schools, but as time passes and the fish grow these schools break up and the fish spread up and down the stream, selecting individual small "territories", from which they drive other fish of the same size or somewhat larger.

The fry in the shallows feed avidly and grow rapidly. The individual fry rise to nearly every small object drifting downstream or falling into the water, selecting those that are suitable and rejecting those that are not. Following their rise, they return to the original position.

Soon after the first steelhead have emerged from the gravel, marked differences in size are to be noted among the fish of the season, within the same section of stream. For example, 20 fish seined in one pool in Waddell Creek on July 12, 1932, by J. H. Wales ranged from 43 to 77 mm. in length. Such differences result principally from the prolonged spawning season and therefore prolonged hatching and emergence periods of the steelhead. Of course, different growth rates of individuals play some role in creating fish of different sizes, but the long spawning

season is the principal cause. In addition, the fish of the lower portions of the stream, with the warmer temperatures, are on the average larger than those of the upper portions. Larger average size in the warmer portions of the stream results both from a more rapid growth rate and a somewhat shortened hatching period, so that these fish have a head start on those from the cooler waters.

Soon after the peak of emergence there is a marked decline in the numbers of fry in the stream, due to mortality. Possible causes of losses at Waddell Creek are predators, drying stream channels, and disease, and have already been discussed in the comparable section on silver salmon. Predatory fishes are believed to make the greatest inroads.

As the fish grow, they gradually move into deeper water and eat coarser food. However, unlike the silver salmon, in late summer the young steelhead do not appear to move into the deep, quiet pools, but inhabit the moderately swift portions of the stream. Diurnal movements within limited areas may occur, but have not been studied in any detail. At this time the growth rate of the fish begins to slow down (probably not as early nor as markedly as in the case of the silver salmon) in association with the period of maximum stream temperatures and minimum flow, with some evidence to indicate that the former plays the greatest part. During the period of heavy rainfall and lowest temperatures, December through February, feeding is generally quite light and growth negligible, according to measurements and scale readings. It appears that during this period of floods and great turbidity the young steelhead, like the silver salmon, are not swept downstream and do not migrate downstream voluntarily in large numbers, but make use of backwater and eddies in maintaining their position in the stream.

Following the period of maximum precipitation, the fish start making extremely rapid growth (usually in March), as witnessed by the sharp increase in average size of fish and new growth registered on the scales. The resumption of heavy feeding is probably influenced both by rising temperatures and an abundance of aquatic food organisms. Although a steady lowering of stream flow takes place during the ensuing months, adverse water conditions ordinarily are not reached before midsummer.

Some data are available regarding the sex ratio among stream steelhead and indicate that great care should be taken in drawing conclusions, for the reason that apparent differences may depend upon the time of year at which the fish are taken and the manner in which they are caught. Actual differences may exist in certain age groups (especially the older ones) and certain categories (e.g., upstream or downstream migrants), although the available data have not yet revealed such differences. Probably the sex ratio is close to 1:1 among stream steelhead two years of age or under.

Snyder (1938), reporting on data obtained from upwards of 1,000 trout caught by Theodore J. Hoover by hook and line in Waddell Creek between May 1, 1927, and May 1, 1928, found that of 866 fish sexed 466 (53.8 percent) were males and 400 (46.2 percent) females. However, the sex representation among fish caught by angling is not necessarily representative of the sex ratio of a stream population, and, moreover, in the case under discussion the numbers caught in the different months were not equal. Males predominated in the catches most strongly during the period February-July, while females predominated or the

sex ratio was approximately equal during the period August-January. Snyder concludes that "A seasonal variation in the sex is indicated . . . although the numbers involved are too small to warrant definite conclusions."

Shepherd (1928) reported on 55 stream steelhead caught by hook and line in Waddell Creek in October, 1926, July and December, 1927, and January, 1928. Of the 55, 32 (58.2 percent) were males and 23 (41.8 percent) females. There was a slight predominance of males in all four months, but the figures are too small to make comparative analyses. Data obtained during the course of the present experiments support the evidence that males predominate in anglers' catches in the spring of the year. Of 24 trout caught by two anglers in the East Branch of Waddell Creek (above the closed area) on May 1, 1942, 23 were males. Nineteen of the 23 males were ripe; the female was spawned out. It is not unlikely that at least during the spawning season males strike at a baited hook or lure more readily than do females. If this is the case, it is interesting to speculate that a short angling season during the spring months may create a marked shortage of males where an intensive fishery exists.

The sex ratio of yearling steelhead held in rearing ponds at the Big Creek State Fish Hatchery was, on the basis of six samples, approximately 1:1. These samples contained a total of 207 males and 193 females.

At this point it may be noted that the young steelhead exhibit much greater variation in individual behavior than do the juvenile silver salmon. This is most markedly brought out by the fact that the young steelhead migrate down at various ages from + to 4, while practically all of the silver salmon migrate downstream as yearlings. While the salmon go to sea almost immediately, some of the steelhead remain for a whole season in the lagoon or the lower portion of the stream, after which some move out to sea, while others make an upstream migration and then a second downstream migration. While most of the steelhead go to sea before maturing, some fish of both sexes spawn before going to sea, while still others complete their life cycles without going to sea at all. (Among the silver salmon perhaps a few males reach precocious sexual maturity prior to their seaward migration, but none of the females do so.) There are other variations in the behavior of individual young steelhead; for example, although most of the fish diminish feeding and growth in the late summer or early autumn, some continue to feed and make rapid growth deep into the winter. Some resume heavy feeding and growth in the middle of the winter, while others do not do so until spring. Some diminish feeding and growth for a prolonged period, while others resume feeding and growth after only a brief interlude. These variations in behavior are reflected in the structure of the scales; for example, some scales are just beginning to form an annulus at the same time that others show considerable new growth. Some of the variations in regard to growth and annulus formation undoubtedly are associated with sexual maturity and migration.

The various migrations made by stream steelhead will be discussed in subsequent sections.

TABLE 37

Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, by Seasons and Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	2	6	60	21	5	131	225	28
Oct. 8-14		--	7	3	10	59	84	11	25	199	24
Oct. 15-21		--	--	3	12	4	20	1	97	137	17
Oct. 22-28		--	--	--	15	12	14	44	70	155	19
Oct. 29-Nov. 4		1	--	--	26	216	6	43	145	437	55
Nov. 5-11		10	--	--	24	42	22	14	43	155	19
Nov. 12-18		66	14	11	107	2	11	18	32	261	33
Nov. 19-25		21	71	8	131	2	--	8	7	248	31
Nov. 26-Dec. 2		8	10	1	35	285	2	6	7	354	44
Dec. 3-9	3	5	11	2	23	174	--	2	87	307	34
Dec. 10-16	28	9	15	6	26	47	20	1	31	183	20
Dec. 17-23	5	3	2	26	5	220	13	134	34	442	49
Dec. 24-30	8	15	77	102	1	80	20	3	23	329	39
Dec. 31-Jan. 6	--	12	330	90	8	43	11	6	1	501	56
Jan. 7-13	--	7	53	12	5	65	7	15	1	165	18
Jan. 14-20	4	--	19	10	7	33	--	10	1	84	9
Jan. 21-27	3	1	8	5	9	32	3	9	--	70	8
Jan. 28-Feb. 3	3	4	6	3	--	37	--	1	9	63	7
Feb. 4-10	16	9	1	17	1	17	2	--	--	63	7
Feb. 11-17	11	4	3	18	--	6	3	3	4	52	6
Feb. 18-24	30	3	3	23	14	2	2	4	13	94	10
Feb. 25-Mar. 3	27	3	16	19	11	2	2	2	42	124	14
Mar. 4-10	22	12	68	37	3	26	2	1	79	250	28
Mar. 11-17	70	20	83	28	19	40	3	33	8	304	34
Mar. 18-24	159	50	105	10	2	77	54	31	26	514	57
Mar. 25-31	201	54	81	15	1	297	17	25	152	843	94
Apr. 1-7	308	126	43	40	10	369	1	1	209	1,107	123
Apr. 8-14	411	18	83	31	30	511	11	1	89	1,185	132
Apr. 15-21	344	53	173	33	46	414	58	50	8	1,179	131
Apr. 22-28	391	85	118	41	29	559	28	74	52	1,377	153
Apr. 29-May 5	150	101	147	57	45	348	9	24	161	1,042	116
May 6-12	105	51	94	75	108	649	37	244	223	1,586	176
May 13-19	111	32	248	142	174	404	33	287	225	1,656	184
May 20-26	138	50	213	236	235	243	47	521	480	2,163	240
May 27-June 2	68	62	207	246	187	68	218	400	112	1,568	174
June 3-9	225	84	102	374	163	37	213	397	400	1,995	222
June 10-16	67	68	224	217	98	147	165	552	621	2,159	240
June 18-23	13	159	345	108	183	84	120	842	421	2,275	253
June 24-30	2	108	309	95	352	14	293	416	390	1,979	220
July 1-7	41	136	29	379	212	69	251	145	265	1,527	169
July 8-14	49	20	55	519	183	69	153	57	333	1,438	160
July 15-21	28	76	138	162	170	16	116	117	308	1,131	126
July 22-28	19	47	82	20	214	44	150	164	128	868	96
July 29-Aug. 4	9	57	59	10	66	21	519	31	44	816	91
Aug. 5-11	11	55	26	92	57	37	401	19	18	716	80
Aug. 12-18	18	20	101	61	43	48	175	11	23	500	56
Aug. 19-25	6	5	87	33	77	21	48	22	9	308	34
Aug. 26-Sept. 1	6	26	50	20	87	46	32	21	8	296	33
Sept. 2-8	4	12	12	42	46	9	17	39	18	199	22
Sept. 9-15	3	16	7	28	16	28	27	119	31	275	31
Sept. 16-22	--	3	5	9	26	21	15	240	15	334	37
Sept. 23-30	--	4	3	8	32	33	8	391	62	541	60
Totals	3,117	1,791	3,943	3,529	3,390	6,189	3,484	5,615	5,721	36,779	--

Downstream Migration of Stream Fish

Time and Size of the Migration

During the nine seasons of operation of the trap,²⁹ 36,779 stream steelhead were checked on their downstream migration. The number taken during each weekly period in each season is shown in Table 37 and Figures 11-19.

The length of these fish from tip of snout to fork of caudal fin was recorded in mm., measurement being made to the next highest mm.³⁰

Scale samples were taken from the great majority of the fish during the first six seasons of operation, i.e., 1933-34 through 1938-39.³¹ Scale samples were not taken during the last three seasons, 1939-40 through 1941-42, largely because it was believed that further scale samples from downstream steelhead would not yield information commensurate with the effort expended.

Time permitted "reading" of only a portion (1,695) of the scale samples taken. Of these, 1,412 were measured as well as read.

From Table 37 and Figures 11-19 it is apparent that some stream steelhead, unlike the juvenile silver salmon, migrate downstream at all times of the year, but that the largest numbers migrate in the spring and summer, with a secondary migration in the late fall or early winter. It is also seen that during January and February the migration is very light.

Age and Size of the Fish

Since it was impossible to examine scales from all of the fish, some alternative system of age analysis had to be adopted. Assignment of fish to age classes at any given point of time in one season on the basis of scale reading for another season proved unsatisfactory because of seasonal differences resulting from (1) varying time of the migration as a whole, (2) varying growth rate (and consequently size of fish) of one or more age classes, (3) varying numerical size of one or more age classes, and (4) other changes in the pattern of the downstream migration of one or more age classes brought about by their place of origin in the stream, rate of migration, etc. Therefore, the logical method that presented itself was that of segregation of age classes according to modal groups of length frequencies, with reading of scales where overlaps between the modal groups occurred.

By definition in this paper, an age + fish becomes age 1 with the completion of its first annulus, an age 1 fish becomes age 2 with the completion of its second annulus, etc. In Waddell Creek, annulus formation is generally completed in December or January, but varies

²⁹ In 1933-34, the first season of operation, the trap was not put into operation until the week of December 3-9.

³⁰ From May 29th through September 30th of the 1933-34 season and from October 1st through November 20th of the 1934-35 season the fish were measured only as three inches or under or over three inches (approximately 76 mm. or under or over 76 mm.). This system was in effect during a period when a regular observer was not available and the fish were checked by hatchery personnel. The demarcation line of three inches was chosen as the approximate line between fish of the season, which made up the bulk of the fish taken during this period, and older fish.

³¹ The major exceptions include the period May 28-September 30 in 1933-34, October 1-November 20 and July 4-September 30 in 1934-35, October 1-December 8, December 10-29, and July 1-September 30 in 1935-36, October 1-December 16 and July 17-September 30 in 1936-37, October 1-27 in 1937-38, and October 1-9 and June 14-September 30 in 1938-39. Also, scales were not taken from a number of fish under 80 mm. in length during other portions of these seasons, but were taken from samples of fish under 80 mm. at various times.

widely for individual fish. However, for the sake of simplicity, in the tables and figures dealing with stream steelhead the break between seasons (September 30-October 1) has been used as the changeover point from one age to another. Thus, fish of the season's hatch are called age +, fish of the previous season's hatch (although including some fish that have not yet formed an annulus) are called age 1, fish of the second previous season's hatch (although including a few fish that have not yet formed a second annulus) are called age 2, etc.

In Table 38 (and Tables A-19 to A-27 for the individual seasons, in the Appendix) the different age classes stand out rather conspicuously, with occasional overlaps. We see that in general the two youngest age classes in each season (i.e., the fish of the season and of the previous season's hatch) stand out as separate entities. The older age classes, however, although generally distinct from the younger ones, are not distinct from each other, but tend to form unimodal groups. These older age class groups are composed principally of fish of one age class (fish completing their second year or in their third year, depending upon the portion of the season in which they are recorded), with fish of older age classes scattered through most of the length-frequency group.

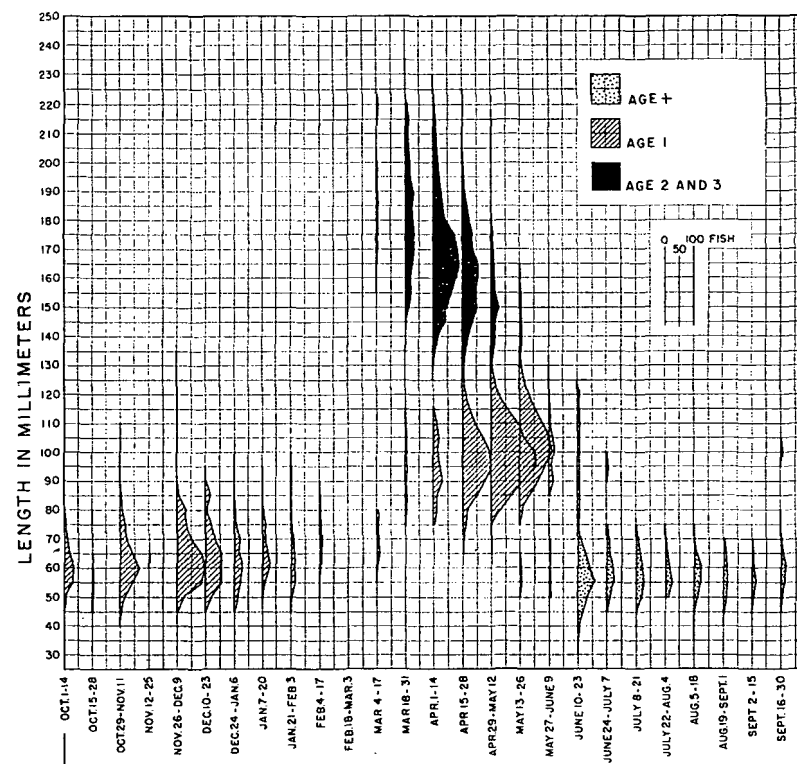


FIGURE 28. Stream steelhead checked through the downstream trap at Waddell Creek during the 1938-39 season; length frequencies by two-week periods.

Figure 28 shows the downstream migration for the 1938-39 season by time-length-number. In this graph the modal groups stand out even more clearly than they do in some other seasons and there is little overlap. The modal groups for the fish of the season (which begin their downstream migration almost immediately after emergence from the gravel), and for the next older age class are clearly discernible. The fish of the other age classes are not distinct from each other but form a series of single modal groups which are highly skewed in the direction of the greater lengths. Fish completing their second year and entering their third (and called age 2) form the majority of fish in this series of modal groups. Older fish are scattered throughout, but tend to be more prevalent in the upper, skewed portions, especially toward the earlier part of the migration. Such older fish in turn are composed principally of one age class, with only an occasional older fish.

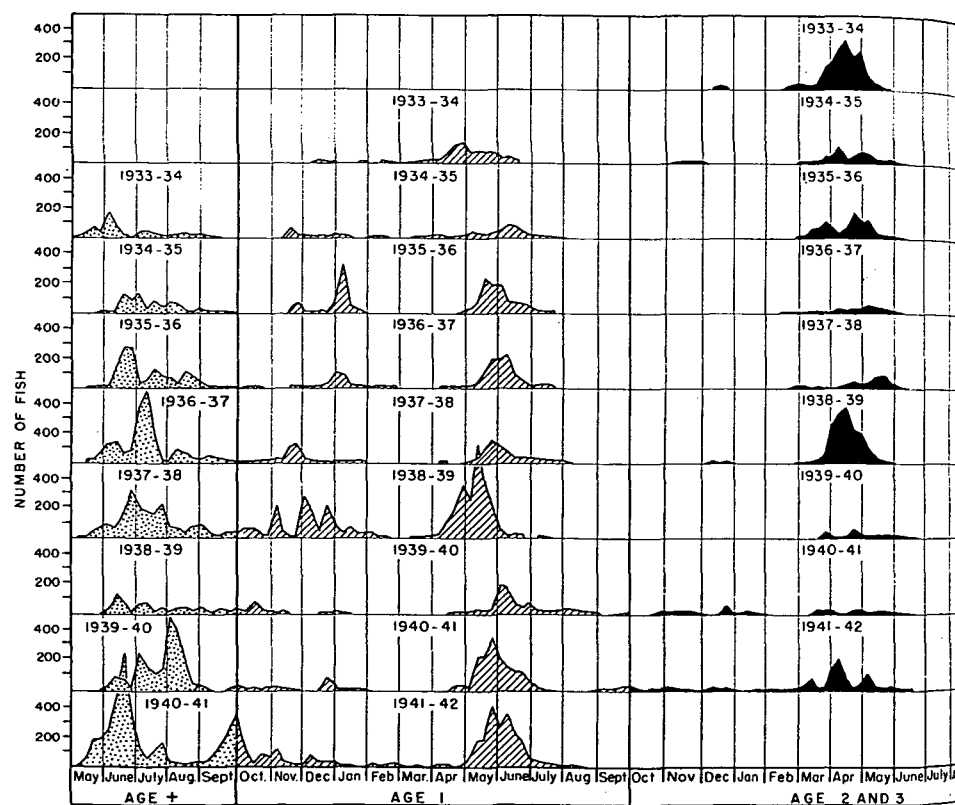


FIGURE 29. Stream steelhead checked through the downstream trap at Waddell Creek, by age groups.

Figures 11-19 and 29 show the age composition of the downstream migration in each season. From these graphs it is seen that the four age classes which, except for an occasional older fish, make up the downstream migration in each season, move down in sequence during the main (spring) migration. The oldest fish appear first and are followed by progressively younger fish. There is often considerable overlap in the migration times of the different age groups, but ordinarily there is a distinct time interval between the occurrence of the *peak numbers* of each group.

The dividing lines used to separate the age classes are shown in Table 38 (and A-19 to A-27 of the Appendix). Where an overlap occurs, the dividing line does not indicate that all of the fish below the line are thought to belong to one age class and those above it to another, but it does indicate that the two modal groups have been separated to show the correct *numbers* of fish in the two age classes. If the slope of the curves of the two modal groups is the same at the overlap (no skewness or equal skewness) and the number of fish in each modal group is the same, there will be equal numbers from each modal group (and therefore age class) above and below the line, respectively, and the dividing line will decrease the apparent size range of *each age class equally*. If the slope of the curves is not the same or the number of fish in each modal group is not the same, the dividing line will decrease the apparent size range of the *age class that has the smaller numbers and/or the greater skewness*, but will *increase the apparent size range of the other age class, with the larger number of fish and/or the lesser skewness*. In general, the length-frequency distributions of each age class are skewed positively, i.e., in the direction of the larger fish.

For the great bulk of the data at hand, the method of dividing the age classes by eye is considered to be quite satisfactory. The great majority (probably over 90 percent) of all the downstream migrants are so grouped that there can be little question regarding their assignment to the proper age. Of the remainder (approximately 10 percent), those occurring at points of overlap can be divided with a high degree (probably 90 percent) of accuracy, even without scale reading, since the pattern of each modal group for any given weekly or two-week period is usually fairly obvious from its pattern in the preceding and following periods. Reading of scales at various points of overlap has served to further increase the accuracy of assignment of these doubtful fish to the proper age classes. The greatest difficulty is encountered in segregating age 2 from age 3 fish in the spring migration at those points at which no scale reading was done, because by the time the fish have reached this size and age their size range is so scattered that the fish do not form sharply defined modal groups. However, scale reading for the entire size range of these two age groups combined, carried out for some periods in different seasons, indicates that the age 3 fish are greatly in the minority (forming approximately 5 percent of the fish in the modal group for these two age classes combined) and occur mostly in the earlier portion of the spring migration.

It is believed that over 95 percent of all the fish in the downstream migrations were assigned to the correct age class.³²

The numbers of fish of each age group passing through the downstream trap in each season, by weekly periods, are shown in Tables 40-44. Their proportionate representation in the various seasons is shown in Tables 45 and 46.

The question now arises to what extent the migration through the trap is representative of the total downstream migration (i.e., migration through the trap plus the uncounted migration over the dam and migration of fish produced below the dam), as regards time of migration and age of fish. An estimate of the numbers and age composition of the fish passing uncounted over the dam will be made in the section on "Survival" (pages 204-239), but there is no way of showing the time at which such fish migrated.

During the fall all of the water passes through the trap, so that the numbers of fish shown in Figures 11-19 are the entire numbers migrating downstream at that time. The very light migration at this time is therefore an actual thing and is almost certainly influenced by the minimum flow which is reached during that period. The very light migration at this time (not only of the downstream stream steelhead but also of other categories of steelhead and other fishes), coupled with

³² The fact that the age classes stand out sufficiently as modal groups to permit them to be picked out readily is shown by the fact that out of 19,688 fish in the five seasons for which two observers (Leo Shapovalov and E. S. Herald) assigned all of the fish to age classes, there was disagreement in the case of only 769 fish, or less than 4 percent. The disagreement was not greater than 6 percent in any one season. Since the disagreement was not all in one direction, the disagreement regarding numbers assigned to each age class is even less. Table 39 shows that the effect of these differences of opinion is practically negligible in showing the number of fish in any given age class expressed as a percentage of fish in all age classes.

TABLE 39

Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap; Assignment to Age Groups by Two Observers

Season	Observer	Number of age + migrants	Percentage of migration	Number of age 1 migrants	Percentage of migration	Number of age 2 migrants	Percentage of migration	Number of age 3 migrants	Percentage of migration	Number of age 4 migrants	Percentage of migration
1933-34	L.S.	604	19	741	24	1,657	53	112	4	3	+
	E.S.H.	604	19	748	24	1,673	54	89	3	3	+
1935-36	L.S.	1,365	35	1,655	42	830	21	90	2	3	+
	E.S.H.	1,370	35	1,567	40	937	24	66	2	3	+
1936-37	L.S.	1,875	53	1,191	34	451	13	11	+	1	+
	E.S.H.	1,856	52	1,181	33	413	12	78	2	1	+
1939-40	L.S.	2,239	64	945	27	292	8	7	+	1	+
	E.S.H.	2,221	64	943	27	286	8	33	1	1	+
1940-41	L.S.	3,306	59	2,049	36	251	4	9	+	0	+
	E.S.H.	3,463	62	1,797	32	328	6	27	+	0	+
Totals (19,688)	L.S.	9,389	48	6,581	33	3,481	18	229	1	8	+
	E.S.H.	9,514	48	6,236	32	3,637	18	293	1	8	+

TABLE 40

Waddell Creek, Steelhead: Age + Stream Fish Checked Through Downstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	--	--	--	--	--	--	--	--	--	--	--
Oct. 8-14	--	--	--	--	--	--	--	--	--	--	--
Oct. 15-21	--	--	--	--	--	--	--	--	--	--	--
Oct. 22-28	--	--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4	--	--	--	--	--	--	--	--	--	--	--
Nov. 5-11	--	--	--	--	--	--	--	--	--	--	--
Nov. 12-18	--	--	--	--	--	--	--	--	--	--	--
Nov. 19-25	--	--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2	--	--	--	--	--	--	--	--	--	--	--
Dec. 3-9	--	--	--	--	--	--	--	--	--	--	--
Dec. 10-16	--	--	--	--	--	--	--	--	--	--	--
Dec. 17-23	--	--	--	--	--	--	--	--	--	--	--
Dec. 24-30	--	--	--	--	--	--	--	--	--	--	--
Dec. 31-Jan. 6	--	--	--	--	--	--	--	--	--	--	--
Jan. 7-13	--	--	--	--	--	--	--	--	--	--	--
Jan. 14-20	--	--	--	--	--	--	--	--	--	--	--
Jan. 21-27	--	--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3	--	--	--	--	--	--	--	--	--	--	--
Feb. 4-10	--	--	--	--	--	--	--	--	--	--	--
Feb. 11-17	--	--	--	--	--	--	--	--	--	--	--
Feb. 18-24	--	--	--	--	--	--	--	--	--	--	--
Feb. 25-Mar. 3	--	--	--	--	--	--	--	--	--	--	--
Mar. 4-10	--	--	--	--	--	--	--	--	--	--	--
Mar. 11-17	--	--	--	--	--	--	--	--	--	--	--
Mar. 18-24	--	--	--	--	--	--	--	--	--	--	--
Mar. 25-31	--	--	--	--	--	--	--	--	--	--	--
Apr. 1-7	--	--	--	--	--	--	--	--	--	--	--
Apr. 8-14	--	1	--	--	--	--	--	--	--	1	+
Apr. 15-21	1	--	--	--	--	--	--	3	--	4	+
Apr. 22-28	2	--	--	--	--	--	--	4	--	6	1
Apr. 29-May 5	4	--	--	--	--	--	--	1	1	6	1
May 6-12	8	--	--	--	2	1	--	5	7	23	3
May 13-19	38	--	4	7	4	5	--	49	24	131	15
May 20-26	70	1	7	16	49	8	--	176	47	374	42
May 27-June 2	30	10	6	58	71	7	6	168	21	377	42
June 3-9	189	--	19	158	86	26	16	200	125	819	91
June 10-16	59	--	140	139	67	124	81	413	244	1,267	141
June 17-23	13	131	276	58	150	67	74	709	189	1,667	185
June 24-30	2	92	272	82	324	14	253	342	230	1,611	179
July 1-7	40	129	24	369	200	60	241	105	218	1,386	154
July 8-14	48	19	54	508	172	68	148	41	300	1,358	151
July 15-21	26	75	134	159	165	15	113	98	288	1,073	119
July 22-28	18	47	82	20	210	44	139	150	128	838	93
July 29-Aug. 4	9	57	59	10	66	20	494	29	43	787	87
Aug. 5-11	11	55	25	92	57	37	388	17	18	700	78
Aug. 12-18	17	20	101	61	42	47	164	8	21	481	53
Aug. 19-25	6	5	87	32	77	21	41	20	8	297	33
Aug. 26-Sept. 1	6	25	49	20	84	45	25	20	6	280	31
Sept. 2-8	4	12	11	41	46	7	15	36	14	186	21
Sept. 9-15	3	13	7	28	16	27	24	114	24	256	28
Sept. 16-22	--	3	5	9	26	19	12	228	10	312	35
Sept. 23-30	--	4	3	8	32	29	5	370	43	494	55
Totals	604	699	1,365	1,875	1,946	691	2,239	3,306	2,009	14,734	--

1637/4R

TABLE 41

Waddell Creek, Steelhead: Age 1 Stream Fish Checked Through Downstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record			2	6	60	19	3	126	216	27
Oct. 8-14			7	3	9	57	71	9	25	181	23
Oct. 15-21				2	11	4	18	1	91	127	16
Oct. 22-28					15	12	14	26	67	134	17
Oct. 29-Nov. 4					26	215	4	33	125	403	50
Nov. 5-11		6			24	42	21	12	38	143	18
Nov. 12-18		56	14	10	104	2	11	16	29	242	30
Nov. 19-25		13	67	8	128	2		8	7	233	29
Nov. 26-Dec. 2		7	10	1	33	284	2	4	5	346	43
Dec. 3-9	1	5	9	2	22	168		2	74	283	31
Dec. 10-16	13	9	15	6	21	47	14	1	30	156	17
Dec. 17-23	3	2	2	24	5	216	13	101	30	396	44
Dec. 24-30	6	14	76	101	1	80	15	2	23	318	35
Dec. 31-Jan. 6		10	324	85	7	42	9	6	1	484	54
Jan. 7-13		6	48	12	5	64	1	9	1	146	16
Jan. 14-20	2		19	10	7	33		8		79	9
Jan. 21-27	3	1	6	5	6	32	2	9		64	7
Jan. 28-Feb. 3		3	2	2		36		1	8	52	6
Feb. 4-10	11	8	1	11	1	16	1			49	3
Feb. 11-17	5	2	3	6		5		1	3	25	3
Feb. 18-24	3		2	8	3			4	6	26	3
Feb. 25-Mar. 3	2		4	1			2	3	12	1	1
Mar. 4-10	2	3	6	3		11			2	27	3
Mar. 11-17	4	3	5	2	4	7		4	1	30	3
Mar. 18-24	10	3	1	1	1	4	2	2		24	3
Mar. 25-31	10	1	2			12	1		1	27	3
Apr. 1-7	23	15	2	4	2	20	1	1	10	78	9
Apr. 8-14	59	3	3	1	2	113	2	1	9	193	21
Apr. 15-21	115	9	2	1		185	6	25	1	344	38
Apr. 22-28	124	9	8	1	1	349	3	47	7	549	61
Apr. 29-May 5	61	41	30	2	4	241	3	13	58	453	50
May 6-12	66	32	67	20	29	599	22	224	187	1,246	138
May 13-19	68	22	231	92	81	381	18	228	189	1,310	146
May 20-26	65	37	206	200	149	227	28	335	411	1,658	184
May 27-June 2	35	51	199	184	105	60	194	230	86	1,144	127
June 3-9	36	83	82	216	76	11	185	195	272	1,156	128
June 10-16	8	68	84	78	31	23	76	139	375	882	98
June 17-23		28	69	49	33	17	46	133	232	607	67
June 24-30		16	37	13	28		40	74	160	368	41
July 1-7	1	7	4	10	12	8	10	40	47	139	15
July 8-14	1	1	1	11	11	1	5	16	33	80	9
July 15-21	2	1	4	3	5	1	3	19	20	58	6
July 22-28	1						11	14		30	3
July 29-Aug. 4						1	25	2	1	29	3
Aug. 5-11			1				13	2		16	2
Aug. 12-18	1				1	1	11	3	2	19	2
Aug. 19-25				1			7	2	1	11	1
Aug. 26-Sept. 1		1	1		2	1	7	1	2	16	2
Sept. 2-8			1			2	2	3	4	12	1
Sept. 9-15		2				1	3	5	7	18	2
Sept. 16-22						2	3	12	5	22	2
Sept. 23-30						4	3	21	19	47	5
Totals	741	578	1,655	1,191	1,015	3,699	945	2,049	2,834	14,707	--

1634/YR

TABLE 42

Waddell Creek, Steelhead: Age 2 Stream Fish Checked Through Downstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record							2	5	9	1
Oct. 8-14					1	2	12	2		17	2
Oct. 15-21				1	1		1		6	9	1
Oct. 22-28								18	3	21	3
Oct. 29-Nov. 4		1				1	2	10	20	34	4
Nov. 5-11		4					1	2	5	12	2
Nov. 12-18		7		1	3			2	3	16	2
Nov. 19-25		8	4		3					15	2
Nov. 26-Dec. 2		1			2	1		2	2	8	1
Dec. 3-9	1		2		1	6			11	21	2
Dec. 10-16	15				4		6		1	26	3
Dec. 17-23	2	1		2		4		33	4	46	5
Dec. 24-30	2	1		1			4	1		9	1
Dec. 31-Jan. 6		2	5	5	1	1	2			16	2
Jan. 7-13		1	5			1	6			19	2
Jan. 14-20	2							1	1	4	+
Jan. 21-27			2		3		1			6	1
Jan. 28-Feb. 3	2	1	4	1		1			1	10	1
Feb. 4-10	5	1		6		1	1			14	2
Feb. 11-17	6	2		12		1	3	1	1	26	3
Feb. 18-24	25	3	1	14	9	2	2		7	63	7
Feb. 25-Mar. 3	20	3	9	16	9	2	2		37	98	11
Mar. 4-10	12	6	55	30	3	14	2	1	70	193	21
Mar. 11-17	50	14	56	25	12	25	3	27	5	217	24
Mar. 18-24	128	41	85	8	1	68	47	27	24	429	48
Mar. 25-31	178	46	63	15	1	256	16	24	143	742	82
Apr. 1-7	272	103	39	36	8	336			190	984	109
Apr. 8-14	337	14	75	30	26	386	9		80	957	106
Apr. 15-21	221	44	169	32	44	229	52	22	7	820	91
Apr. 22-28	257	76	103	39	27	205	25	23	45	800	89
Apr. 29-May 5	83	60	116	55	39	106	6	9	102	576	64
May 6-12	31	19	24	54	77	47	15	15	29	311	35
May 13-19	5	10	9	43	85	18	15	9	12	206	23
May 20-26	2	12		20	37	7	19	10	21	128	14
May 27-June 2	1	1	2	4	11		18	2	5	44	5
June 3-9		1	1		1		12	2	3	20	2
June 10-16							8			8	1
June 17-23											
June 24-30											
July 1-7			1							1	+
July 8-14											
July 15-21											
July 22-28											
July 29-Aug. 4											
Aug. 5-11											
Aug. 12-18											
Aug. 19-25											
Aug. 26-Sept. 1					1					1	+
Sept. 2-8				1						1	+
Sept. 9-15		1								1	+
Sept. 16-22											
Sept. 23-30											
Totals	1,657	484	830	451	410	1,720	292	251	843	6,938	--

771/YR

TABLE 43

Waddell Creek, Steelhead: Age 3 Stream Fish Checked Through Downstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	--	--	--	--	--	--	--	--
Oct. 8-14		--	--	--	--	--	--	--	--	--	--
Oct. 15-21		--	--	--	--	--	1	--	--	1	+
Oct. 22-28		--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4		--	--	--	--	--	--	--	--	--	--
Nov. 5-11		--	--	--	--	--	--	--	--	--	--
Nov. 12-18		1	--	--	--	--	--	--	--	1	+
Nov. 19-25		--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2		--	--	--	--	--	--	--	--	--	--
Dec. 3-9		1	--	--	--	--	--	--	1	2	+
Dec. 10-16	--	--	--	--	1	--	--	--	--	1	+
Dec. 17-23	--	--	--	--	--	--	--	--	--	--	--
Dec. 24-30	--	--	1	--	--	--	1	--	--	2	+
Dec. 31-Jan. 6	--	--	1	--	--	--	--	--	--	1	+
Jan. 7-13	--	--	--	--	--	--	--	--	--	--	--
Jan. 14-20	--	--	--	--	--	--	--	1	--	1	+
Jan. 21-27	--	--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3	1	--	--	--	--	--	--	--	--	1	+
Feb. 4-10	--	--	--	--	--	--	--	--	--	--	--
Feb. 11-17	--	--	--	--	--	--	1	--	--	1	+
Feb. 18-24	2	--	--	1	2	--	--	--	--	5	1
Feb. 25-Mar. 3	5	--	3	2	2	--	--	--	2	14	2
Mar. 4-10	7	3	6	4	--	1	--	--	7	28	3
Mar. 11-17	16	3	22	1	3	7	--	2	2	56	6
Mar. 18-24	21	6	19	1	--	5	5	2	2	61	7
Mar. 25-31	12	7	16	--	--	29	--	1	8	73	8
Apr. 1-7	13	8	2	--	--	12	--	--	9	44	5
Apr. 8-14	15	--	5	--	2	12	--	--	--	34	4
Apr. 15-21	7	--	2	--	2	--	--	--	--	11	1
Apr. 22-28	8	--	7	1	1	5	--	--	--	22	2
Apr. 29-May 5	2	--	--	--	2	1	--	1	--	6	1
May 6-12	--	--	3	1	--	2	--	--	--	6	1
May 13-19	--	--	3	--	4	--	--	1	--	8	1
May 20-26	--	--	--	--	--	1	--	--	1	2	+
May 27-June 2	2	--	--	--	--	1	--	--	--	3	+
June 3-9	--	--	--	--	--	--	--	--	--	--	--
June 10-16	--	--	--	--	--	--	--	--	1	1	+
June 17-23	--	--	--	--	--	--	--	--	--	--	--
June 24-30	--	--	--	--	--	--	--	--	--	--	--
July 1-7	--	--	--	--	--	1	--	--	--	1	+
July 8-14	--	--	--	--	--	--	--	--	--	--	--
July 15-21	--	--	--	--	--	--	--	--	--	--	--
July 22-28	--	--	--	--	--	--	--	--	--	--	--
July 29-Aug. 4	--	--	--	--	--	--	--	--	--	--	--
Aug. 5-11	--	--	--	--	--	--	--	--	--	--	--
Aug. 12-18	--	--	--	--	--	--	--	--	--	--	--
Aug. 19-25	--	--	--	--	--	--	--	--	--	--	--
Aug. 26-Sept. 1	--	--	--	--	--	--	--	--	--	--	--
Sept. 2-8	--	--	--	--	--	--	--	--	--	--	--
Sept. 9-15	--	--	--	--	--	--	--	--	--	--	--
Sept. 16-22	--	--	--	--	--	--	--	--	--	--	--
Sept. 23-30	--	--	--	--	--	--	--	--	--	--	--
Totals	112	28	90	11	19	77	7	9	33	386	--

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TABLE 44

Waddell Creek, Steelhead: Age 4 Stream Fish Checked Through Downstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	--	--	--	--	--	--	--	--
Oct. 8-14		--	--	--	--	--	1	--	--	1	+
Oct. 15-21		--	--	--	--	--	--	--	--	--	--
Oct. 22-28		--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4		--	--	--	--	--	--	--	--	--	--
Nov. 5-11		--	--	--	--	--	--	--	--	--	--
Nov. 12-18		--	2	--	--	--	--	--	--	2	+
Nov. 19-25		--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2		--	--	--	--	--	--	--	--	--	--
Dec. 3-9		--	--	--	--	--	--	1	--	1	+
Dec. 10-16	--	--	--	--	--	--	--	--	--	--	--
Dec. 17-23	--	--	--	--	--	--	--	--	--	--	--
Dec. 24-30	--	--	--	--	--	--	--	--	--	--	--
Dec. 31-Jan. 6	--	--	--	--	--	--	--	--	--	--	--
Jan. 7-13	--	--	--	--	--	--	--	--	--	--	--
Jan. 14-20	--	--	--	--	--	--	--	--	--	--	--
Jan. 21-27	--	--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3	--	--	--	--	--	--	--	--	--	--	--
Feb. 4-10	--	--	--	--	--	--	--	--	--	--	--
Feb. 11-17	--	--	--	--	--	--	--	--	--	--	--
Feb. 18-24	--	--	--	--	--	--	--	--	--	--	--
Feb. 25-Mar. 3	--	--	--	--	--	--	--	--	--	--	--
Mar. 4-10	1	--	1	--	--	--	--	--	--	2	+
Mar. 11-17	--	--	--	--	--	1	--	--	--	1	+
Mar. 18-24	--	--	--	--	--	--	--	--	--	--	--
Mar. 25-31	1	--	--	--	--	--	--	--	--	1	+
Apr. 1-7	--	--	--	--	--	1	--	--	--	1	+
Apr. 8-14	--	--	--	--	--	--	--	--	--	--	--
Apr. 15-21	--	--	--	--	--	--	--	--	--	--	--
Apr. 22-28	--	--	--	--	--	--	--	--	--	--	--
Apr. 29-May 5	--	--	1	--	--	--	--	--	--	1	+
May 6-12	--	--	--	--	--	--	--	--	--	--	--
May 13-19	--	--	1	--	--	--	--	--	--	1	+
May 20-26	1	--	--	--	--	--	--	--	--	1	+
May 27-June 2	--	--	--	--	--	--	--	--	--	--	--
June 3-9	--	--	--	--	--	--	--	--	--	--	--
June 10-16	--	--	--	--	--	--	--	--	1	1	+
June 17-23	--	--	--	1	--	--	--	--	--	1	+
June 24-30	--	--	--	--	--	--	--	--	--	--	--
July 1-7	--	--	--	--	--	--	--	--	--	--	--
July 8-14	--	--	--	--	--	--	--	--	--	--	--
July 15-21	--	--	--	--	--	--	--	--	--	--	--
July 22-28	--	--	--	--	--	--	--	--	--	--	--
July 29-Aug. 4	--	--	--	--	--	--	--	--	--	--	--
Aug. 5-11	--	--	--	--	--	--	--	--	--	--	--
Aug. 12-18	--	--	--	--	--	--	--	--	--	--	--
Aug. 19-25	--	--	--	--	--	--	--	--	--	--	--
Aug. 26-Sept. 1	--	--	--	--	--	--	--	--	--	--	--
Sept. 2-8	--	--	--	--	--	--	--	--	--	--	--
Sept. 9-15	--	--	--	--	--	--	--	--	--	--	--
Sept. 16-22	--	--	--	--	--	--	--	--	--	--	--
Sept. 23-30	--	--	--	--	--	--	--	--	--	--	--
Totals	3	2	3	1	0	2	1	0	2	14	--

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TABLE 45

Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, by Age Groups and Seasons

Season	Number of age + migrants	Percent- age of mi- gration	Number of age 1 migrants	Percent- age of mi- gration	Number of age 2 migrants	Percent- age of mi- gration	Number of age 3 migrants	Percent- age of mi- gration	Number of age 4 migrants	Percent- age of mi- gration	Number of all migrants
1933-34.....	604	19	741	24	1,657	53	112	4	3	+	3,117
1934-35.....	699	39	578	32	484	27	28	2	2	+	1,791
1935-36.....	1,365	35	1,655	42	830	21	90	2	3	+	3,943
1936-37.....	1,875	53	1,191	34	451	13	11	+	1	+	3,529
1937-38.....	1,946	57	1,015	30	410	12	19	1	0	0	3,390
1938-39.....	691	11	3,699	60	1,720	28	77	1	2	+	6,189
1939-40.....	2,239	64	945	27	292	8	7	+	1	+	3,484
1940-41.....	3,306	59	2,049	36	251	4	9	+	0	0	5,615
1941-42.....	2,009	35	2,834	50	843	15	33	1	2	+	5,721
Totals.....	14,734	40	14,707	40	6,938	19	386	1	14	+	36,779

the fact that the steelhead and silver salmon have virtually completed their growth of the season, makes the end of September a convenient point to end a season.

Except by general observation, there is no way of knowing how many fish migrate downstream over the dam during the apparent slack period of January-February. This is a period of heavy rainfall and the stream is often at flood stage and turbid. General observations at Waddell and Scott creeks and data obtained from other streams all indicate that actually there is little downstream migration of steelhead during this period. Comparatively few steelhead have been observed



FIGURE 30. Mouth of Waddell Creek after a storm. Photograph by Leo Shapovalov, January 11, 1936.

TABLE 46

Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, by Age Groups and Weekly Periods, All Seasons Combined

Period	Number of age + migrants	Percent- age of age group (during season)	Percent- age of all age groups (during week)	Number of age 1 migrants	Percent- age of age group (during season)	Percent- age of all age groups (during week)	Number of age 2 migrants	Percent- age of age group (during season)	Percent- age of all age groups (during week)
Oct. 1-7.....	216	1	96	9	+	4			
Oct. 8-14.....	181	1	91	17	+	9			
Oct. 15-21.....	127	1	93	9	+	6			
Oct. 22-28.....	134	1	86	21	+	14			
Oct. 29-Nov. 4.....	403	3	92	34	+	8			
Nov. 5-11.....	143	1	92	12	+	8			
Nov. 12-18.....	242	2	93	16	+	6			
Nov. 19-25.....	233	2	94	15	+	6			
Nov. 26-Dec. 2.....	346	2	98	8	+	2			
Dec. 3-9.....	283	2	92	21	+	7			
Dec. 10-16.....	156	1	85	26	+	14			
Dec. 17-23.....	306	3	90	46	1	10			
Dec. 24-30.....	318	2	97	9	+	3			
Dec. 31-Jan. 6.....	484	3	97	16	+	3			
Jan. 7-13.....	146	1	88	19	+	12			
Jan. 14-20.....	79	1	94	4	+	5			
Jan. 21-27.....	64	+	91	6	+	9			
Jan. 28-Feb. 3.....	52	+	83	10	+	16			
Feb. 4-10.....	49	+	78	14	+	22			
Feb. 11-17.....	25	+	48	26	+	50			
Feb. 18-24.....	26	+	28	63	1	67			
Feb. 25-Mar. 3.....	12	+	10	98	1	79			
Mar. 4-10.....	27	+	11	193	3	77			
Mar. 11-17.....	30	+	10	217	3	71			
Mar. 18-24.....	24	+	5	429	6	83			
Mar. 25-31.....	27	+	3	742	11	88			
Apr. 1-7.....	78	1	7	984	14	89			
Apr. 8-14.....	1	+	193	16	957	14	81		
Apr. 15-21.....	4	+	344	29	820	12	70		
Apr. 22-28.....	6	+	549	40	800	12	58		
Apr. 29-May 5.....	6	+	453	43	576	8	55		
May 6-12.....	23	+	1,246	8	79	4	20		
May 13-19.....	131	1	8	1,310	9	79	3	12	
May 20-26.....	374	3	17	1,658	11	77	2	6	
May 27-June 2.....	377	3	24	1,144	8	73	4	3	
June 3-9.....	819	6	41	1,156	8	58	20	1	
June 10-16.....	1,267	9	59	882	0	41	8	+	
June 17-23.....	1,667	11	73	607	4	27	---	---	
June 24-30.....	1,611	11	82	368	2	19	---	---	
July 1-7.....	1,386	9	91	139	1	9	1	+	
July 8-14.....	1,358	9	94	80	1	6	---	---	
July 15-21.....	1,073	7	95	58	+	5	---	---	
July 22-28.....	838	6	97	30	+	3	---	---	
July 29-Aug. 4.....	787	5	96	29	+	4	---	---	
Aug. 5-11.....	700	5	98	16	+	2	---	---	
Aug. 12-18.....	481	3	96	19	+	4	---	---	
Aug. 19-25.....	297	2	96	11	+	4	---	---	
Aug. 26-Sept. 1.....	280	2	95	15	+	5	1	+	
Sept. 2-8.....	186	1	93	12	+	6	1	+	
Sept. 9-15.....	256	2	93	18	+	7	1	+	
Sept. 16-22.....	312	2	93	22	+	7	---	---	
Sept. 23-30.....	494	3	91	47	+	9	---	---	
Totals.....	14,734	---	40	14,707	---	40	6,938	---	19

TABLE 46—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, by Age Groups and Weekly Periods, All Seasons Combined

Period	Number of age 3 migrants	Percentage of age group (during season)	Percentage of all age groups (during week)	Number of age 4 migrants	Percentage of age group (during season)	Percentage of all age groups (during week)	Number of all migrants
Oct. 1-7	---	---	---	---	---	---	225
Oct. 8-14	---	---	---	1	7	1	199
Oct. 15-21	1	+	1	---	---	---	137
Oct. 22-28	---	---	---	---	---	---	155
Oct. 29-Nov. 4	---	---	---	---	---	---	437
Nov. 5-11	---	---	---	---	---	---	155
Nov. 12-18	1	+	+	2	14	1	261
Nov. 19-25	---	---	---	---	---	---	248
Nov. 26-Dec. 2	---	---	---	---	---	---	354
Dec. 3-9	2	1	1	1	7	+	307
Dec. 10-16	1	+	1	---	---	---	183
Dec. 17-23	---	---	---	---	---	---	442
Dec. 24-30	2	1	1	---	---	---	329
Dec. 31-Jan. 6	1	+	+	---	---	---	501
Jan. 7-13	---	---	---	---	---	---	165
Jan. 14-20	1	+	1	---	---	---	84
Jan. 21-27	---	---	---	---	---	---	70
Jan. 28-Feb. 3	1	+	2	---	---	---	63
Feb. 4-10	---	---	---	---	---	---	63
Feb. 11-17	1	+	2	---	---	---	52
Feb. 18-24	5	1	5	---	---	---	94
Feb. 25-Mar. 3	14	4	11	---	---	---	124
Mar. 4-10	28	7	11	2	14	1	250
Mar. 11-17	56	15	18	1	7	+	304
Mar. 18-24	61	16	12	---	---	---	514
Mar. 25-31	73	19	9	1	7	+	843
Apr. 1-7	44	11	4	1	7	+	1,107
Apr. 8-14	34	9	3	---	---	---	1,185
Apr. 15-21	11	3	1	---	---	---	1,179
Apr. 22-28	22	6	2	---	---	---	1,377
Apr. 29-May 5	6	2	1	1	7	+	1,042
May 6-12	6	2	+	---	---	---	1,586
May 13-19	8	2	+	1	7	+	1,656
May 20-26	2	1	+	1	7	+	2,163
May 27-June 2	3	1	+	---	---	---	1,568
June 3-9	---	---	---	---	---	---	1,995
June 10-16	1	+	+	1	7	+	2,159
June 17-23	---	---	---	1	7	+	2,275
June 24-30	---	---	---	---	---	---	1,979
July 1-7	1	+	+	---	---	---	1,527
July 8-14	---	---	---	---	---	---	1,438
July 15-21	---	---	---	---	---	---	1,131
July 22-28	---	---	---	---	---	---	868
July 29-Aug. 4	---	---	---	---	---	---	816
Aug. 5-11	---	---	---	---	---	---	716
Aug. 12-18	---	---	---	---	---	---	500
Aug. 19-25	---	---	---	---	---	---	308
Aug. 26-Sept. 1	---	---	---	---	---	---	296
Sept. 2-8	---	---	---	---	---	---	199
Sept. 9-15	---	---	---	---	---	---	275
Sept. 16-22	---	---	---	---	---	---	334
Sept. 23-30	---	---	---	---	---	---	541
Totals	386	---	1	14	---	+	36,779

moving downstream during this period at Waddell and Scott creeks and at the various counting and egg taking stations of the California Department of Fish and Game, such as the ones at Benbow Dam on the South Fork of Eel River, Van Arsdale Dam on the Eel River, San Lorenzo Egg Taking Station on the San Lorenzo River, Sweasey Dam on the Mad River, and various stations in the Klamath River system. Pautzke and Meigs (1940), drawing on unpublished data of Loyd A. Royal and C. H. Ellis for the Minter Creek Experimental Station in the State of Washington, state that no downstream steelhead were taken in their trap from September 1, 1938, to April 2, 1939. At Minter Creek, all fish passing downstream are taken, since large rotary screens prevent the escape of any past the trap.

Evidence based on general observations at Waddell and Scott creeks and data obtained from other streams also indicate that the largest numbers of stream steelhead migrate downstream at the approximate times indicated in Figures 11-19. Pautzke and Meigs (1940), quoting Royal and Ellis, state that of the total of 672 steelhead downstream migrants counted through the trap between April 2, 1939, and June 11, 1939, 449 or 71.6 percent passed through the trap during the three-week period from May 1st to May 21st. Part-season counts and observations at the various counting and egg taking stations of the California Department of Fish and Game indicate a heavy migration during this same period and a marked tapering-off in September and October.

The fact that the same flows at which the main migration takes place through the trap are often reached at times when no migration occurs through the trap (Figures 11-19) is a strong indication that the migrations through the trap are in general indicative of the migration taking place in the stream as a whole.

Although heavy and light migrations of downstream stream steelhead in the stream as a whole occur at the times shown in Figures 11-19, it is probable that the numbers shown in this graph are not proportionate to the numbers migrating down in the stream as a whole, especially during the period of heaviest migration. Probably the time of beginning of the spring migration is shown fairly accurately on the graph, but it is to be expected that, because of the large volume of water passing over the dam, proportionately larger numbers than are shown by the graph migrate downstream over the dam in the early stages of the spring migration. As less and less water passes over the dam (except for occasional freshets), the proportion of fish passing through the trap increases, until the water stops flowing over the dam and all of the fish enter the trap. If the age groups making up the downstream migration occurred in the same proportions throughout the season, Figure 29 would show the correct age composition of the downstream migration, even if it did not show the true distribution of numbers at all times of the season. However, the age composition of the downstream migration is very different at different times of the season, as we saw from Figures 11-19. Since the older age classes migrate first in the spring migration, it is to be expected that they will be the most affected by fish passing over the dam and so will show up in disproportionately small numbers among the fish taken in the trap and shown in Figures 11-19 and 29.

Since only about one-fourth of the returning adults are marked it would appear, at first glance, that three-fourths of the fish (1) passed downstream over the dam uncounted, (2) were produced in Waddell Creek below the dam, or (3) strayed from other streams. The amount of straying from other streams will be shown to be a very minor factor (pages 197-201). The fish that spawn below the dam form only about 5 percent of the total spawning run into the stream. Thus, it would still appear that a considerable number of fish pass downstream over the dam, uncounted and unmarked. However, it will be shown, in the discussion of the survival of the different age classes among the marked fish that there is a much higher survival rate among the fish of the older age classes. Comparatively small numbers of age 2 and 3 fish, the ones that are migrating after the spring migration has started but while there is yet considerable water going over the dam, produce the bulk of the marked adults. This being the case, it becomes evident that comparatively small numbers of fish of these older classes could pass over the dam and still produce the unmarked adults "unaccounted for", i.e., the unmarked adults not resulting from fish produced below the dam or straying from other streams. That is probably what actually happens.

Sex Ratio

Sufficient numbers of downstream migrants have not been sexed to determine quantitatively the representation of sexes. The sex ratio may vary somewhat with the age of the fish. Probably it approaches 1:1 among the fish two years old and younger, but may deviate from equal representation among the older fish.

Factors Influencing the Time of Migration and Size at Migration

Possible factors influencing the time of migration and the size of the fish, and their interrelationships, were discussed for the silver salmon (pages 86-88). The reader is referred to that discussion, since most of it is also applicable to the steelhead, except in that the situation for the latter is made still more complex because a heterogeneous population is involved, while the silver salmon formed a homogeneous population. The steelhead downstream migrants form a heterogeneous population not only because they are formed of different age classes, but also because this migration is composed of offspring of sea-run fish which (a) have made a previous downstream migration and are going to sea in the current season, (b) are making their initial downstream migration and are going to sea in the current season, and (c) are making their initial downstream migration but will not go to sea until the following season, and to a minor extent of other offspring of sea-run fish that will not go to sea and offspring of stream fish that may or may not go to sea. No attempt was made and no method is known to distinguish these various groups, except in individual cases, nor to determine the extent of the representation of these groups in the downstream migrations.

In applying the discussion of influencing factors contained in the section on silver salmon to the steelhead, each age class must be treated as a separate unit.

From Figures 11-19 we see that the main (spring) migration as a whole occurs later or earlier in some seasons than in others, as was the case with the silver salmon. Similarly, Figures 11-19 reveal that the early seasons are those with generally low stream levels for the same dates during the migration period (notably 1933-34 and 1938-39), while the late seasons are those with generally high stream levels for the same dates during the migration period (notably 1934-35, 1937-38, 1939-40, and 1940-41). The effects of the absolute stream levels on the time of migration are probably modified by rate of drop in stream level, sudden spring freshets, etc.

The fish that migrate down in the late fall are principally of the previous season's year class. From an examination of Figures 11-19, it is apparent that there is a great deal of fluctuation in the size of this migration from season to season and also that this migration may have several peaks within a season. Both of these phenomena are accounted for by the fact that this migration, or rather series of migrations, is associated with rainfall, which is fairly well brought out in Figures 11-19. However, these graphs probably do not bring out the association between migration and rainfall as clearly as graphs showing rainfall³³ or the proper combination of rainfall and stream flow would do. Naturally, there is an association between rainfall and stream flow, but the early rains are not as well reflected in the stream flow immediately following as are the later rains, when the ground has become soaked and a much larger proportion of the precipitation goes into surface runoff. The fall migrations appear to be influenced by the rainfall out of proportion to its effect on the amount of stream flow. Since the autumn rains vary greatly, both regarding amount and time of occurrence, the migrations occurring at this time assume a fluctuating character.

The fall migration, although often occurring near the beginning of the season chosen for the present studies, probably should properly be thought of as the tail-end of the migration of fish of the season in the previous season, which has been interrupted by low water and perhaps other factors associated with low water. The basis for this view lies principally in the fact that in some years there is no break between the fish of the fall migration and the fish of the same year class in the previous season's spring-summer migration (e.g., 1937-38 to 1938-39 and 1940-41 to 1941-42), while there is always a break between the fall migration and the following spring migration of fish of the same year class. Also, it appears characteristic for a migration of a given age class to rise rather steadily and rapidly to a peak and then taper off for a longer period. Normally, in the spring the migration of fish of the season rises steadily and rapidly to a peak and stretches out, with fluctuations, far into the summer, so that it appears correct to consider the secondary rise in numbers of fish of the same year class as the tail-end of the spring-summer migration, rather than as the fluctuating beginning of the spring migration.

Climatic factors not only affect the general starting time of the main migration, but also create breaks in the pattern once it has gotten

³³ No record of rainfall at Waddell Creek is included in this publication. Such a record for a point at the dam would mean little, since the rainfall in different parts of the stream is greatly different, being approximately twice as heavy in the headwaters as at the mouth.

under way. However, a given factor does not have the same effect at all times of the year but can, on the contrary, have an opposite effect from one time to another. For example, during the normal period of heavy migration a rain stops or markedly slows down the migration, while a rain during a period when there is normally very little migration accelerates it. This phenomenon is true also of other streams. For example, J. H. Wales (unpublished data) reports the following regarding the stream steelhead downstream migration during May, 1942, in the Grenada irrigation ditch of the Klamath River system, Siskiyou County, California:

"Fairly good catches were made in the irrigation ditch [with a fyke net] just below the bar screen on those days when the steelhead fingerlings were migrating downstream. A cold rain storm caused an abrupt cessation of the run but with warm weather this migration was resumed." (Monthly report to the Division of Fish and Game for May, 1942.)

As the spring migration as a whole is pushed backward or forward within a season, so the age composition pattern within the migration is pushed backward or forward. The result of this is, of course, that the age composition of the fish migrating at any given time or brief period of time, such as a weekly or two-week period, in two seasons may be quite different.

From an examination of Figures 11-19, it is also apparent that the strength of a given age class, i.e., its representation within a season both in absolute numbers and in proportion to the other age classes individually and as a whole, varies considerably from season to season. The result of this is, of course, that even when the growth rate and the water levels are the same in two seasons, so that the fish of a given age class start migrating at the same time and are of the same size when they migrate in the two seasons, their proportionate representation among all the fish migrating at any given point of time may be quite different, and so the age composition of the total migration at the same point of time will be different.

An examination of Table 38 and Figure 28 reveals that there is, as a rule, a distinct increase in length of the fish of a given age class within a season between the end of the fall migration and the beginning of the spring migration. Since the fall migration is composed largely of fish of a single year class (age + fish, which become age 1 fish in the spring), in the tables and graph this is evident only for that age class, but from a careful analysis of scattered fish of older year classes in all seasons is also true for them. An examination of a large number of scales reveals that the great majority of the fish in the fall migration have nearly completed growth of the season or are forming an annulus, while the great majority in the spring migration, even in the early part of the migration, have started growth of the new season. The increase in size within the age class therefore represents a growth made by that age class as a whole, rather than a migration of the smaller fish of the age class in the fall, followed by a spring migration of the larger fish of the same age class. (The early start of the growing season at Waddell Creek, fairly evident in the tables and graph under discussion, has been discussed on pages 73, 157.) (It happens that the fall migration of 1938-39, shown in Figure 28, was

the largest in numbers and extended farther into the winter in steady numbers than that of any other season and so from this standpoint is atypical.)

It will also be seen from an examination of Table 38 and Figure 28 that once a migration of a given age class begins, there is often, although not always, a decrease in the average size of the migrating fish of that age class. Quite obviously, *individuals* do not become smaller, and so this phenomenon must result because the larger individuals of a given age class migrate earlier than the smaller ones. The same phenomenon was encountered in the case of the silver salmon and discussed on pages 87-88; it is evident from that discussion that it could come about in any one of three ways.

Since the later migrants are sometimes smaller than the earlier migrants, it is evident that the law of "growth for age" at migration—that the quick growers migrate first, but that the later migrants are always a little bigger when they go to sea than the quicker growers which migrated earlier—held by British investigators (e.g., Went, 1942) to be generally operative for the Atlantic salmon (*Salmo salar*), is not applicable to the Waddell Creek steelhead. It is still possible, however, that among the latter the earlier migrants are the quick growers. If this is true, it is possible either that they are quick growers because of inherent factors, or simply because they happen to be in the portions of the stream with conditions suitable for rapid growth.

Rapid growth does not necessarily mean large size of fish; but, other things being approximately equal, size and rapid growth are associated. (Two cases in which rapid growth would not mean large size of fish may be given. Case 1. Of two fish hatched at the same time in different portions of the stream, one has an inherent rapid growth rate, while the other has a slow growth rate; the fish with the rapid growth rate, hatching in a portion of the stream with less favorable growing conditions than the slow grower, makes less absolute growth in a season than does the slow grower, and so at the end of the season is smaller than the slow grower. Case 2. Two fish, one with an inherent rapid growth rate and the other with an inherent slow growth rate, are hatched in the same section of stream, or in sections having equally favorable conditions; however, the rapid grower is hatched considerably later than the slow grower and again makes less absolute growth during the season than the slow grower. If the rapid grower happened to hatch both later in the season and in a portion of the stream with less favorable growing conditions, the result previously cited would be further accentuated.)

(British investigators have concluded that Atlantic salmon making the best growth in their first year continue to make the best growth throughout life, and that the average length of juvenile Atlantic salmon (parr) which migrate to sea at a particular age is always greater than that of those of the same age which remain for an additional year, or years, in fresh water. This has not been worked out in the case of the Waddell Creek steelhead.)

The hypothetical picture of the downstream migration of silver salmon, as regards time of migration and size of fish, presented on pages 87-88, applies also to the steelhead, with different age classes considered separately.

Characteristics of the Migration

The extent of schooling at migration time has not been noted sufficiently to be recorded at this time. Young steelhead do school in streams under certain conditions, individuals of the same size tending to group together. Yearling steelhead planted at one point in the San Lorenzo River on one day have been observed gathered in a school of over 1,000 individuals on the following day approximately one-half mile below the point of stocking.

Quantitative observations were not made in regard to diurnal distribution of the migration. General observations indicate that some fish move down at all hours of the day and night, but that the bulk of the fish move downstream during the night or at least in the early morning or late evening.

General color notes were taken for a number of the 1933-34 season migrants, during the period December through April. They indicate that on the fish of smaller size the parr marks are generally pronounced and that such fish are not "silvery," while the larger fish are silvery. There are various individual variations; some of the silvery fish are a "silvery blue," while others are silvery with a pink or red lateral stripe. Aside from noting the association of "silveriness" with size of fish, no attempt was made to correlate coloration with sex, sexual development, or other such characteristics of the fish. Both in 1933-34 and in subsequent seasons individuals with "rainbow" coloration, prominent parr marks and rich body and fin coloration, have been noted among the downstream migrants. Examination of such fish has usually revealed them to be sexually mature, and these fish are believed to be mainly the offspring of stream fish.

*Upstream Migration of Stream Fish**Time and Size of the Migration*

During the nine seasons of operation of the trap,³⁴ 3,104 stream steelhead were checked on their upstream migration. The number taken during each weekly period in each season is shown in Table 47.

The length of all of these fish from tip of snout to fork of caudal fin was recorded in mm., measurement being made to the next highest mm.

Scale samples were taken from practically all of the fish during the first six seasons of operation, i.e., 1933-34 through 1938-39. Scale samples were not taken during the last three seasons, 1939-40 through 1941-42, largely because it was believed that further scale samples from these fish would not yield information commensurate with the effort expended.

Of the 1,245 scale samples taken, 1,126 were mounted and read (131 for 1933-34 read only, those for other seasons read and measured), including all for the 1933-34, 1934-35, 1935-36, and 1936-37 seasons, 480 for the 1937-38 season, and a few scattered ones for other seasons.

Table 47 is an over-all presentation of the upstream migration, without distinction as to age or origin of the fish involved. Even without

³⁴ In 1933-34, the first season of operation, the trap was not put into operation until the week of December 3-9 and was not operated from June 3d to the end of the season.

TABLE 47

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, by Seasons and Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average	
Oct. 1-7	No Record	--	--	--	--	--	--	--	5	5	1	
Oct. 8-14		--	--	--	--	--	--	1	6	7	1	
Oct. 15-21		--	--	--	--	1	--	--	2	3	+	
Oct. 22-28		--	--	--	--	--	--	3	1	4	1	
Oct. 29-Nov. 4		--	--	--	--	1	22	11	7	41	5	
Nov. 5-11		--	--	--	--	--	8	4	5	--	17	2
Nov. 12-18		4	--	2	--	2	13	--	--	3	24	3
Nov. 19-25		--	--	--	--	2	17	--	--	3	22	3
Nov. 26-Dec. 2		--	--	--	--	3	24	2	7	10	46	6
Dec. 3-9		4	5	9	1	7	29	1	6	16	78	9
Dec. 10-16		5	2	--	--	150	17	2	3	40	219	24
Dec. 17-23		15	1	--	8	110	4	5	77	766	986	110
Dec. 24-30		6	--	33	2	129	5	4	68	75	322	36
Dec. 31-Jan. 6		27	4	68	2	120	6	1	61	215	504	56
Jan. 7-13		7	2	48	--	14	15	--	12	24	122	14
Jan. 14-20		16	--	38	2	10	1	17	4	50	138	15
Jan. 21-27		4	4	8	1	15	4	7	8	2	53	6
Jan. 28-Feb. 3		1	11	6	13	2	2	--	3	14	52	6
Feb. 4-10		10	1	--	11	3	5	1	5	4	40	4
Feb. 11-17		5	--	4	4	2	1	1	10	4	31	3
Feb. 18-24		--	2	4	--	1	--	4	5	--	16	2
Feb. 25-Mar. 3		2	--	1	2	--	--	--	2	--	7	1
Mar. 4-10		1	1	--	--	1	2	2	3	2	12	1
Mar. 11-17		1	--	--	--	1	--	1	2	2	7	1
Mar. 18-24		1	--	1	--	--	--	--	1	--	3	+
Mar. 25-31		--	--	--	--	--	--	--	1	--	1	+
Apr. 1-7	1	--	--	2	4	--	--	1	2	10	1	
Apr. 8-14	--	--	--	2	--	--	--	1	1	4	+	
Apr. 15-21	1	--	--	2	3	--	--	--	1	7	1	
Apr. 22-28	1	--	--	2	--	--	--	10	--	13	1	
Apr. 29-May 5	4	--	--	--	1	--	--	5	--	10	1	
May 6-12	2	--	1	--	--	--	--	1	--	4	1	
May 13-19	9	--	--	--	--	--	--	3	2	14	2	
May 20-26	8	--	1	1	1	--	--	5	--	16	2	
May 27-June 2	--	--	--	1	5	8	--	7	1	22	2	
June 3-9	No Record	--	--	--	--	2	1	1	2	6	1	
June 10-16		--	--	--	--	--	1	1	--	3	+	
June 17-23		--	--	5	2	3	2	7	--	19	2	
June 24-30		--	4	1	1	--	1	6	2	15	2	
July 1-7		--	--	1	1	--	5	1	--	8	1	
July 8-14		--	--	8	--	1	--	1	2	12	2	
July 15-21		--	--	6	2	--	6	3	--	17	2	
July 22-28		--	2	1	--	--	24	46	--	73	9	
July 29-Aug. 4		--	--	--	4	--	6	25	2	37	5	
Aug. 5-11		--	--	--	4	--	6	3	--	13	2	
Aug. 12-18		--	--	2	--	--	4	--	--	6	1	
Aug. 19-25		--	--	--	--	--	5	--	--	5	1	
Aug. 26-Sept. 1		--	1	4	1	--	5	--	--	11	1	
Sept. 2-8		--	--	--	1	--	1	3	2	7	1	
Sept. 9-15		--	--	--	1	--	--	2	--	3	+	
Sept. 16-22		--	--	--	--	--	--	5	--	5	1	
Sept. 23-30		--	--	1	--	--	--	--	3	4	1	
Totals	131	37	229	91	601	190	119	435	1,271	3,104	*365	

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

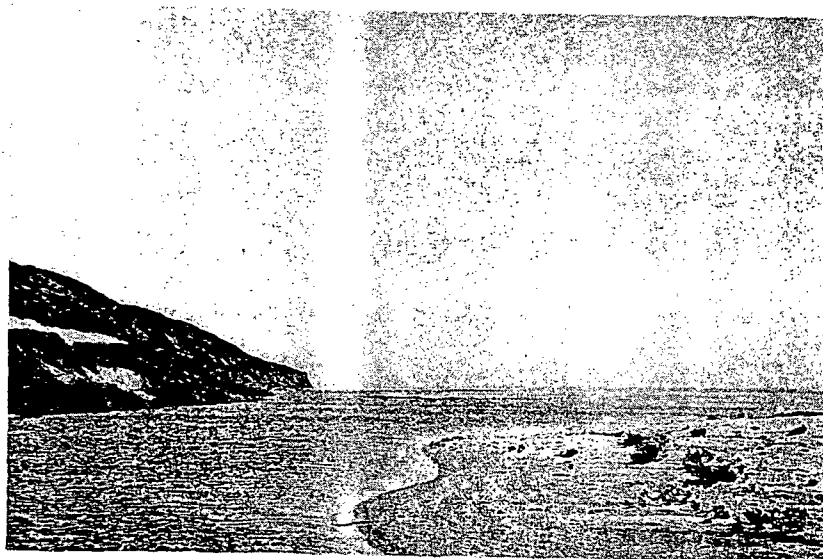


FIGURE 31. Waddell lagoon at full size, showing sand spit and ocean in background. Photograph by Paul R. Needham.

a breakdown into age groups, it is apparent that this upstream migration is not a haphazard affair, but follows a definite pattern, with the peak of migration usually occurring close to the beginning of the calendar year, and a secondary, quite minor rise occurring near the end of July. As will be seen from the subsequent discussion, the latter migration is not comparable to the main, or winter, migration and is composed of fish younger than those in the winter migration.

There is tremendous fluctuation in the size of the upstream migration from season to season and the weekly total and average figures for all seasons are influenced by one season (1941-42). However, the pattern in other seasons is much the same as that in the 1941-42 season.

Unlike the downstream migrations, the upstream migrations do not involve sampling, but represent the entire runs (with the possible exception of a few quite small fish—mostly fish of the season—that may have wanted to migrate upstream during the summer but were too small to make the ascent of the fishway).

The upstream migration is composed of fish that had previously migrated downstream and spent some time in the lagoon (or the section of the stream below the dam) and fish that had hatched in the section of the stream below the dam. Like the downstream migrants, they are probably composed largely of offspring of sea-run fish but to a minor extent of offspring of stream fish. Most of the upstream migrants make a subsequent downstream migration in the same season (some after spawning). In 1933-34, for example, 72 of the 129 upstream fish were recorded downstream in the same season. Since some fish probably went downstream over the dam (unrecorded), it is quite likely that the number returning downstream was even higher.

Probably following their second downstream migration most of the fish go to sea. That some of them go to sea is known from marking.

Age and Size of the Fish

Since scales were not examined from all of the fish, the system of dividing lines (used for separating the age groups in the downstream migrants and discussed on pages 165-166) was used to supplement the segregation into age groups according to scale readings. As in the case of the downstream migrants, the dividing lines were drawn more or less arbitrarily by eye, but taking into consideration the pattern of the migration, including time, size of age classes, and size of fish in the age classes. Where numbers of fish were not sufficient to form conspicuous modal groups, the dividing lines used for the downstream migrants were used as a guide, with allowance made for the fact (as will be discussed later) that the upstream fish of a given age class are not quite of the same size as the downstream fish of the same age class at the same time. The dividing lines used are shown in Table 48. It is believed that over 95 percent of all the fish in the upstream migrations were assigned to the correct age classes. Length-frequency distributions of upstream stream fish in each season are shown in Tables A-28 to A-36 of the Appendix.

From Tables 49-55 it is apparent that not only does the size of the entire migration fluctuate considerably from season to season, but also that the strength of a given age class, i.e., its representation within a season both in absolute numbers and in proportion to the other age classes individually and as a whole, varies considerably from season to season.

Sex Ratio

Data regarding the sex of upstream stream steelhead are not sufficient to warrant definite conclusions regarding the sex ratio. In the one season in which the upstream fish were killed and examined internally (1934-35), the run consisted of 14 males and 14 females. However, the run was small and the fish below average in size, so the sex ratio may not be representative of conditions in other seasons. In other seasons individual males and females were recognized in the case of fish with flowing sexual products, but were not sufficiently numerous to establish sex ratios. Secondary sexual characters are not sufficiently developed in most of the upstream stream steelhead to permit sex differentiation on the basis of external characters.

Factors Influencing the Time of Migration and Size at Migration

In all probability the great majority of the upstream stream steelhead have spent a summer in the lagoon. Possibly or probably a few have spent all or part of the time between the dam and the lagoon, and some may have migrated in and out of the lagoon with the tides (i.e., out to sea). In all probability, then, the size of the upstream migration will depend upon the physical conditions that have existed in the lagoon during the preceding summer, especially the size of the lagoon and the closing and opening dates of the bar at the mouth. The physical character of the lagoon and the opening and closing dates have fluctuated considerably during the course of the experiments. Undoubtedly the food supply in the lagoon is also influenced by these factors, and in turn influences the number of fish produced and their size.

TABLE 48

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, All Seasons Combined; Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29-Nov. 11	Nov. 12-25	Nov. 26-Dec. 9	Dec. 10-23	Dec. 24-Jan. 6	Jan. 7-20	Jan. 21-Feb. 3	Feb. 4-17	Feb. 18-Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
61-65														
70						1			1					
75						14			1					
80			1	1	2	31	2	2		2				
85					2	55	2	3	2					
90			2	1	2	63	4			3	2	2		
95	5		1		2	57	3	2		1	1			
100	1			1	3	58	3	1	3	2	1	1		
105			2	3	6	51	11	1	2	2	2			1
110			2	1	2	36	5	2	6	2	2		1	2
115	2	1			5	36	5	1	2	2	1			
120			2	1	5	31	8	1	3			2		
125		1	1	1	2	29	5	7	5	1	1	2		2
130			3	2		25	16	1	6	2		1		
135	1		2	2	2	18	10	5	2	1		1	1	3
140			1		1	23	9	6	3	1	1			1
145		1	2	2	6	32	16	9	4	2	1	2		2
150			4	2	3	29	26	5	5					
155			5	3	8	43	40	10	2		1			
160			2	4	1	54	38	9	3	2		1	1	
165			4	4	3	61	47	12	3	2		1		
170		1	1		3	57	59	13	1	2				1
175	1		1	4	4	63	64	14	4					
180		1	1	4	9	50	53	17	3	2		1		
185		1	1	4	9	60	60	8	2					
190	2		3	1	9	51	55	13	5	3	1			
195		1			5	30	49	10	8	1				
200			3	1	4	25	34	16	6	4		1		2
205			4		3	24	20	11	5	1				
210		1	3	1	3	8	22	9	1	2				
215			3	2	5	8	11	7	1	5				
220					6	16	16	10	1	1				
225			1			8	28	18	1	2	3			
230					1	12	22	5	2	3	1			
235					3	10	14	5	2	2	1			
240						8	19	7		2	1	1		
245					1	4	10	4						
250						2	13	2	1					
255					1	2	4	5	1	4	1			
260			1			5	6	2	2	2		1		
265						4	4	2	1	2				
270						4	3		3					
275						2	1							
280				1	2	1	1	1					1	
285			1			3	3			2				
290								1	1		1			
295						1	1	1		1				
300							1		1	2				
Totals	12	7	58	46	124	1,205	826	260	105	71	23	19	4	14

* Recorded only as 31 cm.

† 4 at 33 cm.; 4 at 35 cm.; 2 at 39 cm.; 1 at 40 cm.; 1 at 44 cm.

TABLE 48—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, All Seasons Combined; Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29-May 12	May 13-26	May 27-June 9	June 10-23	June 24-July 7	July 8-21	July 22-Aug. 4	Aug. 5-18	Aug. 19-Sept. 1	Sept. 2-15	Sept. 16-30	Totals
61-65						1							1
70						1		1				1	5
75	1					1		3					20
80				1		1	1	4				3	51
85			AGE 1			1	3	3			1		72
90						2	1	1			3	1	87
95			1	2			3	3			1		82
100	2	1	2			1	2						83
105		1	1	4	3	1		1				1	93
110	4		1	2		1	1	1					72
115	3	2	2	3	3	1		3		1	1		74
120		1	2	2		2				1			62
125		1	3	1	5	1	2		1			1	72
130			4	1	2			3	2	1			69
135	1		4	2	2	1	2	2	1	2			65
140		1	1	2	1	1	1	2					55
145	1		1		1	2	2	11		1		1	100
150		1	2			1		11	2	1			92
155	1				1	1	1	12		1			129
160				1		1	1	23	1	2			143
165	1					1	1	12	3		2		157
170	1			2		1	1	9	2		1		155
175	1		1				2	1	1	1		1	163
180			1				1		2	2			146
185							2	1		1			149
190								1		2			146
195			AGE 2		3	1			1	1			110
200										1			97
205													68
210				1									51
215	1							1					44
220								1					51
225													62
230				1									48
235			1										39
240	2												40
245													19
250													18
255			AGE 3										18
260						1							20
265													13
270	1			1									12
275													3
280		1			1								8
285		1											11
290							1						3
295		1											5
300			1										4
Totals	20	14	30	28	22	23	29	110	19	16	10	9	3,104

*5

†12

TABLE 49

Waddell Creek, Steelhead: Age + Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	--	--	--	--	--	--	--	--
Oct. 8-14		--	--	--	--	--	--	--	--	--	--
Oct. 15-21		--	--	--	--	--	--	--	--	--	--
Oct. 22-28		--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4		--	--	--	--	--	--	--	--	--	--
Nov. 5-11		--	--	--	--	--	--	--	--	--	--
Nov. 12-18		--	--	--	--	--	--	--	--	--	--
Nov. 19-25		--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2		--	--	--	--	--	--	--	--	--	--
Dec. 3-9		--	--	--	--	--	--	--	--	--	--
Dec. 10-16	No Record	--	--	--	--	--	--	--	--	--	--
Dec. 17-23		--	--	--	--	--	--	--	--	--	--
Dec. 24-30		--	--	--	--	--	--	--	--	--	--
Dec. 31-Jan. 6		--	--	--	--	--	--	--	--	--	--
Jan. 7-13		--	--	--	--	--	--	--	--	--	--
Jan. 14-20		--	--	--	--	--	--	--	--	--	--
Jan. 21-27		--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3		--	--	--	--	--	--	--	--	--	--
Feb. 4-10		--	--	--	--	--	--	--	--	--	--
Feb. 11-17		--	--	--	--	--	--	--	--	--	--
Feb. 18-24	No Record	--	--	--	--	--	--	--	--	--	--
Feb. 25-Mar. 3		--	--	--	--	--	--	--	--	--	--
Mar. 4-10		--	--	--	--	--	--	--	--	--	--
Mar. 11-17		--	--	--	--	--	--	--	--	--	--
Mar. 18-24		--	--	--	--	--	--	--	--	--	--
Mar. 25-31		--	--	--	--	--	--	--	--	--	--
Apr. 1-7		--	--	--	--	--	--	--	--	--	--
Apr. 8-14		--	--	--	--	--	--	--	--	--	--
Apr. 15-21		--	--	--	--	--	--	--	--	--	--
Apr. 22-28		--	--	--	--	--	--	--	--	--	--
Apr. 29-May 5	No Record	--	--	--	--	--	--	--	--	--	--
May 6-12		--	--	--	--	--	--	--	--	--	--
May 13-19		--	--	--	--	--	--	--	--	--	--
May 20-26		--	--	--	--	--	--	--	--	--	--
May 27-June 2		--	--	--	--	--	--	--	--	--	--
June 3-9		--	--	--	--	--	--	--	--	--	--
June 10-16		--	--	--	--	--	--	--	--	--	--
June 17-23		--	--	--	--	--	--	--	--	--	--
June 24-30		--	--	--	--	--	--	--	--	--	--
July 1-7		--	--	--	--	--	--	--	--	--	--
July 8-14	No Record	--	--	--	--	--	--	--	--	--	--
July 15-21		--	--	--	--	--	--	--	--	--	--
July 22-28		--	--	--	--	--	--	--	--	--	--
July 29-Aug. 4		--	--	--	--	--	--	--	--	--	--
Aug. 5-11		--	--	--	--	--	--	--	--	--	--
Aug. 12-18		--	--	--	--	--	--	--	--	--	--
Aug. 19-25		--	--	--	--	--	--	--	--	--	--
Aug. 26-Sept. 1		--	--	--	--	--	--	--	--	--	--
Sept. 2-8		--	--	--	--	--	--	--	--	--	--
Sept. 9-15		--	--	--	--	--	--	--	--	--	--
Sept. 16-22	No Record	--	--	--	--	--	--	--	--	--	--
Sept. 23-30		--	--	--	--	--	--	--	--	--	--
Totals	0	0	0	4	3	0	20	12	5	44	*5

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

TABLE 50

Waddell Creek, Steelhead: Age 1 Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	--	--	--	--	--	4	4	1
Oct. 8-14		--	--	--	--	--	--	1	3	4	1
Oct. 15-21		--	--	--	--	--	--	--	1	1	+
Oct. 22-28		--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4		--	--	--	--	5	--	--	2	7	1
Nov. 5-11		--	--	--	--	1	2	--	3	3	+
Nov. 12-18		--	1	--	--	--	--	--	3	4	1
Nov. 19-25		--	--	--	2	--	--	--	1	3	+
Nov. 26-Dec. 2		--	--	--	--	5	1	--	5	11	1
Dec. 3-9		--	1	7	--	3	1	1	3	16	2
Dec. 10-16	No Record	--	--	--	7	1	--	--	17	25	3
Dec. 17-23		--	--	--	7	1	1	2	446	457	51
Dec. 24-30		--	--	1	--	--	--	9	12	22	3
Dec. 31-Jan. 6		--	--	1	--	--	--	4	8	17	2
Jan. 7-13		1	--	4	--	--	--	1	2	8	1
Jan. 14-20		--	--	7	1	--	--	--	1	9	1
Jan. 21-27		--	--	3	--	--	--	3	1	7	1
Jan. 28-Feb. 3		--	1	2	--	--	--	--	11	14	2
Feb. 4-10		3	--	--	--	--	1	--	2	6	1
Feb. 11-17		--	--	1	--	--	--	4	3	8	1
Feb. 18-24	No Record	--	1	--	--	--	2	1	--	4	+
Feb. 25-Mar. 3		1	--	1	1	--	--	2	--	5	1
Mar. 4-10		--	--	--	--	--	--	1	2	3	+
Mar. 11-17		--	--	--	--	--	--	1	1	2	+
Mar. 18-24		--	--	--	--	--	--	--	--	--	--
Mar. 25-31		--	--	--	--	--	--	1	--	1	+
Apr. 1-7		--	--	--	2	--	--	1	2	5	1
Apr. 8-14		--	--	--	--	--	--	--	1	1	+
Apr. 15-21		--	--	1	--	--	--	--	1	2	+
Apr. 22-28		--	--	1	--	--	--	7	--	8	1
Apr. 29-May 5	1	--	--	--	1	--	--	4	--	6	1
May 6-12	1	--	--	--	--	--	--	1	--	2	+
May 13-19	8	--	--	--	--	--	--	3	1	12	1
May 20-26	6	--	1	1	--	--	--	3	--	11	1
May 27-June 2	--	--	--	--	3	7	--	6	1	17	2
June 3-9	No Record	--	--	--	--	2	--	1	1	4	+
June 10-16		--	--	--	--	1	1	--	--	2	+
June 17-23		--	--	--	4	2	3	--	7	16	2
June 24-30		--	3	1	1	--	--	1	4	10	1
July 1-7		--	--	1	1	--	--	2	--	4	+
July 8-14		--	--	8	--	1	--	--	1	10	1
July 15-21		--	--	3	1	--	--	2	2	8	1
July 22-28		--	2	--	--	--	14	46	--	62	7
July 29-Aug. 4		--	--	--	2	--	2	24	2	30	3
Aug. 5-11		--	--	4	--	--	6	3	--	13	1
Aug. 12-18	No Record	--	--	2	--	--	4	--	--	6	1
Aug. 19-25		--	--	2	--	--	5	--	--	5	1
Aug. 26-Sept. 1		--	1	4	1	--	5	--	--	11	1
Sept. 2-8		--	--	--	1	--	--	1	--	3	+
Sept. 9-15		--	--	--	--	--	--	1	--	1	+
Sept. 16-22		--	--	--	--	--	--	--	--	--	--
Sept. 23-30		--	--	--	--	--	--	3	--	3	+
Totals	21	4	34	31	36	30	51	145	541	893	*105

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

TABLE 49

Waddell Creek, Steelhead: Age + Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	--	--	--	--	--	--	--	--
Oct. 8-14		--	--	--	--	--	--	--	--	--	--
Oct. 15-21		--	--	--	--	--	--	--	--	--	--
Oct. 22-28		--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4		--	--	--	--	--	--	--	--	--	--
Nov. 5-11		--	--	--	--	--	--	--	--	--	--
Nov. 12-18		--	--	--	--	--	--	--	--	--	--
Nov. 19-25		--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 2		--	--	--	--	--	--	--	--	--	--
Dec. 3-9		--	--	--	--	--	--	--	--	--	--
Dec. 10-16		--	--	--	--	--	--	--	--	--	--
Dec. 17-23		--	--	--	--	--	--	--	--	--	--
Dec. 24-30		--	--	--	--	--	--	--	--	--	--
Dec. 31-Jan. 6		--	--	--	--	--	--	--	--	--	--
Jan. 7-13	No Record	--	--	--	--	--	--	--	--	--	--
Jan. 14-20		--	--	--	--	--	--	--	--	--	--
Jan. 21-27		--	--	--	--	--	--	--	--	--	--
Jan. 28-Feb. 3		--	--	--	--	--	--	--	--	--	--
Feb. 4-10		--	--	--	--	--	--	--	--	--	--
Feb. 11-17		--	--	--	--	--	--	--	--	--	--
Feb. 18-24		--	--	--	--	--	--	--	--	--	--
Feb. 25-Mar. 3		--	--	--	--	--	--	--	--	--	--
Mar. 4-10		--	--	--	--	--	--	--	--	--	--
Mar. 11-17		--	--	--	--	--	--	--	--	--	--
Mar. 18-24		--	--	--	--	--	--	--	--	--	--
Mar. 25-31		--	--	--	--	--	--	--	--	--	--
Apr. 1-7	No Record	--	--	--	--	--	--	--	--	--	--
Apr. 8-14		--	--	--	--	--	--	--	--	--	--
Apr. 15-21		--	--	--	--	--	--	--	--	--	--
Apr. 22-28		--	--	--	--	--	--	--	--	--	--
Apr. 29-May 5		--	--	--	--	--	--	--	--	--	--
May 6-12		--	--	--	--	--	--	--	--	--	--
May 13-19		--	--	--	--	--	--	--	--	--	--
May 20-26		--	--	--	--	--	--	--	--	--	--
May 27-June 2		--	--	--	--	--	--	--	--	--	--
June 3-9		--	--	--	--	--	--	--	--	--	--
June 10-16	No Record	--	--	--	--	--	--	--	--	--	--
June 17-23		--	--	--	--	--	--	--	--	--	--
June 24-30		--	--	--	--	--	--	--	--	--	--
July 1-7		--	--	--	--	--	3	1	2	3	+
July 8-14		--	--	--	--	--	--	--	2	2	+
July 15-21		--	--	2	1	--	4	1	--	8	1
July 22-28		--	--	1	--	--	9	--	--	10	1
July 29-Aug. 4		--	--	--	1	--	4	1	--	6	1
Aug. 5-11		--	--	--	--	--	--	--	--	--	--
Aug. 12-18		--	--	--	--	--	--	--	--	--	--
Aug. 19-25		--	--	--	--	--	--	--	--	--	--
Aug. 26-Sept. 1		--	--	--	--	--	--	--	--	--	--
Sept. 2-8	No Record	--	--	--	--	--	3	1	--	4	1
Sept. 9-15		--	--	--	1	--	--	1	--	2	+
Sept. 16-22		--	--	--	--	--	5	--	--	5	1
Sept. 23-30		--	--	1	--	--	--	--	--	1	+
Totals	0	0	0	4	3	0	20	12	5	44	*5

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

TABLE 50

Waddell Creek, Steelhead: Age 1 Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record	--	--	--	--	--	--	--	4	4	1
Oct. 8-14		--	--	--	--	--	--	1	3	4	1
Oct. 15-21		--	--	--	--	--	--	--	1	1	+
Oct. 22-28		--	--	--	--	--	--	--	--	--	--
Oct. 29-Nov. 4		--	--	--	--	5	--	--	2	7	1
Nov. 5-11		--	--	--	--	1	2	--	--	3	+
Nov. 12-18		--	1	--	--	--	--	--	3	4	1
Nov. 19-25		--	--	--	2	--	--	--	1	3	+
Nov. 26-Dec. 2		--	--	--	--	5	1	--	5	11	1
Dec. 3-9		--	1	7	--	3	1	1	3	16	2
Dec. 10-16	No Record	--	--	--	7	1	--	--	17	25	3
Dec. 17-23		--	--	--	7	1	1	2	446	457	51
Dec. 24-30		--	--	1	--	--	--	9	12	22	3
Dec. 31-Jan. 6		--	--	1	--	4	--	4	8	17	2
Jan. 7-13		1	--	4	--	--	--	1	2	8	1
Jan. 14-20		--	--	7	--	1	--	--	1	9	1
Jan. 21-27		--	--	3	--	--	--	3	1	7	1
Jan. 28-Feb. 3		--	1	2	--	--	--	--	11	14	2
Feb. 4-10		3	--	--	--	--	1	--	2	6	1
Feb. 11-17		--	--	1	--	--	--	4	3	8	1
Feb. 18-24	No Record	--	1	--	--	--	2	--	1	4	+
Feb. 25-Mar. 3		1	--	1	1	--	--	2	5	5	1
Mar. 4-10		--	--	--	--	--	--	1	2	3	+
Mar. 11-17		--	--	--	--	--	--	1	1	2	+
Mar. 18-24		--	--	--	--	--	--	--	--	--	--
Mar. 25-31		--	--	--	--	--	--	1	--	1	+
Apr. 1-7		--	--	--	--	2	--	1	2	5	1
Apr. 8-14		--	--	--	--	--	--	--	1	1	+
Apr. 15-21		--	--	--	1	--	--	--	7	8	1
Apr. 22-28		--	--	--	1	--	--	4	--	6	1
Apr. 29-May 5	1	--	--	--	--	1	--	1	--	2	+
May 6-12	1	--	--	--	--	--	--	3	--	12	1
May 13-19	8	--	--	--	--	--	--	3	1	11	1
May 20-26	6	--	1	1	--	--	--	6	1	17	2
May 27-June 2	--	--	--	--	3	7	--	1	1	4	+
June 3-9	No Record	--	--	--	--	2	--	1	--	2	+
June 10-16		--	--	--	--	1	1	--	--	16	2
June 17-23		--	--	--	4	2	3	--	7	10	1
June 24-30		--	3	1	1	--	--	4	--	4	+
July 1-7		--	--	1	1	--	2	--	--	10	1
July 8-14		--	--	8	--	1	--	1	--	8	1
July 15-21		--	--	3	1	--	2	2	--	62	7
July 22-28		--	2	--	--	--	14	46	--	30	3
July 29-Aug. 4		--	--	--	2	--	2	24	2	13	1
Aug. 5-11		--	--	4	--	--	6	3	--	6	1
Aug. 12-18	No Record	--	--	2	--	--	4	--	--	5	1
Aug. 19-25		--	--	2	--	--	5	--	--	11	1
Aug. 26-Sept. 1		--	1	4	1	--	5	--	--	3	+
Sept. 2-8		--	--	--	1	--	1	--	1	1	+
Sept. 9-15		--	--	--	--	--	--	1	--	--	--
Sept. 16-22		--	--	--	--	--	--	--	3	3	+
Sept. 23-30		--	--	--	--	--	--	--	--	--	--
Totals	21	4	34	31	36	30	51	145	541	893	*105

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

TABLE 51

Waddell Creek, Steelhead: Age 2 Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record								1	1	+
Oct. 8-14									3	3	+
Oct. 15-21					1				1	2	+
Oct. 22-28									1	1	+
Oct. 29-Nov. 4					1	17		4	5	27	3
Nov. 5-11						7	2	2		11	1
Nov. 12-18		2			1	13				18	2
Nov. 19-25				2		17			2	19	2
Nov. 26-Dec. 2					3	19	1	5	3	31	4
Dec. 3-9		3	2	1	7	21		1	9	44	5
Dec. 10-16		2			134	15	2		22	175	19
Dec. 17-23	1	1		7	101	2	4	8	315	439	49
Dec. 24-30	2		5	2	125	5	3	20	61	223	25
Dec. 31-Jan. 6		1	1	1	112	2		29	203	349	39
Jan. 7-13			3		13	13		3	22	56	6
Jan. 14-20	9		13	2	5	1	16	1	48	95	11
Jan. 21-27	3	4	4	1	14	4	6	2	1	39	4
Jan. 28-Feb. 3	1	7	2	9	2			1	3	25	3
Feb. 4-10	2			7	3	2		1	2	17	2
Feb. 11-17	1			3	2	1	1	4	1	13	1
Feb. 18-24							2	3		5	1
Feb. 25-Mar. 3	1									1	+
Mar. 4-10	1				1	1	2	1		6	1
Mar. 11-17	1				1		1		1	4	+
Mar. 18-24			1					1		2	+
Mar. 25-31											
Apr. 1-7	1			2	2				5	1	+
Apr. 8-14				2				1		3	+
Apr. 15-21	1			1					2	+	+
Apr. 22-28	1			1				2		4	+
Apr. 29-May 5								1		1	+
May 6-12											
May 13-19											
May 20-26	2				1			2		5	1
May 27-June 2					2	1		1		4	+
June 3-9											
June 10-16				1			2			3	+
June 17-23										1	+
June 24-30			1					1		1	+
July 1-7											
July 8-14											
July 15-21											
July 22-28							1			1	+
July 29-Aug. 4					1					1	+
Aug. 5-11	No Record										
Aug. 12-18											
Aug. 19-25											
Aug. 26-Sept. 1											
Sept. 2-8											
Sept. 9-15											
Sept. 16-22											
Sept. 23-30											
Totals	29	20	32	42	532	141	43	94	704	1,637	*193

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

TABLE 52

Waddell Creek, Steelhead: Age 3 Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record										
Oct. 8-14											
Oct. 15-21											
Oct. 22-28								3		3	+
Oct. 29-Nov. 4								6		6	+
Nov. 5-11								3		3	+
Nov. 12-18					1					1	+
Nov. 19-25											
Nov. 26-Dec. 2								2	1	3	+
Dec. 3-9	4	1				3		4		16	2
Dec. 10-16	5				8	1		3	1	18	2
Dec. 17-23	14			1	2	1		63	5	86	10
Dec. 24-30	4		26		4		1	34	2	71	8
Dec. 31-Jan. 6	27	1	63		4	4	1	28	3	131	15
Jan. 7-13	4		37		1	2		7		51	6
Jan. 14-20	7		17		1		1	3	1	30	3
Jan. 21-27	1		1		1		1	2		6	1
Jan. 28-Feb. 3		3	1	4		1		2		11	1
Feb. 4-10	4	1						4		13	1
Feb. 11-17	4		3			2		1		8	1
Feb. 18-24		1	4		1			1		7	1
Feb. 25-Mar. 3											
Mar. 4-10								1		1	+
Mar. 11-17								1		1	+
Mar. 18-24	1									1	+
Mar. 25-31											
Apr. 1-7											
Apr. 8-14											
Apr. 15-21					3					3	+
Apr. 22-28								1		1	+
Apr. 29-May 5	2									2	+
May 6-12	1									1	+
May 13-19	1								1	2	+
May 20-26											
May 27-June 2											
June 3-9									1	1	+
June 10-16											
June 17-23											
June 24-30								1		1	+
July 1-7											
July 8-14											
July 15-21											
July 22-28											
July 29-Aug. 4											
Aug. 5-11	No Record										
Aug. 12-18											
Aug. 19-25											
Aug. 26-Sept. 1											
Sept. 2-8											
Sept. 9-15											
Sept. 16-22											
Sept. 23-30											
Totals	79	7	152	7	26	14	4	170	19	478	* 56

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

TABLE 53

Waddell Creek, Steelhead: Age 4 Stream Fish Checked Through Upstream Trap, by Weekly Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Weekly total	Weekly average
Oct. 1-7	No Record										
Oct. 8-14											
Oct. 15-21											
Oct. 22-28											
Oct. 29-Nov. 4											
Nov. 5-11											
Nov. 12-18		1								1	+
Nov. 19-25										1	+
Nov. 26-Dec. 2									1	1	+
Dec. 3-9						2				2	+
Dec. 10-16					1					1	+
Dec. 17-23								4		4	+
Dec. 24-30			1					5		6	1
Dec. 31-Jan. 6		2	3	1					1	7	1
Jan. 7-13		2	4							7	1
Jan. 14-20			1		3					4	+
Jan. 21-27								1		1	+
Jan. 28-Feb. 3			1							2	+
Feb. 4-10	1			2		1				4	+
Feb. 11-17				1				1		2	+
Feb. 18-24											
Feb. 25-Mar. 3				1						1	+
Mar. 4-10		1				1				2	+
Mar. 11-17											
Mar. 18-24											
Mar. 25-31											
Apr. 1-7											
Apr. 8-14											
Apr. 15-21											
Apr. 22-28											
Apr. 29-May 5	1									1	+
May 6-12											
May 13-19											
May 20-26											
May 27-June 2				1						1	+
June 3-9							1			1	+
June 10-16								1		1	+
June 17-23											
June 24-30											
July 1-7											
July 8-14											
July 15-21				1						1	+
July 22-28											
July 29-Aug. 4											
Aug. 5-11											
Aug. 12-18											
Aug. 19-25											
Aug. 26-Sept. 1											
Sept. 2-8											
Sept. 9-15											
Sept. 16-22											
Sept. 23-30											
Totals	2	6	10	7	4	5	1	14	2	51	*6

* The average seasonal total is based on 8.5 years, since 1933-34 was only a half year.

Characteristics of the Migration

At least in some seasons, many of the upstream stream steelhead are sexually mature. For example, many ripe fish were encountered during the 1940-41 season. Others, however, probably do not spawn in the season in which they migrate upstream, and the reason for their migration is not known.

Sea Life

As in the case of the silver salmon, the extremely rapid growth made in the sea, as compared with that made in fresh water, is well known and has been directly observed in the case of Waddell Creek by measurements of juveniles descending to the sea and of fish of the same age classes returning to spawn in the following and in subsequent seasons. Since the seaward migration consists of several age classes, and since the periods covered both by the seaward and spawning migrations are spread over a number of months, it is not possible to present an accurate picture of the growth made, as was done for the silver salmon.

Practically nothing is known regarding the movements of steelhead in the sea. For unknown reasons, very few are caught at sea by commercial salmon trollers. Snyder (1921a) described 16 such fish caught off the coast near Fort Bragg, California, and brought into the harbor in the nearby Noyo Estuary from July 23 to August 25, 1920. These steelhead measured 19 to 29 inches, and weighed 2½ to 9¼ pounds.

No Waddell Creek steelhead have been reported caught at sea, either by commercial fishermen or sports anglers. One steelhead tagged at the Scott Creek Egg Collecting Station on March 19, 1934 (male, 57 cm., Tag No. 88463) was caught off Santa Cruz during early March, 1935, by a commercial fisherman. However, considerable numbers of steelhead, along with silver salmon, are taken by sports anglers in Monterey Bay off the coast of Santa Cruz County, especially between Watsonville Beach and Santa Cruz. The usual size of such fish, caught mostly in October and November, just prior to the opening of the mouths of the spawning streams, is 15 to 19 inches. Most of them are caught from piers or from boats operating within half-a-mile of shore. Five steelhead marked in the San Lorenzo River and two marked in Scott Creek are known to have been caught in this fishery. Also, marked fish from Scott Creek have been checked upstream at Waddell Creek and marked fish from Waddell Creek at Scott Creek. It is evident from these records that all steelhead do not simply remain near the mouth of the stream from which they migrated. The greatest minimum distance that any of the fish in the above records had traveled is approximately 19 miles (Scott Creek to Capitola Pier), but some steelhead almost certainly travel considerably greater distances. To what extent fish as adults return to the stream from which they migrated or stray to other streams will be discussed in the following section of this paper.

As was noted in the comparable section on silver salmon, along the California coast the continental shelf extends approximately 100 miles from the shoreline, and there is some evidence to indicate that all of the anadromous salmonids remain within its limits.

Probably the young steelhead, on first migrating to the ocean, remain fairly close to the shoreline. How soon and to what extent they

TABLE 54

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, by
Age Groups, All Seasons Combined

Weekly period	Number of age + migrants	Percentage of age group (during season)	Percentage of all age groups (during season)	Number of age 1 migrants	Percentage of age group (during season)	Percentage of all age groups (during season)	Number of age 2 migrants	Percentage of age group (during season)	Percentage of all age groups (during season)
Oct. 1-7.....	---	---	---	4	+	0.1	1	+	+
Oct. 8-14.....	---	---	---	4	+	0.1	3	+	0.1
Oct. 15-21.....	---	---	---	1	+	+	2	+	0.1
Oct. 22-28.....	---	---	---	---	---	---	1	+	+
Oct. 29-Nov. 4.....	---	---	---	7	1	0.2	27	2	0.9
Nov. 5-11.....	---	---	---	3	+	0.1	11	1	0.4
Nov. 12-18.....	---	---	---	4	+	0.1	18	1	0.6
Nov. 19-25.....	---	---	---	3	+	0.1	19	1	0.6
Nov. 26-Dec. 2.....	---	---	---	11	1	0.4	31	2	1.0
Dec. 3-9.....	---	---	---	16	2	0.5	44	3	1.4
Dec. 10-16.....	---	---	---	25	3	0.8	175	11	5.6
Dec. 17-23.....	---	---	---	457	51	14.7	439	27	14.2
Dec. 24-30.....	---	---	---	22	2	0.7	223	14	7.2
Dec. 31-Jan. 6.....	---	---	---	17	2	0.5	349	21	11.3
Jan. 7-13.....	---	---	---	8	1	0.3	56	3	1.8
Jan. 14-20.....	---	---	---	9	1	0.3	95	6	3.3
Jan. 21-27.....	---	---	---	7	1	0.2	39	2	1.3
Jan. 28-Feb. 3.....	---	---	---	14	2	0.5	25	2	0.8
Feb. 4-10.....	---	---	---	6	1	0.2	17	1	0.5
Feb. 11-17.....	---	---	---	8	1	0.3	13	1	0.4
Feb. 18-24.....	---	---	---	4	+	0.1	5	+	0.2
Feb. 25-Mar. 3.....	---	---	---	5	+	0.2	1	+	+
Mar. 4-10.....	---	---	---	3	+	0.1	6	+	0.2
Mar. 11-17.....	---	---	---	2	+	0.1	4	+	0.1
Mar. 18-24.....	---	---	---	---	---	---	2	+	0.1
Mar. 25-31.....	---	---	---	1	+	+	---	---	0.2
Apr. 1-7.....	---	---	---	5	1	0.2	5	+	0.1
Apr. 8-14.....	---	---	---	1	+	+	3	+	0.1
Apr. 15-21.....	---	---	---	2	+	0.1	2	+	0.1
Apr. 22-28.....	---	---	---	8	1	0.3	4	+	0.1
Apr. 29-May 5.....	---	---	---	6	1	0.2	1	+	+

May 6-12.....	---	---	---	2	+	0.1	---	---	---
May 13-19.....	---	---	---	12	1	0.4	---	---	0.2
May 20-26.....	---	---	---	11	1	0.4	5	+	0.1
May 27-June 2.....	---	---	---	17	2	0.5	4	+	---
June 3-9.....	---	---	---	4	+	0.1	---	---	---
June 10-16.....	---	---	---	2	+	0.1	---	+	0.1
June 17-23.....	---	---	---	16	2	0.5	3	+	+
June 24-30.....	3	7	0.1	10	1	0.3	1	+	+
July 1-7.....	3	7	0.1	4	+	0.1	1	+	---
July 8-14.....	2	5	0.1	10	1	0.3	---	---	---
July 15-21.....	8	18	0.3	8	7	2.0	1	+	+
July 22-28.....	10	23	0.3	62	3	1.0	1	+	+
July 29-Aug. 4.....	6	14	0.2	30	1	0.4	---	---	---
Aug. 5-11.....	---	---	---	13	1	0.2	---	---	---
Aug. 12-18.....	---	---	---	6	1	0.2	---	---	---
Aug. 19-25.....	---	---	---	5	1	0.2	---	---	---
Aug. 26-Sept. 1.....	---	---	---	11	1	0.4	---	---	---
Sept. 2-8.....	4	9	0.1	3	+	0.1	---	---	---
Sept. 9-15.....	2	5	0.1	1	+	+	---	---	---
Sept. 16-22.....	5	11	0.2	---	---	---	---	---	---
Sept. 23-30.....	1	2	+	3	+	0.1	---	---	---
Totals.....	44	---	1.4	893	---	28.8	1,637	---	52.7

TABLE 54—Continued
Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, by
Age Groups, All Seasons Combined

Weekly period	Number of age 3 migrants	Percent- age of age group (during season)	Percent- age of all age groups (during season)	Number of age 4 migrants	Percent- age of age group (during season)	Percent- age of all age groups (during season)	Number of age 5 migrants	Percent- age of age group (during season)	Percent- age of all age groups (during season)	Number of all migrants	Percent- age of total migration all seasons
Oct. 1-7.....	---	---	---	---	---	---	---	---	---	5	0.2
Oct. 8-14.....	---	---	---	---	---	---	---	---	---	7	0.2
Oct. 15-21.....	---	---	---	---	---	---	---	---	---	3	0.1
Oct. 22-28.....	3	1	0.1	---	---	---	---	---	---	4	0.1
Oct. 29-Nov. 4.....	6	1	0.2	1	2	+	---	---	---	41	1.3
Nov. 5-11.....	3	1	0.1	---	---	---	---	---	---	17	0.5
Nov. 12-18.....	1	+	+	1	2	+	---	---	---	24	0.8
Nov. 19-25.....	---	---	---	---	---	---	---	---	---	22	0.7
Nov. 26-Dec. 2.....	3	1	0.1	1	2	+	---	---	---	46	1.5
Dec. 3-9.....	16	3	0.5	2	4	0.1	---	---	---	78	2.5
Dec. 10-16.....	18	4	0.6	1	2	+	---	---	---	219	7.1
Dec. 17-23.....	86	18	2.8	4	8	0.1	---	---	---	986	31.8
Dec. 24-30.....	71	15	2.3	6	12	0.2	---	---	---	322	10.4
Dec. 31-Jan. 6.....	131	27	4.2	7	14	0.2	---	---	---	504	16.2
Jan. 7-13.....	51	11	1.6	7	14	0.2	---	---	---	122	3.9
Jan. 14-20.....	30	6	1.0	4	8	0.1	---	---	---	138	4.4
Jan. 21-27.....	6	1	0.2	1	2	+	---	---	---	53	1.7
Jan. 28-Feb. 3.....	11	2	0.4	2	4	0.1	---	---	---	52	1.7
Feb. 4-10.....	13	3	0.4	4	8	0.1	---	---	---	40	1.3
Feb. 11-17.....	8	2	0.3	2	4	0.1	---	---	---	31	1.0
Feb. 18-24.....	7	1	0.2	---	---	---	---	---	---	16	0.5
Feb. 25-Mar. 3.....	---	---	---	1	2	+	---	---	---	7	0.2
Mar. 4-10.....	1	+	+	2	4	0.1	---	---	---	12	0.4
Mar. 11-17.....	1	+	+	---	---	---	---	---	---	7	0.2
Mar. 18-24.....	1	+	+	---	---	---	---	---	---	3	0.1
Mar. 25-31.....	---	---	---	---	---	---	---	---	---	1	+
Apr. 1-7.....	---	---	---	---	---	---	---	---	---	10	0.3
Apr. 8-14.....	---	---	---	---	---	---	---	---	---	4	0.1
Apr. 15-21.....	3	1	0.1	---	---	---	---	---	---	7	0.2
Apr. 22-28.....	1	+	+	---	---	---	---	---	---	13	0.4
Apr. 29-May 5.....	2	+	0.1	1	2	+	---	---	---	10	0.3
May 6-12.....	1	+	+	---	---	---	1	100	+	4	0.1
May 13-19.....	2	+	0.1	---	---	---	---	---	---	14	0.5
May 20-26.....	---	---	---	1	2	+	---	---	---	16	0.5
May 27-June 2.....	---	---	---	1	2	+	---	---	---	22	0.7
June 3-9.....	1	+	+	1	2	+	---	---	---	6	0.2
June 10-16.....	---	---	---	---	---	---	---	---	---	3	0.1
June 17-23.....	---	---	---	---	---	---	---	---	---	19	0.6
June 24-30.....	1	+	+	---	---	---	---	---	---	15	0.5
July 1-7.....	---	---	---	---	---	---	---	---	---	8	0.3
July 8-14.....	---	---	---	---	---	---	---	---	---	12	0.4
July 15-21.....	---	---	---	1	2	+	---	---	---	17	0.5
July 22-28.....	---	---	---	---	---	---	---	---	---	73	2.3
July 29-Aug. 4.....	---	---	---	---	---	---	---	---	---	37	1.2
Aug. 5-11.....	---	---	---	---	---	---	---	---	---	13	0.4
Aug. 12-18.....	---	---	---	---	---	---	---	---	---	6	0.2
Aug. 19-25.....	---	---	---	---	---	---	---	---	---	5	0.2
Aug. 26-Sept. 1.....	---	---	---	---	---	---	---	---	---	11	0.4
Sept. 2-8.....	---	---	---	---	---	---	---	---	---	7	0.2
Sept. 9-15.....	---	---	---	---	---	---	---	---	---	3	0.1
Sept. 16-22.....	---	---	---	---	---	---	---	---	---	5	0.2
Sept. 23-30.....	---	---	---	---	---	---	---	---	---	4	0.1
Totals.....	478	---	15.4	51	---	1.6	1	---	+	3,104	---

TABLE 55
Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, by Age Groups and Seasons

Season	Number of age + migrants	Percent- age of migration	Number of age 1 migrants	Percent- age of migration	Number of age 2 migrants	Percent- age of migration	Number of age 3 migrants	Percent- age of migration	Number of age 4 migrants	Percent- age of migration	Number of age 5 migrants	Percent- age of migration	Number of all migrants
1933-34	No record	----	*21	16	*29	22	*79	60	*2	2	*0	*0	131
1934-35	0	0	4	11	20	54	7	19	6	16	0	0	37
1935-36	0	0	34	15	32	14	152	66	10	4	1	+	229
1936-37	4	4	31	33	42	46	7	8	7	8	0	0	91
1937-38	3	+	36	6	532	89	26	4	7	1	0	0	601
1938-39	0	0	30	16	141	74	14	8	4	3	0	0	190
1939-40	20	17	51	43	43	36	4	7	5	1	0	0	119
1940-41	12	3	145	33	94	21	170	39	14	3	0	0	435
1941-42	5	+	541	43	704	55	19	1	2	+	0	0	1,271
Totals.....	44	1	893	29	1,637	53	478	15	51	2	1	+	3,104

* No record prior to December 31 nor after June 24.

begin to spread out is not known. Almost nothing is known of the extent to which steelhead from different streams mix while in the sea. It is not known, but is not improbable, that steelhead in the sea, like the Pacific salmon, migrate in schools.

Homing and Straying

As pointed out in the comparable section for silver salmon, considerable literature exists regarding "homing" among anadromous members of the salmon family. Because of the general importance of the subject and the valuable contribution derived from the Waddell Creek data, the views of the writers will here be repeated. It is the opinion of the present writers that evidence obtained through marking experiments carried out by scientific workers in this and other countries has established as a fact the existence of homing among anadromous salmonids. Briefly, young salmonids which descend from fresh water to the sea return to their "parent stream" for spawning purposes (young fish artificially hatched and liberated return to the stream in which they were liberated, not to the stream to which their parents returned or in which they were hatched). A review of the subject of homing in trout and salmon and the important literature concerning it are contained in a paper by Shapovalov (1941b) and the reader is referred to this paper for details.

Taft and Shapovalov (1938) presented preliminary data for the extent of homing and straying among steelhead between Waddell Creek and Scott Creek, $4\frac{1}{2}$ air-line miles to the south. Table 56 shows the complete figures for nine seasons of marking (1931 through 1938-39) and the nine seasons during which returns were obtained (1933-34 through 1941-42). Fish listed as returning include only those taken at the traps in each season, to obtain as nearly comparable a basis as is possible. Males and females have been grouped together in the table, since no significant sexual differentiation has been revealed in the straying fish as compared with those of the same year class returning to their parent stream. It should be kept in mind that the fish marked and liberated at Scott Creek were hatchery-reared.

From Table 56 it is seen that during the entire period 476 (98.1 percent) of the fish marked at Waddell Creek returned there and 9 (1.9 percent) strayed to Scott Creek. Of those marked at Scott Creek, 932 (97.1 percent) returned there and 28 (2.9 percent) strayed to Waddell Creek. These figures show conclusively that the rate of straying among steelhead is considerably less than among silver salmon for the streams involved.

In the case of the silver salmon, it appeared (page 93) that the amount of straying from a given stream is fairly constant for a given year class, but may vary considerably from year class to year class and consequently from the total run entering in one season to the total run entering in another season. Among the steelhead, the rate of straying is so small that it is difficult to formulate definite conclusions regarding this phase of the subject, but there is some indication that the rule postulated for the silver salmon applies to the steelhead as well. Among the fish marked at Scott Creek in 1938-39, greater than average straying in 1939-40 was followed by greater than average straying in 1940-41.

TABLE 56

Waddell and Scott Creeks, Steelhead: Homing and Straying of Marked Fish

Place and season of marking	Mark	Returned to Waddell Creek								
		1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42
Waddell Creek										
1931.....	Ad-LV	3 (100%)	3 (100%)							
1932.....	Ad-LV									
1933-34.....	Ad-RP		65 (98.5%)	62 (98.4%)	15 (100%)	1 (100%)				
1934-35.....	Ad-LP			17 (100%)	38 (100%)	17 (100%)	4 (100%)			
1935-36.....	Both P				27 (90.0%)	43 (95.6%)	26 (100%)	1 (100%)		
1936-37.....	Ad-RP					13 (100%)	53 (100%)	15 (93.8%)	1 (100%)	
1937-38.....	Ad-LP						15 (100%)	37 (97.4%)	15 (100%)	5 (100%)
Scott Creek										
1932-33.....	Ad-RV	0	0	0	0					
1933-34.....	Both V		0	1 (1.2%)	0					
1934-35.....	Ad-LV			1 (0.5%)	5 (2.7%)	0	0			
1935-36.....	Ad-RV				0	0	0			
1935-36.....	Ad-Ant 1/2D				0	1 (14.3%)	0	0		
1935-36.....	Both V				0	0	0			
1937-38.....	Ad-LV				0	0	0	1 (4.3%)	1 (33.3%)	
1938-39.....	Ad-RV						0	8 (5.9%)	10 (8.3%)	0

TABLE 56—Continued

Waddell and Scott Creeks, Steelhead: Homing and Straying of Marked Fish

Place and season of marking	Mark	Returned to Scott Creek								
		1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42
Waddell Creek										
1931.....	Ad-LV	0	0							
1932.....	Ad-LV									
1933-34.....	Ad-RP		1 (1.5%)	1 (1.6%)	0	0				
1934-35.....	Ad-LP			0	0	0	0	0		
1935-36.....	Both P				3 (10.0%)	2 (4.4%)	0	1 (6.2%)	0	
1936-37.....	Ad-RP					0	0	1 (2.6%)	0	
1937-38.....	Ad-LP						0			0
Scott Creek										
1932-33.....	Ad-RV	9 (100%)	39 (100%)	4 (100%)	10 (100%)	48 (100%)	1 (100%)			
1933-34.....	Both V		38 (100%)	79 (98.8%)	177 (97.3%)	2 (100%)	0			
1934-35.....	Ad-LV			197 (99.5%)	0	0	0			
1935-36.....	Ad-RV				6 (100%)	6 (85.7%)	0	1 (100%)		
1935-36.....	Ad-Ant 1/2D				0	6 (100%)	1 (100%)			
1935-36.....	Both V						22 (100%)	22 (95.7%)	2 (66.6%)	
1937-38.....	Ad-LV							128 (94.1%)	110 (91.7%)	24 (100%)
1938-39.....	Ad-RV									

Although it appears likely that the *rate* of straying from Waddell Creek to Scott Creek and *vice versa* may vary to some extent with each year class, the rate of straying even when it is greatest apparently is so small that the various calculated survivals (discussed in the following section), which are based partly on unmarked fish of unknown origin, are not seriously affected. In view of this and because data on straying of marked fish both from Waddell Creek to Scott Creek and from Scott Creek to Waddell Creek are not available for the whole period of the experiments, it was decided that for the purpose of the present studies it was satisfactory to assume that the rate of straying between the two streams was the same.

Even if the *rate* of straying between the two streams is the same, differences in the *numbers* of strays contributed by each stream would result from different numbers of returning adults of a given year class produced by each stream. During most of the seasons under consideration the runs into Scott Creek have been considerably larger than those into Waddell Creek, and so it is not improbable that the contribution made by Scott Creek to Waddell Creek has been somewhat greater than *vice versa*, but it was decided that because of the low rate of straying and the complexity of the problem, involving various year classes with the same mark and different survival rates, any calculations based on the runs into each stream might result in greater errors than calculations based on the assumption that the numbers of steelhead that strayed from Waddell Creek to Scott Creek were equal to the numbers that strayed from Scott Creek to Waddell Creek.

It is not considered probable that streams other than Scott Creek have contributed sufficient strays to alter the survival figures appreciably. The San Lorenzo River, $13\frac{1}{2}$ miles to the south of Scott Creek, possesses a run of steelhead, but no marked Waddell or Scott Creek fish have been taken at the egg collecting station on that stream, shown in Figure 3. Neither have any marked steelhead from Waddell or Scott creeks been taken in the San Lorenzo River by anglers, of whom there are a considerable number.

As noted in the previous section, some marked Scott Creek and San Lorenzo River steelhead have been caught by anglers in the surf or offshore along the Santa Cruz County coast, mostly in October and November. Without further evidence, however, these fish cannot be treated as strays. In answer to the view that such fish are "lost" and will not return to the parent stream, and that only fish which remain under the influence of water from the parent stream will return to it, it is pointed out that the mouths of most California steelhead streams are closed by sand bars during the summer months and that in some cases the lower courses of the streams are entirely dry, so that no fresh water reaches the ocean. In this connection it may be well to consider again the case recorded by Taft and Shapovalov (1938) of a marked Scott Creek steelhead that was first taken in Waddell Creek and later in Scott Creek, without spawning first in Waddell Creek. This case, although perhaps an isolated one, apparently indicates that we can never quite conclude that a marked fish which wanders into another stream is really "lost" until we are definitely sure that it has spawned in the strange stream. This finding points to the possibility that supposed large-scale wandering among salmonids cited in the literature

may have been only temporary straying. For example, this may have been the situation in the experiments described by White (1936), in which marked Atlantic salmon in numbers entered the West Branch of Apple River, Nova Scotia, as well as the East Branch, in which they had been marked, especially since these streams have a common estuary, and approximately the lower mile of each of them is also tidal. Certainly, those fish which have been taken in the sea at any place away from the parent stream might eventually have come back if they had not been taken.

Between Scott Creek and the San Lorenzo River are several small streams, namely, San Vincente, Liddell, Respini, Laguna, Coja, Baldwin, and Medler creeks; the runs of steelhead in these streams are smaller than those in Waddell and Scott creeks. No marked fish have been reported from any of these streams, although no facilities to secure returns were in operation in them, and any reports would have resulted from chance catches made by anglers.

To the north of Waddell Creek are three small streams, Finny, Año Nuevo, and Whitehouse creeks, which have very small steelhead runs. Cazos Creek, $6\frac{1}{2}$ miles north of Waddell, and Pescadero Creek, $14\frac{1}{2}$ miles north, both have steelhead runs of fair extent, but again, no marked Waddell fish have been reported from these two localities, in which no special facilities to secure returns were in operation.

From the preceding discussion we saw that the amount of straying between Waddell and Scott creeks is so small that it is difficult to pick out trends, but that there was some indication that, as in the case of the silver salmon, a given rate of straying is associated with fish returning in different seasons but resulting from a single year class (or marking). If this is true, it appears that the rate of straying that will result is determined by the time that adults first start returning (as 1/1 fish) and is more dependent upon conditions existing up to the time than on conditions existing at the time of entry into the streams for spawning. Until contradictory evidence is presented, it appears satisfactory to set up the same hypothesis which was set up for the silver salmon, namely, that conditions existing at the time of the migration to the ocean determine the rate of straying that will take place in the years of return of the fish to fresh water. What these conditions are, it has not been found possible to state definitely on the basis of the data which are available and have been analyzed, but attention was called to certain possibilities in the case of the silver salmon, and it appears not improbable that the same considerations apply to the steelhead. In the case of the salmon, there was found to be (1) a tendency toward a positive correlation between size of downstream migration and rate of straying and (2) a tendency toward a negative correlation between average size of fish and rate of straying. In other words, the greater the numbers of downstream migrants and the smaller the size of downstream migrants, the greater is the amount of straying. Possible explanations for these correlations were (1) that an unusually large number of downstream migrants attracts predators out of proportion to the average, with the result that the fish entering the ocean are rapidly scattered or in some other way affected so they do not return to their home stream in average

TABLE 57

Waddell Creek, Steelhead: Allocation of Fish Which Jumped Upstream Over the Dam and Spawned Below the Dam to Total Age Classes

Run in season	2	3	4	5	6	7	Pre- vious spawn- ers	Totals	Total fish
1933-34									
♂	15	61	58	4	---	---	28	166	
% ♂	9.0%	36.7%	34.9%	2.4%	---	---	16.9%	---	
Dam jumpers	3	12	12	1	---	---	5	33	
Below dam spawners	2	7	7	1	---	---	3	20	219 ♂ ♂
♀	3	40	132	12	---	---	36	223	
% ♀	1.3%	17.9%	59.2%	5.4%	---	---	16.1%	---	
Dam jumpers	---	2	5	1	---	---	1	9	
Below dam spawners	---	6	21	2	---	---	6	35	267 ♀ ♀
Mean	23	128	235	21	---	---	79	486	486
1934-35									
♂	5	121	115	17	---	---	7	265	
% ♂	1.9%	45.7%	43.4%	6.4%	---	---	2.6%	---	
Dam jumpers	---	2	1	---	---	---	3	7	
Below dam spawners	---	3	3	1	---	---	7	274	275 ♂ ♂
♀	4	76	160	20	---	---	14	274	
% ♀	1.5%	27.7%	58.4%	7.3%	---	---	5.1%	---	
Dam jumpers	---	---	---	---	---	---	---	---	
Below dam spawners	---	1	3	1	---	---	5	279 ♀ ♀	
Mean	9	203	282	39	---	---	21	554	554
1935-36									
♂	7	76	67	11	---	---	41	202	
% ♂	3.5%	37.6%	33.2%	5.4%	---	---	20.3%	---	
Dam jumpers	1	16	14	2	---	---	9	42	
Below dam spawners	---	3	2	---	---	---	2	7	251 ♂ ♂
♀	5	40	119	36	2	---	46	248	
% ♀	2.0%	16.1%	48.0%	14.5%	0.8%	---	18.5%	---	
Dam jumpers	---	1	3	1	---	---	1	6	
Below dam spawners	---	1	4	1	---	---	2	8	262 ♀ ♀
Mean	13	137	209	51	2	---	101	513	513
1936-37									
♂	---	63	113	16	---	---	36	228	
% ♂	---	27.6%	49.6%	7.0%	---	---	15.8%	---	
Dam jumpers	---	3	5	1	---	---	1	10	
Below dam spawners	---	3	5	1	---	---	2	11	249 ♂ ♂
♀	3	60	116	22	---	---	44	245	
% ♀	1.2%	24.5%	47.3%	9.0%	---	---	18.0%	---	
Dam jumpers	---	---	---	---	---	---	---	---	
Below dam spawners	---	2	5	1	---	---	2	10	255 ♀ ♀
Mean	3	131	244	41	---	---	85	504	504
1937-38									
♂	---	50	55	18	1	---	41	165	
% ♂	---	30.3%	33.3%	10.9%	0.6%	---	24.8%	---	
Dam jumpers	---	3	3	1	---	---	3	10	
Below dam spawners	---	8	8	3	---	---	6	25	200 ♂ ♂
♀	3	56	50	23	5	---	71	208	
% ♀	1.4%	26.9%	24.0%	11.1%	2.4%	---	34.2%	---	
Dam jumpers	---	---	---	---	---	---	---	---	
Below dam spawners	---	5	5	2	1	---	7	20	228 ♀ ♀
Mean	3	122	121	47	7	---	128	428	428

TABLE 57—Continued

Waddell Creek, Steelhead: Allocation of Fish Which Jumped Upstream Over the Dam and Spawned Below the Dam to Total Age Classes

Run in season	2	3	4	5	6	7	Pre- vious spawn- ers	Totals	Total fish
1938-39									
♂	6	102	72	4	2	---	26	212	
% ♂	2.8%	48.1%	34.0%	1.9%	0.9%	---	12.3%	---	
Dam jumpers	---	---	---	---	---	---	1	5	217 ♂ ♂
Below dam spawners	---	2	2	---	---	---	57	243	
♀	2	85	88	11	---	---	23.5%	---	
% ♀	0.8%	35.0%	36.2%	4.5%	---	---	2	6	249 ♀ ♀
Dam jumpers	---	---	---	---	---	---	---	---	
Below dam spawners	---	2	2	---	---	---	---	---	
Mean	8	191	164	15	2	---	86	466	466
1939-40									
♂	33	134	32	3	---	---	12	214	
% ♂	15.4%	62.6%	15.0%	1.4%	---	---	5.6%	---	
Dam jumpers	4	16	4	---	---	---	1	25	
Below dam spawners	2	6	2	---	---	---	21	10	249 ♂ ♂
♀	18	108	79	2	---	---	9.2%	---	
% ♀	7.9%	47.4%	34.6%	0.9%	---	---	1	5	
Dam jumpers	---	2	2	---	---	---	1	10	243 ♀ ♀
Below dam spawners	1	5	3	---	---	---	---	---	
Mean	58	271	122	5	---	---	36	492	492
1940-41									
♂	27	116	33	---	1	---	28	205	
% ♂	13.2%	56.6%	16.1%	---	0.5%	---	13.7%	---	
Dam jumpers	3	14	4	---	---	---	4	25	
Below dam spawners	1	6	2	---	---	---	1	10	240 ♂ ♂
♀	9	58	62	6	---	---	50	185	
% ♀	4.7%	31.4%	33.5%	3.3%	---	---	27.0%	---	
Dam jumpers	---	2	2	---	---	---	1	5	
Below dam spawners	1	3	3	---	---	---	3	10	200 ♀ ♀
Mean	41	199	106	6	1	---	87	440	440
1941-42									
♂	34	54	37	3	---	---	37	165	
% ♂	20.6%	32.7%	22.4%	1.8%	---	---	22.4%	---	
Dam jumpers	6	10	7	---	---	---	7	30	
Below dam spawners	3	5	4	---	---	---	4	16	211 ♂ ♂
♀	9	33	79	17	---	---	73	212	
% ♀	4.2%	15.6%	37.3%	8.0%	---	---	34.4%	---	
Dam jumpers	---	2	4	1	---	---	3	10	
Below dam spawners	1	2	6	1	---	---	6	16	238 ♀ ♀
Mean	53	106	137	22	---	1	130	449	449

numbers, and (2) that unfavorable growing conditions (resulting in small size of fish) in some way affect the fish so they do not return to their home stream in average numbers. For the present, because of the complex life history categories among the steelhead, the above mentioned correlations have not been tested. As in the case of the silver salmon, it would be of interest and profitable to carry out marking experiments planned to reveal and to test the indicated tendencies.

One other phase of homing remains to be considered, and that is the extent to which fish returning to the parent stream return to the same portion of the stream. Taft and Shapovalov (1938) found that

within a large river system, the Klamath in Northern California, the amount of straying among sea-run steelhead between tributaries was not greater than between Waddell and Scott creeks. For Waddell Creek an attempt to determine this matter was made on the basis of the distribution of marked and unmarked adults above and below the dam. The problem was made difficult by the fact that only fish which had completed spawning could be used with certainty, with the result that the number of such fish found below the dam (9) was too small to obtain conclusive evidence. None of these was marked, but for the purposes of the present studies the proportion of marked to unmarked fish has been considered to be the same above and below the dam.

Survival

The simplest procedure to calculate survival to maturity among sea-run steelhead at Waddell Creek is to calculate the number of eggs deposited in a given season and then to total the numbers of sea-run fish of that year class returning to spawn for the first time. Survival calculated in this manner may be termed *primary over-all survival*: primary in the sense that it is calculated to first spawning, and does not include survival to subsequent spawnings, which may be termed secondary survival, and over-all in the sense that it is calculated from egg to sea-run fish, without a breakdown into survival at intervening stages.

In calculating primary over-all survival, the first spawners among the fish comprising the total estimated runs into Waddell Creek (see Table 35) were divided into total age classes. In this division, the numbers of fish estimated to have jumped upstream over the dam and to have spawned below the dam, respectively, were segregated into first and repeat spawners and the first spawners assigned to total age classes according to the ratios of first and repeat spawners and age classes in fish checked through the upstream trap (Table 30). It was not necessary to assign ages to the repeat spawners, since they do not enter into the calculation of primary survival. The results of the division are shown in Table 57.

From Table 57 it was possible to assign all returning first spawners to the proper brood season (season in which they were produced), and to express them as a percentage of the number of eggs which produced them.³⁵ The results are shown in Table 58.

From an examination of Table 58 it is seen that the percentage of survival varies from 0.017 to 0.028 for the four seasons for which returns are complete or practically complete, and from 0.017 to 0.029 if an additional season (1937-38), for which the number of five-year-old returning fish was not available but was calculated on the basis of the

³⁵ In the present paper any offspring of sea-run steelhead which do not go to sea and return as adults are included among "mortality" in calculation of primary over-all survival. For example, if by the time that the fish of a given year class have finished coming in as sea-run fish for their first spawning there are present any fish of sea-run parentage of the same year class remaining in the stream they must be counted as "mortality," since such fish are lost to the sea-run spawning migrations. This procedure must be followed even in the case of those fish which attain sexual maturity as stream fish, for the following reasons: (1) Some of them probably appear later among the sea-run first spawners (it is difficult to recognize with surety the spawning mark on the stream steelhead scales), (2) among the upstream fish it is difficult to recognize fish that are going to spawn in the current season unless they are approaching ripeness, (3) resident fish might be included if fish other than sea-run individuals were included in primary over-all survival.

average return of five-year-olds in the other four seasons, is included. In the former case the mean percentage of return is 0.021 and in the latter case it is 0.023. Of course, these are so close to each other that the selection of one or the other would make very little difference, but for the purposes of the present report the latter figure will be used, especially since the partially assumed survival percentage for 1937-38 is in harmony with the figures for other seasons.

One of the striking features to be noted in Table 58 is the inverse correlation between the total egg production and the survival percentage. The fact that the same phenomenon is encountered among the silver salmon (see page 96 and Table 18), and also in general for both steelhead and silver salmon when the survival is calculated from the downstream migration rather than from the eggs produced, indicates strongly that the correlation is not due to chance but is real. The fact that there is a chronological sequence as well in the present instance might lead one to believe that specific or general improving environmental conditions, rather than the size of the egg production, were responsible for the steady increase in the survival rate, except for the fact that this chronological sequence does not prevail in the case of the silver salmon nor in the case of the survival following downstream migration.

In Table 58, the numbers of fish listed under the heading "Spawning run" are the total fish estimated to have spawned in Waddell Creek in each season, including fish of all ages and all life histories, and both marked and unmarked fish. They include fish which were checked upstream through the trap (the great majority of the fish), those which jumped upstream over the dam, and those which spawned below the dam. It was necessary to include all three groups for the reason that in calculating survival it is impossible to recognize the fish produced in one group from those produced by another group. Survival may also

TABLE 58

Waddell Creek, Steelhead: Primary Over-all Survival

Brood season	Spawning run		Total egg production	Returned as adult first spawners						Total	Percentage survival
	♂	♀		2 yr.	3 yr.	4 yr.	5 yr.	6 yr.	7 yr.		
1933-34.....	219	267	1,654,239	13	131	121	15	---	---	280	0.017
1934-35.....	275	279	1,567,366	3	122	164	5	1	1	296	0.019
1935-36*.....	251	262	1,523,360	3	191	122	6	---	?	322	0.021
1936-37†.....	249	255	1,459,534	8	271	106	22	?	?	407	0.028
1937-38‡.....	200	228	1,422,641	58	199	137	(15)	?	?	(409)	(0.029)
1938-39.....	217	249	---	41	106	?	?	?	?	---	---
1939-40.....	249	243	---	53	?	?	?	?	?	---	---
1940-41.....	240	200	---	?	?	?	?	?	?	---	---
1941-42.....	211	238	---	?	?	?	?	?	?	---	---
Totals.....			7,627,140							1,716	0.022
Mean.....											0.023

* No returns possible for 7-year fish.

† No returns possible for 6- or 7-year fish.

‡ No returns possible for 5-, 6-, or 7-year fish, but the average (3.7 percent) return for 5-year fish in previous seasons has been used.

TABLE 61

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1930-31

Season when first marked downstream	Mark	Probable age as downstream migrant	Age as returning adult	Season of return as adult																					
				1932-33	1933-34		1934-35		1935-36		1936-37		1937-38		Total										
					♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀									
1931-32	No marking	1	1/1	No Records	?	?	?	?	?	?	?	?	?	?	?										
1930-31	No marking	+	1/2																						
1931-32	No marking	1	1/2																						
1932-33	No marking	2	2/1																						
1931-32	No marking	1	2/1																						
1931-32	No marking	1	1/3																						
1932-33	No marking	2	2/2																						
1931-32	No marking	1	2/2																						
1933-34	Ad-RP	3	3/1																						
1932-33	No marking	2	3/1																						
1932-33	No marking	2	2/3																						
1933-34	Ad-RP	3	3/2																						
1932-33	No marking	2	3/2																						
1933-34	Ad-RP	3	4/1																						
1934-35	Ad-LP	4	4/1																						
1933-34	Ad-RP	3	3/3																			0	0		
1934-35	Ad-LP	4	4/2																			0	0		
1934-35	Ad-LP	4	4/3																					0	0
Totals				?	?	?	5+?	3+?	3+?	8+?	0	0	0	0	8+?	11+?									

TABLE 62

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1931-32

Waddell Creek, Steelhead: Marked fish returning (as first spawners), 1931-1936																	
Season when first marked downstream	Mark	Probable age as downstream migrant	Age as returning adult	Season of return as adult													
				1933-34		1934-35		1935-36		1936-37		1937-38		1938-39		Total	
				♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1932-33	No marking	1	1/1	?	?	?	?									?	?
1931-32	No marking	+	1/2			?	?									?	?
1932-33	No marking	1	1/2			?	?									42	14
1932-33	Ad-RP	2	2/1			42	14									?	?
1933-34	Ad-RP	1	2/1			?	?									?	?
1932-33	No marking	1	1/3					?	?							15	22
1932-33	No marking	2	2/2					15	22							?	?
1933-34	Ad-RP	1	2/2					?	?							0	2
1932-33	No marking	3	3/1					0	2							0	2
1934-35	Ad-LP	3	3/1					0	2							0	0
1933-34	Ad-LP	2	3/1							0	0					0	0
1933-34	Ad-RP	2	2/3							0	1					0	1
1934-35	Ad-LP	3	3/2							0	0					0	0
1933-34	Ad-LP	3	3/2							0	0					2	5*
1933-34	Ad-RP	2	3/2							2	5*					0	0
1934-35	Ad-LP	3	4/1							0	0					0	0
1935-36	Both P	4	4/1													0	0
1934-35	Ad-LP	3	3/3									0	0			1	4
1934-35	Ad-LP	3	4/2									0	0			0	0
1935-36	Both P	4	4/2											0	0	0	0
1935-36	Both P	4	4/3													0	0
Totals				?	?	42+?	14+?	15+?	26+?	2	6	1	4	0	0	60+?	50+?

* One of these marked Ad + Both P (marked downstream both in 1934-35 and 1935-36).

TABLE 63

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1932-33

Season when first marked downstream	Mark	Probable age as down- stream migrant	Age as returning adult	Season of return as adult													
				1934-35		1935-36		1936-37		1937-38		1938-39		1939-40		Total	
				♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1933-34	Ad-RP	1	1/1	0	1											0	1
1932-33	No marking	+	1/2			?	?									?	?
1933-34	Ad-RP	1	1/2			0	1									0	1
1934-35	Ad-LP	2	2/1			9	3									9	3
1933-34	Ad-RP	1	2/1			0	0									0	0
1933-34	Ad-RP	1	1/3					0	0							0	0
1934-35	Ad-LP	2	2/2					4	7							4	7
1933-34	Ad-RP	1	2/2					1	0							1	0
1935-36	Both P	3	3/1					5	3							5	3
1934-35	Ad-LP	2	3/1					6	6*							6	6*
1934-35	Ad-LP	2	2/3							0	0					0	0
1935-36	Both P	3	3/2							2	0					2	0
1934-35	Ad-LP	2	3/2							0	2					0	2
1936-37	Ad-RP	4	4/1							0	0					0	0
1935-36	Both P	3	3/3									0	0			0	0
1936-37	Ad-RP	4	4/2									0	0			0	0
1936-37	Ad-RP	4	4/3											0	0	0	0
Totals				0	1	9	4	16	16	2	2	0	0	0	0	27	23

* One of these marked Ad + Both P (marked downstream both in 1934-35 and 1935-36).

TABLE 64

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1933-34

Season when first marked downstream	Mark	Probable age as down- stream migrant	Age as returning adult	Season of return as adult													
				1935-36		1936-37		1937-38		1938-39		1939-40		1940-41		Total	
				♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1934-35	Ad-LP	1	1/1	0	1											0	1
1933-34	Ad-RP	+	1/2			0	0									0	0
1934-35	Ad-LP	1	1/2			0	1									0	1
1935-36	Both P	2	2/1			10	7									10	7
1934-35	Ad-LP	1	2/1			1	2									1	2
1934-35	Ad-LP	1	1/3					0	0							0	0
1935-36	Both P	2	2/2					12	7							12	7
1934-35	Ad-LP	1	2/2					0	3							0	3
1936-37	Ad-RP	3	3/1					0	0							0	0
1935-36	Both P	2	3/1					0	1							0	1
1935-36	Both P	2	2/3							1	0					1	0
1936-37	Ad-RP	3	3/2							0	0					0	0
1935-36	Both P	2	3/2							1	3					1	3
1937-38	Ad-LP	4	4/1							0	0					0	0
1936-37	Both P	3	3/3									0	0			0	0
1937-38	Ad-LP	4	4/2									0	0			0	0
1937-38	Ad-LP	4	4/3											0	0	0	0
Totals				0	1	11	10	12	11	2	3	0	0	0	0	25	25

TABLE 65

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1934-35

Season when first marked downstream	Mark	Probable age as downstream migrant	Age as returning adult	Season of return as adult												Total	
				1936-37		1937-38		1938-39		1939-40		1940-41		1941-42			
				♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1935-36	Both P	1	1/1	0	0											0	0
1934-35	Ad-LP	+	1/2			0	0									0	0
1935-36	Both P	1	1/2			0	0									0	0
1936-37	Ad-RP	2	2/1			9	4									9	4
1935-36	Both P	1	2/1			5	7									5	7
1935-36	Both P	1	1/3					0	0							0	0
1936-37	Ad-RP	2	2/2					5	6							5	6
1935-36	Both P	1	2/2					6	8							6	8
1937-38	Ad-LP	3	3/1					1	0							1	0
1936-37	Ad-RP	2	3/1					0	1							0	1
1936-37	Ad-RP	2	2/3							0	0					0	0
1937-38	Ad-LP	3	3/2							0	0					0	0
1936-37	Ad-RP	2	3/2							0	0					0	0
1938-39	No marking	4	4/1							?	?					?	?
1937-38	Ad-LP	3	3/3									0	0			0	0
1937-38	Ad-LP	3	4/2									1	0			1	0
1938-39	No marking	4	4/2									?	?			?	?
1938-39	No marking	4	4/3											?	?	?	?
Totals				0	0	14	11	12	15	0+?	0+?	1+?	0+?	?	?	27+?	26+?

TABLE 66

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1935-36

Season when first marked downstream	Mark	Probable age as downstream migrant	Age as returning adult	Season of return as adult												Total	
				1937-38		1938-39		1939-40		1940-41		1941-42		1942-43			
				♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		♂	♀	
1936-37	Ad-RP	1	1/1	0	0										0	0	
1935-36	Both P.	+	1/2			0	0								0	0	
1936-37	Ad-RP	1	1/2			1	0								1	0	
1937-38	Ad-LP	2	2/1			7	4								7	4	
1936-37	Ad-RP	1	2/1			16*	20								16*	20	
1936-37	Ad-RP	1	1/3					0	0						0	0	
1937-38	Ad-LP	2	2/2					2	6						2	6	
1936-37	Ad-RP	1	2/2					3	7						3	7	
1938-39	No marking	3	3/1					?	?						?	?	
1937-38	Ad-LP	2	3/1					1	1						1	1	
1937-38	Ad-LP	2	2/3							0	0				0	0	
1938-39	No marking	3	3/2							?	?				?	?	
1937-38	Ad-LP	2	3/2							0	0				0	0	
1939-40	No marking	4	4/1							?	?				?	?	
1938-39	No marking	3	3/3									?	?		?	?	
1939-40	No marking	4	4/2									?	?		?	?	
1939-40	No marking	4	4/3											?	?	?	
Totals				0	0	24	24	6+?	14+?	0+?	0+?	?	?	?	30+?	38+?	

* One of these marked Ad + Both P (D) (marked downstream both in 1936-37 and 1937-38).

TABLE 67

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1936-37

Season when first marked downstream	Mark	Probable age as down- stream migrant	Age as returning adult	Season of return as adult											
				1938-39		1939-40		1940-41		1941-42		1942-43	1943-44	Total	
				♂	♀	♂	♀	♂	♀	♂	♀			♂	♀
1937-38.....	Ad-LP.....	1	1/1	1	0									1	0
1936-37.....	Ad-RP.....	1	1/2			0	0							0	0
1937-38.....	Ad-LP.....	1	1/2			2	1							2	1
1938-39.....	No marking.....	2	2/1			?	?							?	?
1937-38.....	Ad-LP.....	1	2/1			6	17							6	17
1937-38.....	Ad-LP.....	1	1/3					0	0					0	0
1938-39.....	No marking.....	2	2/2					?	?					?	?
1937-38.....	Ad-LP.....	1	2/2					1	4					1	4
1939-40.....	No marking.....	3	3/1					?	?					?	?
1938-39.....	No marking.....	2	3/1					?	?					?	?
1938-39.....	No marking.....	2	2/3							?	?			?	?
1939-40.....	No marking.....	3	3/2							?	?			?	?
1938-39.....	No marking.....	2	3/2							?	?			?	?
1940-41.....	No marking.....	4	4/1							?	?			?	?
1939-40.....	No marking.....	3	3/3									?		?	?
1940-41.....	No marking.....	4	4/2									?		?	?
1940-41.....	No marking.....	4	4/3										?	?	?
Totals.....				1	0	8+?	18+?	1+?	4+?	?	?	?	?	10+?	22+?

TABLE 68

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), Brood Year of 1937-38

Season when first marked downstream	Mark	Probable age as downstream migrant	Age as returning adult	Season of return as adult										
				1939-40		1940-41		1941-42		1942-43	1943-44	1944-45	Total	
				♂	♀	♂	♀	♂	♀				♂	♀
1938-39	No marking	1	1/1	?	?									
1937-38	Ad-LP	+	1/2			0	1						0	1
1938-39	No marking	1	1/2			?	?						?	?
1939-40	No marking	2	2/1			?	?						?	?
1938-39	No marking	1	2/1			?	?						?	?
1938-39	No marking	1	1/3					?	?	No Records			?	?
1939-40	No marking	2	2/2					?	?				?	?
1938-39	No marking	1	2/2					?	?				?	?
1940-41	No marking	3	3/1					?	?				?	?
1939-40	No marking	2	3/1					?	?				?	?
1939-40	No marking	2	2/3							No Records			?	?
1940-41	No marking	3	3/2										?	?
1939-40	No marking	2	3/2										?	?
1941-42	No marking	4	4/1										?	?
1940-41	No marking	3	3/3										?	?
1941-42	No marking	4	4/2									?	?	
1941-42	No marking	4	4/3									?	?	
Totals				?	?	0+?	1+?	?	?	?	?	?	0+?	1+?

marked, and (5) all unmarked fish have been excluded, since none of them is comparable to those marked on a downstream migration.

The data are arranged according to the returns in all seasons from marked fish of a given brood year, for males and females separately. The total number of marked first spawners resulting from a given brood year is shown in the extreme right-hand column of each table. In addition, the first spawners returning from fish *marked in a given season*, irrespective of brood year, have also been obtained from these data. These tabulations must be obtained from more than one table.

Only those freshwater plus ocean age combinations which have actually been encountered among Waddell Creek returning adult first-spawning steelhead during the seasons of 1933-34 through 1941-42 have been listed (three of these combinations, 1/3, 3/3, and 4/3, have not been encountered among the *marked* fish; among the unmarked fish, only one has been found in each of these combinations, and the scale readings for the latter two of them are somewhat doubtful, so these three combinations do not play a significant role).

The first column shows the season in which the fish was first marked on a downstream migration. (Three fish among the marked first spawners made an upstream migration subsequent to the downstream migration on which they were first marked and then a second downstream migration, on which they were again marked. These fish thus carry the mark Ad-Both P and are individually noted.) Seasons during which no marking was carried on are shown for those age combinations for which returns have been obtained in other seasons.

The second column shows the mark given, or carries the notation "No marking".

The third column shows the *probable* age of the fish at the time that it was first marked on a downstream migration. It must be kept in mind that the mark given shows only the *season* in which the fish was marked, and not the age. In most cases, returning adults with *different* marks will have *different* life histories, but a few may have different marks but the same life history. For example, a fish marked in September of one season and one marked in October of the following season (i.e., in the following month) will have different marks, but could well have the same life histories. In the case of fish marked during the principal (spring) migrations those with different marks will have different life histories in those cases in which the fish went to sea in the same season in which they were marked. However, as was noted previously, a number of fish remain in fresh water for one season after their first downstream migration, i.e., migrate to sea in the season following the one in which they were marked. Such fish are shown in bold face type in the columns under "Season of return as adult".

The fourth column shows the age combination (life history category) of the fish as a returning adult.

The remaining columns show the season in which the fish returned as a first spawner. Similarly to the case of the first column, those seasons in which the upstream trap was not operated ("No Records") or in which no returns were possible because no marking had been carried on in the proper season are shown for those combinations for which returns have been obtained in other seasons. Such returns, which might have occurred if marking had been carried on and the upstream trap

had been operated, are indicated by a question mark, "?". A zero, "0", means that no returns were obtained, but that marking had been carried out and the upstream trap operated.

There are nine brood years, 1929-30 through 1937-38, for which at least partial returns could be expected, on the basis of the marking carried out, the seasons during which the upstream trap was operated (nine seasons, 1933-34 through 1941-42), and the life history categories which have been encountered among Waddell Creek adult first-spawning steelhead. At least partial returns were obtained for all but the 1929-30 brood year, for which returns for only three minor age combinations were possible. Complete returns were possible for only two brood years, 1932-33 and 1933-34, but nearly complete returns (complete except for minor age combinations) were possible for two other brood years, 1934-35 and 1935-36. The largest returns were obtained for still another brood year, 1931-32, despite the fact that returns for two major age combinations were not possible.

Altogether, returns were obtained for 383 marked first spawners. (One marked fish, male Ad-LP, 71 cm., taken during the 1936-37 season had all of the scales badly regenerated and was omitted from this series of tabulations. It is not known whether this fish was a first spawner or not. For all other marked fish the scales were sufficiently complete to determine whether or not the fish were spawning for the first time.) These 383 fish were composed of 187 (48.8 percent) males and 196 (51.2 percent) females. This is almost exactly the sex ratio among all 3,220 first spawners checked upstream through the trap (Table 28). Returns for the two complete brood years (1932-33 and 1933-34) (Tables 63 and 64) and for the four complete or nearly complete brood years (1932-33 through 1935-36) (Tables 63-66) also show a sex ratio

TABLE 69

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), All Brood Years Combined

Probable age as downstream migrant	Age as returning adult	Number ♂♂	Number ♀♀	Number ♂♂ + ♀♀	Number of seasons*
1.....	1/1	1	2	3	5
1.....	1/2	3	3	6	5
+.....	1/2	0	1	1	5
2.....	2/1	77	32	109	5
1.....	2/1	28	46	74	5
1.....	1/3	0	0	0	5
1.....	2/2	38	48	86	5
1.....	2/2	11	22	33	5
3.....	3/1	11	8	19	5
2.....	3/1	7	11	18	5
2.....	2/3	1	0	1	5
3.....	3/2	4	8	12	5
2.....	3/2	1	5	6	5
4.....	4/1	1	0	1	5
3.....	4/1	2	6	8	5
3.....	3/3	0	0	0	5
4.....	4/2	0	0	0	5
3.....	4/2	2	4	6	5
4.....	4/3	0	0	0	5
Totals.....	--	187	196	383	--

* Number of seasons for which returns were possible.

of approximately 1:1. In the former case it is 52 (52.0 percent) males and 48 (48.0 percent) females and in the latter case 109 (49.3 percent) males and 112 (50.7 percent) females.

An analysis of the data (Table 69) shows that of the 383 marked adult first spawners, 220 (57.4 percent) had made their initial downstream migration as age 2 fish (in their second year), 116 (30.3 percent) as age 1 fish, and 45 (11.8 percent) as age 3 fish. There was one fish apiece in the + and 4 groups. This sequence, but not order of magnitude, is also true for each sex. It is seen that there were more males than females in the 2 group, whereas the reverse was true in the 1 and 3 groups. These sexual differences are probably real.

For purposes of comparison with the returning adults, Table 70 also shows the age at initial downstream migration of the 12,679 downstream stream fish which were marked and produced those adults. From this table it is seen that the ages at initial downstream migration of adult steelhead first spawners occur in quite different proportions from those of the stream fish producing them. This results both from differing survival rates among downstream stream fish of different ages and the fact that many of the downstream stream fish remain in the stream for an additional season, the percentage doing so varying considerably with age.

That many of the fish which migrate downstream do not go to sea in the same season, but remain in the stream until the following season, has been noted previously and is seen clearly from Table 71. Of the 383 fish under discussion, 237 (61.9 percent) migrated to sea in the same season, while 146 (38.1 percent) migrated in the following season. Of the 146 fish that migrated to sea in the following season, three made an upstream migration and a second downstream migration, while the remainder stayed in the stream below the dam, most likely in the lagoon in the great majority of cases.

In this connection, a striking difference in behavior is to be noted in the different age groups. Among the age 1 group, only 9 (7.8 percent) had migrated in the same season and 107 (92.2 percent) had migrated in the following season; among the age 2 group, 196 (89.9

TABLE 70

Waddell Creek, Steelhead: Age at Initial Downstream Migration of Marked Adult First Spawners and Marked Downstream Stream Fish, All Seasons Combined

Age	Adults						Stream fish	
	♂ ♂		♀ ♀		♂ ♂ + ♀ ♀		Number	Percentage
	Number	Percentage	Number	Percentage	Number	Percentage		
+	0	--	1	0.5	1	0.3	3,820	30.1
1	43	23.0	73	37.2	116	30.3	4,811	38.0
2	124	66.3	96	49.0	220	57.4	3,793	29.9
3	19	10.2	26	13.3	45	11.8	249	2.0
4	1	0.5	0	--	1	0.3	6	+
Totals	187	--	196	--	383	--	12,679	--

percent) had migrated in the same season and only 24 (10.1 percent) in the following season; among the age 3 group, 31 (68.9 percent) had migrated in the same season and 14 (31.1 percent) in the following season.

This sequence, but not order of magnitude, is also true for each sex. Among the males, 136 (72.7 percent) had migrated to sea in the same season and 51 (27.3 percent) in the following season, while among the females 101 (51.5 percent) had migrated in the same season and 95 (48.5 percent) in the following. Thus, a greater proportion of the fish had migrated to sea in the same season following their initial downstream migration among the females than among the males. Among the age 1 group, 9.3 percent of the males and 6.8 percent of the females had migrated in the same season and 90.7 percent of the males and 93.2 percent of the females in the following; among the age 2 group, 93.5 percent of the males and 83.3 percent of the females had migrated in the same season and 6.5 percent of the males and 16.7 percent of the females in the following; among the age 3 group, 78.9 percent of the males and 61.5 percent of the females had migrated in the same season and 21.1 percent of the males and 38.5 percent of the females in the following. It is seen, then, that within each group a greater proportion of the females than of the males had migrated in the following season.

Any definite quantitative explanation of the relation between downstream migration and actual entry into the ocean would involve data regarding the actual or proportionate numbers of marked downstream migrants that went to sea during the same season and during the following season, respectively. Such data are not available, and we know only the numbers that survived out of unknown numbers of such fish.

TABLE 71

Waddell Creek, Steelhead: Comparison of Fish Migrating to Sea in the Season of Their Initial Downstream Migration With Those Migrating in the Following Season, Among Marked Adult First Spawners, All Seasons Combined

Probable age as downstream migrant	Season of migration to sea*	♂ ♂		♀ ♀		♂ ♂ + ♀ ♀	
		Number	Percentage	Number	Percentage	Number	Percentage
+	Same	0	--	0	0.0	0	0.0
	Following	0	--	1	100.0	1	100.0
1	Same	4	9.3	5	6.8	9	7.8
	Following	39	90.7	68	93.2	107	92.2
2	Same	116	93.5	80	88.3	196	89.9
	Following	8	6.5	16	16.7	24	10.1
3	Same	15	78.9	16	61.5	31	68.9
	Following	4	21.1	10	38.5	14	31.1
4	Same	1	100.0	0	--	1	100.0
	Following	0	0.0	0	--	0	0.0
Totals		187	--	196	--	383	--

* In relation to season of initial downstream migration.

However, it might be pointed out that the same results could be obtained whether the numbers of fish which went to sea in the season of their initial downstream migration and in the following season, respectively, were proportionate to the representation of the two categories among the adult first spawners, or greatly out of proportion to them. If they were proportionate to them, it necessarily means that *after* the fish within each age group had made their initial downstream migration the rate of mortality was the same in the fish that went to sea in the same season as in those that went to sea in the following season. On the other hand, if, for example, *equal* numbers of age 1 group downstream migrants migrated to sea in the same season and in the following season, but the ocean mortality was much greater than the freshwater mortality, there would be a much higher survival of the fish that migrated to sea in the season following their downstream migration, with results among the adults corresponding to those obtained. At the same time, among the age 2 group, *many* more fish might migrate to sea in the same season than in the following season, with results again corresponding to those obtained, despite higher ocean mortality.

Whatever the proportions of these categories among the downstream migrants, it is probable that the great majority of the fish in the age 1 and 2 groups are sexually immature and that their behavior in regard to time of migration to sea is not governed by sexual development. It is possible that the fish of the age 1 group have a strong tendency to remain in the lower stream and lagoon in order to make use of the extremely favorable growing conditions to be found there, while the fish of the age 2 group, having reached a size at which they can most favorably make use of the growing conditions (including kind and size of food) to be found in the ocean, migrate to sea in the season of their downstream migration. The shift back to a higher percentage remaining for another season among the age 3 group might then be accounted for by the attainment of sexual maturity among a greater percentage of this group than of the age 1 and 2 groups. A different approach to this phase of the discussion, one that would lay the stress on the fundamental biology of the species rather than on the environmental conditions, would be to say that it is in the nature of the species to migrate to sea as age 2 group fish and that deviations from such behavior occur only when either environmental conditions (favorable or unfavorable) or sexual development are strong enough to overbalance the fundamental behavior pattern. To a greater or less extent, this is probably what happens. When population pressure or other ecological factors cause some of the fish to migrate downstream as age 1 group fish, these fish still have a strong tendency to remain in fresh water into the following season, conforming to their fundamental behavior pattern, while those that migrate downstream as age 2 group fish have a strong tendency to migrate to sea during the same season.

The fact that among the downstream migrants the age 1 and 2 groups form by far the largest age groups, combined with the fact that the great majority of the age 1 group probably remain in fresh water until the following season, while the great majority of the age 2 group probably migrate to sea in the same season, results, of course, in the fact that the great majority of the downstream migrants migrate to sea as

TABLE 72

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), All Brood Years Combined

Age at entry into ocean	Returning as adults					
	♂♂		♀♀		♂♂ + ♀♀	
	Number	Percentage	Number	Percentage	Number	Percentage
+	0	0.0	0	0.0	0	0.0
1	4	2.1	6	3.1	10	2.6
2	155	82.9	148	75.5	303	79.1
3	23	12.3	32	16.3	55	14.4
4	5	2.7	10	5.1	15	3.9
Totals	187	--	196	--	383	--

fish of the age 2 group. This is shown in Table 72, from which it is seen that of the 383 fish under discussion, 303 (79.1 percent) had migrated to sea as fish of the age 2 group, 55 (14.4 percent) as fish of the age 3 group, 15 (3.9 percent) as fish of the age 4 group, and 10 (2.6 percent) as fish of the age 1 group. In examining these percentages and others previously noted, it must constantly be kept in mind that the discussion deals with percentages among returning adults, and that these percentages did not necessarily prevail among the downstream marked migrants. This point has often been overlooked or not sufficiently stressed by various investigators who have discussed age at time of migration among salmonids. The same sequence and approximate order of magnitude for the different age groups migrating to sea prevails in the two sexes, although there may be a somewhat greater tendency for females to remain longer in fresh water.

A comparison of Table 69 (probable age as downstream migrant) with Table 72 (age at entry into ocean) shows strikingly the differences in the representation of the different age groups in these two groups. Although the age 2 group is dominant in both cases, it is much stronger among the latter group. The age 1 group represents 30.3 percent of the former group, but slumps to only 2.6 percent in the latter one. These examples show very clearly how easy it would be to reach erroneous conclusions regarding survival by considering the downstream migrants to be equivalent to seaward migrants.

Table 73 shows the number of fish in each life history category among the 383 marked adult first spawners. It is seen that the 2/1 fish predominate (47.8 percent), followed strongly by the 2/2 group (31.1 percent). The other categories are represented as follows: 3/1 (9.7 percent), 3/2 (4.7 percent), 4/1 (2.3 percent), 1/2 (1.8 percent), 4/2 (1.6 percent), 1/1 (0.8 percent), and 2/3 (0.3 percent). It is to be noted that in both males and females the life history categories occur in the same sequence, but not in the same magnitude. In the 2/1 group the males predominate, while in all other categories of importance the females predominate. These sexual differences, borne out by the much more extensive data for all first spawners, shown in Table 28, mean

TABLE 73

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), by Life History Categories, All Seasons Combined

Age as returning adult	Number returning as adults						
	♂		♀		♂ + ♀		
	Number	Order of rank	Number	Order of rank	Number	Percentage	Order of rank
1/1-----	1	8	2	8	3	0.8	8
1/2-----	3	5	4	6	7	1.8	6
2/1-----	105	1	78	1	183	47.8	1
1/3-----	0	--	0	--	0	--	--
2/2-----	49	2	70	2	119	31.1	2
3/1-----	18	3	19	3	37	9.7	3
2/3-----	1	8	0	--	1	0.3	9
3/2-----	5	4	13	4	18	4.7	4
4/1-----	3	5	6	5	9	2.3	5
3/3-----	0	--	0	--	0	--	--
4/2-----	2	7	4	6	6	1.6	--
4/3-----	0	--	0	--	0	--	--
Totals-----	187	--	196	--	383	--	--

that the males on the average mature at an earlier total age (fresh-water and ocean years combined) than the females, as is shown more clearly in Table 74. The data for marked first spawners are in general agreement with those for all first spawners checked upstream through the trap (Table 28).

Table 74 shows the total age at maturity among the 383 fish under discussion. It is seen that 190 (49.6 percent) or about one-half matured at 3 years of age, 156 (40.7 percent) or approximately two-fifths at 4, 28 (7.3 percent) at 5, 6 (1.6 percent) at 6, and 3 (0.8 percent) at 7. The sequence is somewhat different in the two sexes. Among the males the ages occur in the following sequence: 3 (57.8 percent), 4 (35.8 percent), 5 (4.8 percent), 6 (1.1 percent), and 0 (0.5 percent). Among

TABLE 74

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), by Ages, All Seasons Combined

Age as returning adult	Returning as adults					
	♂		♀		♂ + ♀	
	Number	Percentage	Number	Percentage	Number	Percentage
2-----	1	0.5	2	1.0	3	0.8
3-----	108	57.8	82	41.8	190	49.6
4-----	67	35.8	89	45.4	156	40.7
5-----	9	4.8	19	9.7	28	7.3
6-----	2	1.1	4	2.0	6	1.6
7-----	0	--	0	--	--	--
Totals-----	187	--	196	--	383	--

TABLE 75
Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), by Season of Marking

Season of marking	Mark	Number marked	Number returning as adults				Number of seasons*	Number returning as adults in each season								
			♂	♀	♂ + ♀	Percentage		First			Second			Third		
								♂	♀	♂ + ♀	♂	♀	♂ + ♀	♂	♀	♂ + ♀
1933-34	Ad-RP	2,454	65	51	116	4.7	8	47	18	65	17	33	50	1	0	1
1934-35	Ad-LP	1,013	24	37	61	6.0	7	10	6	16	13	22	35	1	9	10
1935-36	Both P.	3,116	42	36	78	2.5	6	15	10	25	19	15	34	8	11	19
1936-37	Ad-RP	2,744	34	38	72	2.6	5	9	4	13	22	27	49	3	7	10
1937-38	Ad-LP	3,352	22	34	56	1.7	4	9	4	13	11	25	36	2	5	7
Totals		12,679	187	196	383	3.0	--	90	42	132	82	122	204	15	32	47

* Number of seasons during which upstream trap was operated following season of marking.

TABLE 76

Waddell Creek, Steelhead: Secondary Survival of Marked Fish, by Seasons

Brood year	Mark*	Number marked age + †	Survival				Number marked age 1 †	Survival				Number marked age 2 †	Survival			
			♂	♀	♂+♀	Per- cent- age		♂	♀	♂+♀	Per- cent- age		♂	♀	♂+♀	Per- cent- age
1929-30.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1930-31.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1931-32.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	1,652	57	38	95	5.8
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1932-33.....	Ad-RP.....	--	--	--	--	--	687	1	2	3	0.4	--	--	--	--	--
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	470	19	17	36	7.9
	Ad-Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--
	Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1933-34.....	Ad-RP.....	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-LP.....	--	--	--	--	--	507	1	7	8	1.6	--	--	--	--	--
	Ad-Both P.....	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--
	Both P.....	--	--	--	--	--	--	--	--	--	--	820	24	18	42	5.1
	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1934-35.....	Ad-LP.....	6	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Both P.....	--	--	--	--	--	1,481	11	15	26	1.8	--	--	--	--	--
	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	443	14	11	25	5.6
	Ad-Both P.....	--	--	--	--	--	--	--	--	--	--	4	--	--	--	--
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1935-36.....	Both P.....	724	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-RP.....	--	--	--	--	--	1,146	19	27	46	4.2	--	--	--	--	--
	Ad-Both P.....	--	--	--	--	--	--	1	--	1	--	--	--	--	--	--
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	404	10	11	21	5.2
1936-37.....	Ad-RP.....	1,142	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-LP.....	--	--	--	--	--	988	10	22	32	3.2	--	--	--	--	--
1937-38.....	Ad-LP.....	1,945	--	1	1	--	--	--	--	--	--	--	--	--	--	--
Totals.....		3,820	--	1	1	--	4,811	43	73	116	--	3,793	124	96	220	--
Percentage survival.....		--	--	--	--	+	--	--	--	--	2.4	--	--	--	--	5.8

TABLE 76—Continued
Waddell Creek, Steelhead: Secondary Survival of Marked Fish, by Seasons

Brood year	Mark*	Number marked age 3†	Survival				Number marked age 4†	Survival				Total number marked	Survival			
			♂	♀	♂ + ♀	Per-centage		♂	♀	♂ + ♀	Per-centage		♂	♀	♂ + ♀	Per-centage
1929-30.....	Ad-RP.....	--	--	--	--	--	2	--	--	--	--	2	--	--	--	0.0¶
1930-31.....	Ad-RP.....	110	7	11	18	16.4	--	--	--	--	--	111	8	11	19	17.1¶
	Ad-LP.....	--	--	--	--	--	1	1	--	1	100.0	--	--	--	--	--
1931-32.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	1,682	60	50	110	6.5¶
	Ad-LP.....	27	3	12‡	15	55.6	--	--	--	--	--	--	--	--	--	--
	Both P.....	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--
1932-33.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	1,245	27	23	50	4.0§
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Both P.....	88	7	3	10	11.4	--	--	--	--	--	--	--	--	--	--
1933-34.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	1,341	25	25	50	3.7§
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-RP.....	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1934-35.....	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	1,949	27	26	53	2.7‡
	Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-LP.....	15	2	--	2	13.3	--	--	--	--	--	--	--	--	--	--
1935-36.....	Both P.....	--	--	--	--	--	--	--	--	--	--	2,274	30	38	68	3.0‡
	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-Both P.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1936-37.....	Ad-RP.....	--	--	--	--	--	--	--	--	--	--	2,130	10	22	32	1.5¶
	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1937-38.....	Ad-LP.....	--	--	--	--	--	--	--	--	--	--	1,945	--	1	1	+¶
Totals.....		249	19	26	45	--	6	1	--	1	--	12,679	187	196	383	--
Percentage survival ..		--	--	--	--	18.1	--	--	--	--	16.7	--	--	--	--	3.0¶

* Final mark given.

† Age at time of first marking.

‡ One of these marked Ad-Both P (must be error; thought to have been 4/1 adult marked downstream in both 1934-35 and 1935-36 and first migrating downstream at age 3).

§ Complete.

|| Complete except for minor age combinations.

¶ Incomplete.

TABLE 77

Waddell Creek, Steelhead: Marked Fish Returning (as First Spawners), by Season of Marking and Age

Season of marking	Mark	Total number marked	Marked fish by ages												Survival U	1 + 2 L
			+		1		2		3		4					
			a	b	c	d	e	f	g	h	i	j				
			Number	Per- centage	Number	Per- centage	Number	Per- centage	Number	Per- centage	Number	Per- centage				
1933-34	Ad-RP	1	2,454	0.6	3	0.1	687	28.0	1,652	67.3	110	4.5	2	0.1	4.7	95.3
1934-35	Ad-LP	4	1,013	0.1	6	0.6	509	50.4	470	46.4	27	2.7	1	0.1	6.0	96.8
1935-36	Both P	2	3,116	0.8	724	23.2	1,481	47.6	820	26.4	88	2.8	3	0.1	2.5	74.0
1936-37	Ad-RP	3	2,744	0.2	1,142	41.6	1,146	41.6	447	16.3	9	0.3	--	--	2.6	57.9
1937-38	Ad-LP	5	3,352	0.6	1,945	58.0	988	29.4	404	12.1	15	0.4	--	--	1.7	41.5
Total			12,679	--	--	--	--	--	--	--	--	--	--	--	--	--

↑
TABLE 75

$$L = (e + c) / M$$

$$M = a + c + e + g + i = \text{TOTAL \# MARKED AT AGE}$$

$$U = \text{CALCULATED OCEAN SURVIVAL} = \text{RETURNED MARKED / MARKED}$$

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returns for the last marking, that of 1937-38, were complete, since the upstream trap was operated for four seasons following. This analysis indicates that probably in most California coastal streams in which it is desired to carry out marking of stream juvenile steelhead and secure survival rates in terms of returning first-spawning, sea-run adults, returns should be sought for three seasons following season of marking, but need not be watched for beyond that. For each marking fewer fish have returned in the third season following marking than in either the first or second season. With the exception of the 1933-34 marking, for which the largest number returned in the first season, the largest number of fish have returned in the second season following marking. From the marking of 1934-35, which yielded the greatest returns, 26.2 percent of the fish returned in the first season, 57.3 percent in the second season, and 16.4 percent in the third, while from the marking of 1937-38, which yielded the smallest returns, 23.2 percent returned in the first season, 64.3 percent in the second, and 12.5 percent in the third. Thus, it is seen that the *pattern* of return is much the same for the returns from the two markings which exhibited the greatest difference in rate of survival.

A comparison of Table 76 with Table 20 for the silver salmon seems to indicate basic similarities as regards survival. The average return from the number marked at the same age (1) is much the same for both species (2.4 percent for steelhead and 2.3 percent for silver salmon). Although an inverse correlation between the number of fish marked and the number returning does not follow in sequence through the five years for the silver salmon, as it does in the case of the steelhead, it is still true that the lowest return was obtained from the largest number marked and the second highest return from the smallest number marked. When survival is based on the estimated total number of downstream migrants, including both marked and unmarked fish, it is seen (Table 22) that an inverse correlation does exist for the four years for which data are available. In other words, it appears that in the silver salmon the number of fish marked is *roughly* correlated with the total downstream migration, that the number of adults returning has a *true* relationship (inverse correlation) to the number in the downstream migration, and that this relationship (inverse correlation) exists between the number of marked downstream migrants and the number of marked adults returning only to the extent that the marked downstream migrants form a portion of the total downstream migration. (A possible explanation of the inverse correlation has already been given.) In the case of the silver salmon the situation is easier to analyze than in the case of the steelhead, since the downstream migrants (except for a few unmarked fish of the season) in the former are all of one age class and all migrate to sea in the same season that they migrate downstream. Thus, the mark given represents not only the season of marking but also the age class. In the case of the steelhead, as we have seen, several age classes migrate down during one season and are given the same mark and, conversely, fish of the same age class migrate down in different seasons and are given different marks. Furthermore, a large number of the downstream migrants do not migrate to sea until the following season, and some migrate upstream and make a second downstream migration. In the case of the steelhead, when an estimate

is made of the total downstream migration it is found that an inverse correlation does exist between the number of downstream migrants and the number of returning adults, with certain variations. It is also found that the number of fish marked is *roughly* correlated with the total downstream migration, which accounts for the approximate inverse correlation found between the number of fish marked and the number of marked adults returning. The variations just mentioned which occur in the case of the steelhead are brought about by the varying proportions of age classes, and consequently sizes of fish, in the total downstream migrations of different seasons. In other words, the phenomenon of inverse correlation of number of fish in the downstream migration to the number of adults returning operates, but is modified by the size composition of the downstream migration. Now, the size composition of the fish marked on the downstream migration is not identical with the size composition of the total downstream migration, and so some variation in the degree of inverse correlation may be expected in the two groups. The fact that a rough inverse correlation does exist between the number of fish marked on the downstream migration and the number of marked fish returning indicates (1) that there is a rough correlation between the number of fish marked and the total downstream migration, (2) that there is a rough correlation between the size-age composition of the fish marked downstream and of the total downstream migration, and (3) that the size-age composition of both the fish marked downstream and the total downstream migration is approximately the same.

From the discussion of the comparable section for silver salmon (page 97) it has been seen that in both the salmon and steelhead there is rough correlation between the season of marking and the survival, when fish of the same age (1) are compared. In the same discussion it was also noted that there appears to be no correlation between the mark given and the survival among either the salmon or the steelhead. From Table 76 it is seen that the same mark used in different seasons for fish of the same age resulted in both high and low survivals.

In the preceding pages we have determined the survivals from eggs deposited to returning adult first spawners (primary over-all survival) for the stream as a whole and from downstream migrants to adults returning to the trap for marked fish. In order also to determine the survival from eggs deposited to downstream migrants it is necessary to know the *total* number of downstream migrants, including those that went over the dam uncounted and those that were produced below the dam.

In the case of the steelhead, all of the young fish do not migrate to the ocean at the same age at which they migrate downstream, so the total number of downstream migrants can not be calculated simply by applying the ratio of marked to unmarked fish among the adults of a given brood year to the marked downstream migrants of the same brood year, as was done for the silver salmon. The calculation of the total number of downstream migrants must therefore be made by a less direct method. This method is illustrated by Tables 78 and 79.

Table 78 shows the stream history and the survival from time of downstream migration for the *marked* adult first spawners. In this table

the adults are grouped according to age as stream fish at the time of migration to the ocean and then regrouped according to age at time of downstream migration and marking at the dam. (In the case of the *marked* adults the age at which they had entered the ocean is known from scale readings, and the age at which they had migrated downstream past the dam is known from the combined interpretation of scale readings and marks used.) It is seen that of the 10 adults that had entered the ocean at age 1, 10 percent had migrated downstream at age + and 90 percent had migrated downstream at age 1, and so on for the other age groups. To calculate survival in the marked fish the adults are regrouped in column 8 of the table on the basis of age at time of downstream migration and are then shown in column 9 as percentages of the total number of downstream migrants of those ages marked at the dam.

In the case of the *unmarked* fish only the age at which they had entered the ocean is known. The age at which they had migrated downstream is not known. However, it is assumed that the *unmarked* fish entering the ocean had migrated downstream in the same proportions as the marked fish of corresponding ages. There are no observational or theoretical considerations to indicate that such an assumption is questionable. Therefore, in Table 79 the unmarked adults (taken at

TABLE 78

Waddell Creek, Steelhead: Stream History and Survival From Time of Downstream Migration Among Marked First Spawners

Stream history					Survival			
To ocean		Downstream			Downstream			
Age	Number	Age	Percent-age	Number	Age	Number stream fish	Number adults	Percent-age survival
1	10	+	10.0	1	+	3,820	1	0. +
		1	90.0	9		4,811	116	2.4
2	303	1	35.3	107				
		2	64.7	196	2	3,793	220	5.8
3	55	2	43.6	24				
		3	56.4	31	3	249	45	18.1
4	15	3	93.3	14				
		4	6.7	1	4	6	1	16.7
Totals	383			383		12,679	383	

the trap) are arranged as were the marked fish in Table 78 as to age at time of entry into the ocean and then regrouped as to age at downstream migration in proportion to the known percentages for the marked adults of similar stream history.

To calculate the number of downstream migrants that produced the unmarked adults it is only necessary to use the survival percentages for the marked fish. The number of unmarked downstream migrants (217,849) is then added to the number of marked downstream migrants (12,679) to obtain the total production (230,528) of downstream fish which produced the adult first spawners taken at the trap.

This number of downstream migrants was derived from an estimated 7,627,000 eggs (Table 58). Survival from eggs deposited to downstream migrants was therefore $\frac{230,528}{7,627,000}$, or 3.0 percent.

The survival figures obtained for Waddell Creek should approach fairly closely the "natural" survival and mortality for the stream, since no angling has been carried on and since the amount of poaching is thought to have been negligible. As has been noted previously, there is no commercial fishery for steelhead in California, but there is a considerable sport fishery in the northern part of Monterey Bay. Since the

TABLE 79

Waddell Creek, Steelhead: Stream History and Survival From Time of Downstream Migration Among Unmarked First Spawners

Stream history					Survival			
To ocean		Downstream			Downstream			
Age	Number	Age	Percent-age*	Number†	Age	Number stream fish†	Number adults†	Percent-age survival*
1	341	+	10.0	34	+	149,880	34	0. +
		1	90.0	307	1	40,667	976	2.4
2	1,895	1	35.3	669				
		2	64.7	1,226	2	25,328	1,469	5.8
3	558	2	43.6	243				
		3	56.4	315	3	1,956	354	18.1
4	42	3	93.3	39				
		4	6.7	3	4	18	3	16.7
Totals	2,836			2,836			2,836	

* Assumed, on basis of Table 78.

† Calculated.

fish caught in this fishery are largely ripening fish, undoubtedly a large percentage of the fish would otherwise have returned to their parent stream to spawn, and so the fishery affects the "natural" mortality and survival rates. Just what influence this fishery has on the individual streams is not known. Two steelhead which were marked at Scott Creek in 1938-39 (Ad-RV) were taken off Capitola on October 21 and 31, 1939, but the total number of marked fish caught is not known. The number of Waddell Creek fish caught in this fishery probably is not large.

Another possible source of "unnatural mortality" is the marking and other handling of the fish, both stream fish and adults. All evidence points to the conclusion that this is a negligible source of mortality. This evidence is based on (1) holding experiments conducted with marked fish at Waddell Creek, (2) holding experiments conducted with marked fish at other localities in California (especially with steelhead at the Fall Creek State Fish Hatchery on the Klamath River), (3) experiments conducted with the same lot of hatchery fish given different marks at Scott Creek, and (4) general observations on the behavior and mortality of marked fish liberated at Waddell Creek.

One factor that may influence the calculation of survival is the presence in unknown numbers of the offspring of stream fish in the downstream juvenile migrations. If the latter do not participate in the

TABLE 80

Calculated and Actual Survival for Sea-run Steelhead, If Offspring of Stream Fish Take Part in Downstream Migration But Do Not Go to Sea

Marked or unmarked	Parents	Eggs	Downstream	Adults
	Stream	1,000 MD	→ 100 ME	→ 0 MF
Marked	Sea-run	100,000 MA	→ 1,000 MB	→ 100 MC
	Sea-run	100,000 UA	→ 1,000 UB	→ 100 UC
Unmarked	Stream	1,000 UD	→ 100 UE	→ 0 UF
Survival	Calculated		Actual	
Eggs to adults	✓	MA + UA → MC + UC 200,000 → 200		Same as calculated
Downstream to adults	—	MB + ME : MC : UB : UC 1,100 : 100 :: x : 100 100 x = 110,000 x = 1,100		MB : MC : UB : UC 1,000 : 100 :: x : 100 100 x = 100,000 x = 1,000
Eggs to downstream	+	Number of downstream taken from preceding calculation MA + UA → MB + UB + ME 200,000 → 2,100		Number of sea-run downstream taken from preceding calculation MA + UA → MB + UB 200,000 → 2,000

Categories in boxes are those whose numbers are known. Plus, minus, and check signs show whether survival to stage in bold face type is too great, too small, or correct.

downstream migration, of course no error will result. But if the offspring of stream fish participate in the downstream migration to an appreciable extent they will affect the *calculated* survival rate for offspring of sea-run fish, whether they themselves go to sea and return as sea-run fish or not. If the offspring of stream fish participate in the downstream migration but do not go to sea, they will have *no effect* on the calculated survival from eggs to adults, will *decrease* the calculated survival from downstream migrants to adults, and will *increase* the calculated survival from eggs to downstream migrants. If the offspring of stream fish participate in the downstream migration and go to sea and return as adults, they will *increase* the calculated survival from eggs to adults, and also from eggs to downstream migrants, but will have no effect on the calculated survival from downstream migrants to adults. Actually, there will be an error in the latter case as well, for the calculated numbers of *both* the downstream migrants and the adults will be too high in terms of the eggs from which these fish were produced, although the survival from downstream migrants to adults will be correct.

Tables 80 and 81 show the quantitative effects for the possible situations described in the preceding paragraph. In the tables, the ratio of eggs produced by stream fish to eggs produced by sea-run fish is arbitrarily taken to be 1:100, and the survival rates for the fish resulting

TABLE 81

Calculated and Actual Survival for Sea-run Steelhead, If Offspring of Stream Fish Take Part in Downstream Migration and Go to Sea and Return as Adults

Marked or unmarked	Parents	Eggs	Downstream	Adults
	Stream	1,000 MD	→ 100 ME	→ 10 MF
Marked	Sea-run	100,000 MA	→ 1,000 MB	→ 100 MC
	Sea-run	100,000 UA	→ 1,000 UB	→ 100 UC
Unmarked	Stream	1,000 UD	→ 100 UE	→ 10 UF
Survival	Calculated		Actual	
Eggs to adults	MA + UA → MC + UC + MF + UF 200,000 → 210	MA + UA + MD + UD → MC + UC + MF + UF 202,000 → 210		
Downstream to adults	MB + ME : MC + MF : UB + UE : UC + UF 1,100 : 110 :: x : 110 110 x = 121,000 x = 1,100	Same as calculated		
Eggs to downstream	Number of downstream taken from preceding calculation MA + UA → MB + UB + ME + UE 200,000 → 2,200	Number of sea-run downstream taken from preceding calculation MA + UA → (MB + UB) - (ME + UE) 200,000 → 2,000		

Categories in boxes are those whose numbers are known. Plus, minus, and check signs show whether survival to stage in bold face type is too great, too small, or correct.

from both groups of eggs are arbitrarily taken to be the same. Actually, there appears to be no way of knowing either the numbers present or the survival rate, since the offspring of stream fish were not distinguished from those of sea-run parents (except as scattered individual fish) among the downstream migrants and returning adults during the experiments. However, the direction, although not the magnitude, of the effects on the calculated survivals will be the same, whatever the numbers of stream fish in the migrations and whatever their survival rate.

As outlined above, there appears to be no way of knowing whether offspring of stream fish are present or absent in the downstream and upstream migrations nor their numbers and survival rates if they are present. However, a picture of the situation as it is thought to exist is here presented, on the basis of various observations and more or less indirect evidence for Waddell Creek and other streams.

Of the fish resulting from eggs deposited from sea-run steelhead, a large proportion migrate downstream and thence to sea, either in the same season or the following one, as previously discussed. Others, composed of both males and females, mature sexually in the stream and spawn. Probably a few stream males fertilize the eggs of some sea-run females (it is definite that they are capable of doing so), while it is doubtful that any—or more than a negligible number—of stream females are fertilized by sea-run males. Of the fish resulting from the spawning of stream fish which were the offspring of sea-run parents, some probably go to sea and others remain to spawn in the stream, but whether in the same proportions as the offspring of sea-run parents or not is not known. Of the stream parents that were the offspring of sea-run fish, some probably then go to sea and return as sea-run fish, while others remain in the stream for additional spawnings. In addition, in Waddell Creek and other coastal streams there are probably one or more populations (races, strains) of resident fish which are largely nonmigratory (especially insofar as going to sea is concerned). In Waddell Creek, such a population exists above the main falls in the East Branch, which are impassable to sea-run steelhead. Whether or not any of the members of such populations migrate to sea and return as sea-run fish is not known. Whether or not any of the members of such populations participate in spawning with sea-run fish or stream fish that are the offspring of sea-run parents also is not known, but probably some do, especially with stream fish that are the offspring of sea-run parents. Probably at least some of the offspring of such "crosses" go to sea, while others remain to spawn in the stream without going to sea, but in what proportions is not known.

Although the spawning seasons for both sea-run and stream steelhead are quite long, even in such a small stream as Waddell Creek, the great bulk of the sea-run fish and stream fish that are the offspring of sea-run fish spawn at a different time (earlier) than the resident fish. This is determined as much or more by stream conditions, especially temperatures, as by any inherent factors in the populations. That is, the majority of the resident fish are in the upper reaches of the streams, where cooler temperatures prevail, while the majority of the sea-run fish and offspring of sea-run fish are in the lower reaches of the streams, where the water is warmer. Thus, even though the members of the different

populations would otherwise interbreed, there is a strong tendency for them to be kept apart in spawning both from the standpoint of time and spawning localities.

The interbreeding of the different populations, of minor extent but varying in amount from year to year, probably further accentuates the variability in the life history pattern of the steelhead that occurs not only within one year class but also from one year class to another. Thus, there is a constant interplay of the forces of inheritance and environment. In streams in which stocking is being carried on, especially stocking with fish from other streams, the variability of the life history pattern is further accentuated through the addition and at least partial integration of the stocked fish.

From the above discussion it is clear that we can not think of the total steelhead population in a stream or stream system as a static thing, to which simply numbers are added or subtracted through fishing, stocking, natural propagation, etc., but as a dynamic whole in a constant state of flux.

In the discussion of the preceding pages of the present section, we have discussed primary over-all survival from egg to downstream migration and from downstream migration to return as adults. In preceding sections we learned something of the survival from egg to hatching and from hatching to emergence from the gravel, on the basis of data derived from certain experiments, work done in other streams, and general observations (not strictly quantitative) on the emergence of fish from the gravel at Waddell Creek. In summing up, it may be stated that the percentage of eggs fertilized is high and constant, while the percentages hatching and emerging from the gravel (the two may be quite different) probably vary considerably from season to season as well as within a season. These percentages are probably influenced most of all by the amount of silting due to floods and by the destruction of the redds through their re-utilization by newly arrived spawners. Under favorable conditions the percentages of eggs hatching and fish emerging from the gravel may both be quite high, but even when they are low the number of fish emerging from the gravel is vastly greater than the number surviving to time of downstream migration. Among the fish making their initial downstream migration, some go to sea in the same season and some in the following season. The proportion behaving in each manner is correlated primarily with age and secondarily with sex. Of those that go to sea in the following season, some make an upstream migration and then a second downstream migration before going to sea, while others spend the time in the lagoon near the mouth of the stream. Whether the fish go to sea in the same season or the following season, the survival from time of initial downstream migration to adult first spawning is correlated positively with age (and therefore size) at time of downstream migration, varying from almost zero survival for fish migrating down at age 4 to 18.1 percent survival for those migrating at age 3. The normal survival from time of initial downstream migration to adult first spawning for any year class, migrating downstream over the course of several years, is probably in the neighborhood of between 3 and 4 percent. There apparently also exists a negative correlation between the numbers of fish migrating to sea and the rate of survival. It probably operates on the principal that

the greater the numbers, the greater *proportionately* are the inroads made by predators. If it is a generally operative principle, it is undoubtedly modified by the age composition of the migration to sea, and the latter probably exercises a greater influence than does the number of fish. In general, it appears that survival to various stages of life history follows essentially the same pattern in the various species of trout and salmon and that usually local conditions (amount of silting, character of bottom, size of spawning run, and spawning runs of other species of salmonids present) play a more important role than do the factors peculiar to the species involved.

So far, the discussion of survival has dealt only with *primary* survival, i.e., survival to first spawning. It is also of interest and practical significance in fisheries management to consider *secondary* survival, i.e., survival following spawning. Here again we shall deal with survival among sea-run fish, since it is only for them that we have quantitative data.³⁶

From a viewpoint of fisheries management, we desire to know what percentage of sea-run steelhead survive to spawn more than once under normal and optimum conditions, in order to know what efforts should be expended to enable spent adults to reach the sea. If the number of fish that would return to spawn for a second time or more is sufficiently large to warrant such efforts, they could be directed toward (1) greater protection of spent fish in the streams, by (a) maintenance of flow and screening of diversions in streams in which diversions and dams exist, (b) protection against predators, and (c) legislation, and (2) greater protection by more careful handling at egg collecting stations.

From Table 57 it is seen that the percentage of fish returning to spawn for a second time or more varies considerably from season to season. Among the fish taken in the upstream trap, it has varied from 2.6 (1934-35) to 24.6 (1937-38) percent for the males and from 5.1 (1934-35) to 34.4 (1941-42) percent for the females. Averages for the nine years are 13.9 percent for males, 20.0 percent for females, and 17.1 percent for males and females combined. In other words, in the spawning run approximately one fish in seven among the males, one fish in five among the females, and one fish in six among males and females combined is returning to spawn for a second time or more. The percentage of females returning to spawn for a second time or more is higher than that of the males in seven out of the nine years, so the higher secondary survival among females is apparently real (the sex ratio among the first spawners has been shown to be approximately 1:1). At first thought, this may appear to be somewhat surprising, since it might be expected that the spawning and redd building act would be harder on the females than the males and since among the first spawners the males on the average are younger than the females. However, the males are believed to serve more than one female and so in the end not only exhaust themselves more but also remain in the stream longer, thus lessening their chances of survival. At least theoretically, an excess of males over females in a given season, including repeat spawners, should

³⁶ Scales of various stream fish examined at Waddell Creek, including both upstream and downstream migrants, show that some of them spawn more than one time, but no attempt has been made to analyze these data.

increase the number of male repeat spawners in the following season, and a reverse situation should have the reverse effect. At Waddell Creek, the difference in sex ratio in any season probably has not been great enough to prove this theory, if it is true. In support of this theory, it might be pointed out that the two seasons of greatest excess of females over males (1933-34 and 1938-39) were followed by seasons in which the lowest percentages of repeat spawners were obtained among the males, and that the one season of marked excess of males over females (1940-41) was followed by the second highest percentage of repeat spawners among the males. At the same time, it will be noted that the 1934-35 and 1939-40 seasons were also the ones with the lowest percentages of female repeat spawners, and that in general seasons with a high percentage of repeat spawners for one sex are also seasons with a high percentage of repeat spawners for the other sex, and that seasons with a low percentage of repeat spawners for one sex are also seasons with a low percentage of repeat spawners for the other sex. It appears, then, that environmental conditions existing at the time of first spawning, or occurring between the time of first spawning and second spawning, exercise a greater influence than does the sex ratio at first spawning, although the sex ratio, in line with the theory advanced, may be a contributing factor.

What are the factors that have caused poor or good survival of first spawners at Waddell Creek, where fishing and diversions of water have played no part or at most a very minor role? A plausible explanation is readily found for the two low survivals. In 1933-34 the disease called furunculosis was extremely severe, and may well have accounted for the small number of repeat spawners in the following season. In 1938-39 the precipitation was light and water conditions very poor, and these conditions may well have resulted in the small number of repeat spawners in the following season.

Pathology

Diseases

The occurrence of disease among trout and salmon under natural and artificial conditions was discussed in the comparable section on silver salmon (pages 101-102).

Some mortality, especially among adults, has resulted at Waddell Creek during the course of the experiments from some form or strain of furunculosis, which is caused by a bacterium, *Bacillus salmonicida*. J. H. Wales of the department made cultures of the bacteria from kidney blood of dead and dying adult steelhead in Waddell Creek in February and April, 1934. Frederic Fish of the U. S. Fish and Wildlife Service also examined adults at Waddell Creek and tentatively confirmed the identification of the disease. Although the symptoms caused by the disease at Waddell Creek are not entirely typical of those present among salmonids in the British Isles, it appears that the disease organism is at least closely allied to the form found there, and so will be referred to as "furunculosis" in the present paper.

Furunculosis as manifested at Waddell Creek is not evident among the adult steelhead in the early fish, but appears around February or March, perhaps associated with higher water temperatures. Some of the

fish show boils and lesions along the sides of the body, and bleeding at the vent, while others die without exhibiting external signs of the disease. The kidneys have an abnormal appearance in most of the fish examined.

As stated previously, the relationship of the form of furunculosis present in Waddell Creek to that found in the British Isles, and also to other strains along the Pacific Coast, is not yet entirely clear. Neither is it known whether the disease is indigenous to the Pacific Coast or was introduced from some other area. Snyder (1914) noted that "The dead bodies of large steelheads were occasionally seen in Uvas, Arroyo Seco, the Nacimiento Creeks" (tributaries of the Pajaro and Salinas rivers, tributary to Monterey Bay), but the cause of death is not known. Outbreaks of the disease occurred regularly in the steelhead held in the tanks at the Scott Creek Egg Collecting Station at least since the spring of 1932, appearing about the same time as at Waddell Creek.

Wales and Berrian (1937) found that fingerlings of Scott Creek steelhead and silver salmon, Klamath River steelhead, eastern brook trout from Mt. Whitney Hatchery, and brown trout from Mt. Shasta Hatchery were all susceptible to one strain of furunculosis (from eastern brook trout from Mt. Shasta Hatchery). This strain was introduced into the food of these fish, which were held together in a pond at the Big Creek Hatchery, on August 14, 1936. During the course of the disease, which ran approximately 70 days, the losses ranged from 98 percent for the eastern brook trout to 50 percent for the brown trout. Although the different lots were not equally susceptible, the authors correctly point out that differences due to age, fin rot, or some other predisposing influence may have played a part.

At Waddell Creek many of the adults have succeeded in spawning before succumbing to furunculosis, but some mortality has occurred among unspawned steelhead, particularly during the 1933-34 season, when 161 dead adults in all were found. It is estimated that 17 females died without spawning during this season. In all other seasons mortality is believed to have been very much less, although variations in water conditions prevented uniformity in searching for fish. Estimates of the numbers which died without spawning or spawned only partially were made for each season and considered in calculating egg production and survival.

Abnormal mortality among adults, such as that caused by furunculosis in 1933-34, of course results in abnormally low numbers of repeat spawners in subsequent seasons. Thus, in 1934-35 the number of repeat spawners was the lowest on record, a further indication that mortality in 1933-34 was correctly assessed as being the heaviest during the course of the experiments.

The extent of losses from furunculosis among the stream steelhead is not known exactly, but is not believed to have been nearly as severe as among adults. Observations on the stream have not shown large numbers dead in the stream at any time. Only occasional fish among the downstream migrants have possessed red spots on the body (usually at the bases of the fins) or shown other external signs of disease. Particularly in 1933-34 many of the downstream fish bled

abnormally when a pectoral fin was clipped off in marking; it is possible that furunculosis played a part in this, but this is not known definitely.

It was pointed out in the comparable section on silver salmon that during the 1933-34 season an abnormally large number of dead fish, including juvenile silver salmon, adult and stream steelhead, sculpins, and sticklebacks, were found, but that absence of external signs of disease or injury made assessment of mortality to different causes very difficult. It was also noted that during the same season an abnormally large number of other animals, mostly rodents, was found dead in the stream, but that their relation to the dead fish was not known.

Fungus (*Saprolegnia parasitica*) is present in all or practically all trout and salmon streams; it is a secondary infection which gains a foothold on breaks in the skin caused by mechanical injury or disease. Under normal conditions it does not cause much damage to salmonids in their natural environment.

As a rule many of the downstream migrants, especially yearlings and older fish, possess from a few to many cysts under the skin on the sides of the body, but otherwise appear to be in good condition. These cysts, which appear in the form of blackish spots, are formed by encysted strigeid larvae (Trematoda).

The upstream stream steelhead also not infrequently possess cysts. For example, in 1934-35 out of 28 upstream fish examined (December 3-February 23, size range 93-254 mm.) 19 possessed cysts, especially on the caudal fin.

Freshwater copepods are found attached to many of the downstream migrants, but apparently cause no serious damage. Apparently these copepods are specific, being found much more frequently on the steelhead than on the salmon migrating downstream at the same time. The species found in Waddell Creek has been identified as *Salmincola californiensis* Dana by Charles B. Wilson. In the stream fish it is found most commonly attached to the bases of the fins, especially the pectorals and dorsal. Occasional specimens may be found attached to almost any part of the fish, including the ventrals, adipose, head, branchiostegal membranes, and gills. Usually not more than one or two are found on a fish. On adults which have remained in the stream for some time following spawning, copepods may be found in much larger numbers. Steelhead which have summered over in Waddell Creek have been found with copepods swarming in the mouth and on the gills. Their prevalence in the mouths of such fish evidently results from the cessation of feeding by the fish. Circumstantial evidence is strong that these copepods die when the fish reach salt water, since no adult steelhead (or salmon) returning from the ocean with these parasites have been encountered. Another species of freshwater copepod, *Salmincola falcata*, has been taken from an adult steelhead from Shackleford Creek, tributary of Scott River, in Northern California (identification by Charles B. Wilson).

Marine copepods ("sea lice") probably occur on adult fish entering the stream, but have never been found on any of the fish by the time that they have reached the dam.

Nematodes (unidentified) were sometimes extruded along with eggs from adults during the course of spawning operations at the Scott Creek Egg Collecting Station. These probably also occur in the fish at Waddell Creek, but have not been recorded from there. They are not known to do particular damage to the fish.

Diseases or parasites other than those noted above have not been observed in the steelhead at Waddell Creek, but have been noted among fish in other California coastal streams, particularly in association with unfavorable environmental conditions. For example, during periods of exceptionally hot weather (water temperatures reaching 80-85 degrees F.) mass mortality of varying severity occurs almost every year among the juvenile steelhead in portions of the Eel River system in Northern California. Many of the affected young steelhead turn a pale yellow, due to loss of black pigment, and stand out clearly in the water. Parasites commonly found on these fish are the following four (identifications by J. H. Wales): *Ichthyophtherius* sp.; bacterium in the mouth (not identified); fin rot (one or more bacteria, not identified); and *Lernaea* sp. (anchor parasite). Losses occurring in July, 1938, were particularly severe and were described in detail by Wales (1938). It is of interest that furunculosis has not been observed in connection with these outbreaks.

Two other instances of *Lernaea* attacking *Salmo gairdneri* in natural waters or reservoirs in California are known to the present writers. In July, 1943, C. E. Holladay and the writer collected infested specimens at the head of Stevens Creek Reservoir, Santa Clara County. Previously A. C. Taft had observed *Lernaea* to be common on trout in Little Rock Reservoir, Los Angeles County. (The parasite attacks many other species of fishes in natural waters in California.)

Lampreys, which sometimes cause damage when they attach themselves to fish, do not occur in Waddell Creek.

As in the adult silver salmon, fish that were blind or partially blind in one or both eyes, as evidenced by opaqueness of the eye, were fairly common among the adult steelhead but were met with only rarely among the juveniles. Consideration is here given only to fish in which no mechanical injury to the eye was apparent. The writers believe that such opaqueness often, if not usually, is the result of fish scraping the eye after entering fresh water, e.g., in leaping falls, passing through log jams, spawning, or being handled in nets at traps. This condition has been noted frequently at various egg collecting stations, especially when the fish had been handled in dip nets made of seine material with prominent knots.

The records at Waddell Creek indicate that the diseases encountered, including the external parasites, have not been associated with size of fish, within an age class.

At Waddell Creek there has been no known loss of steelhead because of high temperatures or lack of oxygen.

Teratology

Deformities are rare among trout and salmon in their natural environment, and this general rule has held good at Waddell Creek. Of particular interest are abnormalities of the fins, because of their relation to marking programs.

Although abnormal or naturally missing fins were watched for in all seasons among the downstream migrants, it is possible that a few were missed. No fish with fins completely missing were recorded, however, and only on rare occasion one with an atrophied or partially missing fin. The occurrence of salmonids with missing fins in other streams and the relation of naturally missing fins to marking programs has been discussed in the comparable section on silver salmon.

The occurrence of missing and deformed fins among adult fish was somewhat greater than among juveniles, principally due to injuries to these fins that had taken place at sea. Several fish with the adipose or other single fins missing were encountered. Since in each case the possibility existed that the fish was one in which another fin had been missed in the course of marking at Waddell or Scott creeks, or a hatchery fish whose fin had been destroyed by disease (this applies particularly to the dorsal being destroyed by *Gyrodactylus* or fin rot) or bitten off by another fish, no record of such fish is presented in this paper.

Deformities of the body, like abnormalities in the fins, are rare among salmonids in their natural environment. Occasionally steelhead with deformed upper or lower jaws have been taken among the juveniles and the adults. Trout with various deformities are much more common among hatchery fish, but such fish rarely survive to return as sea-run spawners.

Food

One of the greatest difficulties in analyzing the food of steelhead in coastal streams lies in the fact that usually the investigator is not able to distinguish individuals of sea-run stock from those of resident stock. Idyll (1942), studying steelhead,³⁷ Cutthroat Trout (*Salmo clarki*), and brown trout 25.4-50.8 cm. (10-20 inches) long in the Cowichan River, British Columbia, found that fish formed an insignificant proportion of the food of the steelhead, but were an important item in the food of the brown trout and an exceedingly important item in the food of the cutthroat trout. Among the fish of the size listed, individuals consuming fish were as follows: of 104 steelhead, 4 (3.8 percent); of 37 cutthroat trout, 29 (78.3 percent); and of 67 brown trout, 39 (58.4

³⁷ The author lists these fish by the scientific name "*Salmo gairdneri*," but by the common name "rainbow trout".

TABLE 82

Waddell Creek, Steelhead: Foods Consumed by 22 Stream Fish *

Class of food	Total number present	Percentage of total
Trichoptera (Caddisflies).....	557	50.5
Diptera (True flies).....	400	36.3
Hemiptera (True bugs).....	56	5.1
Coleoptera (Beetles).....	53	4.8
Hymenoptera (Ants, bees, wasps).....	13	1.2
Miscellaneous.....	23	2.1
Total.....	1,102	

* Taken August 9, 19, 1933. Average length, 4 inches; maximum, 6.9 inches; minimum, 2.6 inches.

percent). If such differences exist between species and are significant, the possibility exists that differences, although perhaps of not equal magnitude, also exist between migratory and nonmigratory races or strains of steelhead in the same stream. In the present state of our knowledge it is necessary to consider foods eaten by fish listed as *Salmo gairdneri* by the authors on an equal basis, unless the author specifically notes that the fish which he studied were nonmigratory.

Table 82 is based on data from Needham (1934a).

Of the 557 caddisflies eaten, only one was eaten in the adult stage, at the surface of the water. All the rest were taken as larvae or pupae below the water surface, where they normally live in their immature stages.

Shepherd (1928) found that 55 steelhead from Waddell Creek had eaten the items listed in Table 83.

It will be seen from this table that caddisflies, as in the case of the fish cited by Needham, form the dominant food. Of the 1,615 caddisflies eaten, all but two were in the larval stage. It is of interest that 71 percent of all the insects found in the 55 stomachs were larvae belonging to the genus *Notidobia*, larvae living in small cornucopia-shaped cases. As Shepherd (*loc. cit.*) states: "Their great abundance may be accounted for in the following manner: (1) The larvae have a general distribution and are very abundant along the whole length of Waddell Creek; (2) the larvae are typically bottom feeders and as a result may easily be taken into the mouths of the fishes; (3) the larvae are protected by a type of portable case which may easily be swallowed; (4) ordinarily the larvae are gregarious, feeding in groups, either in the shallow or deep water."

TABLE 83

Waddell Creek, Steelhead: Foods Consumed by 55 Stream Fish *

Class of food	Total number present	Percentage of total number of organisms	Percentage of total number of insects (2,135)
Trichoptera (Caddisflies).....	1,615	43.5	75.6
Diptera (True flies).....	393	10.6	18.4
Hemiptera (True bugs).....	22	0.6	1.0
Homoptera (Leafhoppers).....	10	0.3	0.5
Coleoptera (Beetles).....	24	0.6	1.1
Plecoptera (Stoneflies).....	39	1.1	1.8
Ephemeroptera (Mayflies).....	24	0.6	1.1
Odonata (Dragonflies).....	1	+	+
Hymenoptera (Ants, bees, wasps).....	6	0.2	0.3
Corrodentia (Psocids).....	1	+	+
Arachnida (Water mites).....	7	0.2	
Isonoda (Isopods).....	1,046	28.0	
Amphipoda (Amphipods).....	424	11.4	
Nemathelminthes (Roundworms) (probably parasitic)	91	2.5	
Salmon eggs.....	35	--	
Total.....	3,738		

* Fish taken October 16, 1928 (2), July 2, 1927 (12), July 4, 1927 (12), December 27, 1927 (5), January 7, 1928 (10), January 8, 1928 (13), and January 9, 1928 (1). Average length, 16.9 cm.; maximum, 41.7 cm.; minimum, 10.1 cm. (The 41.7 cm. fish may have been a sea-run individual; the next largest fish was 25.2 cm. long.)

TABLE 84
Waddell Creek, Steelhead: Foods Consumed by 28 Upstream Stream Fish, 1934-35

Fish number	Length in mm.	Salmon eggs	Diptera (true flies)	Ephemero- ptera (mayflies)	Neuropt- era (dob- son flies)	Plecopt- era (stoneflies)	Trichop- tera (caddis- flies)	Isopoda	Diplopoda	Debris	Empty
5	146	--	--	--	--	--	1	--	--	--	--
6	143	--	--	--	--	--	25	--	--	--	--
7	118	--	--	19	--	1	11	--	--	+	--
8	115	--	--	--	--	2	9	--	--	--	--
9	111	--	--	--	--	--	1	--	--	--	--
10	142	--	6	1	--	--	7	--	--	--	--
11	134	--	--	1	--	--	1	--	1	--	--
12	128	--	--	--	--	--	14	--	--	--	--
13	206	3	--	--	--	--	3	--	--	--	--
14	103	--	1	2	--	1	16	--	--	--	--
15	127	+	--	--	--	--	5	--	--	--	--
16	139	5	--	--	--	--	33	--	--	+	--
17	141	--	--	--	--	--	1	--	--	--	--
18	102	+	--	1	1	--	+	--	--	--	--
19	131	--	--	--	--	--	--	--	--	--	x
20	200	--	--	--	--	--	4	--	--	--	--
21	254	--	--	--	--	--	--	1	--	--	--
22	115	--	--	--	--	--	+	--	--	--	--
23	171	+	--	--	--	--	1	--	--	+	--
24	119	--	--	--	--	--	+	--	--	--	--
25	124	5	--	--	--	--	+	--	--	--	--
26	120	--	--	--	--	--	--	--	--	--	--
27	126	+	--	--	--	--	--	--	--	--	--
28	141	+	--	--	--	--	--	--	--	--	--
29	179	--	--	--	--	--	--	--	--	--	x
30	252	--	--	--	--	--	--	--	--	--	x
31	251	12	--	--	--	--	6	--	--	--	--
32	93	--	--	1	--	--	1	1	--	--	--
Number of times item occurred.....		9	2	6	1	3	20	2	1	3	3
Number of each item.....		25+	7	25	1	4	141+	2	1		

TABLE 85

Analysis of Food of Steelhead From the Cowichan River System, British Columbia, Arranged According to Size of Fish and Types of Organisms Eaten

Length in cm.	Number	Aquatic										Terrestrial					Fish	Fish eggs
		Trichoptera	Simuliidae	Chironomidae	Ephemeroptera	Plecoptera	Odonata	Hydracarina	Amphipoda	Gastropoda	Miscellaneous	Coleoptera	Homoptera and Hemiptera	Formicoidea and Apoidea	Isoptera	Miscellaneous		
0-5-----	12 A	0	2	193	15	2	--	--	--	--	--	--	4	--	--	--	--	--
	B	2.7	0.9	86.5	6.7	0.9	--	--	--	--	--	--	1.8	--	--	--	--	--
	C	33.3	8.3	91.6	91.6	16.6	--	--	--	--	--	--	16.6	--	--	--	--	--
5-10-----	3 A	1	2	23	6	32	--	--	--	--	--	--	--	--	--	--	--	--
	B	1.6	3.1	36.0	9.4	50.0	--	--	--	--	--	--	--	--	--	--	--	--
	C	33.3	33.3	100.0	100.0	100.0	--	--	--	--	--	--	--	--	--	--	--	--
10-15-----	48 A	379	500	11	61	11	--	--	2	--	10	4	--	10	--	3	16	--
	B	37.1	48.9	1.0	5.9	1.0	--	--	0.2	--	1.0	0.3	--	1.0	--	0.2	1.5	--
	C	85.5	31.4	18.5	27.0	12.5	--	--	2.5	--	9.0	8.0	--	6.0	--	6.0	4.0	--
15-20-----	55 A	346	37	13	40	40	2	8	3	13	--	12	7	196	6	7	3	--
	B	48.4	4.9	1.7	5.1	5.1	0.2	1.0	0.4	1.7	--	1.6	0.8	27.6	0.8	0.8	0.4	--
	C	82.7	25.0	11.5	34.0	34.0	3.8	5.7	5.7	3.8	--	17.3	7.6	28.7	3.8	5.6	3.8	--
20-25-----	30 A	223	5,574	25	23	13	8	--	1	88	--	203	6	238	22	4	1	--
	B	3.4	85.1	0.5	0.3	0.2	0.1	--	--	1.3	--	3.1	--	5.3	0.3	--	--	--
	C	86.6	60.0	36.6	13.3	16.7	23.3	--	3.3	10.0	--	30.0	16.7	36.7	3.3	13.2	3.3	--
25.5-30.5-----	32 A	727	2,994	6	16	26	2	--	--	58	6	22	--	748	--	13	4	--
	B	16.0	66.0	0.1	0.3	0.5	--	--	--	1.2	0.1	0.4	--	14.3	--	0.3	--	--
	C	78.1	37.5	12.8	25.0	18.7	3.0	--	--	12.5	9.0	25.0	--	31.0	--	27.3	6.0	--
30.5-35.5-----	18 A	401	3,720	33	15	11	4	--	--	51	2	122	--	40	--	14	--	1
	B	9.0	84.0	0.7	0.2	0.3	0.1	--	--	1.1	--	2.7	--	1.0	--	0.3	--	--
	C	72.1	55.5	33.0	22.0	37.7	16.5	--	--	16.0	11.0	27.7	--	44.0	--	55.0	--	5.5
35.5-40.5-----	8 A	209	1,774	40	2	18	--	--	--	74	1	--	--	--	6	--	5	33
	B	11.4	81.9	1.8	--	0.8	--	--	--	3.4	--	--	--	--	0.3	--	0.2	1.5
	C	37.5	25.0	25.0	25.0	12.5	--	--	--	12.5	12.5	--	--	--	12.5	--	12.5	12.5
40.5-45.5-----	9 A	109	5,208	8	20	15	--	--	--	1	--	4	--	12	--	2	--	--
	B	1.9	96.7	0.1	0.3	0.2	--	--	--	--	--	22.2	--	1.1	--	22.2	--	--
	C	100.0	66.6	44.4	33.3	22.2	--	--	--	11.1	--	--	--	11.1	--	--	--	--
45.5-51.0-----	5 A	24	677	--	--	6	--	--	--	3	--	1	--	14	--	--	--	--
	B	3.1	93.6	--	--	0.8	--	--	--	0.4	--	0.1	--	1.8	--	--	--	--
	C	40.0	40.0	--	--	40.0	--	--	--	40.0	--	20.0	--	40.0	--	--	--	--

A = total number of organisms eaten; B = percentage of total number eaten; C = percentage of stomachs containing this organism.

It will be noted that although in the case of the fish cited by Needham all forms other than insects formed only 2.1 percent of all items eaten, in the case of the fish cited by Shepherd isopods (pill bugs) formed 28.0 percent of all the organisms and amphipods 11.4 percent. This difference emphasizes the fact that conclusions regarding the food of steelhead in a given stream must be based on adequate sampling, which takes into account the time of year, size of fish, sexual development of fish, locality in the stream, and method of capture and preservation. In regard to the latter point, it is not improbable that mayflies are represented in the food of the Waddell Creek steelhead much more strongly than is indicated by Shepherd's analysis, which is based on fish caught by angling and not preserved immediately. This statement is based on the great abundance of mayflies at Waddell Creek and their tendency to be digested quickly. The 35 salmon eggs were eaten by 14 fish caught on January 7 and 8, 1928; the maximum number of eggs in a single stomach was five. Since all of these fish were caught on Tyee (salmon egg clusters), it appears possible that at least some of the eggs were preserved ones used for bait. Shepherd makes no statement in this regard.

Chapman and Quistorff (1938) examined the stomach contents of 819 steelhead 32 to 240 mm. in length collected from various portions of the north central Columbia River drainage in 1937 (May 14 to October 2) and 1938 (May 1 to October 29). The organisms contained formed a wide variety, comprising 11 orders of insects, two orders of arachnids, annelid worms, crustaceans, mollusks, and fish, as well as some vegetable matter. However, insects formed the great bulk of the foods eaten. Among the insects, the nymphs and larvae of stoneflies, mayflies, dragonflies, and caddisflies, "although everywhere abundant in the streams", were not well represented in the stomachs. A considerable amount of the insect food was composed of purely terrestrial forms which had fallen into the water. Only five fish, none of which was a salmonid, were found in the 819 stomachs, despite the abundance of various small fishes in the streams.

The stomach contents of 27 stream steelhead taken in the upstream trap at Waddell Creek during the 1934-35 season are listed in Table 84.

It will be seen from this table that caddisflies, as in the cases of the fish cited by Needham and by Shepherd, were the principal food eaten and formed over 50 percent of the items. Mayflies, which were entirely absent from the fish taken in August, 1933, appear as the second most numerous insects in the upstream fish, and salmon eggs (which are not available in August) also form an item of some importance. The majority of eggs eaten probably had been washed out of the spawning beds or dislodged from them by other spawning fish. Eggs of whatever species of salmonids are spawning at the time are generally found in the stomachs of various species of trouts in all parts of the world.

Idyll (*loc. cit.*) found no appreciable change in the type of food as size of fish increased for the Cowichan River steelhead. Insects were distinctly dominant for every size group, true flies (particularly Simuliidae) being eaten in the greatest numbers, although caddisflies were found in a larger number of stomachs. The foods eaten by these fish are shown in Table 85 (Table I of Idyll).

Idyll (*loc. cit.*) also presents data on the winter food of steelhead. These data are reproduced in Table 86. Salmon eggs, mainly from silver salmon spawnings, constituted the principal food during this period (October to February), although insects were still important. No fish had been consumed.

A comparison of the data in the preceding tables indicates essential harmony of results. Insects are the most important summer food, caddisflies and true flies predominating among the aquatic foods. In some streams and at certain times of the year mayflies and stoneflies are also of some importance, perhaps, as noted, out of proportion to their representation in the tables. During the winter salmonid eggs are of definite importance. Other observations indicate additional seasonal changes, with terrestrial organisms contributing considerably more to the diet in the summer months than in the winter months.

The data presented in the preceding tables do not indicate other fish to be an item of importance, but it is known that under certain conditions steelhead do consume fish. Various authors have found fish to be present in considerable quantities in the stomachs of "rainbow trout" from interior waters of the United States, particularly in larger fish. A steelhead 165 mm. long (female), taken in the downstream trap at Waddell Creek on December 4, 1934, contained four steelhead, 47, 53, 57, and 60 mm. long. A downstream migrant steelhead six inches long, taken at Benbow Dam on the South Fork of Eel River, contained nine fry, four of which were silver salmon one to one and one-fourth inches long, and the other five fish too digested to be identifiable. Another from the same locality, 135 mm. long, taken on April 28, 1939, contained a "small salmon in throat."

It is of interest that none of the steelhead listed in this section had eaten sculpins or sticklebacks. The present writers believe that these fishes do not form an important part of the steelhead diet, although they may be eaten occasionally.

The food organisms found in the lagoons of California streams are considerably different from those found in the streams proper, and the diet of the steelhead resident in the lagoons is also quite different. Needham (1940) presented data on the foods consumed by 14 out of 100 yearling steelhead held in a cage (dimensions: 3 x 3 x 4 feet) in the

TABLE 86
Winter Food of Steelhead From the Upper Cowichan River, British Columbia

Class of food	35 steelhead (20 - 35.5 cm.)		
	A	B	C
Trichoptera (larvae, pupae, adults).....	47	7.4	34.3
Simuliidae (larvae, pupae, adults).....	26	4.1	11.3
Chironomidae (larvae, pupae, adults).....	10	1.6	22.7
Plecoptera (nymphs, adults).....	4	0.5	5.6
Arachnida.....	3	0.4	5.6
Gastropoda.....	11	1.7	5.6
Salmonid eggs.....	529	84.0	65.6

A = total number of organisms eaten; B = percentage of total number eaten; C = percentage of stomachs containing this organism.

middle of Waddell Creek lagoon during the spring of 1933. These are shown in Table 87. Needham also presented data on foods present in Waddell Creek lagoon and compared them with those eaten by the trout in the experimental cage. As he points out, such a comparison may not be truly representative of foods consumed under natural conditions, since the fish were confined and dependent upon organisms entering the cage. The data do show that steelhead in the lagoon *will* eat the organisms indicated and make growth (0.93 inches in 91 days, February 28-May 30, 1933).

Conditions in Waddell Creek lagoon are similar to or paralleled by conditions in lagoons of other Pacific Coast streams. The crustaceans and fishes common in Waddell Creek lagoon, or their close relatives, are generally distributed in brackish water along the Pacific Coast.

Studies by Needham (1934b, 1940) indicate that Waddell Creek compares favorably with other streams as regards its supply of bottom organisms. However, an expression of the adequacy of such organisms to support a certain trout population is impossible at the present time, for we do not fully know (1) the amount of natural foods of various kinds required to produce a given weight of trout, (2) the amounts of the same food organisms consumed by fishes other than trout, and (3) the relation of so-called "available" or "potential" foods to the foods actually consumed.

In Waddell Creek and all or practically all other salmon and trout streams other fishes which are competitors of the salmonids are present. Both sculpins and sticklebacks are competitors of trout. An examination of a number of sculpin stomachs at Waddell Creek has shown that many of the food items are also eaten by steelhead. Munro and Clemens (1937) have shown the food of *Cottus asper* and of Three-spined Sticklebacks to include many items consumed by trout. Further studies in regard to the foods consumed by sculpins and sticklebacks in comparison with the importance of sculpins and sticklebacks as foods for salmonids are needed.

Evidence indicates that the composition of the foods actually eaten by trout in a given locality may be different from that of the so-called "available" or "potential" foods (Needham, 1938, p. 142; Chapman and Quistorff, 1938, p. 2; and others). These differences probably result from (1) the degree of accessibility of the different potential food organisms and (2) selectivity practiced by the trout. Of the more important items, mayflies and stoneflies are usually represented more

TABLE 87

Foods Consumed by 14 Yearling Steelhead Held in Cage in Waddell Creek Lagoon, Spring of 1933 *

Class of food	Number	Percentage
<i>Gammarus confervicolis</i>	122	93.8
<i>Corophium spinicorne</i>	0	0.0
<i>Ezospharoma oregonensis</i>	5	3.8
Miscellaneous.....	3	2.3
Totals.....	130	

* Average size of fish 3.4 inches; range 2.8 to 4.7 inches. Fish were removed for stomach examination between March 1st and March 10th.

strongly on the stream bottom than they are in the stomachs, while the reverse is true for caddisflies. It is the belief of the present writers that considerable selectivity is practiced by steelhead in their choice of food. The data for the three species of trout in the Cowichan River (Idyll, *loc. cit.*) suggest that the fish may discriminate among potential food organisms and that definite selection may therefore take place.

Adult steelhead, like the Pacific salmon, do not commonly eat during their spawning migration in fresh water. Examinations by the writers of stomachs of steelhead from various California streams, as well as findings by other workers (e.g., Chapman and Quistorff, 1938), support this view.

Feeding in fresh water following spawning is not typical, but has been noted in the case of some Waddell Creek fish, although the stomachs of only a few individuals have been examined. A spent male, 56 cm. in length, taken in good condition in the downstream trap on June 16, 1937, contained seven caddisfly larvae. A spent female, 49 cm. in length, taken in the downstream trap on July 10, 1937, had eaten two steelhead, 81 and 86 mm. in length, and one silver salmon, 80 mm. in length. A spent male, 40 cm. in length, taken in the downstream trap on April 28, 1939, was listed as having its stomach "full of young fish; one tail had not yet disappeared"; it is assumed the "young fish" listed by the field observer were salmonids. The stomachs of a few dead spent adults have also been examined and found to be empty.

Very little is known of the food of steelhead in the sea, although because of similarities in morphology it is probably not grossly different from that of silver salmon.

Summing up, it is not improbable that throughout the life history of the steelhead its food in its general character is similar to that of the silver salmon: juveniles in fresh water live very largely upon insects, both aquatic and terrestrial, smaller individuals in salt water depend heavily upon marine invertebrates (and those in brackish water, especially in lagoons, on brackishwater crustaceans), and the larger fish in salt water are chiefly piscivorous.

PREDATORS

Inasmuch as one of the main purposes of the Waddell Creek project was to study a stream under as nearly as possible natural conditions, hesitation was felt in killing suspected predators, because of the danger of upsetting the biological balance. However, it is believed worth while to make evaluations of the effects of various possible predators on the basis of incomplete data and observations on other streams.

Predators in Fresh Water

In previous sections of this paper it was stated that tremendous losses occurred soon after the fish had emerged from the gravel, and that these losses were caused principally by fishes. Under normal conditions, in Waddell Creek and other California streams the greatest numbers of juvenile silver salmon and steelhead are probably eaten by juvenile steelhead. Freshwater sculpins (*Cottus*) are probably an important predator in most Pacific Coast streams; at Waddell Creek and probably in most other streams the species which causes the greatest damage

is *Cottus asper*. During the period immediately following emergence from the gravel some young fish may also be eaten by juvenile silver salmon of older year classes; this has not been noted in Waddell Creek but has been reported from another stream (Pritchard, 1936b). Other predators on fish of such small size are limited in Waddell Creek and most other California streams to the Dipper and to garter snakes. Usually these two are not sufficiently numerous to be the principal cause of loss at this stage. A few are consumed by crayfish and giant water bugs.

As the young salmon and trout grow, the percentage of loss declines, but they become attractive as food to an increasing number of predators. When they are too large to be taken by the Dipper, the smaller garter snakes, and many of the steelhead, they are taken in varying amounts by fish-eating birds (kingfishers, blue herons, and others). In some cases, striped bass may make serious inroads into the seaward migrants. The losses caused by each of these depend upon a variety of factors, including the size of the populations of trout and salmon and the predators, the abundance of other foods for the predators, the character of the stream and the particular portion of the stream, and climatic and water conditions. Some of the predators are able to secure fish in appreciable quantities only when the latter are confined to drying pools or some spot like the traps at Waddell Creek. Figure 32 shows the common food interrelations at Waddell Creek.

Sea-run steelhead and silver salmon, except individuals dying after spawning or from old age, disease, or injury, are subject to very little predation from any source once they have entered fresh water. It is probable that less than 1 percent of the run of either species is normally taken by predators in any stream in California.

Fishes

(a) *Steelhead*. Because of the nature of the program at Waddell Creek, it was not possible to make a detailed study of the predation of steelhead on other steelhead and silver salmon. However, from scattered data it is known that it is not uncommon for stream steelhead to prey upon both of them. The numbers and sizes consumed depend upon the size and composition of the populations of both species, the time of year, the abundance of other food, and other factors.

A steelhead 165 mm. long, taken in the downstream trap on December 4, 1934, contained four steelhead, 47, 53, 57, and 60 mm. long.

A downstream migrant steelhead six inches long, taken at Benbow Dam on the South Fork of Eel River, contained nine fry, four of which were silver salmon one to one and one-fourth inches long, and the other five fish too digested to be identifiable.

Nine out of 32 upstream juvenile steelhead taken during the 1934-35 season contained several to 12 or more silver salmon eggs apiece. Most of these eggs probably had been washed out of the spawning beds.

Idyll (1942) found that salmonids formed only a small proportion of the food of steelhead³⁸ 25.4-50.8 cm. (10-20 inches) long from the Cowichan River, British Columbia.

³⁸The author lists these fish by the scientific name "*Salmo gairdneri*," but by the common name "rainbow trout".

As a general rule, adult steelhead do not feed in fresh water. Apparently a few resume feeding while still in fresh water after spawning, but the inroads into the salmon and trout populations made by such fish cannot be considered important.

(b) *Silver Salmon*. As in the case of the steelhead, it was not possible to make a detailed study of the predation of silver salmon on other silver salmon and steelhead. During their first year of life the silver salmon are so nearly of the same size as other silver salmon and steelhead of the same age class that they probably rarely eat them. In their second year of life at Waddell Creek and in most other California streams the silver salmon migrate to sea before the bulk of the silver salmon and steelhead of the following year class have emerged from the gravel, and so probably consume comparatively few fish of the season.

The preceding statements do not mean that silver salmon are not fish eaters when they have the opportunity to be so. Pritchard (1936b) studied pink salmon predators at McClinton Creek, British Columbia, from February to June in the springs of 1931 and 1933. The stomachs of 385 yearling silver salmon (including 76 which were empty) 2 to 6½ inches long contained a total of 1,027 pink salmon fry (average 2.7 per stomach, maximum 13), 10 chum salmon fry, and 35 silver salmon fry and fingerlings. None of the stomachs contained other food. These results were corroborated by examination of 1,523 additional stomachs from a mixture of silver salmon and cutthroat trout, of which over 90 percent were young silver salmon.

Pritchard correctly points out that the results of the analyses may be more extreme than those which would be obtained under natural conditions, since the pink salmon fry were concentrated along the screens and in the pen of a counting fence. On the basis of stomach examinations and general observations on the numbers of the different predatory fishes in the stream, Pritchard assessed the absolute damage caused to the young pink salmon in the stream, from greatest to least, in the following order: silver salmon, cutthroat trout, Dolly Varden Trout (*Salvelinus malma spectabilis*), and sculpins (*Cottus* sp.).

We are led to conclude that in Waddell Creek and other California streams, silver salmon cannot be considered serious predators on silver salmon or steelhead. In those streams in which king salmon are also present, silver salmon yearlings may do considerable damage, since the king salmon hatch earlier than do the steelhead and silver salmon and since many of them migrate to sea as fish of the season, about the same time as do the yearling silver salmon.

With extremely rare exceptions, adult silver salmon do not feed in fresh water and therefore are not predators.

(c) *Sculpins* (*Cottus*). Two species of freshwater sculpins are present in Waddell Creek and a number of other California coastal trout and salmon streams: *Cottus asper* and *C. aleuticus*. The former is the larger and more abundant species.

These species appear to be of considerable interest in a discussion of salmon and trout predators, first, because it appears that they may make considerable inroads into the populations of these fishes and affect survival rates noticeably, and second, because a practicable method of control appears to exist.

One of the things discovered upon start of operation of the traps was the existence of a definite annual downstream migration of the two species, and to some extent an upstream migration. The downstream migration takes place in connection with high water during the winter and spring months, and is evidently a spawning migration, since most of the fish are large and sexually mature. The extent of the upstream migration that would occur under *natural* conditions is not known, since the sculpins are not leapers and so had only partial success in passing through the fishway into the upstream trap. At first some of the upstream migrants were put upstream, but when it became apparent that most of them could not enter the upstream trap it was decided to "go the whole hog" and kill them.

That this downstream migration, with the upstream migration stopped, was steadily diminishing the population of sculpins above the dam seems evident from Table 88. Tabulations for the two species separately (Tables A-37 and A-38 of the Appendix) show that more than 90 percent of the downstream migrants were the larger *Cottus asper*.

It seems, then, that low dams (\pm three feet high) across the lower parts of streams might prove an effective way of eliminating the sculpin populations above such dams. Dams of this height would not stop adult salmon and steelhead if they were constructed without an apron. Nearby Scott Creek seems to be an example of a stream in which the elimination of sculpins above a dam actually took place. This dam was built for egg taking purposes about 1908. Extensive seining and observations during the 1930's revealed *no* sculpins above the dam, while they were plentiful below it. An old-time resident told Shapovalov that sculpins were abundant above the site of the dam before the dam was built.

There remains the possibility that such dams might cause an unnatural concentration of sculpins below them. Elimination of sculpins below the dams might be accomplished through chemical treatment of

TABLE 88

Waddell Creek: Sculpins Checked Through Downstream Trap, by Four-week Periods
(*Cottus asper* and *Cottus aleuticus*)

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28.....	--	--	--	--	--	--	1	--	--	1
Oct. 29-Nov. 25.....	--	23	--	--	--	--	--	--	--	23
Nov. 26-Dec. 23.....	92	18	--	--	21	--	--	--	--	131
Dec. 24-Jan. 20.....	124	618	199	26	34	11	2	10	1	1,025
Jan. 21-Feb. 17.....	2,075	771	258	163	38	20	19	19	15	3,378
Feb. 18-Mar. 17.....	944	278	108	86	25	26	8	7	5	1,487
Mar. 18-Apr. 14.....	94	99	41	43	9	16	5	13	6	326
Apr. 15-May 12.....	20	24	37	17	13	1	8	4	2	126
May 13-June 9.....	8	5	4	1	--	7	1	1	1	28
June 10-July 7.....	--	1	2	1	--	6	--	--	--	10
July 8-Aug. 4.....	--	--	2	--	12	2	--	3	--	19
Aug. 5-Sept. 1.....	--	--	--	--	1	2	1	4	--	8
Sept. 2-Sept. 30.....	--	--	2	--	2	--	--	--	--	4
Totals.....	3,357	1,837	653	337	155	91	45	61	30	6,566

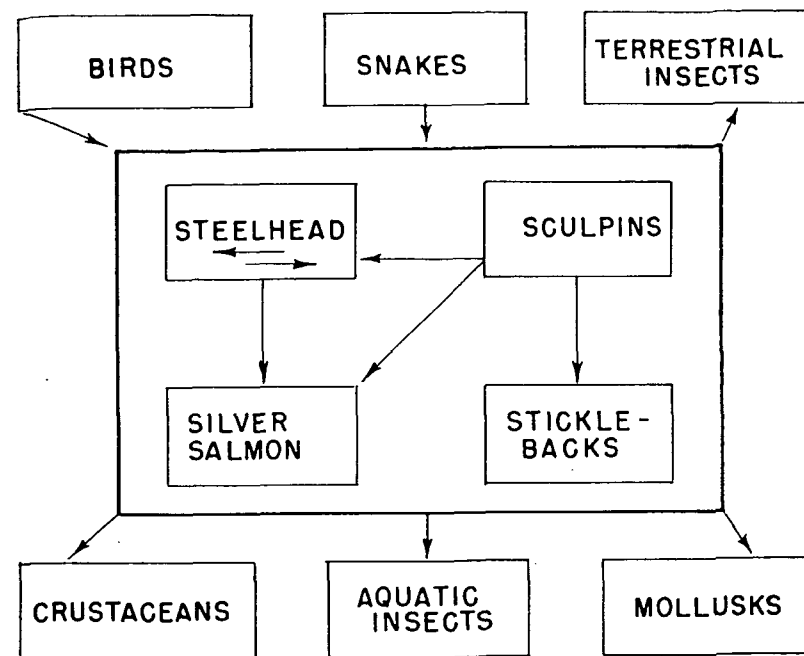


FIGURE 32. Waddell Creek food interrelationships.

the streams below them at low water. Elimination of sculpins below the dams should not be attempted until the populations above had been eliminated through the downstream migrations.

The upstream migrations of sculpins in Waddell Creek are shown in Table A-39 of the Appendix. The upstream migrations occur generally later in the season than the downstream migrations. The average size of the upstream migrants is definitely less than that of the downstream migrants.

Stomachs of sculpins taken from the downstream trap have revealed considerable numbers of young trout and salmon. That confinement of the fishes in the trap aided the sculpins in capturing their prey is probable. At the same time, on various occasions sculpins have been observed to rise to the surface of the pool below the dam and seize freshly liberated downstream migrant salmon and trout. Fish at least as large as 111 mm. long have been observed to be taken by sculpins in this manner. It is possible that such trout and salmon had been temporarily weakened by measuring, marking, and scale-taking operations. Under natural conditions sculpins probably more often secure salmon and trout by sudden darts when their prey is close to the bottom of the stream, since sculpins are not capable of sustained rapid swimming away from the bottom.

Sculpins from the downstream trap have also contained salmon and trout eggs. Most of these eggs probably had been washed out of the spawning beds. *C. asper*, being the larger and more abundant species,

probably does the greater damage. Sculpins continue to feed during sexual maturity.

Pritchard (1936b) examined the stomachs of 165 sculpins (*Cottus* sp.) from McClinton Creek, British Columbia, from February to June in the springs of 1931 and 1933, and found them to contain: 175 pink salmon fry (maximum in single stomach, 8) 2 chum salmon fry, and 10 silver salmon fry and fingerlings; only one stomach contained other materials (insects), and 98 out of the 165 were empty. These data are presented in Table 89. Concentration of the salmon along the screens and in the pen of a counting fence probably aided the sculpins in capturing them. Munro and Clemens (1937) record silver salmon fry and steelhead eggs from the stomachs of *C. asper* from British Columbia.

Measurements were made of nearly all of the downstream and upstream sculpins taken in all seasons except 1933-34, and of some of those taken in 1933-34, but are not presented in this paper.

Some of the sculpins taken in the traps were marked or tagged, but the returns were not sufficient to warrant discussion at this time.

It is believed by the writers that a concentration of sculpins below the dam during the 1933-34 season may have contributed to the poor survival of the year class (1932-33) migrating downstream at that time, although disease (see pages 239-242) or some other factor may have been of greater importance.

(d) *Three-spined Stickleback*. The food of the stickleback at Waddell Creek was not studied. In view of its small size, it is doubtful that

TABLE 89

Stomach Contents of Sculpins Taken at McClinton Creek, British Columbia (After Pritchard, 1936b)

	<i>Cottus</i> sp.	
	1931	1933
Size.....	1¾"—7"	1¾"—7"
Number examined.....	81	84
Number empty.....	59	39
Number containing:		
1 pink salmon fry.....	7	13
2 pink salmon fry.....	3	12
3 pink salmon fry.....	3	9
4 pink salmon fry.....	5	6
5 pink salmon fry.....	1	2
6 pink salmon fry.....	--	1
7 pink salmon fry.....	--	--
8 pink salmon fry.....	1	2
Total pink salmon in stomachs.....	55	120
Average number per stomach.....	0.7	1.4
Total chum salmon fry.....	2	--
Total silver salmon fry and fingerlings.....	8	2
Stomachs containing insects.....	--	1

this species is a serious predator on even small trout and salmon. However, it is considered at this point because of its reputation in this regard in certain quarters, as noted by Kincaid (1919): "The damage done by the Stickleback is out of proportion to his size as he is able to kill the fry of larger fish, notably the salmon, for which reason the Stickleback is known locally as the Salmon Killer." Kincaid does not cite supporting evidence for his statement and it is the belief of the writers that it cannot be accepted without adequate data. Munro and Clemens (1937) found no fish remains in 61 stickleback stomachs from British Columbia.

(e) *Striped Bass*. Under certain conditions striped bass which have entered a stream may consume large quantities of seaward migrant trout and salmon, as shown by Shapovalov (1936). In that paper the writer described the stomach contents of 47 striped bass seined by A. C. Taft and himself in the upper end of Waddell Creek lagoon on April 26, 1935. The larger of these fish (37 to 49 cm. long) had been feeding largely on silver salmon and steelhead fingerlings and sculpins (*Cottus*), while the smaller bass (20 to 31 cm. long) had been feeding almost entirely on small crustaceans (*Gammarus*, *Exosphaeroma*, and *Corophium*), sticklebacks (*Gasterosteus*), and gobies (*Eucyclogobius*).

Shapovalov (*loc. cit.*) also reported on a collection of young trout and salmon from the stomachs of six striped bass taken in the Coos Bay region, Oregon, in April and June, 1930 and 1931. These striped bass contained 10, 11, 14, 15, 20, and 22 trout and salmon fingerlings, respectively. The salmon were practically all silver salmon 100-140 mm. long, evidently seaward migrants.

It is evident from the foregoing that striped bass may cause serious depredations, especially when they are in a position to intercept all seaward migrants, as were the 47 fish seined from the narrow upper end of Waddell Creek lagoon in 1935. It is also possible, although no data are at hand, that striped bass may consume numbers of trout and salmon that have entered salt water.

The effect of the presence of striped bass on survivals at Waddell Creek is not evident, since in 1935 they were seined out about the time of the beginning of the seaward migrations and in other seasons they may have entered the lagoon without being noticed, because of the depth and the murky condition of the water, although a watch was kept for them. It is known that some striped bass have entered Waddell Creek in various years, as shown by the following record:

1927. Unknown number of striped bass of second, fifth, sixth, seventh, and eighth age groups seined in Waddell Creek in May (Seo-field, 1931).

1931. Two dozen striped bass of approximately the same size composition as those taken in 1935 seined in Waddell Creek lagoon by A. C. Taft and J. H. Wales on November 24th. One large, dead striped bass found at the same time.

1932. Two one-year-old striped bass 113 and 114 mm. long seined in Waddell Creek lagoon by J. H. Wales and Leo Shapovalov on April 26th.

1934. One dead striped bass 260 mm. long found in Waddell Creek lagoon by Leo Shapovalov on March 23d.

1935. Forty-seven striped bass 20 to 49 cm. long seined in upper end of Waddell Creek lagoon by A. C. Taft and Leo Shapovalov on April 26th, but first noticed during the early part of March. A few fish escaped the seining.

1938. The field observer, J. H. Cook, caught a 13-inch striped bass in the surf several hundred yards north of the mouth of Waddell Creek in July (?), and afterwards caught two other small striped bass in the surf along the beach near Waddell Creek.

1939. Several striped bass were reported to be present in the upper end of Waddell Creek lagoon in late June. Report not verified.

1941. Anglers caught numerous striped bass in the surf from the beach adjacent to Waddell Creek during the first two weeks of April. One fish is reported to have weighed 16 pounds.

Reptiles

The only aquatic or semiaquatic reptiles found at Waddell Creek are the Pacific Pond Turtle (*Clemmys m. marmorata*) and garter snakes (*Thamnophis*).

(a) *Pacific Pond Turtle*. During the nine seasons of operations only seven Pacific pond turtles were recorded as being taken from the downstream trap, and only very occasionally has an individual been observed in the stream. The seven from the trap were taken between April 8-14 and August 26-September 1. Not more than two were taken in any one season. The Pacific pond turtle is largely a scavenger and bottom feeder and probably is rarely, if ever, a trout or salmon predator. Most individuals probably hibernate during the greater portion of the salmonid spawning season and for this reason, if no other, eat very few eggs.

(b) *Garter Snakes*. Garter snakes in general have been accused of extensive depredations on young trout and salmon by anglers. Fitch (1941) stated that the feeding habits of the different species vary widely, and that some commonly enter water, while others are largely terrestrial.

During the nine seasons of operations, 160 garter snakes were taken from the downstream tank, with the seasonal number varying from 1 to 45. The earliest garter snake was taken April 1-7 and the latest October 22-28. During the same time of year garter snakes were often observed in and about the stream. During the period October through March garter snakes usually hibernate in the Waddell Creek area. The occurrence of garter snakes in the downstream tank during the various seasons is shown in Table A-40 of the Appendix.

According to known distributional records and information recently supplied by Mr. Jay M. Savage, Stanford University (personal communication to Shapovalov, February 28, 1954), the Common Garter Snake (*Thamnophis sirtalis infernalis*) and the Coast Aquatic Garter Snake (*T. couchi atratus*) are known to occur at Waddell Creek, while a third, the Coast Terrestrial Garter Snake (*T. elegans terrestris*),

although not recorded from there, almost certainly is present. Mr. Savage states that the first two are aquatic forms, while the latter is a terrestrial type.

Unfortunately, an attempt to identify the species taken in the trap was not made until the season of 1941-42, and in that season only one individual was taken. This individual, taken in the trap on June 10, 1942, was probably *T. c. atratus*. However, there is considerable doubt regarding the identity of the other individuals taken during the various seasons.

As stated previously, many, if not most, of the salmonids taken by garter snakes are those from drying portions of a stream. At Waddell Creek, the depredations of garter snakes are probably not of major proportions, both because garter snakes are not very abundant and because dropping stream levels do not isolate many pools.

Birds

The fish-eating birds of some importance at Waddell Creek are the Western Belted Kingfisher, California Heron, and Dipper. Birds present but whose fish-eating propensities in this area are not well known are the Common Loon, Pacific Loon, Red-throated Loon, American Egret, Black-crowned Night Heron, American Bittern, Red-breasted Merganser, Southern Bald Eagle, and Caspian Tern. None in this group is present in sufficient numbers to be a serious factor. The American Osprey and American Merganser, which may be serious predators in other California salmon and trout waters, are absent from the Waddell Creek area or are rare visitants. Fish-eating birds which have not been observed to take fish from fresh water in this area, such as the California Brown Pelican, are omitted from consideration.

Of the above birds the only species large enough to attack and eat sea-run steelhead and silver salmon are the California Heron and Southern Bald Eagle, and possibly the American Egret and American Bittern. Altogether, the adult fish killed by all birds form probably less than 1 percent of the runs.

Orr (1942) has given an account of the birds of the Waddell Creek area, but does not discuss their foods.

(a) *Western Belted Kingfisher*. The Western Belted Kingfisher is undoubtedly more adept at catching trout and salmon than any of the other birds present at Waddell Creek, with the possible exception of the Dipper. Very likely an individual bird consumes a considerable number of trout and salmon during the course of a year. However, the number of birds along Waddell Creek is not believed to be large, probably not numbering over a dozen. The Western Belted Kingfisher appears to show a decided preference for the lower, more open portions of the stream over the upper portions in the redwood forest. It is the writers' opinion that the complete elimination of this bird from Waddell Creek would not affect the survival of either steelhead or silver salmon to an appreciable degree.

(b) *California Heron*. The population of California Herons in the Waddell Creek drainage was not large, numbering probably less than half-a-dozen birds. Some time prior to the start of the experiments in 1933 some California Herons, which then roosted in a large tree beside

Waddell Creek in its lower portion, were shot. Since the start of the experiments never more than two birds were seen on any single occasion.

Because of its size, the California Heron is capable of consuming large numbers of fair-sized fish, but it is probably rarely that such an occasion presents itself at Waddell Creek or in other streams unless isolated pools have formed.

In the majority of instances in which California Herons have been observed in the Waddell Creek area they have been in areas not inhabited by trout and salmon, such as the marshy areas around the lagoon and the grassy fields. It is probable that the California Heron finds frogs, rodents, and other foods preferable to or easier to obtain than trout or salmon.

Both at Waddell Creek and at Scott Creek an occasional unspent adult fish with a deep, round hole at the nape, but otherwise in good condition, has been taken in the upstream trap. These holes are believed to have been made by the bills of California Herons.

(c) *Dipper*. The Dipper has often been accused by anglers of extensive depredations on trout, not only because of the fish consumed, but also because of a habit of catching fish and leaving them on exposed stones. One angler told Shapovalov of seeing 22 small trout laid out on a stone by a Dipper (not at Waddell Creek). Shapovalov has also seen a single bird consume 15 small trout that had died in a hatchery in the Sierra Nevada and had been thrown into the adjacent stream. To secure these trout the bird had to dive to the bottom of a fairly deep pool.

In favor of the bird it may be said that it is known to feed extensively on other foods, such as aquatic insects, and that it is not usually abundant. By its own size the Dipper is limited to fish of small size. There is no way of estimating the effect of the Dipper on the trout and salmon populations at Waddell Creek, but the writers do not believe it to be serious.

(d) *Southern Bald Eagle*. Southern Bald Eagles have been seen in the Waddell Creek area on various occasions, but they may be classed as only occasional visitors. As regards adult steelhead and silver salmon, these birds probably very largely consume spent dead or dying fish. Southern Bald Eagles probably are not a factor of consequence to the salmon and trout populations of any streams in California.

Mammals

The only terrestrial fish-eating mammal found at Waddell Creek is the California coon. Coons eat considerable quantities of adult steelhead and silver salmon, but the writers believe that the fish consumed are very largely dead or dying spent individuals, and that it is doubtful that coons have an appreciable adverse effect on the salmon and trout populations of the stream or of other streams.

As coons eat the fish, they peel the skins back from head to tail until the empty skin is left like a glove turned inside out. During the 1933-34 season, when the adult steelhead were tagged, it was often necessary to turn the skins right side out to locate and remove tags.

Crayfish

The species present in Waddell Creek has been identified by W. L. Schmitt of the U. S. National Museum as *Astacus klamathensis*, which is found also in the Columbia, Smith, and Klamath rivers.³⁹ Its origin in Waddell Creek remains obscure. It may be endemic, since there are early records of crayfish in neighboring streams. On the other hand, various individuals have informed Shapovalov of transplantings of crayfish made by different persons in neighboring streams during the past 40 or so years, so the species may have been introduced. This view is supported by the statement of Rathbun (1884, page 813) that *A. nigrescens* was "the only species found in the vicinity of San Francisco" at that time. Mr. Theodore Hoover, owner of the property, had not seen crayfish in the stream until some were taken in the trap. The rapid increase of the species in Waddell Creek during the course of the experiments indicates either a comparatively recent introduction or a tremendous population increase. During the first five seasons of operations (1933-34 through 1937-38) Shapovalov made repeated trips along the stream, wading the length of the lower portions many times, but saw only one or two small individuals. During the same five seasons not over two were taken in the downstream trap. In 1938-39 three were taken in the downstream trap, in 1939-40 there were 77, in 1940-41, 276, and in 1941-42, 471. At the close of the experiments they were quite common in sections of the stream where very few were seen during the first five seasons. The numbers taken in the downstream trap in each season by four-week periods are shown in Table A-41 of the Appendix.

The significance of the downstream migration has not been determined. Crayfish with eggs have been recorded from October 8-14 through December 31-January 6. One with two young (11 and 14 mm. long) was taken during the week of March 4-10, 1942.

Crayfish have sometimes been accused of predation on young salmon and trout. At Waddell Creek, however, many hours of observation (by several observers) failed to indicate such predation.

Crayfish were found rather to subsist largely on organic detritus stirred up from the stream bottom, and occasionally on carrion. They sometimes caught small steelhead and silver salmon in the trap, although they were never seen to stalk them there. It is probable that the confinement of the trap aided the capture. Crayfish probably capture some diseased and injured fish in the stream, but it is doubtful that they are capable of catching healthy fish.

Insects

At Waddell Creek, two species of giant water bugs (family Belostomatidae) are present and may occasionally prey on young trout and salmon when the opportunity presents itself. However, their fish depredations probably play a minor role in the economy of the stream.

It is of interest that both species, a very large one, *Lethocerus americanus* (Leidy), and a small, oval one, *Abedus hungerfordi* De Carlo (identifications by Robert L. Usinger of the University of California), migrate downstream, especially during the spring and summer months. Table A-42 of the Appendix shows this. In the table the two

³⁹ In accordance with recent nomenclature, the generic name becomes *Pacifastacus*.

species have been lumped together, since the field notes did not distinguish the species in all instances, but probably 90 percent of the total is represented by the smaller species, *Abedus hungerfordi*. The males of this species, but not those of the larger one, carry the eggs on their backs. The significance of the downstream migrations is not known to the present writers, and the cause of the apparent decline in numbers of migrants during the course of the experiments is not apparent.

In the comparatively limited confines of the downstream trap the giant water bugs occasionally seize and eat a small trout or salmon, but it is doubtful that they have an opportunity to do so in the open stream, unless the fish are sick or injured.

The giant water bugs just discussed represent the two common species in California.

Predators at Sea

As has been seen in the sections on "Survival", considerable losses occur among both silver salmon and steelhead between the time that they leave fresh water and the time that they return as adults. Little is known of the life of salmon and trout at sea, and so little of the proportionate toll taken by predators, disease, and lack of food. The latter cause of mortality, if and when a factor of importance, probably occurs only soon after the fish have entered salt water.

It is not improbable that the major mortality in the ocean is caused by predators, of which there are some capable of preying on salmon and trout of all sizes.

Sea lions have been accused of extensive depredations on steelhead and salmon by sportsmen and commercial fishermen. The extent of such depredations is difficult to determine, largely because of the difficulty in securing stomachs of sea lions at the proper time of the year. Individuals swimming in the water are difficult to shoot, and many of those that are shot sink or cannot be recovered because of difficulties in reaching them.

It must be recognized that because of their size and agility sea lions are capable of catching large, fast-swimming fishes. Therefore, if they are partial to salmon and steelhead, they may be expected to cause extensive depredations, because of their large numbers along the northern and central California coasts.⁴⁰ Whether they actually favor salmon and steelhead as a food over other forms of marine life is a moot point. Many individuals have reported seeing sea lions catch salmon and steelhead along the coast, particularly near piers and wharves. Observers have reported that occasionally the sea lions on catching a large fish have not eaten it, but have tossed it into the air and gone to another fish, as in play. Uncertainties in identification of the fish involved help to make it difficult to analyze the significance of such reports.

Circumstantial evidence that sea lions feed on salmon and steelhead lies in the appearance of the sea lions near the mouths of California

⁴⁰ Two species of sea lions are found along the coast of California. The Steller Sea Lion (*Eumetopias jubata*) ranges from the Channel Islands of southern California northward to the Bering Sea, while the California Sea Lion (*Zalophus californianus*) occurs from Pt. Reyes and the Farallone Islands off San Francisco southward into Mexico. The former is by far the more abundant species off the California coast.

streams during the time of entry of the salmon and steelhead. From one to half-a-dozen sea lions may usually be seen at the mouth of Waddell Creek (and other streams of comparable size) during the times that the salmon and steelhead are entering. During these periods the animals come very close to shore, swimming through the breakers. At Waddell Creek they have been seen to approach within 50 yards of the mouth of the stream. It is not known whether the same individuals are seen during the course of the steelhead and silver salmon spawning season, or whether they are replaced by others.

A considerable number of the silver salmon and steelhead taken in the upstream traps at Waddell Creek and at Scott Creek have had scars in the form of a "V" or "W" or some portion of a "V" or "W," or an inverted "V" or "W," on their sides. Usually these scars, the lines of which are several inches long, are well healed. It has been suspected that these scars were made by sea lions, but this has not been proved. During portions of several seasons a graphic record was made of all scars on silver salmon and steelhead taken in the traps at Waddell Creek and at Scott Creek; it is hoped to analyze this record at some future time.

Further knowledge regarding the extent of depredations by sea lions would be of particular interest in the case of Waddell Creek in view of the fact that the largest Steller sea lion rookery in California is located only a little over three miles away, at Año Nuevo Island. The herd there numbers 2,500 animals at times, and up to 200 California sea lions have also been counted at this rookery. According to Bonnot, Clark, and Hatton (1938) the sea lion population along the entire coast of California at the time numbered on the average approximately 5,600 Steller sea lions and 1,600 California sea lions. Bonnot (1951) listed 9,000 as the approximate number of sea lions along the coast of California.

An accurate picture of the relationship of sea lions to salmon and steelhead could be obtained only by examining stomachs taken from animals not only in the open sea or on land but also off the mouths of salmon and steelhead streams during the period of the spawning runs.

The Harbor Seal (*Phoca vitulina*) is occasionally to be seen off the mouth of Waddell Creek. Its relationship to steelhead and silver salmon is not known, but is not believed to be of importance.

RECOMMENDATIONS FOR MANAGEMENT

Proper recommendations for the management of any species should consider that species in relation to its total environment, including the human beings who will be concerned with its utilization. The demands of various segments of the population for its sporting or commercial utilization, the funds, facilities, and personnel available to conservation agencies, and expected changes in these factors must all be considered. To be able to formulate such recommendations, however, it is first necessary to know the basic facts about the biology of the species concerned. To gather these basic facts and present them in usable form has been the main function of the present study.

The problems that concern the steelhead have been well presented by Taft (1933). Intensive fisheries for both the adult and immature

steelhead create too great a drain on the species. In many of our coastal streams the immature fish face the additional difficulty of low water during the dry summer season. Such streams can support only limited numbers of fish of angling size.

By contrast, immature silver salmon (and king salmon) are subjected to relatively little fishing. The adult salmon, however, must withstand, in addition to the sport fishery, an extensive commercial fishery. The numbers of seaward migrants must be great enough to maintain these fisheries with adequate numbers of adults.

Detailed studies such as the present one, although yielding much indispensable information, cannot alone provide direct answers to all problems of management. For example, no matter how definitely, correctly, and completely we know the biology of the steelhead, we cannot on that basis alone answer positively what the bag limit should be. Knowledge of the biology of the fish is essential to an understanding of what effect certain regulatory measures will achieve, but such regulations must also be made on the basis of the factors previously outlined—environment, demand, and management resources—and anticipated changes in these factors.

Although specific management practices will be proposed in this section, it must be realized that even if put completely into effect they will not create *complete* management. The Department of Fish and Game does not have control over the land, except in some limited phases. Many of the problems encountered and many of the ill effects on the fishes have resulted from the methods of land and water use now in effect. Deforestation through lumbering and pasture clearing has caused erosion along the streams, greater floods, higher water temperatures, and lower water in the summer months. Grazing has had approximately the same effects. Many new dams have impeded or blocked the runs of spawning fishes, destroyed spawning areas, diverted the natural flow of the streams, increased water temperatures, and caused fluctuation of the water. Control over these factors lies largely outside the province of the Department of Fish and Game.

One other fact must be realized to evaluate correctly the measures and recommendations proposed and now in effect, namely, that sometimes different management methods will give the same results. For example, the maintenance of the population of silver salmon in a given stream may be expected to be achieved *either* by a given season and bag limit, or a larger bag limit but shorter season, other things being equal. The choice must in this case depend upon the desires of the angling public. Similarly, in another instance a population may be maintained with a certain season and bag limit, and natural propagation, or with a more liberal season and bag limit, and intensive stocking. In this case also the choice must depend upon the desires of the angling public, plus the funds, facilities, and personnel available to conservation agencies.

Of the five species of Pacific salmon found along the Pacific Coast, only the king salmon and silver salmon occur in significant numbers in California. Although the king salmon is still much the more important, the silver salmon may be expected to become increasingly important in the future with the construction of still more dams and diversions. The silver salmon is more commonly found in the smaller streams and

tributaries near the coast, which are less subject to human interference and development than the large stream systems, like the Sacramento-San Joaquin and Klamath, that are favored by the king salmon. The elaborate water utilization plans for these stream systems will ultimately cut off most of the present king salmon spawning areas.

Present trends point toward a vast development of the northern areas of the world: Siberia, Canada, and Alaska. It is to be expected that many phases of this development will adversely affect the salmon fisheries of those areas in the manner that has taken place in the United States, with the result that the salmon fisheries of California will assume a *relatively* more important position.

From this long view of the present and future place of the salmon and trout fisheries in California, we may now proceed to an examination of specific measures to be applied in a management program. A sound program of management should include wise conservation legislation, good enforcement of this legislation, improvement of the physical and biological habitat, pollution control, and fish rescue and artificial propagation, when and if necessary. These various phases of management are treated below.

Regulation

Regulations governing the taking of salmon and steelhead should be designed to provide the *maximum sustained yield*, that is, the widest use of the resource possible without causing depletion. Regulations formulated for any given area should also consider adjacent areas, for if the regulation of adjacent areas is not coordinated, there is danger of an undue burden being placed on one or more of them. This applies especially to seasons. If the trout season opens at different times on two nearby streams, anglers naturally concentrate on one and then the other. Quite naturally, too, the more regulations there are the more confusing and irritating it is to the angler and the more difficult is made the work of the law enforcement officer. A multiplicity of local regulations also hinders studies of the effects of management policies. In general, therefore, regulations should be as uniform as is consistent with basic biological requirements.

The California Fish and Game Commission (like the Oregon Game Commission and the Washington Game Commission) has the power to promulgate regulations governing game fish. Such regulations are formulated annually. Additional laws and regulations concerning game fish are enacted by the state legislatures in all three states.

The take is variously regulated by means of bag limits, size limits, season limits, closed areas, and restrictions on angling gear and methods. One very important fact which must be considered is that only the take of the individual angler is restricted; the total annual take of game fish is not directly limited in any body of water. Under such conditions angling regulations will remain a management tool of limited effectiveness in the maintenance of the steelhead and salmon fisheries.

Since steelhead are taken by anglers as sea-run adults and also as fish which have not yet migrated to salt water, and since the latter are very difficult to distinguish from resident rainbow trout, it is inevitable

that the freshwater regulations governing the species are quite complex. Comparatively little fishing for steelhead exists in offshore waters, and so regulations governing such angling are relatively simple.

It is the general practice in California (and also in Oregon and Washington) to set up a winter season for the sea-run adults and a summer season for the immature and resident fish.

The daily bag limit in the three states during the winter season is mostly two or three fish. Oregon and Washington also have weekly and seasonal limits, while California does not.

Oregon and Washington both employ minimum size limits during the summer season, while California does not, using other means (such as closed areas and closed seasons) to protect the immature steelhead and salmon.

In California, the laws pertaining to steelhead and salmon angling had grown so complex that in January, 1948, the Fish and Game Commission, on the recommendation of the Bureau of Fish Conservation, revised them. These greatly simplified regulations have remained essentially unchanged since then.

The present offshore sport fishing regulations for salmon and trout provide a yearlong open season in the northern part of the State and a season extending from February 15 to November 15 in the southern part with a daily bag limit of three fish in the aggregate in the north and two fish in the south; one undersize salmon may be included in this daily bag limit.

The river fishery regulations provide a winter season and a summer season for taking trout and salmon. The winter season is designed to regulate the fishery for the adult steelhead and salmon. It varies to some extent for different groups of streams, with the longest season for any group extending from November 1st to the last day of February and the largest bag and possession limit consisting of three trout or salmon in the aggregate. Fishing in tributary streams other than those listed in the regulations is prohibited.

The summer season is designed to regulate the fishery for juvenile steelhead and salmon. In northern California steelhead and salmon waters it extends from the end of May through October, with a bag and possession limit of not more than 15 trout and salmon in the aggregate, nor more than 10 pounds and one fish in the aggregate in the round, provided that irrespective of weight at least three such fish in the aggregate may be included in the daily bag and possession limit.

Although these existing regulations are generally satisfactory, some changes are desirable. It is especially important that the summer season in the coastal steelhead and salmon waters, if permitted at all, open not earlier than the end of May. Quite a number of coastal streams are now open during May, which is one of the principal periods of seaward migration of the young steelhead. Most of these fish are under six inches in length. They are too small to provide much pleasure for the true sportsman, yet large enough to take good care of themselves and insure the survival of a sizable proportion as spawning fish a year or two years later. A closed season until the end of May protects large numbers of stream steelhead that have not completed spawning, as well as a certain number of spent sea-run steelhead returning to the ocean. It also affords

great protection to the young silver salmon. Most anglers do not distinguish young silver salmon from young steelhead and are unaware that their catches during the early part of May often contain from 30 to 50 percent young silver salmon. The seaward migration of these fish, practically all of which are under six inches in length, is heaviest during the month of May. *Protection of this migration not only insures better angling for the adult silver salmon in the autumn, but also helps to preserve the important commercial fishery for this species.*

It is also very important that at least the lagoons and tidal waters of all coastal steelhead streams and in some instances additional portions of their lower reaches be closed at all times except during the winter season for adult fish. It is in these portions of the streams that young steelhead make their most rapid growth before entering the sea.

Study is being given to the following possible changes:

(1) Closure of the summer season and bag limit on September 30th instead of October 31st and opening of the winter season on October 1st instead of November 1st.

(2) Extension of the winter season through March 31st instead of the last day of February.

(3) Extension of angling during the winter season to some major tributary streams.

(4) Abolition of or changes in size limits for ocean-caught salmon.

Just what would be accomplished by these changes?

(1) The closure of the summer season on September 30th would greatly curtail the take of young steelhead which had migrated to the lower reaches of the streams in the spring and remained there throughout the summer, making rapid growth. In certain years of late rainfall large numbers of such steelhead have been taken in October, especially in the Eel River.

The September 30th closing date would also provide a considerable measure of protection for the so-called "half-pounders," the young steelhead weighing usually from one to two and one-half pounds. The writers believe that these fish are inadequately protected by present regulations. They usually make their appearance in the lower Eel River in August (sometimes even in July) and *from then until November 1st may be taken legally at the rate of 10 fish weighing one pound each plus one fish of any size.*

Under the proposed regulation these fish could still be taken at this rate through September 30th, but would be protected in October.

From October 1st to the last day of February, inclusive, they could still be taken along with the large fish, so long as the total number of fish did not exceed three. It is hard to believe that a greater daily bag limit may be allowed without causing depletion, unless the taking of small fish be prohibited entirely.

(2) A study of the merit of extending the winter season through March 31st has been proposed because of the possibility that certain segments of the runs are not now contributing to the fishery. In other words, if the late running fish which ascend the streams in March also produce fish which are late running, a resource is not being utilized.

Shapovalov (1954) has shown that in California such an extended winter season would expose 94 percent of all male steelhead and 89 percent of all female steelhead to angling, whereas under the present

general open season 71 percent of the males but only 53 percent of the females are exposed to angling. From the viewpoint of total age, the youngest fish run first during the season and are followed in succession by progressively older fish. Thus, the present general open season of November through February, especially in the first three months, exposes mainly males and younger fish, while an extension of the season through March would expose an additional group in which females and older fish predominated.

Unfortunately, the two most critical factors bearing on an extension of the steelhead season have not been determined: (1) the proportion of the total run which is being harvested by anglers each year in various types of streams is not known; (2) it is not known if the progeny of fish running in March return to spawn primarily in March, like their parents, or scatter throughout the season.

While it is possible that the offspring of steelhead which run in March also return as adults primarily in March, it appears more probable that they do not, in view of the preponderance of females in March. These late-running fish may be important out of all proportion to their numbers in maintaining the runs, since survival of eggs and fry is probably highest from late spawners because of reduced loss from floods and in view of the preponderance of females.

Efforts should be directed toward obtaining the answers to the two problems outlined above, but it will take several years to get the answers. Until we are sure of the facts, it seems wise to take no chance of jeopardizing our valuable steelhead resource. Therefore, the writers recommend against any general extension of the winter steelhead season at the present time.

(3) Consideration should be given to the extension of the winter season to include some major tributaries which are now closed. The purpose of closing the tributaries for adult fish during the winter season has been to protect the fish on their spawning grounds. The theory of such regulation is correct, but the writers do not believe that in practice sufficient fish would be taken in some *major* tributaries now closed to warrant keeping them closed. Extension of the winter season open areas, if carried out judiciously, might prove to be the most effective way of increasing the harvest to the maximum allowable without injury to the resource.

(4) Consideration should be given to changes in the ocean size limit, or to abolition of minimum size limits altogether. Any changes should be made only after careful study, since they could have unforeseen consequences. For example, scale examinations of samples of king salmon caught some 30 years ago and recently indicate that the taking of the larger fish (and therefore the fish of the older year classes) has changed the populations so that now the dominant age at maturity is three years instead of four years.

With the existing size limit, many undersized salmon are caught in the ocean fisheries, both commercial and sport. Except for the single undersized salmon allowed in a daily sport bag limit, such fish are generally released by a flip or violent jerk of the line, which often seriously injures the mouth parts of the fish. Subsequent examination

in streams has shown that many such fish survive these injuries, but it is not known how many die and the whole question of minimum size limits needs further evaluation from this standpoint.

In conclusion, it may be pointed out that regulations are the one form of management which requires no monetary expenditure, except for enforcement. It is obvious that good enforcement of sensible regulations is essential.

Physical Habitat Improvement

Physical habitat improvement is perhaps the most obvious type of management, other than artificial propagation, in that it produces visible results which can be measured at least partially, e.g., in terms of miles of spawning stream opened by removal of a dam or other barrier.

Certainly, it appears sensible to effect all reasonable physical habitat improvement before indulging in other forms of management, if there must be a choice. In northern California, desirable physical habitat improvement includes principally (1) stream clearance (removal of log jams and debris clogging stream channels); (2) removal of unused dams and reduction of natural barriers; (3) maintenance and improvement of stream flows; (4) uniting of flows at mouths of small tributary streams, generally making entrance and exit for fish to and from these streams more accessible; (5) opening channels from streams and pools cut off from the main streams at low water; and (6) screening of water diversions.

There can be but little doubt that improvement of the type outlined above would aid materially in the conservation of salmon and trout in the coastal streams by improving shelter and spawning grounds, making spawning grounds more accessible to adults, facilitating egress of juvenile seaward migrants from tributaries to the main streams, and assisting fingerlings in their ascent of small tributaries when the water in the main streams becomes too warm. However, the activation of such a program remains a complex matter.

The principal obstacles to the carrying out of such a program appear to be (1) private ownership of property and (2) lack of man power. Some of the streams in which improvements would be desirable lie on National Forest land, in State Parks, or on municipally-owned property, but others are on privately-owned land. The matter of personnel from the Department of Fish and Game working on private property involves (1) the question of the propriety of the State's making improvements to private property, and (2) possible damage suits, for example, in the case of damage to property from material from log jams that had been broken up. Despite these obstacles, it is believed by the writers that such improvements would bring so much good to the angling public and to the commercial fisheries, that improvements even on private property would be justified and that releases to preclude damage suits could be arranged.

In years of deficient runoff, late summer flows in the lower reaches of some of the north coast streams, including the Eel River, are not satisfactory. Occasionally large numbers of adult fish, especially king salmon, which have made their entrance from the ocean are unable to ascend upstream and are vulnerable to natural mortality and illegal snagging and spearing.

Possibilities of improving the conditions described above through the construction of dams from which releases would be made during the low-water periods should be explored. For example, the U. S. Corps of Engineers has found that it would be physically possible to provide a minimum flow of up to 300 second-feet in the Eel River at Scotia by the construction of a dam on the South Fork of Eel River near Rattlesnake Creek. Obviously, most such dams cut off some spawning grounds, and in each instance the improvement in flows must be weighed against loss of spawning area.

Physical improvement of streams through the opening of mouths of tributaries into the main streams, uniting of side channels with the main stream, and improving entrances of small tributaries into main streams may be termed the "annual" type of stream improvement, in that much of the work must be repeated each year. Such work is not spectacular, but is well worth while and is not costly.

The above type of work may be carried out in part by the same men who do the fish rescue work, or by regular stream improvement crews. Two men working together form an efficient team that can perform all but the heaviest work, if provided with the proper equipment.

There are but few water diversions in the north coast area and so screening does not present a major problem there. In Trinity and Siskiyou counties, however, diversions are more numerous and adequate screening of them to prevent loss of young salmon and steelhead is highly desirable. For many years unsatisfactory laws formed a major block to an adequate screening program. These laws were revised by the 1951 Legislature and the screening of diversions in these two counties is now about 75 percent complete. The Department's present program in Trinity and Siskiyou counties has been described by Wales (1948) and Wales, Murphey, and Handley (1950).

One of the most important things that could be done for the improvement of the coastal trout and salmon waters would be the prohibition of cutting of trees within a certain distance of any stream, say 50 feet to 50 yards, and the recommendation is here made that legislation to this effect be sought. Such legislation would not only be of help to important fisheries, both commercial and sporting, but would also be of great importance in preventing erosion, thus effecting flood control at the source, and in maintaining a more esthetically pleasing appearance of our streams for the many thousands of sportsmen and vacationists.

The possibility of environmental improvement through the installation of stream improvement devices that are suitable to California's coastal streams from the points of view of durability and creation of desired effect should be explored further. These devices should probably be of the kind that cause the stream to create holes by a digging action. An experimental program to determine the most suitable types of such devices and to study their mechanical action and influence on fish was started at Waddell Creek in 1940. The program was discontinued shortly after the start of World War II, due to lack of man power, and since the results achieved were inconclusive, will not be reported upon at this time.

In summary, physical habitat improvement in northern California salmon and steelhead waters offers definite possibilities which should be immediately and thoroughly explored and exploited when found to

be feasible. The general stream clearance and barrier removal program should be continued. Some of the specific situations would require the expenditure of considerable sums, but might produce results worth much more. Certainly, it seems wise to increase the carrying capacities of the streams to the practicable maximum before spending large sums on other forms of management to increase the numbers of fish.

Biological Habitat Improvement

By biological habitat improvement is meant the improvement of the biological environment for the fishes which it is desired to maintain. It means the control of predators and competitors, and the maintenance of an adequate food supply. Among predators are included animals both within and outside the waters: other fishes and snakes, birds, mammals, and invertebrates. Competitors are composed chiefly of other fishes. These may be competitors for food, for spawning grounds, or simply for space. Predators may affect the adults, the immature fish, or the eggs.

Biological habitat improvement in salmon and steelhead waters has received relatively little study, but several leads which have been uncovered should be followed up. Success in each case is by no means certain, but the potentialities are so great that thorough investigation should not be neglected. Witness the rough fish control programs that have been made possible by the chemical treatment of lakes and reservoirs.

One promising lead was discovered recently when it was found in the course of studies made by the Department in Prairie Creek (Briggs, 1953) that apparently oligochaete worms are causing considerable damage to eggs of salmonids in the spawning gravels. If a means of control could be found, the survival among the eggs might be increased appreciably.

Contrary to the hopes of some sportsmen, there appears to be little reason to expect that much can be accomplished through the introduction of the smaller food organisms or of plants. In general, such organisms spread rapidly and easily by natural means, and the absence of desirable organisms in a body of water usually means that environmental conditions are not suitable for them or comparable forms.

The introduction of fishes, and mammals such as beaver, is easier to accomplish, but is a very complex matter, with manifold ramifications within the field of ecological relationships, and must be studied carefully. It is the belief of the writers that in the coastal streams generally the native salmon and trout should be preserved, and that exotic species of fishes should not be introduced, unless new and very conclusive evidence points in their favor. In nearly all cases the introduction of exotic species of fishes where a valuable game or commercial fishery for native species has existed has yielded unsatisfactory or doubtful results. If a native game or commercial fishery has produced unsatisfactory results, it will usually be found either that various man-introduced factors have produced depletion, or that natural environmental conditions are responsible for the unsatisfactory conditions. Consequently, the introduced species are liable to be affected in the same manner by the depletion-creating factors or the adverse environmental

conditions. The remedy then obviously lies in improving such factors and conditions for the native species, as discussed in other portions of this section.

The improvement of existing stocks through selective breeding and the introduction of various strains or races is a somewhat different matter, and offers some promise, particularly in the case of the steelhead. Some work along these lines has already been started by the California Department of Fish and Game.

The elimination or control of undesirable species offers more promise than the introduction of desirable species, but like the latter is a matter involving complex ecological relationships and therefore possibly unforeseen results.

The role of birds as predators on salmon and steelhead should be determined more exactly. An important start on one phase of this subject was made in 1938 and 1939 by Elden H. Vestal of the Department's staff, who made a study of the feeding habits and other phases of the life history of mergansers, the "fish ducks" of local residents, in the Eel River drainage.

The control of undesirable species of fishes, the so-called "rough fish" or "scrap fish," might be executed by several means. Rough fish could be removed on a large scale by seining, trapping, or chemical treatment, if it is decided that it is desirable to reduce their numbers or to attempt to eliminate them. It might also be possible to control certain of the species (e.g., lampreys, sculpins, suckers, and some cyprinids) by erecting barriers in the streams high enough to bar their upstream migration, but low enough to permit steelhead and salmon to jump them. Lampreys appear to constitute a very real menace to salmon and steelhead in certain instances and should receive further study.

The introduced sunfishes and brown bullhead are probably undesirable elements in stream systems such as the Eel and Klamath, but there appears to be no economically justifiable way of eliminating them from the entire systems. Where they are found locally there is a possibility of eliminating them entirely, if the effort is deemed justifiable.

The matter of predators has been discussed in the preceding section, in which it was pointed out that other fishes are usually the most serious predators. The possibilities for the control or elimination of undesirable species of fish predators have already been noted. The greatest danger in making a great issue of predators in general, as is done by many anglers in California, lies in diverting attention from other causes of depletion, such as diversion of water, deforestation, and overfishing, which alone could cause depletion, even if no predators existed or if all predators were eliminated.

Pollution Control

Strenuous efforts and constant vigilance should be maintained in order that all forms of pollution in the salmon and trout streams be prevented. Any violations of the pollution laws should be vigorously prosecuted and the conditions immediately remedied. In general, industrial pollution is not a major problem in the coastal area, being confined to isolated instances, principally from wineries, creameries, tanneries, dumps, sawmills, and millponds. Pollution from mining silt is of considerable importance in the Klamath River watershed; efforts

are now being made and should be continued to give the utmost possible protection to salmon and trout. Pollution from sewage is not a general problem, but has had ill effects in some cases; a number of communities are now installing sewage disposal systems. Great disregard for proper disposal of slashings and unwanted logs from lumbering operations is still practiced. The log jams thus created block spawning fish, destroy spawning grounds, and so change the character of the stream bottom that fish food organisms are destroyed. In his 1938 survey of the Eel River system, Shapovalov (1939c) found that practically every stream whose watershed had been logged off contained log jams. Conversely, these were rarely found in streams flowing through virgin timber.

Fish Rescue

The fish rescue work in the north coast area has been very worthwhile and should be continued and expanded to provide as complete coverage as possible. It should be improved by planning a regular stocking program for each rescue crew, this program to be based on *need* for stocking, rather than on simply accessibility of the waters being stocked. At least one man with each crew should have had fish rescue experience in that area during a previous year. This is highly important for both the fish rescue and the stream improvement.

Although the numbers of steelhead and salmon rescued in the north coast area are impressive in themselves, they take on added significance from the viewpoint that it is to be expected that their survival is higher than that of hatchery fish of comparable size.

Artificial Propagation

It is difficult to break old concepts and to think along new lines. But when the evidence points strongly in favor of a change of thought, then it is fair and necessary to do so.

For many years it has been the popular conception that artificial propagation of trout and salmon and the stocking of streams were the complete solution to the problem of maintaining the fisheries of a stream or stream system. It is the writers' belief, however, that stocking *alone* cannot hope to maintain fishing at its present level in the coastal streams. Moreover, the writers believe that the *amount* of natural propagation is so great that even with a very favorable survival rate artificially propagated fish would not form more than a minor part of the total production. Shapovalov (1939a, 1939b) made the statement that "probably . . . if no fish cultural work had ever been done on the Eel River the quality of fishing and the size of the spawning runs would be at least 90 percent of what they are today". This statement was based on careful field observations which showed no apparent differences between stocked and unstocked streams, either in the number of fish present or the quality of the fishing. It has been shown definitely that adult silver salmon, steelhead, and king salmon return to the stream which they left on their seaward migration as young fish; consequently, if stocking of the type that had been carried on for many years (small fingerlings planted mostly in midsummer) were producing results that gave the stocked streams a marked advantage over the unstocked streams, the spawning runs in them should have been noticeably larger, but this was not the case. The quoted statement was in a

sense speculative in that it attempted to show what would have taken place had not something else been done. Additional support for the statement now appears from the fact that since the almost complete abandonment of stocking in the Eel River system in 1939 the runs, as judged by the counts of adults at Benbow Dam on the South Fork of Eel River, have not shown a downward trend (Table 90). Of course, change of the opening date of trout season from May 1 to the end of May, a limited amount of stream improvement work, and a greatly expanded fish rescue program, all in effect since 1938, have to varying and unknown extents contributed to the maintenance of the runs.

The indicated inefficiency of stocking as carried on in the Eel River system should by no means be interpreted to mean that all artificial propagation is useless. The experimental programs at Waddell and Scott creeks have shown that although extremely small returns may be expected from fish in their first year of life, on the average approximately 2 to 5 percent of yearling steelhead and silver salmon allowed to descend to sea at their normal migration time may be expected to return as adults, and that survival among older and larger steelhead is considerably higher, increasing with the size and age of the fish. Therefore, some stocking of aged fish may be desirable in the coastal streams, especially in heavily fished streams. In such case, emphasis should be placed on planting yearling fish in barren sections of streams above falls and other barriers and the planting of areas in which adverse climatic conditions or very small spawning runs have caused subnormal natural propagation. In other words, artificial propagation should be considered an *aid* to natural propagation, rather than a replacement of it.

The most hopeful solution to the problem of maintaining successful and *varied* angling in the coastal area of California as a whole appears to be to provide *summer* fishing by planting aged trout in heavily fished bodies of water, often those blocked to sea-run fish, and to have the winter fishing for adult salmon and trout depend largely upon natural propagation, aided by habitat improvement, fish rescue, and specialized

TABLE 90

South Fork of the Eel River (at Benbow Dam): Adult Fish Checked Upstream Through Fishway

Year	King salmon	Silver salmon	Steelhead
1938*	6,051	7,370	12,995
1939	3,424	8,629	14,476
1940	14,691	11,073	18,308
1941	21,011	13,694	17,356
1942	10,612	15,037	25,032
1943	7,264	13,030	23,445
1944	13,966	18,309	20,172
1945	12,488	16,731	13,626
1946	16,024	14,109	19,005
1947	13,160	25,289	18,225
1948	16,312	12,872	13,963
1949	3,803	7,495	13,715
1950	14,357	12,050	15,138
1951	12,476	11,441	13,774
1952	7,256	3,711	19,448

* 1938 refers to counting year 1938-39, etc.

stocking. Under such a program summer fishing in the streams in which a winter fishery is to be maintained should be limited in the ways recommended previously in this report.

SUMMARY

The Steelhead Rainbow Trout, *Salmo gairdneri gairdneri* Richardson, and Silver Salmon, *Oncorhynchus kisutch* (Walbaum), are two of the most important fishes found along the Pacific Coast of North America. Despite the existence of considerable published information about them, quantitative life history data have been lacking. To secure such data, so necessary for sound regulatory, stocking, and other management programs, a program of study was initiated at Waddell Creek, a typical coastal stream in Santa Cruz County, California, in 1932.

The plan of the experiment was to study the steelhead and the silver salmon in their natural habitat.

Waddell Creek was chosen as a representative California coastal stream under more or less natural conditions, large enough to possess a full biota and small enough to be dammed at reasonable cost, and so situated that it could be kept under observational and legal control as a unit, with the general public excluded.

The information gathered at Waddell Creek was complemented by other types of data (especially egg counts) secured at nearby Scott Creek, where a State egg collecting station was located. "Homings" and "straying" between the two streams were also studied.

The basic physical portion of the Waddell Creek experiments consisted of a dam and two-way trap for counting and examining upstream and downstream migrants. This trap has been described in detail by Taft (1936).

The dam and trap were constructed during the summer of 1933 approximately 7,250 to 9,250 feet above the mouth of the stream (the distance depending upon the varying location of the mouth) and 3,300 feet above the uppermost limit of tidewater.

A yearly "season" from October 1 of a given year to September 30 of the following year was chosen for the purpose of the studies. At Waddell Creek and neighboring streams the spawning seasons, hatching seasons, periods of emergence from gravel, and principal upstream and downstream migrations of both juvenile and adult steelhead and silver salmon are completed within this period.

All adult fish entering the trap were sexed and measured and scale samples were taken from them for life history determination. The number of adults of each life history category in each season was thus determined. This was the first and most important step in determining the population fluctuations from season to season.

The second and more difficult step was the determination of the number of juvenile fish of each age moving from the stream to the ocean in each season. During high water only a portion of the water could be strained through the trap and thus only a portion of the downstream migrants could be captured. The percentage of such fish taken in the trap was calculated through the marking of trapped migrants by the removal of alternate pectoral fins and the adipose in

each season from 1933-34 through 1937-38 and the recovery of returning adults. The total number of migrants in any one year was then calculated in accordance with the proportion of marked to unmarked fish of the same life history.

Waddell Creek is located in central California, entering the Pacific Ocean approximately two-thirds of the way from San Francisco to Monterey Bay. In its general characteristics it is typical of the great majority of California coastal streams of like size. Moreover, in miniature it is almost a replica of the larger stream systems, such as the Klamath and the Eel. This fact is of great importance in that the habits and ecology of the trout and salmon in the small streams and large ones are basically similar. Consequently, the conclusions regarding the proper management of these fishes derived from the present study are applicable, at least in the broader aspects, to the coastal streams in general.

Waddell Creek is near the southern border of the humid coast belt. The headwaters of most of the streams in this belt are subject to a great deal of precipitation during the winter months. The headwaters portion of Waddell Creek has a mean annual rainfall of between 55 and 60 inches, while the watershed near the coast receives about 30. More than one-half of the rain falls during December, January, and February.

Because of the distinct wet and dry seasons, there are tremendous fluctuations in the flow of most of the coastal streams.

Like nearly all California coastal streams, Waddell Creek terminates in a drowned mouth or lagoon, which is subject to tidal action when not closed by a sand bar. Some streams have characteristically "large" lagoons, while others have "small" lagoons. The mouths of only a few of the larger California streams (Klamath River, Eel River, Noyo River) regularly stay open during the summer months. At Waddell Creek the permanent closing date varied from May 11 to October 25 and the permanent opening date from October 27 to December 29.

Waddell Creek has its source in the redwood belt of the Santa Cruz Mountains, at an altitude of 1,500 to 2,300 feet. Several small tributaries unite to form two main branches, which in turn create the main stream. The length from mouth to source is approximately 12 miles. The hydrographic basin has an area of 26 square miles.

The distance from the uppermost limit of tidewater to the junction of the East Branch with the West Branch is 14,500 feet. Upstream migrants can ascend the West Branch an additional 14,000 feet, and the East Branch an additional one mile. Natural falls bar their ascent at these points.

The current of Waddell Creek is rapid to moderate throughout its course. Cascades and deep pools typify the upper reaches of the stream, which flow through the Transition Life Zone, characterized here by a forest of redwood and Douglas fir. The redwoods extend to within a mile of the coast at this point. The lower portions are broader and contain fewer deep pools. Gravel and small rubble beds, interspersed with stretches of sandy bottom or coarse rubble, are abundant. The stream banks are lined by red alder, big-leaf maple, buckeye, madrono, California laurel, and, in the lowermost portion, by willows.

The lowermost portion of the stream flows through the Upper Sonoran Life Zone. Here several patches of cultivated grassland and crop fields are scattered through a valley, which is about 2,000 feet wide at its broadest point and extends inland about 6,000 feet. The hillslopes are populated mostly by chaparral, pines, and Douglas fir. The predominant sandstone formation is covered with a loose, diatomaceous shale.

Immediately above the lagoon the stream flows through a small area of marshland. The lagoon is bordered by shifting sand dunes.

Some changes from the primitive condition of the area have taken place as a result of human usage. Part of the redwood forest was logged off by 1870 and is now covered by a second growth. The early lumbering operations have resulted in the creation of several semi-permanent log jams and temporary accumulations of logs, which have hastened erosion of the stream banks, with consequent increase in silting during flood stage.

In common with the other coastal streams from San Francisco to Monterey Bay, Waddell Creek contains no strictly fluvial fishes. The species regularly found in flowing (fresh) water, besides the steelhead and silver salmon, are the Prickly Sculpin (*Cottus asper*), the Aleutian Sculpin (*C. aleuticus*), the Three-spined Stickleback (*Gasterosteus aculeatus*), and the Tidewater Goby (*Eucyclogobius newberryi*). The only introduced species in Waddell Creek is the Striped Bass (*Roccus saxatilis*), which in some years enters the lagoon from the ocean but apparently does not spawn in the drainage. Lampreys do not enter Waddell Creek.

Several species of aquatic or semiaquatic birds are regularly associated with the stream, but none is found in great abundance.

The only mammal known to have a direct relationship to the salmon and trout in Waddell Creek is the California Coon (*Procyon lotor psora*), which eats dead or weakened spent adult steelhead and salmon. No beaver or mink are present.

The assemblage of native aquatic invertebrates in Waddell Creek is quite varied and is rather typical of the invertebrate life in other coastal streams. Nearly all of the aquatic invertebrates have some relation to the trout and salmon and most of them are eaten by these fishes to a greater or less extent. The introduced (?) crayfish *Pacifastacus klamathensis* apparently increased greatly in abundance during the last three years of the studies (1940-42).

Silver Salmon

In Waddell Creek, and over their range as a whole, silver salmon spawn mostly within the period November-January. The earliest fish was taken in the upstream trap during the week ending November 25, and the latest during the week ending March 24. However, 81 percent of the fish were taken during the six weeks December 10-January 20, and 96 percent during the nine weeks December 10-February 10.

During the nine seasons of operation of the upstream trap, 1933-34 through 1941-42, 2,218 adult silver salmon were taken. The seasonal runs varied from 84 (1937-38) to 583 (1934-35).

Scale examinations and marked fish returns indicated that all adults return either as males in the season following downstream migration

(age 1/1, one growing season in ocean) or as males and females in the second season following downstream migration (age 1/2, two growing seasons in ocean). Other workers have reported that the great majority of silver salmon adults fall into the above age categories, but have noted some exceptions. The 1/2 age class is everywhere the dominant one in the fishery.

At Waddell Creek, the 1/1 fish (all males) formed 18.3 percent of the total runs, 1/2 males 39.5 percent, and 1/2 females 42.2 percent. These data are in agreement with expected returns, assuming a 1:1 sex ratio among migrants entering the ocean and an equal mortality among males and females in the ocean, since some of the males return to spawn after only one growing season at sea, while all of the females spend two seasons at sea. They are also in essential agreement with data obtained at Scott Creek and at Benbow Dam on the South Fork of Eel River in northern California.

The mean fork lengths of the respective groups were 40.6, 64.7, and 63.9 cm. (16.0, 25.5 and 25.1 inches). There is a slight, but consistent, tendency for males to attain a larger size than females. In general, the average size attained by fish of one sex in a given season is proportionate to the average size attained by the other sex.

A demarcation line of 49 cm. (19.3 inches) separated 99.1 percent of 1/1 fish from 1/2 fish correctly and appears to have general application.

Over the range of the silver salmon, size of fish does not appear to be correlated with size of stream.

There is no correlation between the mean length attained by the grilse (age 1/1) of a given brood season and the two-year-ocean (1/2) fish of the same brood season. There is also no correlation between the average size of the downstream migrants of a given brood season and the adults of the same brood season. Thus, the growth made during the last growing season outbalances previous growth in determining average size.

Males predominate in the early portions of the run, while females predominate in the latter portion. Since the sexes and age categories are associated, it follows that changes in the representation of the age categories also occur throughout the run.

There is a correlation between the general period of the spawning run and the general period of rainfall. Silver salmon (and steelhead) ascend both on rising and falling stream levels, but cease movement during peak floods. They move upstream mainly during the daytime. The factors influencing fluctuations in upstream movement are "probably multiple with complex inter-relationships" (Chapman, 1941).

Maturation of silver salmon (and other species of Pacific salmon) is accompanied by changes in body form and coloration.

Silver salmon ascend practically all accessible streams within their range flowing into the Pacific Ocean, from the largest to the very smallest. They do not ascend streams for as great distances as do king salmon, red salmon, or steelhead, usually not proceeding upstream in large numbers more than 150 miles even in the larger rivers. In Waddell Creek, they consistently spawned lower than the steelhead, with individual exceptions.

Females choose the redd sites, as is the case with other species of salmon and trout. The site selected is typically near the head of a

rifle (which is also the lower end of a pool) composed of medium and small gravel. Usually the site chosen is close to the point where the smooth water "breaks" into the riffle. The nature of the redd site insures a good supply of oxygen.

In its general features the spawning of silver salmon is similar to that of other species of salmon and trout. The female digs the nest. One or more males, one of which usually becomes the mate, may accompany her, but do not participate in the digging. In digging the nest the female turns partly on her side and with powerful and rapid movements disturbs the bottom materials until a roundish depression, at least as deep and as long as the fish, has been formed. A portion of the eggs is then deposited, simultaneously fertilized by the male, and then covered with gravel by the female. The female may dig several pits to complete spawning, probably normally depositing a few hundred eggs in each one. Probably at least 97 percent of the eggs spawned lodge in the pit and are properly buried. To complete spawning may take a week or more.

Probably the over-all percentage loss of eggs as a result of damage by subsequent spawners is not large. Superimposition probably causes more damage to silver salmon than to steelhead redds, since most of the steelhead in California streams spawn after the salmon.

The rapid burial of eggs precludes any but an insignificant proportion of eggs being eaten by fishes.

All silver salmon die after first spawning. Death results from physiological changes independent of the rigors of spawning.

The calculation of numbers of eggs produced by Waddell Creek silver salmon was based on the numbers produced by Scott Creek silver salmon of known lengths. Measurements of the eggs were carried out according to a method which in essence consisted of dividing the actual total volume of eggs from one fish by the average measured volume per egg for that fish. The total number of eggs contained in these fish was plotted in 200-egg intervals against fish length in 1-cm. intervals and a regression line fitted to the points by the method of least squares. Since the relationship is curvilinear, the regression line was determined on a logarithmic scale and later transposed to a linear scale. Its equation is $\text{Number of Eggs} = 0.01153 \times \text{Length}^{2.9403}$. The correlation ratio, γ , for the relationship between eggs produced and fish length is 0.682. Other workers have found a correlation between number of eggs and size of fish for various species of salmonids, including other species of Pacific salmon.

The number of eggs left in silver salmon after spawning was found to be so small that it was decided not to subtract any number in calculating the eggs deposited by Waddell Creek fish which had completed spawning, but to use the total egg production figures obtained for Scott Creek silver salmon of the same lengths and expressed by the above-cited regression line. However, allowance was made for fish which died without completing spawning in each season.

Although quantitative data for Waddell Creek silver salmon are not available, there is every indication that the percentage of eggs fertilized is very high and rather constant.

The embryology of the silver salmon is in general similar to that of the other Pacific salmon and of trout. The number of days required

for the eggs to hatch varies from about 38 at an average water temperature of 51.3 degrees F. to about 48 at an average temperature of 48.0 degrees F. At the temperatures prevailing in Waddell Creek, the usual hatching time is from 35 to 50 days.

Chemical conditions have some effect on the rate of development of salmon and trout eggs, but probably do not play a significant role within the limits found in Waddell Creek and in the great majority of other coastal streams.

The percentage of silver salmon eggs which hatch probably varies widely under natural conditions, and in Waddell Creek and other coastal streams free from mining is likely dependent principally upon the amount and character of silting caused by floods occurring between fertilization and hatching. Such silting smothers the eggs, i.e., deprives them of the oxygen necessary for development. Mining silt has a similar effect.

Under normal hatchery conditions the hatch is between 80 and 90 percent of silver salmon eggs taken.

In Waddell Creek, serious losses probably occur only in the case of exceptional floods. Utilization of areas used by earlier spawners has been noted on various occasions, but no quantitative estimate of the amount of loss can be made, although it is not believed to form a large percentage of all the eggs deposited.

There is no quantitative basis for estimating the average percentage of silver salmon emerging from the gravel in Waddell Creek, but the writers believe that under favorable conditions it is probably between 65 and 85 percent of the eggs deposited. Again, silting is probably the principal factor determining the survival rate from hatching to emergence from the gravel.

Silver salmon fry start emerging from the gravel two to three weeks after hatching and require in addition two to seven weeks to complete emergence, with peak emergence occurring within three weeks of hatching. Shallow burial, loose gravel, absence of silt, and high temperatures all speed emergence, while the opposite conditions retard it. It is probable that most fish emerge at night.

As the young fish emerge from the gravel they take up residence in the shallow gravel areas, especially at the sides of the stream, where they feed avidly and grow rapidly. At first they tend to congregate in schools, but as the fish grow these schools break up and the fish spread up and down the stream. Following the peak of emergence there is a marked decline in the numbers of fry, caused by mortality rather than emigration. At Waddell Creek predatory fishes are believed to make the greatest inroads.

As the fish grow, they gradually move into deeper water and eat coarser food. Around July or August they move into the deeper pools, often those with overhanging logs. It appears that about this time the fish cease feeding or at least greatly diminish it, since the growth rate slows down. High stream temperatures may be the influencing factor in the cessation of feeding in late summer.

During the period of heavy rainfall and lowest temperatures, December through February, feeding continues to be light and growth negligible.

Following the period of maximum precipitation the fish start making extremely rapid growth (March). Rising temperatures and an abundance of aquatic food organisms likely influence the fish to resume heavy feeding.

Toward the end of March or sometime in April, approximately a year following emergence from the gravel, the fish begin to migrate to the ocean. There is an inverse correlation between average amount of growth made to time of migration and the number of migrants (= total stream population of age 1 fish).

During the nine seasons of operation of the trap, 18,362 juvenile silver salmon were checked on their downstream migration. Of these, 18,256 were age 1 fish and only 106 age + fish.

All scales of *adult* silver salmon taken at Waddell Creek show the fish to have migrated to the ocean at age 1, so the juveniles go to sea in the same season in which they migrate downstream.

The great majority of the fish in the spring migration had started growth of the new season, even in the early part of the migration.

Nearly all of the downstream migrants passing through the trap were taken during April and May. Observations in various streams indicate that there is little downstream migration prior to this and that few fish are swept downstream by high water. Over 95 percent migrated downstream during the nine-week period April 8-June 9 at age 1 and at an average size of from 103 to 117 mm. (4.1 to 4.6 inches). In all seasons the peak of the migration was reached not earlier than the week of April 22-28 and not later than the week of May 20-26.

The migration as a whole occurs later or earlier in some seasons than in others. The "early" seasons are those with generally low stream levels during the migration period for the same dates on which in late seasons stream levels were generally high.

There is a general decrease in the average size of the age 1 fish migrating in the spring (the same phenomenon occurs among the steelhead of a given age class). The hypothesis is advanced that the fish are influenced in starting their downstream migration by both size and environmental factors, with the larger fish from all portions of the stream migrating first.

The migrating fish move down in schools; those seen were composed of some 10 to 50 individuals. General observations indicate that most fish move downstream in the night or twilight, although some may move down during the day.

The sex ratio among the returning adults indicates that approximately a 1:1 sex ratio exists among the downstream migrants.

General color notes taken during the 1933-34 season indicate that the parr marks were prominent in the earliest migrants of the spring migration (March). As the season progressed, the fish became more "silvery," with parr marks barely visible.

The extremely rapid growth made in the sea is well known; it is shown in Figure 21.

Little is known regarding the movements of silver salmon in the sea. Marked salmon from Waddell Creek have been caught off Fort Bragg, 200 miles to the north. There is some evidence that silver salmon (and

other anadromous salmonids) remain within the limits of the continental shelf, which along the California coast extends approximately 100 miles from the shoreline.

Probably the young salmon, on first migrating to the sea, remain fairly close to the shoreline. Very little is known regarding how soon and to what extent they begin to spread out, but after a few months they begin to be taken at various points at sea, sometimes in large numbers away from the mouth of any stream possessing a run of consequence.

Evidence indicates that the migrations of the various Pacific salmon take place in the form of mass movements. Although little is known of the extent to which silver salmon from different streams mix while at sea, it is fairly certain that masses of fish from different streams visit some of the same areas at sea.

It is the opinion of the present writers that evidence obtained through various marking experiments has established as a fact the existence of "homing" among anadromous salmonids. Briefly, young salmonids which descend from fresh water return to their "parent stream" to spawn.

The extent of homing and straying among silver salmon between Waddell Creek and Scott Creek, $4\frac{1}{2}$ miles apart, was studied. Figures for the six seasons of marking (1933-34 through 1938-39) and the seven seasons for which returns were possible (1934-35 through 1940-41) show that 314 (85.1 percent) fish marked at Waddell Creek returned there and 55 (14.9 percent) strayed to Scott Creek. Of those marked at Scott Creek, 41 (73.2 percent) returned there and 15 (26.8 percent) strayed to Waddell Creek. (The percentage of straying is considerably larger than among steelhead.)

It appears that the rate of straying from a given stream is fairly constant for a given *year class*, but may vary considerably from year class to year class, and consequently from the total run entering in one season to the total run entering in another season. From this it appears that by the time adults first start returning (as 1/1 males) the amount of straying that will result has already been determined and is more dependent upon conditions existing up to that time than on conditions existing at the time of entry into the streams for spawning. The hypothesis is advanced that conditions existing at the time of seaward migration determine the amount of straying which will take place one and two seasons later, since there is a tendency toward (1) a positive correlation between size of downstream migration and rate of straying and (2) a negative correlation between average size of fish at downstream migration and rate of straying. In other words, the greater the number of downstream migrants and the smaller their size, the greater is the amount of straying. The significance of these tendencies has not been established.

Over-all survival (survival to maturity from eggs produced) varied from 0.02 to 0.30 percent for the six seasons for which complete returns were possible, with a mean of 0.13 percent. A striking feature was the inverse correlation between total egg production and survival (the same phenomenon was encountered for the steelhead).

The percentage of survival from time of downstream migration (secondary survival) varied from 0.6 to 5.4, with a mean of 2.3, on the

basis of marked adults returning to the trap. (The average return to the trap from the number marked at the same age (1) was 2.4 percent for steelhead.)

The *calculated* percentage of survival from eggs deposited to downstream migrants (primary survival) for the four brood seasons (1933-34 through 1936-37) for which figures were possible was fairly constant, varying from 1.16 to 1.56, with a mean of 1.35. These figures indicate that *within the limits of conditions encountered during the above four seasons* the number of downstream migrants is approximately proportional to the number of eggs deposited.

The *estimated* percentage of survival from downstream migrants to returning adults *for the stream as a whole* varied markedly, from 0.98 to 7.72, with a mean of 4.95, for these four brood seasons. An inverse correlation between the number of downstream migrants and the percentage of return as adults was found. The over-all survival for these four brood seasons was 0.06.

The *calculated* survivals, which are based partly on unmarked fish of unknown origin, may be affected by straying from and to Waddell Creek.

As a rule, disease is not prevalent among trout and salmon in their natural environment. In 1933-34 a disease believed to be furunculosis caused abnormal mortality among juvenile silver salmon and other fishes at Waddell Creek.

Deformities are also rare among salmon and trout in their natural environment. Only a very few fish with naturally missing fins were encountered at Waddell Creek.

In general, young silver salmon in fresh water live very largely on insects, both aquatic and terrestrial; smaller individuals in salt water depend heavily upon marine invertebrates; larger fish in salt water are chiefly piscivorous. Probably in most California streams the food of the young silver salmon is similar to that of steelhead of the same size.

Steelhead

Both over its range as a whole and in individual streams, the spawning season of the steelhead extends over a much longer period of time than does that of the silver salmon. In general, the bulk of the fish enter the streams and spawn in the winter or spring, but it is probable that in the larger rivers, such as the Sacramento, Eel, Klamath, and Columbia, some steelhead enter from the sea in all or nearly all months.

Roughly, steelhead may be divided into those of the spring run (fish in general entering and migrating upstream on dropping stream levels, while quite green, and spawning in the following season) and those of the fall run (fish in general entering on rising stream levels, with sexual products in various stages of development, but spawning within the same season). Spring-run fish do not occur in Waddell Creek or in most other California streams.

In the section on silver salmon it was pointed out that Waddell Creek and most other California streams are closed by sand bars at their mouths during a portion of the annual dry season, as a result of which the entry of the first fish of the spawning run is dependent upon the breaking of the bar with the start of the rainy season. The same consideration, of course, applies to the steelhead. As with the silver salmon,

at Waddell Creek (and Scott Creek) some steelhead have entered the stream with the first opening of the bar, whenever that has occurred. The earliest fish was taken in the upstream trap during the week ending October 28, and the latest during the week ending July 21. However, 96 percent of all fish were taken during the 22 weeks December 3-May 5. Within any of these 22 weeks steelhead may be expected in most California steelhead streams, depending upon seasonal weather and water conditions. Some steelhead enter northern California streams earlier than do any of those running into Waddell Creek and its neighbors, but even in those streams the spawning season takes place about the same time as in the southern ones.

At Waddell Creek there are two peaks, occurring during the weeks ending January 6 and March 17, respectively. These peaks so far apart result because fish of different sex-life history categories run at different times.

It is of interest that 38.7 percent of all fish were taken after February 28, the usual closing date of the winter steelhead season in California. At Benbow Dam on the South Fork of the Eel River 24.2 percent were taken after the end of February, and at Sweasey Dam on the Mad River (both in northern California) 53.1 percent.

During the nine seasons of operation of the upstream trap, 1933-34 through 1941-42, 3,888 adult steelhead were taken. The seasonal runs varied from 373 (1937-38) to 539 (1934-35). (These are the same seasons in which the smallest and largest numbers of salmon were taken in the trap.) There was less fluctuation in the size of the seasonal runs than in the case of the silver salmon.

Steelhead of many life history categories made up the runs in Waddell Creek. Unlike silver salmon, steelhead migrate to sea at various ages and over a long period within a season, spend varying amounts of time in the ocean and return over a fairly long period within a season, are capable of spawning more than once, sometimes spawn before their first journey to sea, and may even remain in fresh water for their entire lives.

Despite the great number of life history categories, on the average only the following four exceeded five percent of the run: 2/1 (29.8 percent), 2/2 (26.5 percent), 3/1 (10.5 percent), and 2/1S.1 (8.1 percent). Together, these four categories formed 75 percent of the run.

First spawners composed 82.8 percent (range 70.0-96.1 percent) of all adults, second spawners 15.0 percent, third spawners 2.1 percent, and fourth spawners 0.1 percent. (At Scott Creek two fish spawning for the fifth time have been recorded.)

Survival beyond first spawning is a function of total age, as well as of number of spawnings. No steelhead with a total age of more than seven years were encountered.

It is believed that on the whole the composition of the runs in Waddell Creek is representative of that in many other Pacific Coast streams under natural conditions. In general, (1) at least 59 percent of the fish (at Waddell, at least 70 percent) are spawning for the first time (excluding fish that have spawned prior to initial entry into salt water); (2) fish spawning for a second time *may* form an important contribution, constituting as high as 36 percent of the total run; (3) fish spawning for the third time form a very minor part of the total run; (4) fish

spawning for the fourth and fifth times form a negligible portion of the run; (5) fish of a total age of over six years form a negligible portion of the run; (6) no fish more than seven years old have been encountered; (7) probably 2/1 and 2/2 fish predominate among normal populations, with 3/1, 1/1, 3/2, and 2/1S.1 occasionally contributing significantly.

The rate of growth is so much greater in the ocean than in fresh water that it is obvious the ocean growth in general determines the size of fish of a given sex and life history category in a given season.

Generally, males tend to reach a larger size than females among fish spending two years at sea before spawning, while females tend to reach a larger size than males among fish spending one year at sea.

Growth is resumed following spawning among all life history categories. The greatest increase is made by the smallest fish.

As in the case of the silver salmon, the size attained by one sex of a given life history category is paralleled by the size attained by the other sex. This fact, coupled with other data, indicates that conditions in the ocean may vary sufficiently from season to season to affect markedly the size of steelhead from a given stream. The summer of 1941 appears to have been a very poor one for growth of both steelhead and silver salmon.

The repeat spawners of a given life history category are markedly smaller than first spawners of the same year class which have spent the same number of seasons in fresh water and in the ocean.

Waddell Creek steelhead achieve approximately the same length as silver salmon of the same life history categories.

It appears that the size of steelhead is not correlated with the size or latitude of the home stream.

In all seasons but one a comparatively small number of steelhead succeeded in jumping over the dam at extreme flood stage. Among such fish males were in excess of females out of all proportion to the sex ratio among fish checked through the upstream trap.

Among both first and second spawners, males predominate in the life history categories forming the fish of the lesser total ages, while females predominate in those forming the fish of the greater total ages.

Survival following spawning is higher among females than among males. The lower survival among males probably results because the males serve more than one female, and so are exposed not only to prolonged physical exertion, but also to the dangers of being stranded by lowering flows and the closing of the bar at the stream mouth.

The sex ratio for the steelhead runs as a whole was one male to 1.1 females. It is evident that some unnatural factors are operating at egg collecting stations and other places where females greatly exceed males, sometimes six to one.

Females are represented to some extent among all categories of steelhead grilse.

As in the case of the silver salmon, males predominate in the early portions of the steelhead runs, while females predominate in the latter portions.

Since the sexes and life history categories are associated, it follows that changes in the representation of the life history categories also occur throughout the run. Of the principal categories, the 2/1 fish of

smaller size predominate in the early part of the run, 2/2 fish reach a peak at midseason, and the larger grilse, composed of the 3/1 fish and the larger 2/1 fish, appear strongly in March or the latter part of February and thenceforth increase in relative abundance during the remainder of the season.

As in the case of the silver salmon, the writers believe that in Waddell Creek and similar small streams there is a definite relationship between ascension of the streams by spawning steelhead and flow of water, which so far it has proved impossible to show quantitatively, because of the existence of several variables. Steelhead, like silver salmon, ascend both on rising and falling stream levels, but cease movement during peak floods. In general, they appear to be less exacting than silver salmon as regards the conditions under which they will spawn or ascend an obstacle in a stream, such as a fishway.

Steelhead (like silver and king salmon) move upstream mainly in the daytime. Fluctuations in movement during the daytime likely are caused by factors which are "probably multiple with complex inter-relationships" (Chapman, 1941).

The changes in body form and coloration which are associated with maturation in sea-run steelhead are of the same character as those in the silver salmon, but usually much less marked.

The spawning of steelhead is very similar to that of silver salmon. It has been described in detail by Needham and Taft (1934). The female chooses the redd site, digs the pit, and covers the eggs. One or more males, one of which becomes the mate, may accompany the female. A female 60 cm. (23.6 inches) long dug six or seven pits to complete spawning, averaging a deposition of from 550 to 1,300 eggs in each. The completed redd was approximately 12 feet long and 5 feet wide (60 square feet). Spawning can be completed within 12 hours, but is believed often to take a week or more.

The writers believe that 97.5 percent would express a minimum average for the number of eggs buried in the redds by steelhead.

It is probable that although the losses resulting from damage to redds by subsequent spawners may be severe in individual nests, the percentage loss for all eggs deposited in Waddell Creek was small.

Spawning sea-run steelhead are very often accompanied by stream trout, which may eat loose eggs, but whose primary purpose in being present probably is to participate in the spawning activities.

The calculations of numbers of eggs produced by Waddell Creek steelhead were based on the numbers produced by Scott Creek steelhead. The relationship between fish length and number of eggs produced was determined from 562 measurements of the amount (volume) of eggs and the size (volume) of individual eggs obtained from manually spawned fish of known lengths. Measurement of the eggs was carried out according to the method described for the silver salmon. Since only about 90 percent of the number of eggs contained in a fish are obtained in ordinary hatchery spawning, to obtain the *total number of eggs* the calculated number was multiplied by 1.1.

The *total number of eggs* was plotted in 400-egg intervals against fish length in 2-cm. intervals and a regression line fitted to the points by the method of least squares. Since the relationship is curvilinear, the regression line was determined on a logarithmic scale and later

transposed to a linear scale. Its equation is $\text{Number of Eggs} = 0.9471 \times \text{Length}^{2.1169}$. The correlation ratio, γ , for the relationship between eggs produced and fish length is 0.838. Regressions of eggs produced on fish length calculated separately for first spawners and second spawners showed such slight differences that a single regression was used.

The number of eggs left in steelhead after natural spawning was found to be so few that no allowance for them was made in calculating total egg deposition in the stream.

Although no quantitative data for Waddell Creek steelhead are available, there is every indication that the percentage of eggs fertilized is consistently very high.

After spawning, the spent adult steelhead which have not succumbed to old age, disease, or predators descend to the sea. At Waddell Creek the bulk of such "downstreamers" have been taken during the period April-June. Spent adult steelhead typically do not resume feeding while in fresh water.

The embryology of steelhead is in general similar to that of other trout and of salmon; it has been described in detail by Wales (1941). The number of days required for steelhead eggs to hatch varies from about 19 at an average temperature of 60 degrees F. to about 80 at an average temperature of 40 degrees F. At the temperatures prevailing in Waddell Creek, the usual hatching time is from 25 to 35 days.

As in the case of the silver salmon, silting occurring between fertilization and hatching is probably the principal cause of pre-hatching losses.

The writers believe that under favorable conditions (principally absence of heavy silting) the percentage of eggs hatching in Waddell Creek is comparable to that of hatchery eggs, or 80 to 90 percent of the eggs deposited.

At time of hatching steelhead are approximately 17 to 18 mm. (0.7 inch) long and weigh about 0.1 gram (270 fish per ounce).

Silting is also probably the principal factor in determining survival rate from time of hatching to emergence from the gravel. The writers believe that under favorable conditions the average percentage of steelhead emerging from the gravel is between 70 and 85 percent of the eggs deposited.

Steelhead fry probably start emerging from the gravel two to three weeks after hatching and require another two to three weeks to complete emergence. Shallow burial, loose gravel, absence of silt, and high temperatures speed emergence, while the opposite conditions retard it. Shallow burial results in premature emergence. At time of emergence from the gravel steelhead are approximately 23 to 26 mm. (0.95 inch) long and weigh about 0.16 gram (180 fish per ounce).

The behavior of juvenile steelhead during their first year of life, especially during the first couple of months following emergence, is generally similar to that of young silver salmon, which has been summarized previously.

Soon after the first steelhead have emerged from the gravel, marked differences in size are noticeable among them. Such differences result principally from the prolonged spawning season and therefore prolonged hatching and emergence periods.

Soon after the peak of emergence there is a marked decline in the numbers of fry in the stream, due to mortality. Predatory fishes are believed to make the greatest inroads.

As the fish grow, they gradually move into deeper water and eat coarser food. However, unlike the silver salmon, in late summer the young steelhead do not appear to move into the deep, quiet pools, but inhabit moderately swift portions of the stream. Diurnal movements within limited areas may occur.

The growth rate of the fish slows down (probably not as early nor as markedly as in the case of the silver salmon) in association with the period of maximum stream temperatures and minimum flow, with some evidence to indicate that the former plays the greatest part.

Feeding continues to be generally quite light and growth negligible until after the period of maximum precipitation, when the fish start making extremely rapid growth (usually in March). The resumption of heavy feeding is probably influenced both by rising temperatures and the abundance of aquatic food organisms.

Probably the sex ratio is close to 1:1 among stream steelhead two years of age or under.

Young steelhead exhibit much greater variation in individual behavior than do juvenile silver salmon. This is most markedly brought out by the fact that the young steelhead migrate downstream at various ages from + to 4, while practically all of the silver salmon migrate downstream as yearlings. While the salmon go to sea almost immediately, some of the steelhead remain for a whole season in the lagoon or the lower portion of the stream, after which some move out to sea, while others make an upstream migration and then a second downstream migration. While most of the steelhead go to sea before maturing, some fish of both sexes spawn before going to sea, while still others complete their life cycles entirely in fresh water. (Among the silver salmon perhaps a few males reach precocious sexual maturity prior to their seaward migration, but none of the females do so.) There are other variations in the behavior of individual young steelhead, especially in regard to feeding and growth. These variations in behavior are reflected in the structure of the scales.

During the nine seasons of operation of the trap, 36,779 stream steelhead were checked on their downstream migration.

Some stream steelhead, unlike the juvenile silver salmon, migrate downstream at all times of the year, but the largest numbers migrate in the spring and summer, with a secondary migration in the late fall or early winter. Migration during January and February is very light.

Since it was impossible to examine scales from all of the fish, the age classes were segregated according to modal groups of length frequencies, with "reading" of scales where overlaps between the modal groups occurred.

The four age classes which, except for occasional older fish, make up the downstream migration in each season move down in sequence during the main (spring) migration. The oldest appear first and are followed by progressively younger fish.

The 36,779 stream steelhead checked through the trap on their downstream migration consisted of 14,734 (40 percent) fish of age +,

14,707 (40 percent) of age 1, 6,938 (19 percent) of age 2, 386 (1 percent) of age 3, and 14 of age 4.

It is probable that the migrations through the trap are indicative of but not strictly proportionate to the numbers migrating down in the stream as a whole. Because of the large volume of water in the early stages of the migration, proportionately larger numbers pass uncounted over the dam. Since the older age classes migrate first in the spring migration, it is to be expected that they show up in disproportionately small number among the fish taken in the trap.

Possible factors influencing the time of migration and the size of fish, and their interrelationships, were summarized for the silver salmon. Most of that discussion is also applicable to the steelhead, except in that the situation is made still more complex because a heterogeneous population is involved. In the steelhead, each age class must be treated as a separate unit.

The main (spring) migration occurs earlier in some seasons than in others, as was the case with the silver salmon. Similarly, the early seasons are those with generally low stream levels, while the late seasons are those with generally high stream levels.

The fish that migrate down in the late fall are principally of the previous season's year class. These migrations exhibit a fluctuating character, apparently through the influence of the fall rains. The fall migration probably should properly be thought of as the tail-end of the spring migration of age + fish, which has been interrupted by low water and perhaps other factors associated with low water.

Climatic factors not only affect the general starting time of the main (spring) migration, but also create breaks in its pattern.

As the spring migration as a whole is retarded or advanced within a season, so the age composition pattern within the migration is pushed backward or forward. As a result, the age composition of the fish migrating at any given time in two seasons may be quite different. Also, the strength of a given age class, i.e., its representation within a season both in absolute numbers and in proportion to the other age classes individually and as a whole, varies considerably from season to season.

As a rule, there is a distinct increase in length of fish of a given age class within a season between the end of the fall migration and the beginning of the spring migration. Scale examinations reveal that the great majority of the fall migrants have completed or nearly completed growth of the season, while the great majority of the spring migrants, even the early ones, have renewed growth. The increase in size within an age class therefore represents growth made by that age class as a whole.

Through the season there is often a decrease in the average size of the migrants of a given age class. This phenomenon results because the larger individuals of the age class migrate earlier than the smaller ones.

The summarized hypothetical picture of the downstream migration of silver salmon, as regards time of migration and size of fish, applies also to the steelhead.

The extent of schooling at migration time has not been noted sufficiently to be recorded at this time. Young steelhead do school in streams

under certain conditions, individuals of the same size tending to group together.

General observations indicate that some fish move down at all hours of the day and night, but that the bulk of the fish move downstream during the night or at least at twilight.

Parr marks are generally pronounced on the smaller migrants and such fish are not "silvery," while the larger ones are silvery. Migrants with "rainbow" coloration (prominent parr marks and rich body and fin coloration) are usually sexually mature and are believed to be mainly the offspring of stream fish.

During the nine seasons of operation of the trap, 3,104 upstream migrant stream steelhead were checked (seasonal variation 37 to 1,271). The peak of this migration usually occurs close to the beginning of the calendar year, and a secondary, quite minor rise takes place near the end of July. The latter migration is composed of fish younger than those migrating in the winter.

The upstream migration is composed of fish that had previously migrated downstream and spent some time in the lagoon (or the section of the stream below the dam) and fish that had hatched below the dam. Like the downstream migrants, they are probably composed largely of offspring of sea-run fish but to a minor extent of offspring of stream fish. Most of the upstream migrants make a subsequent downstream migration in the same season (some after spawning). Probably following this second migration most of them go to sea.

The 3,104 upstream migrants consisted of 44 (1 percent) fish of age +, 893 (29 percent) of age 1, 1,637 (53 percent) of age 2, 478 (15 percent) of age 3, 51 (2 percent) of age 4, and 1 of age 5. The upstream migrations do not involve sampling, but represent the entire runs.

Both sexes are represented in the upstream migration of stream steelhead, but the available data are insufficient to warrant definite conclusions regarding the sex ratio. Many of the fish are sexually mature.

As in the case of the silver salmon, the extremely rapid growth made by steelhead in the sea, as compared with that made in fresh water, is well known. Probably the young steelhead, on first migrating to the ocean, remain fairly close to the shoreline. How soon and to what extent they begin to spread out is not known, and practically nothing is known regarding their movements in the sea. For unknown reasons, very few are caught at sea by commercial salmon trollers. Almost nothing is known of the extent to which steelhead from different streams mix while in the sea. It is not known, but is not improbable, that steelhead in the sea, like the Pacific salmon, migrate in schools.

The views of the writers regarding "homing" among anadromous salmonids were expressed in the summary discussion of silver salmon and will not be repeated. During nine seasons of marking (1931 through 1938-39) and nine seasons during which returns were obtained (1933-34 through 1941-42) 476 (98.1 percent) steelhead marked at Waddell Creek returned there and 9 (1.9 percent) strayed to Scott Creek. Of those marked at Scott Creek, 932 (97.1 percent) returned

there and 28 (2.9 percent) strayed to Waddell Creek. Thus, the rate of straying among steelhead is considerably less than among silver salmon for the streams involved.

The simplest procedure to calculate survival to maturity among sea-run steelhead at Waddell Creek is to calculate the number of eggs deposited in a given season and then to total the numbers of sea-run fish of that brood season returning to spawn for the first time. Survival calculated in this manner may be termed *primary over-all survival*.

In calculating primary over-all survival, the first spawners among the fish comprising the estimated total run into Waddell Creek were divided into total age classes. It was then possible to assign all returning first spawners to the proper brood season (season in which they were produced), and to express them as a percentage of the number of eggs which produced them. The percentage of survival varied from 0.017 to 0.028 for the four seasons for which returns were complete or practically complete, and from 0.017 to 0.029 when an additional season (1937-38), for which the number of five-year-old returning fish was not available but was calculated on the basis of the average return of five-year-olds in the other four seasons, was included. In the former case the percentage is 0.021 and in the latter case it is 0.023. The latter figure is used for the purposes of the present report.

One of the striking features to be noted is the inverse correlation between total egg production and survival percentage (the same phenomenon was encountered among the silver salmon).

In calculating the number of eggs produced by each spawning run, the number of eggs produced by each fish was calculated on the basis of the egg number-fish length relationship previously established.

Altogether, returns were obtained for 383 marked first spawners. Of these, 220 (57.4 percent) had made their initial downstream migration at age 2 (in their second year), 116 (30.3 percent) at age 1, and 45 (11.8 percent) at age 3. There was one fish apiece in the + and 4 groups.

The ages at initial downstream migration of these adult first spawners occur in quite different proportions from those of the 12,679 downstream stream fish which produced them. This results both from differing survival rates among downstream stream fish of different ages and the fact that varying percentages of the downstream fish remain in the stream for an additional season.

Of the 383 fish under discussion, 237 (61.9 percent) migrated to sea in the season of marking, while 146 (38.1 percent) migrated in the following season. Of the latter, three made an upstream migration and a second downstream migration, while the remainder stayed in the stream below the dam, most likely in the lagoon in the great majority of cases.

Among the age 1 group, only 9 (7.8 percent) had migrated in the same season and 107 (92.2 percent) in the following; among the age 2 group, 196 (89.9 percent) had migrated in the same season and only 24 (10.1 percent) in the following; among the age 3 group, 31 (68.9 percent) had migrated in the same season and 14 (31.1 percent) in

the following. This sequence, but not order of magnitude, is also true for each sex. Within *each* age group a greater proportion of the females than of the males had migrated in the following season.

Of the 383 adult first spawners under discussion, 303 (79.1 percent) had migrated to sea at age 2, 55 (14.4 percent) at age 3, 15 (3.9 percent) at age 4, and 10 (2.6 percent) at age 1.

A comparison of probable age as downstream migrant with age at entry into ocean shows striking differences between them in the representation of the different age groups. Although the age 2 fish are dominant in both cases, they are much stronger among the latter group. The age 1 fish represent 30.3 percent of the former group, but slump to only 2.6 percent in the latter. These examples show how easy it would be to reach erroneous conclusions regarding survival by considering the downstream migrants to be equivalent to seaward migrants.

Survival to adult first spawning for the 12,679 fish marked on their initial downstream migration was as follows: age +, 1 out of 3,820 (+ percent); age 1, 116 out of 4,811 (2.4 percent); age 2, 220 out of 3,793 (5.8 percent); age 3, 45 out of 249 (18.1 percent); age 4, 1 out of 6 (16.7 percent). Since size of fish is correlated positively with age, there is also a positive correlation between size at time of marking (initial downstream migration) and survival to first spawning.

In no instance did a marked fish return for first spawning *later than the third season following marking*. Thus, probably in most California coastal streams in which it is desired to carry out marking of stream juvenile steelhead and secure survival rates in terms of returning first-spawning, sea-run adults, returns should be sought for three seasons following season of marking, but need not be watched for beyond that.

In order to determine the survival from eggs deposited to downstream migrants it was necessary to know the *total* number of downstream migrants, including those that went over the dam uncounted and those that were produced below the dam. In the case of the steelhead, all of the young fish do not migrate to the ocean at the same age at which they migrate downstream, so the total number of downstream migrants could not be calculated simply by applying the ratio of marked to unmarked fish among the adults of a given brood year to the marked downstream migrants of the same brood year. The calculation of the total number of downstream migrants was therefore made by a less direct method, illustrated by Tables 78 and 79.

The general occurrence of disease among trout and salmon under natural conditions was summarized for the salmon and will not be repeated. At Waddell Creek some mortality occurred among unspawned steelhead from some form or strain or furunculosis, particularly during the 1933-34 season, when 161 dead adults in all were found. It is estimated that 17 females died without spawning during that season. In all other seasons mortality is believed to have been much less. Estimates of the numbers which died without spawning or spawned only partially were made for each season and considered in calculating egg production and survival.

Abnormal mortality among adults, such as that caused by furunculosis in 1933-34, of course results in abnormally low numbers of repeat

spawners in subsequent seasons. Thus, in 1934-35 the number of repeat spawners was the lowest on record, a further indication that mortality in 1933-34 was correctly assessed as being the heaviest.

The extent of losses from furunculosis among the stream steelhead is not known exactly, but is not believed to have been nearly as severe as among adults.

Freshwater copepods (*Salmincola californiensis*) were found attached to many of the downstream migrants, but apparently cause no serious damage. These copepods were found much more frequently on the steelhead than on the salmon migrating downstream at the same time.

No downstream migrant stream steelhead with fins completely missing were recorded.

It is not improbable that throughout the life history of the steelhead its food is similar to that of the silver salmon: juveniles in fresh water live very largely upon insects, both aquatic and terrestrial; smaller individuals in salt water depend heavily upon marine invertebrates (and those in brackish water, especially in lagoons, on brackishwater crustaceans); the larger fish in salt water are chiefly piscivorous.

Predators

Inasmuch as one of the main purposes of the project was to study a stream under as nearly as possible natural conditions, suspected predators were not killed because of the danger of upsetting the biological balance. Evaluations of the effects of various possible predators are therefore based on incomplete data and observations on other streams.

In Waddell Creek and other California streams juvenile silver salmon and steelhead are probably most heavily preyed upon by juvenile steelhead. Freshwater sculpins (*Cottus*) are probably important predators in most Pacific Coast streams; at Waddell Creek and probably in most other streams *Cottus asper* is the species which causes the greatest damage. Stomachs of sculpins taken from the downstream trap contained considerable numbers of young trout and salmon. That confinement of the fish in the trap aided the sculpins in capturing their prey is probable. During the period immediately following emergence from the gravel some young fish may also be eaten by juvenile silver salmon of older year classes; this has not been noted in Waddell Creek but has been reported from another stream (Pritchard, 1936b). Other predators on fish of such small size are limited in Waddell Creek and most other California streams to the dipper and to garter snakes. Usually these two are not sufficiently numerous to be the principal cause of loss at this stage.

As the young salmon and trout grow, the percentage of loss declines, but they become attractive as food to an increasing number of predators. When they are too large to be taken by the dipper, the smaller garter snakes, and many of the steelhead, they are taken in varying amounts by fish-eating birds (kingfishers, blue herons, and others). In some cases, striped bass may make serious inroads upon the seaward migration. The losses caused by each of these depend upon a variety of factors, including the size of the populations of trout and salmon and the predators, the abundance of other foods for the predators, the character of the stream and the particular portion of the stream, and

climatic and water conditions. Some of the predators are able to secure fish in appreciable quantities only when the latter are confined to drying pools or some spot like the traps at Waddell Creek.

The American osprey and American merganser, which may be serious predators in other California salmon and trout waters, are absent from the Waddell Creek area or are rare visitors.

Sea-run steelhead and silver salmon, except individuals dying after spawning or from old age, disease, or injury, are subject to very little predation from any source once they have entered fresh water. It is probable that less than 1 percent of the run of either species is normally taken by predators in any stream in California.

Considerable losses occur among both silver salmon and steelhead between the time that they leave fresh water and the time that they return as adults. Little is known of the life of salmon and trout at sea, but it is not improbable that the major mortality is caused by predators, of which there are some capable of preying on salmon and trout of all sizes.

Sea lions have been accused of extensive depredations on steelhead and salmon by sportsmen and commercial fishermen. The extent of such depredations is difficult to determine, largely because of the difficulty in securing stomachs of sea lions at the proper time of the year. Circumstantial evidence that sea lions feed on salmon and steelhead lies in the appearance of the sea lions near the mouths of California streams during the time of entry of salmon and steelhead. The extent of depredations by sea lions is of particular interest in the case of Waddell Creek in view of the fact that the largest Steller sea lion rookery in California is located only a little over three miles away, on Año Nuevo Island.

Management

Proper recommendations for the management of any species should consider that species in relation to its total environment, including the human beings who will be concerned with its utilization. To be able to formulate such recommendations, however, it is first necessary to know the basic facts about the biology of the species concerned. To gather these basic facts and present them in usable form has been the main function of the present study.

The problems that concern the steelhead have been well presented by Taft (1933). Intensive fisheries for both the adult and immature steelhead create too great a drain on the species. Most California coastal streams can support only limited numbers of fish of angling size.

By contrast, immature silver salmon (and king salmon) are subjected to relatively little fishing. The adult salmon, however, must withstand, in addition to the sport fishery, an extensive commercial fishery. The numbers of seaward migrants must be great enough to maintain these fisheries with adequate numbers of adults.

Many of the problems encountered and many of the ill effects on the fishes have resulted from the methods of land and water use now in effect. Control over these factors lies largely outside the province of the Department of Fish and Game.

Sometimes different management methods will give the same results. The choice of methods must often depend upon the desires of the

angling public, plus the funds, facilities, and personnel available to conservation agencies.

It is to be expected that many phases of the impending vast development of the northern areas of the world will adversely affect the salmon fisheries of those areas in the manner that has taken place in the United States, with the result that the salmon fisheries of California will assume a *relatively* more important position.

A sound program of management should include wise conservation legislation, good enforcement of this legislation, improvement of the physical and biological habitat, pollution control, and fish rescue and artificial propagation, when and if necessary.

Regulations governing the taking of salmon and steelhead should be designed to provide the *maximum sustained yield*, that is, the widest use of the resource possible without causing depletion. Regulations formulated for any given area should be coordinated with the regulations for adjacent areas, to avoid danger of an undue burden being placed on one or more of them. In general, regulations should be as uniform as is consistent with basic biological requirements.

Since in areas open to public fishing only the take of the individual angler is restricted and the total annual take is not directly limited in any body of water, regulations will remain a management tool of limited effectiveness in the maintenance of the steelhead and salmon fisheries.

The existing regulations are generally satisfactory, but some changes are desirable.

It is especially important that the summer season in the coastal steelhead and salmon waters, if permitted at all, open not earlier than the end of May, to protect the heavy downstream migration of young steelhead and silver salmon at that time.

It is also very important that at least the lagoons and tidal waters of all coastal streams be closed except during the winter angling season. It is here that young steelhead make their most rapid growth before entering the sea.

Physical habitat improvement in northern California salmon and steelhead waters offers definite possibilities which should be immediately and thoroughly explored and exploited when found to be feasible. Certainly, it seems wise to increase the carrying capacities of the streams to the practicable maximum before spending large sums on other, more expensive forms of management to increase the numbers of fish, if there must be a choice.

In northern California, desirable physical habitat improvement includes principally (1) stream clearance (removal of log jams and debris clogging stream channels); (2) removal of unused dams and reduction of natural barriers; (3) maintenance and improvement of stream flows; (4) uniting of flows at mouths of small tributary streams, generally making entrance and exit for fish to and from these streams easier; (5) opening channels from streams and pools cut off from the main streams at low water; and (6) screening of water diversions.

Legislation prohibiting the cutting of trees within a prescribed distance of any stream would contribute importantly to the improvement of the coastal trout and salmon waters.

Biological habitat improvement in salmon and steelhead waters has received relatively little study, but several leads which have been uncovered should be followed up. Success in each case is by no means certain, but the potentialities are so great that thorough investigation should not be neglected.

The improvement of existing stocks through selective breeding and the introduction of various strains or races offers some promise, particularly in the case of the steelhead.

The elimination or control of undesirable fishes offers more promise than the introduction of desirable species, but like the latter is a matter involving complex ecological relationships and therefore possibly unforeseen results. The control of these unwanted fishes might be executed by seining, trapping, or chemical treatment. Control of certain of the species (e.g., lampreys, sculpins, suckers, and some cyprinids) might also be effected by erecting barriers in the streams high enough to bar their upstream migration, but low enough to permit steelhead and salmon to jump them. Lampreys appear to constitute a very real menace to salmon and steelhead in certain instances and should receive further study.

In general, industrial pollution is not a major problem in the coastal area, being confined to isolated instances, principally from wineries, creameries, tanneries, dumps, sawmills, and millponds. Pollution from mining silt is of considerable importance in the Klamath River watershed. Pollution from sewage is not a general problem, but has had ill effects in some cases. Proper disposal of slashings and unwanted logs from lumbering operations is frequently disregarded. The log jams thus created block spawning fish, destroy spawning grounds, and so change the character of the stream bottom that fish food organisms are destroyed.

The fish rescue work in the north coast area has been very worthwhile and should be continued and expanded to provide as complete coverage as possible.

For many years it has been the popular conception that artificial propagation of trout and salmon and the stocking of streams were the complete solution to the problem of maintaining the fisheries of a stream or stream system. It is the writers' belief, however, that stocking *alone* cannot hope to maintain fishing at its present level in the coastal streams. Moreover, the writers believe that the *amount* of natural propagation is so great that even with a very favorable survival rate artificially propagated fish would not form more than a minor part of the total production.

The inefficiency of stocking as carried on in the past does not mean that all artificial propagation is useless. The experimental programs at Waddell and Scott creeks have shown that although extremely small returns may be expected from fish in their first year of life, on the average approximately 2 to 5 percent of yearling steelhead and silver salmon allowed to descend to sea at their normal migration time may be expected to return as adults, and that survival among older and larger steelhead is considerably higher, increasing with the size and age of the fish. Therefore, some stocking of aged fish may be desirable in the coastal streams, especially in heavily fished streams. In such case, emphasis should be placed on planting yearling fish in barren

sections of streams above falls and other barriers and the planting of areas in which adverse climatic conditions or very small spawning runs have caused subnormal natural propagation. In other words, artificial propagation should be considered an *aid* to natural propagation, rather than a replacement of it.

The most hopeful solution to the problem of maintaining successful and *varied* angling in the coastal area of California as a whole appears to be to provide *summer* fishing by planting aged trout in heavily fished bodies of water, often those blocked to sea-run fish, and to have the winter fishing for adult salmon and trout depend largely upon natural propagation, aided by habitat improvement, fish rescue, and specialized stocking. Under such a program summer fishing in the streams in which a winter fishery is to be maintained should be limited in the ways recommended previously in this report.

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APPENDIX

TABLE A-1

Waddell Creek, Silver Salmon: Adults Checked Upstream Through Trap; Mean Lengths (in cm.) by Brood Seasons

Brood season	1/1 ♂♂		1/2 ♂♂		1/2 ♀♀	
	Number	Mean length	Number	Mean length	Number	Mean length
1930-31	--	--	152	65.7	177	65.2
1931-32	118	39.8	275	64.0	287	63.2
1932-33	21	41.2	33	65.8	39	63.9
1933-34	56	41.0	104	65.8	107	64.3
1934-35	3	42.5	42	66.1	22	67.2
1935-36	20	39.6	29	63.2	40	63.6
1936-37	17	39.5	88	67.8	126	65.9
1937-38	52	41.8	93	64.3	105	62.5
1938-39	65	42.4	66	59.2	77	58.9
1939-40	4	40.2	--	--	--	--
Totals	356	40.9*	882	64.7*	980	63.8*

* An average of the seasonal means, the assumption being that seasonal means are representative of seasonal conditions.

TABLE A-2

Scott Creek, Silver Salmon: Data Used in Calculation of Volume Factor (F)

Date	Fish no.	Counted no. eggs	Measured vol. of eggs (cc.)	Vol. per egg (cc.)	Actual vol. of eggs (cc.)	Volume factor (F)	No. eggs measured
Jan. 16, 1936	27	2,789	805	0.213	594	0.738	90 (9 lots)
Jan. 30, 1936*	31	2,782	995	0.2226	619	0.622	50 (5 lots)

$$0.738 + 0.622 = 1.360$$

$$\frac{1.360}{2} = 0.680 = \text{Average volume factor (F)}$$

* Stray from Waddell Creek.

NOTE: The volume factor was also calculated for two other fish, for which the data are tabulated below. However, these data were not used, since the measured egg volumes approached the extremes of the egg volume frequency distribution, Table A-3 of the Appendix. Admittedly, it would be desirable to have a larger series of measurements and counts to test the validity of the volume factor used, but such data are not available. Its validity is substantiated to a certain degree by the closeness of the volume factor found for steelhead (0.674), using the same methods and apparatus.

Date	Fish no.	Counted no. eggs	Measured vol. of eggs (cc.)	Vol. per egg (cc.)	Actual vol. of eggs (cc.)	Volume factor (F)	No. eggs measured
Jan. 8, 1936	13	4,479	1,325	0.187	838	0.632	90 (9 lots)
Feb. 6, 1936	41	1,396	350	0.2103	293	0.840	30 (3 lots)

TABLE A-3

Scott Creek, Silver Salmon: Volumes of Eggs Obtained From 40 Spawned Fish, 1935-36

Measured vol. of eggs (cc.)	No. of fish	Measured vol. of eggs (cc.)	No. of fish
350-399	1	900	4
400	--	950	4
450	--	1,000	1
500	1	1,050	3
550	2	1,100	--
600	5	1,150	--
650	3	1,200	--
700	2	1,250	--
750	6	1,300	1
800	4		
850	3	Total	40

TABLE A-4

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1933-34, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31
21-25													
30													
35													
40													
45													
50													
55													
60													
65													
70													
75													
80						1							
85			No Record							2		1	
90												1	2
95												2	2
100												2	1
105												2	
110												2	
115												2	
120												6	
125													
130													
135													
140												1	
145													
150													
155													
160													
165													
Totals						1				2		4	18

TABLE A-4—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1933-34, by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25														
30														
35														
40				1										1
45		1		1										2
50				2										2
55				2		(1)*						(1)*		(2)*+2
60				4										4
65														
70														
75														1
80														2
85	1													2
90			4	2	1									10
95	1	8	18	5	2								1	38
100	7	47	76	20	3									154
105	22	165	151	23	75 (39)				(1)†					(40)†+369
110	42	313	279	44	4									684
115	54	370	316	44	3									789
120	79	306	288	30	2									711
125	61	165	117	13	2									357
130	17	65	47	5										134
135	3	41	17	4	2									67
140	3	21	6	1										32
145	1	11	5	2	2									21
150		3		1										4
155														
160					1									1
165														
Totals	291	1,516	1,324	204	66		1		1			1	1	3,430

* Recorded only as 3 inches or under.

† Recorded only as over 3 inches.

TABLE A-5

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1934-35, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														4
40														5
45														
50														
55	(4)*	(2)*		(6)*										
60														
65														
70							1							
75								1						
80														1
85								1						2
90												1		6
95														4
100														3
105			(1)†	(4)†									1	1
110														
115														
120														1
125														
130														
135														
140														
145														
150														
155														
160														
165														
Totals	4	2	1	10	--	--	1	2	--	--	2	1	1	27

TABLE A-5—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1934-35, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25													
30													4
35													14
40	9												3
45													(12)*† + 7
50						3							4
55						5	2						3
60					2	2							4
65												1	3
70						1	1						3
75						1	1			1			4
80	1												2
85	3	1											8
90	2	7			1								17
95	9	27	11	7	2								60
100	20	95	72	36	6								232
105	32	188	141	74	7								(5)† + 445
110	34	331	258	91	4								719
115	28	340	247	106	3								724
120	39	304	224	44	5								617
125	33	180	101	28	2	1							345
130	22	89	61	10	1								183
135	9	41	37	3									90
140	3	18	12	3									36
145	1	4	7										12
150	2	5	4										11
155	1	4	3		1								9
160	1	1	1										3
165	--	1	--	--	--	--	--	--	--	--	--	--	1
Totals	249	1,636	1,179	402	34	13	6	--	--	2	--	1	3,573

* Recorded only as 3 inches or under.

† Recorded only as over 3 inches.

TABLE A-6

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1935-36, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														
40														
45														
50														
55														
60				1				2						
65	1			4	1		2							
70				33	5		3	1						
75				92	18		5	3	2	1				
80				125	26		5	2	2		1			
85				96	20		4	9	1		2			
90				44	10		1	4	3		4			
95				18	3			4			3			
100				3	1		2				2	1		
105				1	2							1		
110					1									
115														
120														
125														
130														
135												1		
140													1	
145														
150														
155														
160														
165														
Totals	1	--	--	417	87	--	22	25	8	1	1	12	3	2

TABLE A-6—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1935-36, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25													
30													
35													
40													
45													
50													
55													
60													3
65						1							9
70													42
75													121
80													161
85		1	1	2									137
90		2	5	1									74
95		24	26	5	1								84
100	2	75	112	16	5	1							220
105	4	225	269	30	6								538
110	8	449	387	32									877
115	20	580	377	30									1,007
120	27	521	276	26									850
125	33	335	120	5									493
130	17	137	42	1									198
135	15	50	6										72
140	5	11											16
145	4	3											7
150	1												2
155													
160													
165													
Totals	136	2,413	1,621	148	12	2	--	--	--	--	--	--	4,911

TABLE A-7

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap, 1936-37, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														
40														
45														
50														
55														
60														
65														
70														
75														
80														
85							1	2			1			
90								1		2				
95							2	1		3				
100							1							
105										1				
110														
115														
120														
125														1
130														
135														
140														
145														
150														
155														
160														
165														
Totals...	--	--	--	--	--	--	4	4	--	6	1	--	--	1

TABLE A-7—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap, 1936-37, by Two-week Periods

[illegible]

TABLE A-8

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1937-38, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														
40														
45														
50														
55														
60														
65														
70														
75										1				
80														
85														1
90														
95														
100														1
105														
110														
115														
120														
125														
130														
135														
140														
145														
150														
155														
160														
165														
Totals	--	--	--	--	--	--	--	--	--	1	--	--	--	2

TABLE A-8—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1937-38, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25													
30													
35													
40													
45													
50													
55													
60													
65													
70													
75													1
80													
85				1									2
90			5	2									7
95	1		14	9									24
100	1	1	56	24	2								85
105		3	127	34	1	1							166
110	2	13	216	78	4								313
115		14	328	59	5								406
120	2	23	366	56	2								449
125	2	23	199	31	1								256
130	1	25	110	10	4								150
135		14	33	5	1								53
140		3	3		1								7
145		3	3										6
150		1											1
155													
160													
165													
Totals	9	123	1,460	309	21	1	--	--	--	--	--	--	1,926

TABLE A-9

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1938-39, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														
40														
45														
50														
55														
60														
65														
70														
75														
80														
85														
90														
95														
100														4
105														2
110														3
115														3
120														5
125														4
130														3
135														1
140														2
145														4
150														
155														
160														1
165														
Totals	--	--	--	--	--	--	--	--	--	--	--	--	--	32

TABLE A-9—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1938-39, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25													
30													
35													
40													
45													
50													
55													1
60													2
65													2
70													2
75													
80													
85													
90	1												1
95	6	5	1										12
100	34	14	2										54
105	62	54	7										125
110	101	80	11	1									196
115	94	78	7										182
120	61	44	2										112
125	57	26	2										90
130	22	11											36
135	16	1											18
140	1	5											8
145	4	2											10
150													
155													
160													
165													1
Totals	459	320	33	3	2	--	2	--	1	--	--	--	852

TABLE A-10

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1939-40, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														
40														
45														
50														
55														
60														
65														
70														
75				2			1						1	
80						1	3					1	3	
85				2						1			3	1
90							1					1	1	
95										1		1	1	
100														1
105														
110														
115														
120														
125														
130														
135														
140														
145														
150														
155														
160														
165														
Totals	--	--	--	4	--	1	5	--	--	2	--	3	9	2

TABLE A-10—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1939-40, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25													
30													
35													
40													
45													
50													
55													
60													
65													
70													
75		1											5
80	1												9
85	1	2											10
90	5	1											10
95	18	4	1	2									27
100	30	21	12	15	2								81
105	38	77	81	45	9								250
110	22	104	125	81	4								336
115	25	85	153	122	4	1							390
120	11	45	162	111	1								330
125	1	21	111	77	1								211
130		7	37	24	1								69
135		4	5	2									11
140													
145	1												1
150													
155													
160													
165													
Totals	153	372	687	479	22	1	--	--	--	--	--	--	1,740

TABLE A-11

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1940-41, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25														
30														
35														
40														
45														
50														
55														
60														
65														
70														
75														
80														
85														
90														
95														
100														
105														
110														
115														
120														
125														
130														
135														
140														
145														
150														
155														
160														
165														
Totals	--	--	--	--	--	--	--	--	--	--	--	--	--	--

TABLE A-11—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1940-41, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25													
30													
35													
40													
45													
50													
55													
60													
65					1								1
70													
75						1							1
80					1	1							2
85													
90													
95		2	2										4
100		7	7										14
105	1	12	18	2									33
110	1	18	17	2									38
115		16	9	3									28
120	1	7	6										14
125	1	6	2										9
130		5	1										6
135		2											2
140													
145													
150													
155													
160													
165													
Totals	4	75	62	7	2	2	--	--	--	--	--	--	152

TABLE A-12

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1941-42, by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24- Jan. 6	Jan. 7-20	Jan. 21- Feb. 3	Feb. 4-17	Feb. 18- Mar. 3	Mar. 4-17	Mar. 18-31	Apr. 1-14
21-25.....														
30.....														
35.....														
40.....														
45.....														
50.....														
55.....														
60.....														
65.....														
70.....														
75.....														
80.....														
85.....								1						
90.....								1						
95.....														
100.....														
105.....														
110.....														
115.....														
120.....														
125.....														
130.....														
135.....														
140.....														
145.....														
150.....														
155.....														
160.....														
165.....														
Totals.....	--	--	--	--	--	--	2	--	--	--	--	--	--	2

TABLE A-12—Continued

Waddell Creek, Silver Salmon: Juveniles Checked Through Downstream Trap,
1941-42, by Two-week Periods

Length in mm.	Apr. 15-28	Apr. 29- May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
21-25.....													
30.....													
35.....	1												2
40.....	1	1											2
45.....													
50.....						2	1						3
55.....				1	1	1	3	1					7
60.....					1	3	4						8
65.....						3	1	1	1				6
70.....					1								1
75.....					1								1
80.....						1							1
85.....		1	3	1									6
90.....		6	17	3	2	1							30
95.....		25	51	18	6								100
100.....		37	77	29	10								153
105.....		31	56	48	7								142
110.....		36	28	25	8								97
115.....		36	35	16	3								90
120.....		21	27	3									52
125.....		3	5										8
130.....		1	1										2
135.....													
140.....													
145.....													
150.....													
155.....													
160.....													
165.....													
Totals.....	2	198	300	144	40	11	9	2	1	--	--	--	711

TABLE A-13

Waddell Creek, Silver Salmon: Age + Juveniles Checked Through Downstream Trap; Mean Length (in mm.) by Two-week Periods

Brood season	Item	Two-week period ending:													
		Oct. 14	Oct. 28	Nov. 11	Nov. 25	Dec. 9	Dec. 23	Jan. 6	Jan. 20	Feb. 3	Feb. 17	Mar. 3	Mar. 17	Mar. 31	Apr. 14
1933-34	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1934-35	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	9
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	35.67
1935-36	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1936-37	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1937-38	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1938-39	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1939-40	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1940-41	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1941-42	Number....	--	--	--	--	--	--	--	--	--	--	--	--	--	1
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	--	34.00

TABLE A-13—Continued

Waddell Creek, Silver Salmon: Age + Juveniles Checked Through Downstream Trap; Mean Length (in mm.) by Two-week Periods

Brood season	Item	Two-week period ending:												Total
		Apr. 28	May 12	May 26	June 9	June 23	July 7	July 21	Aug. 4	Aug. 18	Sept. 1	Sept. 15	Sept. 30	
1933-34	Number....	1	--	10	--	--	--	--	--	--	--	--	--	11 + 3 not meas- ured = 14
	Mean length	44.00	--	52.00	--	--	--	--	--	--	--	--	--	
1934-35	Number....	9	--	--	--	2	12	6	--	--	2	--	1	41
	Mean length	37.56	--	--	--	58.50	55.50	62.33	--	--	78.50	--	64.00	
1935-36	Number....	--	--	--	--	--	1	--	--	--	--	--	--	1
	Mean length	--	--	--	--	--	64.00	--	--	--	--	--	--	
1936-37	Number....	--	1	1	3	3	--	--	--	--	--	--	--	8
	Mean length	--	41.00	43.00	35.00	38.67	--	--	--	--	--	--	--	
1937-38	Number....	--	--	--	--	--	--	--	--	--	--	--	--	0
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	
1938-39	Number....	--	--	1	2	2	--	1	--	1	--	--	--	7
	Mean length	--	--	51.00	57.50	52.50	--	58.00	--	65.00	--	--	--	
1939-40	Number....	--	--	--	--	--	--	--	--	--	--	--	--	0
	Mean length	--	--	--	--	--	--	--	--	--	--	--	--	
1940-41	Number....	--	--	--	--	2	2	--	--	--	--	--	--	4
	Mean length	--	--	--	--	70.50	73.50	--	--	--	--	--	--	
1941-42	Number....	2	1	--	1	4	10	9	2	1	--	--	--	31
	Mean length	37.50	36.00	--	52.00	63.25	57.70	56.56	57.50	65.00	--	--	--	

TABLE A-14

Waddell Creek, Silver Salmon: Age 1 Juveniles Checked Through Downstream Trap;
Mean Length (in mm.) by Two-week Periods

Brood season	Item	Two-week period ending:									
		Oct. 14	Oct. 28	Nov. 11	Nov. 25	Dec. 9	Dec. 23	Jan. 6	Jan. 20	Feb. 3	Feb. 17
1932-33	Number	--	--	--	--	--	1	--	--	--	2
	Mean length	--	--	--	--	--	71.00	--	--	--	78.00
1933-34	Number	--	--	--	--	--	--	1	2	--	--
	Mean length	--	--	--	--	--	--	69.00	78.00	--	--
1934-35	Number	1	--	--	417	87	--	22	25	8	1
	Mean length	62.00	--	--	79.13	80.48	--	77.09	81.12	81.00	72.00
1935-36	Number	--	--	--	--	--	--	4	4	--	6
	Mean length	--	--	--	--	--	--	91.75	86.75	--	93.67
1936-37	Number	--	--	--	--	--	--	--	--	--	1
	Mean length	--	--	--	--	--	--	--	--	--	71.00
1937-38	Number	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--
1938-39	Number	--	--	--	4	--	1	5	--	--	2
	Mean length	--	--	--	79.25	--	76.00	79.80	--	--	87.00
1939-40	Number	--	--	--	--	--	--	--	--	--	--
	Mean length	--	--	--	--	--	--	--	--	--	--
1940-41	Number	--	--	--	--	--	--	2	--	--	--
	Mean length	--	--	--	--	--	--	87.00	--	--	--

TABLE A-14—Continued

Waddell Creek, Silver Salmon: Age 1 Juveniles Checked Through Downstream Trap;
Mean Length (in mm.) by Two-week Periods

Brood season	Item	Two-week period ending:									
		Mar. 3	Mar. 17	Mar. 31	Apr. 14	Apr. 28	May 12	May 26	June 9	June 23	July 7
1932-33	Number	--	4	18	291	1,515	1,324	194	27	--	--
	Mean length	--	89.50	108.83	115.82	114.20	112.57	111.28	112.89	--	--
1933-34	Number	2	1	1	18	240	1,636	1,179	402	32	1
	Mean length	104.00	89.00	101.00	92.56	113.80	113.47	113.59	110.35	109.38	123.00
1934-35	Number	1	12	3	2	136	2,413	1,621	148	12	1
	Mean length	85.00	89.42	110.33	140.00	121.89	114.37	110.80	108.36	100.75	98.00
1935-36	Number	1	--	--	1	40	470	438	92	3	--
	Mean length	78.00	--	--	118.00	112.32	118.49	115.40	114.66	116.33	--
1936-37	Number	--	--	--	2	9	123	1,460	309	21	1
	Mean length	--	--	--	92.00	113.00	121.94	114.86	111.37	116.33	105.00
1937-38	Number	--	--	--	32	459	320	32	1	--	--
	Mean length	--	--	--	121.00	118.63	111.62	108.37	106.00	--	--
1938-39	Number	--	3	9	2	153	372	687	479	22	1
	Mean length	--	87.33	81.56	90.00	103.61	109.95	114.38	114.28	108.18	111.00
1939-40	Number	--	--	--	--	4	75	62	7	--	--
	Mean length	--	--	--	--	114.25	111.19	107.18	108.57	--	--
1940-41	Number	--	--	--	1	--	197	300	143	36	1
	Mean length	--	--	--	120.00	--	105.10	102.40	102.45	100.83	86.00

TABLE A-14—Continued
Waddell Creek, Silver Salmon: Age 1 Juveniles Checked Through Downstream Trap;
Mean Length (in mm.) by Two-week Periods

Brood season	Item	Two-week period ending:					Total
		July 21	Aug. 4	Aug. 18	Sept. 1	Sept. 15	Sept. 30
1932-33	Number.....	—	—	—	—	—	3,376+40 not measured = 3,416
1933-34	Mean length.....	—	—	—	—	—	113.52*
1934-35	Number.....	—	—	—	—	—	3,515+17 not measured = 3,532
1935-36	Mean length.....	—	—	—	—	—	113.26*
1936-37	Number.....	—	—	—	—	—	4,910
1937-38	Mean length.....	—	—	—	—	—	113.06*
1938-39	Number.....	—	—	—	—	—	1,089
1939-40	Mean length.....	—	—	—	—	—	116.61*
1940-41	Number.....	—	—	—	—	—	1,926
	Mean length.....	—	—	—	—	—	114.77*
	Number.....	1	—	—	—	—	845
	Mean length.....	123.00	—	—	—	—	112.40*
	Number.....	—	—	—	—	—	1,740
	Mean length.....	—	—	—	—	—	112.40*
	Number.....	—	—	—	—	—	148
	Mean length.....	—	—	—	—	—	109.47*
	Number.....	—	—	—	—	—	680
	Mean length.....	—	—	—	—	—	103.11*
Total.....							112.07†

* Mean length of four consecutive periods forming largest total.

† Arithmetic mean of means.

TABLE A-15
Waddell Creek, Steelhead: Changes in Life History Category Composition of the
Spawning Run, by Months *

Month	First spawners				Second spawners		Total
	1/1	2/1	3/1	2/2	2/1S.1	2/1.1S.1	
October.....	—	2	—	—	—	—	2
November.....	0.1% 4	0.2% 7	—	—	—	—	0.3% 12
December.....	1.5% 59	4.6% 179	0.2% 8	1.2% 48	0.8% 31	0.1% 5	8.5% 330
January.....	1.8% 69	8.6% 336	1.6% 61	6.4% 250	2.0% 76	0.6% 24	21.0% 816
February.....	0.5% 20	5.9% 231	2.1% 81	8.7% 338	2.7% 106	1.1% 44	21.1% 820
March.....	0.6% 23	7.8% 304	5.3% 205	7.8% 303	1.8% 71	1.1% 41	24.4% 947
April.....	0.1% 3	2.2% 86	2.1% 83	1.8% 70	0.4% 14	0.2% 8	6.8% 264
May.....	—	0.1% 5	—	0.1% 5	—	—	0.3% 10
June.....	—	1	—	—	—	—	1
Totals.....	4.6% 178	29.6% 1,151	11.3% 439	26.1% 1,014	7.7% 298	3.1% 122	82.4% 3,202

* Percentages are percentages of total run of all fish.

TABLE A-16

Scott Creek, Steelhead: Data Used in Calculation of Volume Factor (F)

Date	Fish no.	Counted no. eggs	Measured vol. of eggs (cc.)	Vol. per egg (cc.)	Actual vol. of eggs (cc.)	Volume factor (F)	No. eggs measured
1932-----	--	3,874	550	0.0978	379	0.689	100 (10 lots)
Mar. 5, 1936--	--	6,172	900	0.0958	591	0.657	110 (11 lots)
Mar. 5, 1936--	--	4,013	568	0.0958	384	0.676	110 (11 lots)

$$0.689 + 0.657 + 0.676 = 2.022$$

$$\frac{2.022}{3} = 0.674 = \text{Average volume factor (F)}$$

NOTE: The latter two sets of data represent complete and partial counts and measured egg volumes from the same fish. The volume factor was also calculated for three other fish, for which the data are tabulated below. However, these data were not used, since either the measured egg volumes approached the extremes of the egg volume frequency distribution, Table A-17 of the Appendix, or the number of eggs measured for individual volume was too small.

Date	Fish no.	Counted no. eggs	Measured vol. of eggs (cc.)	Vol. per egg (cc.)	Actual vol. of eggs (cc.)	Volume factor (F)	No. eggs measured
Feb. 2, 1933---	87,927	8,859	1,325	0.101	895	0.675	10
Feb. 13, 1933--	87,950	4,217	425	0.070	295	0.694	10
Feb. 19, 1935--	54	2,403	190	0.053	127	0.668	20 (2 lots)

TABLE A-17

Scott Creek, Steelhead: Volumes of Eggs Obtained From 537 Spawned Fish, 1932-33

Measured volume of eggs (cc.)	No. of fish	Measured volume of eggs (cc.)	No. of fish
100-149-----	1	900-----	47
150-----	4	950-----	33
200-----	11	1,000-----	16
250-----	20	1,050-----	14
300-----	16	1,100-----	16
350-----	17	1,150-----	10
400-----	31	1,200-----	2
450-----	22	1,250-----	3
500-----	27	1,300-----	3
550-----	23	1,350-----	1
600-----	27	1,400-----	3
650-----	35	1,450-----	--
700-----	49	1,500-----	1
750-----	29		
800-----	48		
850-----	28		
		Total-----	537

TABLE A-18

Scott Creek, Steelhead: Eggs Remaining in Spawned Fish

Date	Fish length in cm.	Age	Vol. per egg (cc.)	Calc. no. eggs obtained	Eggs remaining		Total no. eggs
					Number	Percentage	
1932							
February 25.....	--	--	.087	7,347	325	4.2	7,672
March 10.....	62	2/2	.099	4,174	925	18.1	5,099
April 14.....	66	--	.076	7,476	740	9.0	8,216
April 14.....	--	--	.091	5,294	400	7.0	5,694
April 21.....	52	--	.111	4,591	445	8.8	5,036
April 21.....	51	--	.072	3,395	344	9.2	3,739
April 28.....	58	2/1S.1	.072	4,687	539	10.3	5,226
April 28.....	48	2/1	.058	2,969	264	8.2	3,233
May 5.....	53	27/1	.094	3,150	415	11.6	3,565
May 5.....	53	37/1	.080	2,838	475	14.3	3,313
1933							
February 13.....	72	2(?) / 2	.088	11,153	1,047	8.6	12,200
March 6.....	71	1/1.1S.1	.090	6,122	659	9.7	6,781
Mean.....	--	--	--	--	--	9.92	--

NOTE: The total number of eggs in the fish less 9.92 percent = $1.11 \times$ the number of eggs obtained in spawning. For purposes of calculation of total egg production in this paper, the factor 1.1 has been used to multiply the number of eggs obtained in spawning.

TABLE A-19

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1933-34;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Oct. 1- 14	Oct. 15- 28	Oct. 29- Nov. 11	Nov. 12- 25	Nov. 26- Dec. 9	Dec. 10- 23	Dec. 24- Jan. 6	Jan. 7- 20	Jan. 21- Feb. 3	Feb. 4- 17	Feb. 18- Mar. 3	Mar. 4- 17	Mar. 18- 31
21-25.....	--	--	--	Traps not operated before December 3	--	--	--	--	--	--	--	--	--
30.....	--	--	--		--	--	--	--	--	--	--	--	--
35.....	--	--	--		--	--	--	--	--	--	--	--	--
40.....	--	--	--		--	--	--	--	--	--	--	--	--
45.....	--	--	--		--	--	1	--	--	--	--	--	--
50.....	--	--	--		--	--	2	1	--	--	--	--	--
55.....	--	--	--		--	1	1	--	--	--	--	--	--
60.....	--	--	--		--	--	3	2	--	--	4	--	--
65.....	--	--	--		--	--	4	--	1	1	7	--	--
70.....	--	--	--		--	--	--	--	1	--	3	1	--
75.....	--	--	--		--	--	1	1	--	1	1	--	--
80.....	--	--	--		--	--	--	--	--	--	1	--	--
85.....	--	--	--		--	--	--	--	--	--	--	--	3
90.....	--	--	--		--	--	1	1	--	--	--	--	--
95.....	--	--	--		--	--	--	--	--	--	--	--	--
100.....	--	--	--		--	--	3	1	--	1	--	1	--
105.....	--	--	--		--	--	--	--	--	--	--	--	1
110.....	--	--	--		--	--	1	1	1	--	3	2	--
115.....	--	--	--		--	--	3	--	1	--	6	4	--
120.....	--	--	--		--	1	3	1	1	--	8	2	1
125.....	--	--	--		--	--	4	--	--	--	3	5	2
130.....	--	--	--		--	--	--	--	--	--	2	2	1
135.....	--	--	--		--	--	2	--	1	--	7	3	9
140.....	--	--	--		--	--	1	--	--	1	2	--	--
145.....	--	--	--		--	--	2	--	--	--	3	--	--
150.....	--	--	--		--	--	--	--	--	--	2	2	5
155.....	--	--	--		--	--	--	--	--	--	1	--	5
160.....	--	--	--		--	--	1	--	--	--	--	2	3
165.....	--	--	--		--	1	--	--	--	1	2	7	--
170.....	--	--	--		--	--	--	--	--	--	2	6	19
175.....	--	--	--		--	--	--	--	--	--	--	1	6
180.....	--	--	--		--	--	--	--	--	--	--	3	5
185.....	--	--	--		--	--	1	--	--	--	1	4	25
190.....	--	--	--	--	--	--	--	--	--	--	1	2	
195.....	--	--	--	--	--	--	--	--	--	--	--	3	
200.....	--	--	--	--	--	--	--	--	--	--	--	5	
205.....	--	--	--	--	--	--	--	--	--	2	3	--	
210.....	--	--	--	--	--	--	--	--	--	--	4	4	
215.....	--	--	--	--	--	--	--	--	--	--	2	4	
220.....	--	--	--	--	--	--	--	--	1	--	--	7	
225.....	--	--	--	--	--	--	--	--	--	--	2	2	
230.....	--	--	--	--	--	--	--	--	--	--	4	4	
235.....	--	--	--	--	--	--	--	--	--	--	2	3	
240.....	--	--	--	--	--	--	--	--	--	--	2	1	
245.....	--	--	--	--	--	--	--	--	--	--	--	1	
250.....	--	--	--	--	--	--	--	--	--	--	--	--	
255.....	--	--	--	--	--	--	--	--	--	--	--	1	
260.....	--	--	--	--	--	--	--	--	--	--	--	1	
265.....	--	--	--	--	--	--	--	--	--	--	--	--	
270.....	--	--	--	--	--	--	--	--	--	--	--	--	
Totals.....	--	--	--	--	3	33	8	4	6	27	57	92	360

* Measured only as 3 inches or under.
† Measured only as over 3 inches.

TABLE A-19—Continued

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1933-34;
Length-frequency Distribution by Two-week Periods**

[illegible]

GRAND TOTAL	3,117
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TABLE A-20

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1934-35;
Length-frequency Distribution by Two-week Periods**

[illegible]

* 75 mm. or under.

TABLE A-20—Continued

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1934-35;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Apr. 1- 14	Apr. 15- 28	Apr. 29- May 12	May 13- 26	May 27- June 9	June 10- 23	June 24- July 7	July 8- 21	July 22- Aug. 4	Aug. 5- 18	Aug. 19- Sept. 1	Sept. 2- 15	Sept. 16- 30	
21-25.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
30.....	--	--	--	--	--	--	--	--	AGE +				--	
35.....	1	--	--	--	--	--	--	--	--	--	--	--	--	
40.....	--	--	--	--	--	--	3	--	--	--	--	--	--	
45.....	--	--	--	--	--	--	11	2	5	--	--	--	--	
50.....	--	--	--	--	1	9	21	8	15	14	3	1	--	
55.....	--	--	--	1	4	17	62	14	17	13	7	5	--	
60.....	--	--	--	--	3	26	33	22	18	12	7	3	2	
65.....	--	--	--	--	2	32	35	25	20	20	9	6	4	
70.....	--	--	--	--	--	24	33	10	20	9	3	6	--	
75.....	--	1	--	--	4	14	10	9	5	5	1	2	--	
80.....	2	--	1	--	4	10	5	1	3	1	--	1	1	
85.....	1	1	--	3	4	3	3	2	--	1	--	--	--	
90.....	3	3	6	3	4	6	3	1	--	--	--	--	--	
95.....	--	4	5	9	15	12	2	--	1	--	--	--	--	
100.....	1	1	10	8	23	16	5	--	--	--	--	1	--	
105.....	3	1	13	10	22	11	3	--	--	--	--	--	--	
110.....	2	1	9	6	19	8	7	--	--	--	--	--	--	
115.....	2	2	4	3	14	16	3	--	--	--	--	--	--	
120.....	1	1	9	5	4	3	2	1	--	--	--	--	--	
125.....	3	--	6	4	9	7	--	--	--	--	--	1	--	
130.....	--	3	2	--	7	5	1	1	AGE 1				--	
135.....	--	1	7	3	1	5	--	--	--	--	--	--	--	
140.....	2	7	4	5	2	1	1	--	--	--	--	1	--	
145.....	5	10	5	2	1	1	--	--	--	--	--	--	--	
150.....	8	8	12	2	--	--	1	--	--	--	--	--	--	
155.....	16	21	14	6	1	1	--	--	--	--	--	--	--	
160.....	14	27	12	5	--	--	--	--	--	--	1	--	--	
165.....	10	12	17	2	--	--	--	--	--	--	--	--	--	
170.....	19	11	5	4	2	--	--	--	--	--	--	--	--	
175.....	13	8	6	--	--	--	--	--	--	--	--	--	--	
180.....	8	5	2	1	--	--	--	--	--	--	--	--	--	
185.....	7	4	2	--	--	--	--	--	--	AGE 2				--
190.....	8	3	--	--	--	--	--	--	--	--	--	1	--	
195.....	4	1	--	--	--	--	--	--	--	--	--	--	--	
200.....	2	2	1	--	--	--	--	--	--	--	--	--	--	
205.....	1	--	--	--	--	--	--	--	--	--	--	--	--	
210.....	3	--	--	--	--	--	--	--	--	--	--	--	--	
215.....	2	--	--	--	--	--	--	--	--	--	--	--	--	
220.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
225.....	1	--	--	--	--	--	--	--	--	--	--	--	--	
230.....	2	--	--	--	--	--	--	--	--	AGE 3				--
235.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
240.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
245.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
250.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
255.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
260.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
265.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
270.....	--	--	--	--	--	--	--	--	--	--	--	--	--	
Totals.....	144	138	152	82	146	227	244	96	104	75	31	28	7	
GRAND TOTAL													1,791	

TABLE A-21

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1935-36;
Length-frequency Distribution by Two-week Periods**

[illegible]

* Recorded only as 25 cm.

TABLE A-21—Continued

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1935-36;
Length-frequency Distribution by Two-week Periods**

[illegible]

TABLE A-22

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1936-37;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Oct. 1- 14	Oct. 15- 28	Oct. 29- Nov. 11	Nov. 12- 25	Nov. 26- Dec. 9	Dec. 10- 23	Dec. 24- Jan. 6	Jan. 7- 20	Jan. 21- Feb. 3	Feb. 4- 17	Feb. 18- Mar. 3	Mar. 4- 17	Mar. 18- 31
21-25	--	--	--	--	--	--	--	--	--	--	--	--	--
30	--	--	--	--	--	--	--	--	--	--	--	--	--
35	--	--	--	--	--	--	--	--	--	--	--	--	--
40	--	--	--	--	--	--	--	1	--	--	--	--	--
45	--	--	--	--	--	--	4	--	--	--	--	--	--
50	1	--	--	--	1	2	9	2	--	--	--	--	--
55	1	--	--	1	1	4	20	2	3	3	--	--	--
60	--	--	--	3	--	4	27	1	--	--	--	--	--
65	1	--	--	3	--	7	24	3	1	1	1	--	--
70	2	--	--	4	--	4	33	4	--	1	3	--	--
75	--	--	--	4	1	5	23	2	1	8	--	--	--
80	--	--	--	1	--	2	21	2	--	2	2	--	--
85	--	1	--	1	--	1	6	1	--	--	1	--	1
90	--	--	--	--	--	1	13	2	1	--	1	--	--
95	--	1	--	--	--	--	3	1	--	1	--	--	--
100	--	--	--	1	--	--	2	--	1	--	--	1	--
105	--	--	--	--	--	--	1	1	--	1	1	--	--
110	--	--	--	--	--	--	1	--	--	1	--	1	--
115	--	1	--	--	--	--	1	--	--	2	--	2	--
120	--	--	--	--	--	--	1	--	--	2	2	1	--
125	--	--	--	--	--	1	--	--	--	4	1	--	--
130	--	--	--	--	--	1	1	--	--	1	--	--	--
135	--	--	--	--	--	--	--	--	--	2	3	2	--
140	--	--	--	--	--	--	--	--	--	1	3	1	--
145	--	--	--	--	--	--	--	--	--	1	1	3	--
150	--	--	--	1	--	--	1	--	1	2	2	2	3
155	--	--	--	--	--	--	--	--	--	--	2	3	2
160	--	--	--	--	--	--	--	--	--	--	1	3	7
165	--	--	--	--	--	--	--	--	--	1	1	4	1
170	--	--	--	--	--	--	--	--	--	--	--	6	3
175	--	--	--	--	--	--	--	--	--	1	1	2	1
180	--	--	--	--	--	--	1	--	--	--	7	8	1
185	--	--	--	--	--	--	--	--	--	--	1	4	1
190	--	--	--	--	--	--	--	--	--	--	--	6	1
195	--	--	--	--	--	--	--	--	--	--	5	2	1
200	--	--	--	--	--	--	--	--	--	--	--	6	1
205	--	--	--	--	--	--	--	--	--	--	--	3	1
210	--	--	--	--	--	--	--	--	--	--	1	2	--
215	--	--	--	--	--	--	--	--	--	--	1	1	--
220	--	--	--	--	--	--	--	--	--	--	1	--	1
225	--	--	--	--	--	--	--	--	--	--	--	2	--
230	--	--	--	--	--	--	--	--	--	--	--	--	--
235	--	--	--	--	--	--	--	--	--	--	--	--	--
240	--	--	--	--	--	--	--	--	--	--	--	--	--
245	--	--	--	--	--	--	--	--	--	--	--	--	--
250	--	--	--	--	--	--	--	--	--	--	--	--	--
255	--	--	--	--	--	--	--	--	--	--	--	--	--
260	--	--	--	--	--	--	--	--	--	--	--	--	--
265	--	--	--	--	--	--	--	--	--	--	--	--	--
270	--	--	--	--	--	--	--	--	--	--	--	--	--
Totals	5	3	--	19	3	32	192	22	8	35	42	65	25

* Length not recorded.
† Recorded only as 30 cm.

TABLE A-22—Continued

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1936-37;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Apr. 1- 14	Apr. 15- 28	Apr. 29- May 12	May 13- 26	May 27- June 9	June 10- 23	June 24- July 7	July 8- 21	July 22- Aug. 4	Aug. 5- 18	Aug. 19- Sept. 1	Sept. 2- 15	Sept. 16- 30
21-25													
30				1	4			1					
35					2	14	31	9				2	
40					2	5	102	101	2	8	2	3	
45				1	1	5	83	125	2	23	7	11	4
50				3	4	4	50	91	3	26	11	10	4
55				11	35	11	28	78	9	31	9	16	7
60				5	65	40	12	63	3	29	9	11	2
65				2	70	61	22	46	3	13	7	8	
70					32	41	35	29	4	6	2	3	
75					1	12	33	42	3	10	1	2	
80	1		2	3	2	3	26	37		3	2	1	
85	2	1		3	8	5	19	25	1	2		1	
90	1		1	16	25	5	5	8		2		1	
95				32	33	8	2	5			2		
100		1	2	36	51	4	3	5					
105			3	53	68	16	5	2					
110			8	42	66	20	4	1					
115	1		4	47	53	20	7	5					
120			1	23	43	22	3	3			1		
125			1	12	24	13	2	3					
130	2			9	13	10	1						
135	4	2	2	8	6	2	1	1					
140	2	2	1	3	2	1							
145	4	2	4	5	1	1		1					
150	8	6	10	5	2								
155	5	11	7	11	3	1							
160	8	10	11	8	1								
165	10	8	15	11	1								
170	6	10	19	12									
175	7	5	15	4	1								
180	4	5	13	2									
185		3	4	3									
190	1	5	4	1									
195	3	1	2	3								1	
200	1			1									
205	1	1		1									
210			1										
215					1								
220													
225		1											
230													
235													
240													
245													
250													
255			1										
260													
265													
270			*1	*1		†1							
Totals	71	74	132	378	620	325	474	681	30	153	53	70	17
GRAND TOTAL													3,529

TABLE A-23

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1937-38;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Oct. 1- 14	Oct. 15- 28	Oct. 29- Nov. 11	Nov. 12- 25	Nov. 26- Dec. 9	Dec. 10- 23	Dec. 24- Jan. 6	Jan. 7- 20	Jan. 21- Feb. 3	Feb. 4- 17	Feb. 18- Mar. 3	Mar. 4- 17	Mar. 18- 31
21-25	--	--	--	--	--	--	--	--	--	--	--	--	--
30	--	--	--	--	--	--	--	--	--	--	--	--	--
35	--	--	2	--	--	--	--	--	--	--	--	--	--
40	2	1	4	2	1	2	--	2	--	--	--	--	--
45	2	3	10	11	6	2	1	1	--	--	--	--	--
50	2	1	11	43	9	2	2	2	1	--	--	--	--
55	1	8	10	53	16	3	1	1	--	1	--	--	--
60	3	2	11	55	11	3	1	1	--	--	1	--	--
65	1	1	--	26	3	3	1	3	1	--	--	--	--
70	1	6	2	11	5	2	1	--	--	--	--	--	--
75	--	--	--	8	2	1	--	1	1	--	--	--	--
80	--	2	--	9	2	4	--	--	--	--	--	2	--
85	1	--	--	7	--	1	--	--	--	--	--	--	--
90	1	1	--	5	--	2	--	--	2	--	--	--	--
95	1	--	--	1	--	2	1	1	--	--	--	--	--
100	--	1	--	1	--	1	--	--	1	--	1	--	--
105	--	--	--	--	--	--	--	--	--	--	--	--	--
110	--	--	--	1	--	--	--	--	--	--	--	1	1
115	--	--	--	1	--	--	1	--	--	--	--	1	--
120	--	--	--	--	--	1	--	--	--	--	1	--	--
125	--	1	--	1	--	1	--	--	1	--	--	--	--
130	--	--	--	2	1	1	--	--	1	--	--	--	--
135	--	--	--	--	1	--	--	--	--	--	2	1	--
140	--	--	--	1	--	1	--	--	--	--	1	2	--
145	--	--	--	--	--	--	--	--	1	--	--	1	--
150	1	--	--	--	--	--	--	--	--	--	--	--	--
155	--	--	--	--	--	--	--	--	--	--	1	--	2
160	--	--	--	--	1	--	--	--	--	--	2	1	--
165	--	--	--	--	--	--	--	--	--	--	1	--	--
170	--	--	--	--	--	--	--	--	--	--	2	2	--
175	--	--	--	--	--	--	--	--	--	--	2	1	--
180	--	--	--	--	--	--	--	--	--	--	4	1	--
185	--	--	--	--	--	--	--	--	--	--	1	4	--
190	--	--	--	--	--	--	--	--	--	--	1	2	--
195	--	--	--	--	--	--	--	--	--	--	1	--	--
200	--	--	--	--	--	--	--	--	--	--	--	3	--
205	--	--	--	--	--	--	--	--	--	--	1	--	--
210	--	--	--	--	--	1	--	--	--	--	--	--	--
215	--	--	--	--	--	--	--	--	--	--	1	--	--
220	--	--	--	--	--	--	--	--	--	--	--	--	--
225	--	--	--	--	--	--	--	--	--	--	--	--	--
230	--	--	--	--	--	--	--	--	--	--	--	--	--
235	--	--	--	--	--	--	--	--	--	--	--	--	--
240	--	--	--	--	--	--	--	--	--	--	--	--	--
245	--	--	--	--	--	--	--	--	--	--	--	--	--
250	--	--	--	--	--	--	--	--	--	--	--	--	--
255	--	--	--	--	--	--	--	--	--	--	--	--	--
260	--	--	--	--	--	--	--	--	--	--	--	--	--
265	--	--	--	--	--	--	--	--	--	--	--	--	--
270	--	--	--	--	--	--	--	--	--	--	--	--	--
Totals	16	27	50	238	58	31	9	12	9	1	25	22	3

TABLE A-23—Continued

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1937-38;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Apr. 1- 14	Apr. 15- 28	Apr. 29- May 12	May 13- 26	May 27- June 9	June 10- 23	June 24- July 7	July 8- 21	July 22- Aug. 4	Aug. 5- 18	Aug. 19- Sept. 1	Sept. 2- 15	Sept. 16- 30
21-25.....	--	--	--	--	--	--	--	--	--	--	--	--	--
30-----	--	--	--	--	--	--	1	--	--	--	--	--	--
35-----	AGE +			--	--	--	1	--	--	--	--	--	--
40-----	--	--	--	1	1	1	4	4	11	1	--	--	--
45-----	--	--	--	1	4	1	8	21	31	2	1	--	1
50-----	--	--	--	5	8	1	19	42	44	6	9	--	4
55-----	--	--	1	15	33	6	54	45	44	15	28	13	10
60-----	--	--	1	18	27	29	68	33	37	16	44	10	17
65-----	--	--	--	10	41	43	96	49	36	16	25	15	11
70-----	--	--	--	4	31	76	102	36	24	13	19	12	9
75-----	--	--	--	2	7	35	76	48	14	18	14	2	4
80-----	1	--	--	7	6	17	46	27	16	5	10	3	1
85-----	1	--	1	9	9	4	32	8	7	3	3	3	--
90-----	2	--	--	23	19	5	10	17	6	3	3	1	--
95-----	--	--	1	34	14	--	5	5	3	--	1	1	--
100-----	--	--	3	32	22	9	5	3	3	1	3	1	--
105-----	--	--	10	32	32	9	7	4	3	--	1	1	1
110-----	--	--	8	33	20	12	10	1	--	--	--	--	--
115-----	--	--	4	28	23	10	6	4	1	--	2	--	--
120-----	--	--	2	12	21	11	5	3	--	--	--	--	--
125-----	--	--	2	6	11	4	2	2	--	--	--	--	--
130-----	--	1	2	9	3	2	2	2	AGE 1			--	--
135-----	--	1	2	7	3	4	3	--	--	--	--	--	--
140-----	--	3	--	6	3	1	1	--	--	--	--	--	--
145-----	3	2	6	13	4	1	1	--	--	1	--	--	--
150-----	4	8	20	16	2	1	--	--	--	--	--	--	--
155-----	4	9	17	19	2	--	--	--	--	--	--	--	--
160-----	8	12	14	25	1	--	--	--	--	--	--	--	--
165-----	5	11	16	15	1	--	--	--	--	--	--	--	--
170-----	3	11	19	8	1	--	--	--	--	--	--	--	--
175-----	2	6	12	11	--	--	--	--	AGE 2			--	--
180-----	2	4	3	3	--	--	--	--	--	--	--	--	--
185-----	1	4	5	2	--	--	--	--	--	--	--	--	--
190-----	2	--	2	--	1	--	--	--	--	--	--	--	--
195-----	1	1	--	1	--	--	--	--	--	--	1	--	--
200-----	1	1	1	--	--	--	--	--	--	--	--	--	--
205-----	--	--	--	--	--	--	--	--	--	--	--	--	--
210-----	--	--	--	--	--	--	--	--	--	--	--	--	--
215-----	--	--	--	--	--	--	--	--	--	--	--	--	--
220-----	--	--	1	--	--	--	--	--	--	--	--	--	--
225-----	--	1	--	1	--	--	--	--	--	--	--	--	--
230-----	--	--	--	--	--	--	--	--	--	--	--	--	--
235-----	--	--	--	1	--	--	--	--	AGE 3			--	--
240-----	--	--	--	1	--	--	--	--	--	--	--	--	--
245-----	--	--	--	--	--	--	--	--	--	--	--	--	--
250-----	--	--	--	--	--	--	--	--	--	--	--	--	--
255-----	--	--	--	--	--	--	--	--	--	--	--	--	--
260-----	--	--	--	--	--	--	--	--	--	--	--	--	--
265-----	--	--	--	--	--	--	--	--	--	--	--	--	--
270-----	--	--	--	--	--	--	--	--	--	--	--	--	--
Totals-----	40	75	153	409	350	281	564	353	280	100	164	62	58
GRAND TOTAL													3,390

TABLE A-25

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1939-40;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Oct. 1- 14	Oct. 15- 28	Oct. 29- Nov. 11	Nov. 12- 25	Nov. 26- Dec. 9	Dec. 10- 23	Dec. 24- Jan. 6	Jan. 7- 20	Jan. 21- Feb. 3	Feb. 4- 17	Feb. 18- Mar. 3	Mar. 4- 17	Mar. 18- 31
21-25-----	--	--	--	--	--	--	--	--	--	--	--	--	--
30-----	--	--	--	--	--	--	--	--	--	--	--	--	--
35-----	--	--	--	--	--	--	--	--	--	--	--	--	--
40-----	--	--	--	--	--	--	--	--	--	--	--	--	--
45-----	2	1	--	--	--	--	--	--	--	--	--	--	--
50-----	14	5	2	--	--	1	1	--	--	1	--	--	--
55-----	25	13	4	2	--	6	1	--	--	--	--	--	--
60-----	21	5	6	--	--	6	6	--	--	--	--	--	--
65-----	20	2	10	4	2	6	3	--	--	--	--	--	--
70-----	5	2	2	1	--	6	6	1	1	--	--	--	1
75-----	2	2	--	2	--	--	3	--	--	--	--	--	--
80-----	1	2	--	1	--	2	4	--	1	--	--	--	--
85-----	--	--	1	1	--	--	--	--	--	AGE 1			
90-----	--	--	--	--	--	--	1	--	--	--	--	--	--
95-----	1	--	--	--	--	--	--	--	--	--	--	--	--
100-----	2	1	--	--	--	--	--	--	--	--	--	--	--
105-----	1	--	--	--	--	2	--	1	--	1	--	--	--
110-----	2	--	--	--	--	--	--	1	--	1	--	--	--
115-----	1	--	1	--	--	1	3	--	--	--	--	--	1
120-----	2	--	1	--	--	--	1	2	--	--	--	--	--
125-----	2	--	--	--	--	--	--	1	1	--	1	--	2
130-----	2	--	1	--	--	--	--	--	--	--	--	1	--
135-----	1	--	--	--	--	--	--	--	--	2	--	--	2
140-----	--	--	--	--	--	--	--	--	--	--	1	--	1
145-----	--	--	--	--	--	--	--	1	--	--	1	--	7
150-----	--	--	--	--	--	--	--	--	--	--	1	1	8
155-----	--	--	--	--	--	1	--	--	--	--	--	--	8
160-----	--	--	--	--	--	--	1	--	--	--	--	--	7
165-----	--	--	--	--	--	1	1	--	--	--	--	--	6
170-----	--	--	--	--	--	1	--	AGE 2			--	--	10
175-----	--	--	--	--	--	--	--	--	--	--	--	1	5
180-----	--	--	--	--	--	--	--	--	--	--	--	2	4
185-----	--	--	--	--	--	--	--	--	--	--	--	--	3
190-----	--	--	--	--	--	--	--	--	--	--	--	--	--
195-----	--	--	--	--	--	--	1	--	--	--	--	--	3
200-----	--	--	--	--	--	--	--	--	--	--	--	--	1
205-----	--	--	--	--	--	--	--	--	--	--	--	--	--
210-----	--	--	--	--	--	--	--	--	--	--	--	--	1
215-----	--	--	--	--	--	--	--	--	--	--	--	--	--
220-----	--	1	--	--	--	--	--	--	--	--	--	--	--
225-----	--	--	--	--	--	--	--	--	--	--	--	--	--
230-----	--	--	--	--	--	--	--	--	AGE 3			--	--
235-----	--	--	--	--	--	--	--	--	--	--	--	--	--
240-----	--	--	--	--	--	--	--	--	--	--	--	--	--
245-----	--	--	--	--	--	--	--	--	--	--	--	--	--
250-----	--	--	--	--	--	--	--	--	--	--	--	--	--
255-----	--	--	--	--	--	--	--	--	--	--	--	--	--
260-----	--	--	--	--	--	--	--	--	--	--	--	--	--
265-----	--	--	--	--	--	--	--	--	--	--	--	--	--
270-----	--	--	--	--	--	--	--	--	--	--	--	--	--
275-----	1	AGE 4			--	--	--	--	--	--	--	--	--
Totals-----	105	34	28	11	2	33	31	7	3	5	4	5	71

TABLE A-25—Continued

**Waddell Creek, Steelhead: Stream Fish Checked Through Downstream Trap, 1939-40;
Length-frequency Distribution by Two-week Periods**

Length in mm.	Apr. 1- 14	Apr. 15- 28	Apr. 29- May 12	May 13- 26	May 27- June 9	June 10- 23	June 24- July 7	July 8- 21	July 22- Aug. 4	Aug. 5- 18	Aug. 19- Sept. 1	Sept. 2- 15	Sept. 16- 30
21-25.....	--	--	--	--	--	--	--	--	--	--	--	--	--
30.....	--	--	--	--	1	--	--	--	--	--	--	--	--
35.....	AGE +				--	--	--	--	--	--	--	--	--
40.....	--	--	--	--	--	--	--	--	--	1	--	--	--
45.....	--	--	--	--	1	3	11	--	2	2	2	--	1
50.....	--	--	--	--	3	7	32	16	6	26	5	1	--
55.....	--	--	--	--	2	8	42	30	51	48	9	2	1
60.....	--	--	--	--	4	28	61	39	99	91	18	6	--
65.....	--	--	--	--	5	25	73	42	94	84	13	9	3
70.....	--	--	--	--	4	25	73	31	112	92	9	6	3
75.....	--	--	--	--	2	25	54	31	77	70	6	6	3
80.....	--	1	--	--	4	18	63	19	56	50	1	1	3
85.....	--	2	3	--	6	13	39	24	59	44	2	6	1
90.....	--	--	--	--	7	13	23	14	34	18	1	1	1
95.....	1	--	--	1	7	13	17	6	32	15	--	1	--
100.....	1	3	3	3	8	7	17	6	32	15	--	1	--
105.....	--	1	2	5	30	23	16	8	11	11	--	--	1
110.....	--	--	6	5	32	9	8	3	12	7	1	1	--
115.....	--	1	1	2	46	22	11	1	3	5	3	--	--
120.....	--	--	5	8	64	10	7	--	5	2	1	--	1
125.....	1	--	3	10	58	13	4	1	6	1	1	--	--
130.....	--	--	--	3	44	9	4	2	--	--	2	--	--
135.....	--	--	--	3	36	11	3	1	3	2	2	1	1
140.....	--	7	--	6	23	4	2	--	2	6	1	--	2
145.....	--	7	4	--	13	2	--	--	2	--	2	2	1
150.....	2	13	3	3	8	1	--	--	1	1	--	--	--
155.....	1	18	5	6	6	2	1	--	--	--	--	--	1
160.....	2	11	3	4	5	1	--	--	1	--	1	--	--
165.....	2	9	4	7	7	2	--	--	--	--	--	--	--
170.....	--	9	--	--	7	2	1	--	--	--	--	--	--
175.....	--	1	1	3	3	1	--	--	--	--	--	--	--
180.....	--	1	1	1	2	1	--	--	--	--	--	1	--
185.....	2	--	--	2	3	--	--	--	--	--	--	--	--
190.....	--	--	--	1	2	--	--	--	--	--	--	--	--
195.....	--	1	--	--	--	--	--	--	--	--	--	--	--
200.....	--	--	--	--	--	--	--	--	--	--	--	--	--
205.....	--	--	--	--	--	--	--	--	--	--	--	--	--
210.....	--	--	--	--	--	--	--	--	--	--	--	--	--
215.....	--	--	--	--	--	--	--	--	--	--	--	--	--
220.....	--	--	--	--	--	--	--	--	--	--	--	--	--
225.....	--	--	--	--	--	--	--	--	--	--	--	--	--
230.....	--	--	--	--	--	--	--	--	--	--	--	--	--
235.....	--	--	--	--	--	--	--	--	--	--	--	--	--
240.....	--	--	--	--	--	--	--	--	--	--	--	--	--
245.....	--	--	--	--	--	--	--	--	--	--	--	--	--
250.....	--	--	--	--	--	--	--	--	--	--	--	--	--
255.....	--	--	--	--	--	--	--	--	--	--	--	--	--
260.....	--	--	--	--	--	--	--	--	--	--	--	--	--
265.....	--	--	--	--	--	--	--	--	--	--	--	--	--
270.....	--	--	--	--	--	--	--	--	--	--	--	--	--
275.....	--	--	--	--	--	--	--	--	--	--	--	--	--
Totals.....	12	86	46	80	431	285	544	269	669	576	80	44	23
GRAND TOTAL													3,484

TABLE A-30

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1935-36;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
66-70													
75													
80					1			2		1			
85								3	1				
90					1			1			1		
95					2			1					
100					1			1					
105					2		2	1					
110								2	1				
115													
120							1						
125				1				1	2				
130									1				
135							2	2					
140							1	1					
145								2	1				
150				1		2		1					
155								3					
160								3	1				1
165								1	1				
170								1	1				
175													
180							1	2	1				
185							3	2					
190							2	2					
195							5	2					
200							7	5	1				
205							5	5					
210							3	4					
215							6	5		1			
220							8	4					
225							12	12			2		
230							13	3		1			
235							8	4	1		1		
240							9	5			1		
245							7	2					
250							1	1					
255							1	3					
260							1	1	1				
265							1						
270													
275													
280													
285													
290													
295													
300													
305													
310										1(35 cm.)			
Totals	--	--	--	--	9	--	101	86	14	4	5	--	1

TABLE A-30—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1935-36;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
66-70														--
75														--
80														4
85														4
90														2
95														3
100							1							3
105														5
110														3
115														--
120							1							2
125														4
130														1
135														4
140														2
145														3
150							1				1			7
155														3
160														5
165														2
170									1					3
175														--
180				1										5
185														5
190														4
195							1							8
200														13
205														10
210														7
215														12
220														12
225														26
230														17
235														14
240														15
245														9
250														2
255														4
260														3
265														1
270														--
275														--
280														--
285														--
290														--
295														--
300			1											--
305														*1
310														1
Totals	--	--	1	1	--	--	4	--	2	--	1	--	--	229

* Recorded only as 31 cm.

TABLE A-31

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1936-37;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
66-70													
75													
80													
85													
90													
95													
100													
105													
110													
115													
120													
125													
130				1									
135						1							
140													
145						1							
150				1									
155													
160						1	1						
165						1							
170													
175					1								
180						1	1			2			
185						1							
190						1				1			
195									1				
200									3	3			
205									5				
210							1	1	1				
215										3			
220													
225								1					
230									2	1			
235													
240													
245													
250													
255										1			
260									1				
265													
270						1			1				
275													
280													
285													
290											1		
295													
300							1			1			
305										1 (33 cm.)			
310										1 (44 cm.)			
Totals	--	--	--	2	1	8	4	2	14	15	2	--	--

TABLE A-31—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1936-37;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
66-70														1
75														1
80														1
85								1						1
90								1						1
95														2
100						1								2
105								1						2
110		1												2
115		1				1								1
120											1			1
125				1										2
130						1								4
135	1							2						2
140	1							1						3
145		1						1						3
150														1
155						1	1	1			1			4
160														2
165							1	1		1				4
170	1													2
175		1						1		1				4
180								1						5
185								2						3
190										2				4
195						1				1				4
200	1										1			8
205														5
210														4
215														3
220														1
225														3
230														1
235														3
240														1
245														1
250														1
255														1
260														2
265														2
270														2
275														2
280														2
285														2
290								1						2
295														2
300														2
305														3
310														3
Totals	4	4	--	1	1	5	2	14	1	6	4	--	1	91

TABLE A-32

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1937-38;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-23	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
66-70
75
80
85
90	1
95
100	1
105	1	..	4
110	1	..	1
115	2	1	1
120	2	1
125	..	1	4
130	5	2	1
135	1	5	4	1
140	9	3	1	1
145	13	4
150	1	8	8	1	1	1	..
155	3	13	8
160	20	16	1	..	1
165	17	14	2	2
170	16	26	2	2	1
175	21	32	2	2
180	2	16	22	3	1	..
185	1	2	23	24	..	2
190	1	18	24	..	4
195	1	16	25	3	3	1
200	14	19	..	1	1
205	11	6	1
210	2	5	1
215	1	..	6	1	1
220	4	2	1	1
225	1	1	1
230	4
235	2
240
245
250
255
260	1
265	1
270
275
280	1
285
290
295
300
305
310	1 (39 cm.)
Totals	..	1	1	4	10	260	249	24	17	5	1	2	..

TABLE A-32—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1937-38;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
66-70
75
80
85	1	1
90	1
95	1	1
100	1
105	1	6
110	1	1	..	5
115	1	..	1	..	1	8
120	1	4
125	1	..	1	7
130	1	1	10
135	2	1	14
140	14
145	1	19
150	1	20
155	24
160	1	1	40
165	35
170	1	46
175	57
180	44
185	52
190	47
195	49
200	1	36
205	18
210	8
215	..	1	1	11
220	8
225	3
230	4
235	2
240	..	2	2
245
250
255
260	1
265	1
270
275
280	1
285
290
295
300
305
310	1
Totals	4	3	1	1	5	2	2	2	4	..	1	2	..	601

TABLE A-33

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1938-39;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
66-70.....													
75.....													
80.....													
85.....													
90.....			1										
95.....													
100.....			1		2								
105.....			2			1							
110.....			1										
115.....					3								
120.....			1		2								
125.....			1		1	1							
130.....			2	1									
135.....			2	2									
140.....			1										
145.....			2	2	2	1							
150.....			2	1									
155.....			2	3	4								
160.....				3	1		1					1	
165.....			3	4	2	3		1		1			
170.....					3	2							
175.....				4	1		1						
180.....				3	3	2	1	1	1				
185.....			1	3	3	1							
190.....			3	1	5	3	1						
195.....					3	2	3	1	2				
200.....			2	1	3	2		2					
205.....			1					2		1			
210.....			1	1	1			1					
215.....			1	1	4		1						
220.....					5	1		1					
225.....								2		1			
230.....								2					
235.....					2	1			1				
240.....						1	1			1			
245.....					1			1					
250.....							2						
255.....								1		1			
260.....							1						
265.....													
270.....									1				
275.....													
280.....					1								
285.....													
290.....													
295.....													
300.....										1			
305.....									1*				
310.....					1 (39 cm.)						1 (40 cm.)		
Totals.....	--	--	30	30	53	21	11	16	6	6	--	2	--

TABLE A-33—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1938-39;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
66-70.....														
75.....														
80.....					1									1
85.....														1
90.....					2									2
95.....														3
100.....														4
105.....						1								3
110.....					2									5
115.....					1	1								3
120.....														5
125.....						1		1						3
130.....														5
135.....						1								3
140.....					2									5
145.....														3
150.....														7
155.....														3
160.....														9
165.....														6
170.....														14
175.....					1									6
180.....														6
185.....														11
190.....														8
195.....														13
200.....														11
205.....														10
210.....														4
215.....														4
220.....														7
225.....														7
230.....														3
235.....					1									3
240.....														4
245.....														3
250.....														2
255.....														2
260.....														1
265.....														1
270.....														1
275.....														1
280.....														1
285.....														1
290.....														1
295.....														1
300.....														1
305.....														1
310.....														2
Totals.....	--	--	--	--	10	4	--	1	--	--	--	--	--	190

* Recorded only as 31 cm.

TABLE A-34

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1939-40;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
61-65													
70													
75													
80			1		1	1							
85					1								
90			1		1								
95						2							
100													
105													
110										1	1		
115										1			
120			1		1	1		1				1	
125						1	1	1			1		
130			1				1	2				1	
135								3					
140						1		3			1		
145								1					
150								1	1				
155								1	1				
160								1	1				
165						1		1			1		
170								1					
175						1							
180													
185													
190							1	1					
195													
200								2					
205													
210													
215													
220													
225						1		1					
230													
235													
240							1						
245													
250													
255													
260													
265								1					
270													
275													
280													
285													
290													
295													
300													
305													
310													
Totals	--	--	4	--	3	7	5	17	7	2	4	3	--

TABLE A-34—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1939-40;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
61-65								1						1
70							1		1					2
75							1		2					3
80									3					6
85								2	2					5
90									1					3
95								1	3					6
100														
105									1					2
110									1	1				4
115									2					3
120														5
125						1	1			1				6
130									2		1			7
135							1			1	2			7
140														5
145							1	1	2		1			8
150										1				3
155														1
160									1		2			6
165									5	2				11
170								1	1	1				4
175											1			2
180										2	2			4
185									1		1			2
190														2
195						2								3
200														2
205														
210														
215														
220									1					1
225														2
230														
235														
240														1
245														
250														
255														
260														
265														1
270														
275														
280														
285														
290														
295														
300														
305														
310					1 (35 cm.)									1
Totals	--	--	--	--	1	3	6	6	30	10	10	1	--	119

TABLE A-35

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1940-41;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
66-70													
75							1						
80							1						
85					1	1	2			2		2	
90					1	1	1	1		1			
95	1						2		2		1		
100							6		1				
105							3						1
110						2	4				1		
115						2	5				1		
120							3	1	1	1			
125							7					1	
130							2		1	1			1
135						2	5						
140							6	1		1			
145					1		5			1			
150							3	1			1		
155			1				2	1					
160			2			1	2			1			
165				1			2						
170			1				2						
175			1		2			1					
180			1		2								
185		1				2	2						
190						3	3	1	1	1			
195		1			1	1	2						
200					1	3	3	1					
205			3		2	4	2	1					
210		1	2			3	4						
215			2		1	1	1						
220					1	6	3						
225			1			6	6	1					
230						7	5				1		
235						7	3					1	
240						6	5	2		1			
245						4	1	1					
250						2	9		1				
255						2	3	1		1			
260			1			4	3	1		1		1	
265						3	3		1	2			
270						3	2		1				
275						2	1						
280						1	1						
285			1			2	3			1			
290													
295						1	1	1					
300													
305													
310							1 (33 cm.)						
Totals	1	3	16		13	80	129	16	11	15	7	5	2

TABLE A-35—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1940-41;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
66-70													1	1
75		1											1	1
80								1	1				2	5
85							1					1		4
90												2	1	11
95												1		5
100		2	1	2				1						11
105			1	1	3		1						1	14
110		2												8
115		2	2	1	2	1								14
120			1	1	1									11
125	1			1	1	3		1						13
130														10
135		1				1		1						8
140			1			1	1	2						13
145	1					1	1							20
150								10		1				18
155		1						12						19
160								22						28
165								6				1		11
170							1	7						11
175								1	1					6
180														4
185														5
190														10
195														5
200														5
205														12
210					1									11
215														5
220														10
225				1										15
230				1										14
235							1							11
240														15
245														6
250														12
255														7
260							1							12
265														9
270		1												7
275														3
280						1								3
285														7
290														1
295														3
300														
305														
310														1
Totals	2	10	6	8	8	8	7	4	71	3		5	5	435

TABLE A-36

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1941-42;
Length-frequency Distribution by Two-week Periods

Length in mm.	Oct. 1-14	Oct. 15-28	Oct. 29- Nov. 11	Nov. 12-25	Nov. 26- Dec. 9	Dec. 10-23	Dec. 24 Jan. 6	Jan. 7-20	Jan. 21 Feb. 3	Feb. 4-17	Feb. 18 Mar. 3	Mar. 4-17	Mar. 18-31
66-70						1			1				
75						14			1				
80						30	1						
85					1	54	1		1				
90				1		61	2						
95	4		1			55	2						
100	1			1		57	1		1	1		1	
105					4	46	2			1			
110			1		2	33	1		5	1			
115	2	1				33			1				
120				1	1	26	1	1	1			1	
125				1		23	2	2				1	
130						19	6		1	1			
135	1				1	11	1						
140					1	11							
145		1			2	16	7	3		1			
150			1		1	21	10						
155			2		1	30	29	5	1				
160				1		32	18	3	1				
165			1			40	29	6					
170		1				38	30	9		1			
175	1					37	31	10					
180				1	2	31	28	10					
185					2	30	30	6					
190	2				2	23	23	9					
195						10	13	3	1				
200			1			6	4	4				1	
205					1	9	6	1					
210					2	3	4			1			
215						1	2	1	1				
220						3	2	1					
225													
230					1		1						
235													
240						1	1						
245													
250													
255					1								
260							1						
265						1							
270							1						
275													
280					1								
285													
290													
295													
300													
305													
310													
Totals	11	3	7	6	26	806	290	74	16	8		4	--

TABLE A-36—Continued

Waddell Creek, Steelhead: Stream Fish Checked Through Upstream Trap, 1941-42;
Length-frequency Distribution by Two-week Periods

Length in mm.	Apr. 1-14	Apr. 15-28	Apr. 29 May 12	May 13-26	May 27- June 9	June 10-23	June 24- July 7	July 8-21	July 22- Aug. 4	Aug. 5-18	Aug. 19- Sept. 1	Sept. 2-15	Sept. 16-30	Seasonal total
66-70														2
75														15
80														33
85														58
90														66
95				1										63
100							1							64
105	1				1									55
110	1	1												45
115														37
120					1									33
125													1	30
130														28
135	1													15
140														12
145													1	31
150														33
155														68
160														55
165														77
170														80
175														80
180												1		72
185														68
190														59
195														27
200														16
205														17
210														10
215														5
220														6
225														
230														2
235				1										1
240														2
245														
250														
255														1
260														1
265														1
270					1									2
275														
280														1
285														
290														
295														
300														
305														
310														
Totals	3	1	--	2	3	--	2	2	2	--	--	2	3	1,271

TABLE A-37

Waddell Creek: Numbers of *Cottus asper* Checked Through Downstream Trap, by Four-week Periods

Period	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28	--	--	--	--	--	--	--	--
Oct. 29-Nov. 25	--	--	--	--	--	--	--	--
Nov. 26-Dec. 23	--	--	21	--	--	--	--	21
Dec. 24-Jan. 20	189	25	32	10	2	10	1	269
Jan. 21-Feb. 17	254	160	37	19	19	18	15	522
Feb. 18-Mar. 17	81	83	23	19	8	7	5	226
Mar. 18-Apr. 14	38	43	8	15	4	13	4	125
Apr. 15-May 12	28	11	12	--	7	4	1	63
May 13-June 9	3	--	1	4	1	1	1	11
June 10-July 7	2	1	--	4	--	--	--	7
July 8-Aug. 4	2	--	12	2	--	3	--	19
Aug. 5-Sept. 1	--	--	1	1	--	4	--	6
Sept. 2-Sept. 30	2	--	1	--	--	--	--	3
Totals	599	323	148	74	41	60	27	1,272

TABLE A-38

Waddell Creek: Numbers of *Cottus aleuticus* Checked Through Downstream Trap, by Four-week Periods

Period	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28	--	--	--	--	--	--	--	--
Oct. 29-Nov. 25	--	--	--	--	--	--	--	--
Nov. 26-Dec. 23	--	--	--	--	--	--	--	--
Dec. 24-Jan. 20	10	1	2	1	--	--	--	14
Jan. 21-Feb. 17	7	3	1	1	--	1	--	13
Feb. 18-Mar. 17	26	3	2	7	--	--	--	38
Mar. 18-Apr. 14	3	--	1	1	1	--	2	8
Apr. 15-May 12	9	--	--	1	1	--	1	12
May 13-June 9	1	1	--	3	--	--	--	5
June 10-July 7	--	--	--	2	--	--	--	2
July 8-Aug. 4	--	--	--	--	--	--	--	--
Aug. 5-Sept. 1	--	--	--	1	1	--	--	2
Sept. 2-Sept. 30	--	--	1	--	--	--	--	1
Totals	56	8	7	17	3	1	3	95

TABLE A-39

Waddell Creek: Sculpins Taken in Upstream Trap, by Four-week Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28	--	--	--	--	--	--	1	--	--	1
Oct. 29-Nov. 25	--	--	--	--	--	3	1	--	--	4
Nov. 26-Dec. 23	--	--	--	--	--	1	--	4	1	6
Dec. 24-Jan. 20	--	--	49	--	--	--	5	22	--	76
Jan. 21-Feb. 17	--	--	46	--	--	--	--	21	9	76
Feb. 18-Mar. 17	4	--	7	3	--	--	--	1	--	15
Mar. 18-Apr. 14	5	68	--	5	1	--	--	4	--	83
Apr. 15-May 12	36	17	231	3	--	--	1	1	--	289
May 13-June 9	2	19	108	15	--	--	--	1	--	145
June 10-July 7	--	4	16	18	--	1	2	1	--	42
July 8-Aug. 4	--	--	--	5	--	--	6	2	--	13
Aug. 5-Sept. 1	--	--	--	3	--	--	3	1	--	7
Sept. 2-Sept. 30	--	--	--	--	--	--	3	--	--	3
Totals	47	108	457	52	1	5	22	58	10	760

TABLE A-40

Waddell Creek: Garter Snakes Checked Through Downstream Trap, by Four-week Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28	--	--	--	--	--	1	--	--	--	1
Oct. 29-Nov. 25	--	--	--	--	--	--	--	--	--	--
Nov. 26-Dec. 23	--	--	--	--	--	--	--	--	--	--
Dec. 24-Jan. 20	--	--	--	--	--	--	--	--	--	--
Jan. 21-Feb. 17	--	--	--	--	--	--	--	--	--	--
Feb. 18-Mar. 17	--	--	--	--	--	--	--	--	--	--
Mar. 18-Apr. 14	1	--	--	--	--	2	--	--	--	3
Apr. 15-May 12	--	2	9	3	2	7	--	--	--	23
May 13-June 9	--	16	15	5	5	10	1	2	--	54
June 10-July 7	--	7	9	7	3	8	1	--	1	36
July 8-Aug. 4	--	--	5	5	1	8	2	--	--	21
Aug. 5-Sept. 1	--	--	1	2	4	4	--	--	--	11
Sept. 2-Sept. 30	--	--	2	--	2	5	1	1	--	11
Totals	1	25	41	22	17	45	5	3	1	160

TABLE A-41

Waddell Creek: Crayfish Checked Through Downstream Trap, by Four-week Periods

Period	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28	1	--	10	11	22
Oct. 29-Nov. 25	--	--	2	20	22
Nov. 26-Dec. 23	--	--	1	4	5
Dec. 24-Jan. 20	--	--	4	4	8
Jan. 21-Feb. 17	--	--	1	6	7
Feb. 18-Mar. 17	1	--	6	28	35
Mar. 18-Apr. 14	--	--	10	29	39
Apr. 15-May 12	--	1	11	49	61
May 13-June 9	--	3	13	103	119
June 10-July 7	--	11	68	42	121
July 8-Aug. 4	--	20	77	85	182
Aug. 5-Sept. 1	--	9	28	33	70
Sept. 2-Sept. 30	1	35	45	54	135
Totals	3	79	276	468	826

TABLE A-42

Waddell Creek: Giant Water Bugs Checked Through Downstream Trap, by Four-week Periods

Period	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	Total
Oct. 1-Oct. 28	--	--	--	--	1	1	2	1	--	5
Oct. 29-Nov. 25	--	--	--	6	1	1	--	--	--	8
Nov. 26-Dec. 23	--	--	--	--	--	1	--	--	1	2
Dec. 24-Jan. 20	2	2	3	--	1	--	--	--	--	8
Jan. 21-Feb. 17	--	--	1	--	2	1	--	--	--	4
Feb. 18-Mar. 17	--	--	--	4	1	4	2	--	--	11
Mar. 18-Apr. 14	--	3	1	3	1	3	--	--	--	11
Apr. 15-May 12	--	58	16	7	4	6	2	--	--	93
May 13-June 9	--	106	33	62	28	14	9	1	--	253
June 10-July 7	--	73	33	58	22	12	23	1	--	222
July 8-Aug. 4	--	--	1	14	10	1	24	--	--	50
Aug. 5-Sept. 1	--	--	--	6	7	4	8	1	--	26
Sept. 2-Sept. 30	--	--	3	8	--	1	1	--	--	13
Totals	2	242	91	168	78	49	71	4	1	706

TABLE A-43

Conversion Table, Inches to Millimeters

Inches	Mm.	Inches	Mm.	Inches	Mm.	Inches	Mm.
1/8	3	3 1/8	79	6 1/8	156	9 1/8	232
1/4	6	3 1/4	83	6 1/4	159	9 1/4	235
3/8	10	3 3/8	86	6 3/8	162	9 3/8	238
1/2	13	3 1/2	89	6 1/2	165	9 1/2	241
5/8	16	3 5/8	92	6 5/8	168	9 5/8	244
3/4	19	3 3/4	95	6 3/4	171	9 3/4	248
7/8	22	3 7/8	98	6 7/8	175	9 7/8	251
1	25	4	102	7	178	10	254
1 1/8	29	4 1/8	105	7 1/8	181	10 1/8	257
1 1/4	32	4 1/4	108	7 1/4	184	10 1/4	260
1 1/2	35	4 1/2	111	7 1/2	187	10 1/2	264
1 3/4	38	4 3/4	114	7 3/4	191	10 3/4	267
1 7/8	41	4 7/8	117	7 7/8	194	10 7/8	270
2	44	4 7/8	121	7 7/8	197	10 7/8	273
2 1/8	48	4 7/8	124	7 7/8	200	10 7/8	276
2 1/4	51	5	127	8	203	11	279
2 1/2	54	5 1/8	130	8 1/8	206	11 1/8	283
2 3/4	57	5 1/4	133	8 1/4	210	11 1/4	286
2 7/8	60	5 3/8	137	8 3/8	213	11 3/8	289
3	64	5 1/2	140	8 1/2	216	11 1/2	292
3 1/8	67	5 5/8	143	8 5/8	219	11 5/8	295
3 1/4	70	5 3/4	146	8 3/4	222	11 3/4	298
3 1/2	73	5 1/2	149	8 7/8	225	11 7/8	302
3 3/4	76	6	152	9	229	12	305

TABLE A-44
Waddell Creek: Water Analyses/Chemical Data

Locality	Date	Temp. water °F.*	Oxygen p.p.m.	Oxygen percent saturation	M.O. alk. p.p.m. CaCO ₃	Chlorides p.p.m.	Ca and Mg p.p.m.†	CO ₂ cc/l (approx.)	pH	Sulphates‡	Observer
West Branch.....	11/27/33	48.2	9.5	82	168	36	46	2.2	7.6	Fairly high...	P. A. Shaw
West Branch.....	1/30/34	46.4	10.3	87	108	26	38	---	7.6	-----	P. A. Shaw
West Branch.....	3/24/34	55.4	9.3	88	90	22	34	---	7.6	-----	P. A. Shaw
West Branch.....	4/30/34	56.3	8.5	81	116	26	37	---	7.7	-----	P. A. Shaw
West Branch.....	1/28/41	51.0	15.4	---	32	---	---	---	7.4	-----	M. Moore
West Branch.....	2/ 1/41	53.0	11.2	---	40	---	---	---	7.4	-----	M. Moore
West Branch.....	2/ 5/41	---	11.4	---	52	---	---	---	7.5	-----	M. Moore
West Branch.....	2/ 6/41	---	10.2	---	44	---	---	---	7.4	-----	M. Moore
West Branch.....	4/19/41	53.5	9.5	---	44	---	---	---	7.1	-----	M. Moore
West Branch.....	5/ 2/41	54.5	11.5	---	48	---	---	---	7.3	-----	M. Moore
West Branch.....	5/ 9/41	60.0	9.2	---	52	---	---	---	7.1	-----	M. Moore
West Branch.....	5/24/41	60.5	9.4	---	60	---	---	---	7.3	-----	M. Moore
West Branch.....	6/14/41	60.5	10.4	---	68	---	---	---	7.3	-----	M. Moore
East Branch.....	11/27/33	49.1	9.6	84	156	33	54	1.9	7.6	Fairly high...	P. A. Shaw
East Branch.....	1/30/34	44.6	11.5	94	90	22	40	---	7.7	-----	P. A. Shaw
East Branch.....	3/24/34	55.4	9.8	92.5	84	20	39	---	7.8	-----	P. A. Shaw
East Branch.....	4/30/34	56.3	9.2	87.6	100	23	44	---	7.9	-----	P. A. Shaw
East Branch.....	1/28/41	---	12.4	---	48	---	---	---	7.4	-----	M. Moore
East Branch.....	2/ 1/41	---	13.0	---	52	---	---	---	7.3	-----	M. Moore
East Branch.....	2/ 5/41	---	11.2	---	60	---	---	---	7.2	-----	M. Moore
East Branch.....	2/ 6/41	---	11.2	---	40	---	---	---	7.5	-----	M. Moore
East Branch.....	4/19/41	53.0	9.6	---	32	---	---	---	7.4	-----	M. Moore
East Branch.....	5/ 2/41	54.5	11.9	---	68	---	---	---	7.3	-----	M. Moore
East Branch.....	5/ 9/41	60.5	9.0	---	72	---	---	---	7.2	-----	M. Moore
East Branch.....	5/24/41	61.5	9.0	---	80	---	---	---	7.3	-----	M. Moore
East Branch.....	6/14/41	61.5	10.0	---	88	---	---	---	7.5	-----	M. Moore
Main Stream at Dam.....	11/27/33	50.0	8.5	75	148	35	43	2.6	7.5	Fairly high...	P. A. Shaw
Main Stream at Dam.....	1/30/34	46.4	10.7	90	98	25	39	---	7.5	-----	P. A. Shaw
Main Stream at Dam.....	3/24/34	57.2	9.6	92	86	21	38	---	7.6	-----	P. A. Shaw
Main Stream at Dam.....	4/30/34	59.0	8.4	82.7	105	25	39	---	7.5	-----	P. A. Shaw
Main Stream at Dam.....	3/ 2/36	52.0	---	---	56.5	---	---	---	---	-----	M. Hanavan
Main Stream at Dam.....	3/ 9/36	55.0	8.96	---	59.5	---	---	---	---	-----	M. Hanavan
Main Stream at Dam.....	3/31/36	51.5	11.01	---	56.5	---	---	---	---	-----	M. Hanavan
Main Stream at Dam.....	4/15/36	57.0	10.18	---	69.8	---	---	---	---	-----	M. Hanavan
Main Stream at Dam.....	5/18/36	58.0	9.72	---	71.0	---	---	---	---	-----	M. Hanavan
Main Stream at Dam.....	6/ 2/36	57.0	10.64	---	70.5	---	---	---	---	-----	M. Hanavan
Main Stream at Dam.....	12/18/40	---	9.0	---	176	---	---	---	7.5	-----	Leo Shapovalov
Main Stream at Dam.....	1/28/41	---	15.0	---	36	---	---	---	7.6	-----	M. Moore
Main Stream at Dam.....	2/ 1/41	---	14.0	---	42	---	---	---	7.6	-----	M. Moore
Main Stream at Dam.....	2/ 5/41	51.0	12.8	---	52	---	---	---	7.4	-----	M. Moore
Main Stream at Dam.....	2/ 6/41	52.0	12.4	---	44	---	---	---	7.5	-----	M. Moore
Main Stream at Dam.....	4/19/41	55.5	9.6	---	48	---	---	---	7.3	-----	M. Moore
Main Stream at Dam.....	5/ 2/41	55.5	11.8	---	60	---	---	---	7.3	-----	M. Moore
Main Stream at Dam.....	5/ 9/41	64.5	9.8	---	60	---	---	---	7.4	-----	M. Moore
Main Stream at Dam.....	5/24/41	66.0	9.8	---	72	---	---	---	7.2	-----	M. Moore
Main Stream at Dam.....	6/14/41	65.0	9.4	---	72	---	---	---	7.4	-----	M. Moore
Lagoon.....	2/ 5/41	---	11.2	---	56	---	---	---	7.4	-----	M. Moore
Lagoon.....	2/ 6/41	---	13.6	---	48	---	---	---	7.3	-----	M. Moore
Lagoon.....	4/19/41	57.5	9.2	---	52	---	---	---	7.3	-----	M. Moore
Lagoon.....	5/ 2/41	52.0	11.5	---	56	---	---	---	7.3	-----	M. Moore
Lagoon.....	5/ 9/41	67.0	10.6	---	60	---	---	---	7.6	-----	M. Moore
Lagoon.....	5/24/41	68.5	9.6	---	64	---	---	---	7.3	-----	M. Moore
Lagoon.....	6/14/41	69.5	10.0	---	80	---	---	---	7.3	-----	M. Moore

* Temperatures by Shaw converted from °C. to °F.

† Calcium and magnesium determined together and computed as calcium.

‡ Qualitative tests.