AN ESTIMATE OF MORTALITY OF CHINOOK SALMON IN THE COLUMBIA RIVER NEAR BONNEVILLE DAM DURING THE SUMMER RUN OF 1955

BY THEODORE R. MERRELL, JR.,[1] MELVIN D. COLLINS,[2] AND JOSEPH W. GREENOUGH[3]
BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
AUKE BAY, ALASKA 99821

ABSTRACT

In 1955 the Oregon Fish Commission estimated the numbers of dead chinook salmon, *Oncorhynchus tshawytscha*, near Bonneville Dam and studied the probable causes of death.

The estimates of numbers of dead fish were made from ratios of tagged to untagged floating carcasses below the dam. Tagged salmon carcasses were released at the dam, and the river below the dam was searched systematically to recover tagged and untagged carcasses. The introduced tagged carcasses and the untagged carcasses of fish that died in the river were assumed to have equal chances of recovery, provided they were not too severely mutilated to be recoverable. This assumption was verified experimentally.

On June 30 and July 1, 1955, when riverflows were relatively high, 1,169 tagged chinook salmon carcasses were released at Bonneville Dam. Thirty-one tagged and 117 untagged carcasses were recovered in searches downstream from the release point. On the basis of these recoveries, an estimated 4,412 summer-run chinook salmon died near the dam between June 21 and July 10. On the basis of this estimate, 16.8 percent of the total chinook salmon run died at Bonneville Dam in this period.

The numbers of floating carcasses in 1954 and 1955 were directly related to spillway discharge; greatest numbers of floating dead fish coincided with Columbia River flows in excess of 7,100 c.m.s. At Bonneville Dam fall chinook salmon runs have never been subjected to flows above 7,100 c.m.s. (killing flows); spring runs are exposed to such flows in some years; and summer runs nearly always encounter such flows. Water temperature, turbidity, disease, and injuries from gill nets did not affect the number of carcasses. Although the specific causes of death and the precise areas at Bonneville Dam where death occurred were not determined in our study, the major source of chinook salmon mortality was associated with the spillway during high flows. Other investigators subsequently demonstrated that during high flows the Columbia River that has plunged over dam spillways is supersaturated with atmospheric nitrogen. This supersaturation may be one of the principal causes of death of fish at mainstem dams.

Bonneville Dam is only about 18.3 m. high, and hundreds of thousands of salmon successfully negotiate the fishways each year; yet many salmon are killed during periods of high flow. Complacency about the efficiency of salmon passage over large dams is, therefore, unwarranted, even when elaborate well-designed passage facilities are present and few dead or injured fish are noticed.

The problem of facilitating passage of anadromous fish over dams and evaluating the effects of dams on the fish has become a matter of increasing importance and concern because of the steady increase in the number of dams in the past 2 decades. Each dam is an impediment to migratory fish.

The Columbia River, one of the greatest rivers in the world for chinook salmon, *Oncorhynchus tshawytscha*, now has 11 dams across the main stem and numerous dams across tributaries. Bonneville Dam, the first dam on the lower Columbia River, was completed in 1938; it is 227 km. from the river mouth. Before its construction, anadromous fish migrated with little difficulty into the upper Columbia and Snake Rivers and their tributaries to spawn. The lower river had two natural barriers—Cascade Rapids and Celilo

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[1] Theodore R. Merrell, Jr., Fishery Biologist, Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska 99821. He was Aquatic Biologist with the Oregon Fish Commission at the time of the study.

[2] Melvin D. Collins, Aquatic Biologist, Fish Commission of Oregon Research Laboratory, Clackamas, Oreg. 97015.

[3] Joseph W. Greenough, Biometrician, Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska 99821.

Falls—but fish could readily pass these except in periods of extremely low riverflow. Cascade Rapids was inundated by Bonneville Dam in 1938; Celilo Falls by The Dalles Dam in 1957.

Each year Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, that spawn above Bonneville Dam yield several million dollars to commercial and sport fisheries in the river and ocean. Because of the great value of these fish, it is important to ensure that they pass over the dam with a minimum of loss and delay.

Hanson, Zimmer, and Donaldson (1950) counted many dead fish in the river below Bonneville Dam in various seasons and years, and fishermen in boats below the dam often observed floating dead fish or dying fish on the surface. Chinook salmon were reported most frequently, but other species were also noted: sockeye or Columbia River blueback salmon, *O. nerka*; steelhead trout; American shad, *Alosa sapidissima*; white sturgeon, *Acipenser transmontanus*; carp, *Cyprinus carpio*; and Pacific lamprey, *Entosphenus tridentatus*. Biologists and fishermen suspected that many of these fish died from attempting to find a route over the dam or from being swept downstream through the spillway after ascending a series of gravity-flow fish ladders, the principal means for fish to migrate over the dam. Although many of the fish seemed to negotiate the ladders satisfactorily, Schoning and Johnson (1956) estimated that chinook salmon were delayed an average of 2.6 to 3.0 days in their migration.

This paper reports a study of the magnitude and possible causes of the mortality of fish at Bonneville Dam, with particular reference to the summer run of chinook salmon, which is believed to be more adversely affected than other runs.

Bonneville Dam (fig. 1) consists of two concrete sections—the spillway and the powerhouse—

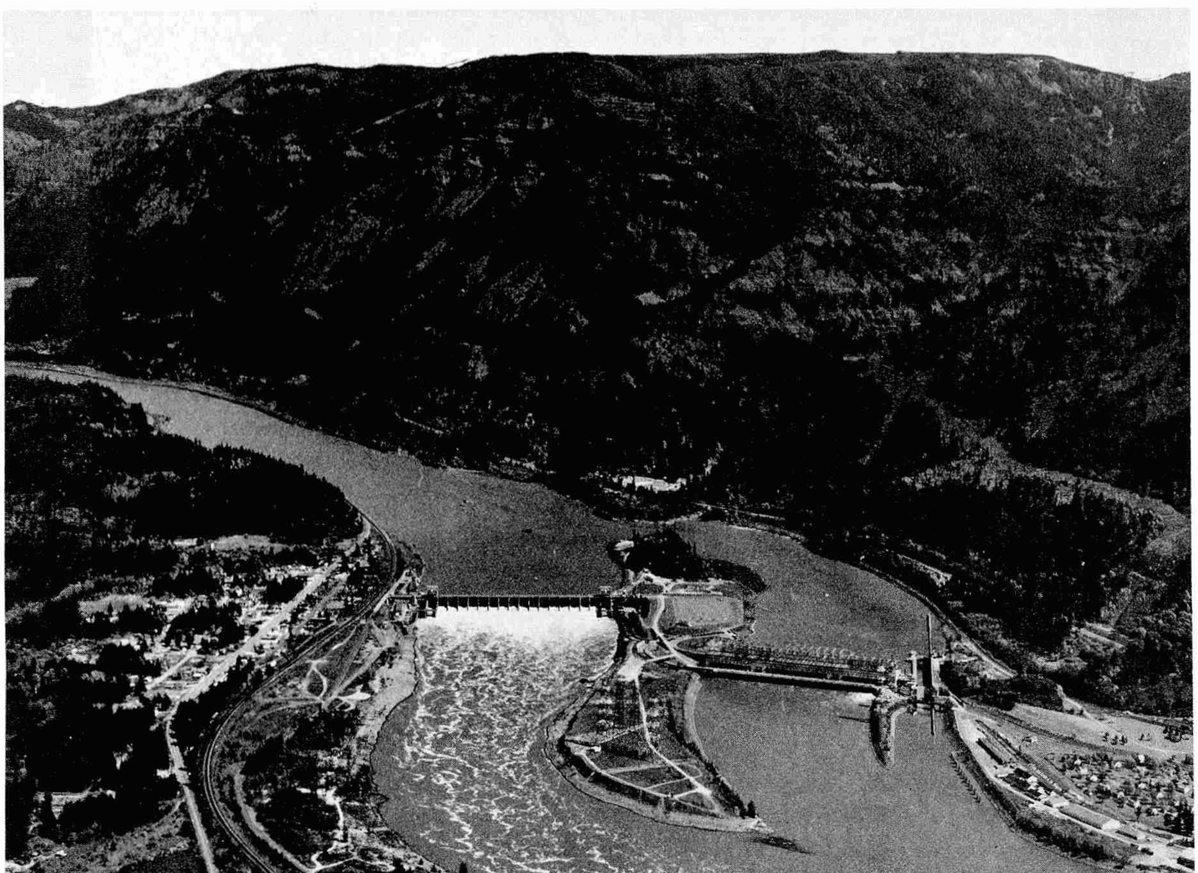

FIGURE 1.—Bonneville Dam, showing the spillway and powerhouse sections and the difference in turbulence between the two sections. Photo taken April 29, 1958, when spillway flow was 4,000 c.m.s. and powerhouse flow, 2,700 c.m.s. (Photo courtesy of U.S. Army Corps of Engineers.)

which are separated by Bradford Island. The spillway spans the Columbia River north of the island, and the powerhouse spans the south channel. The spillway has eighteen 15.2-m.-wide gates that release water not needed for power generation. To attract fish to the adjacent ladder entrances, the gate at each end of the spillway discharges water (except during very high or very low flows). The gates are the vertical-lift type, and water is released under them at a maximum forebay depth of about 17.8 m. (fig. 2). The spillway extends downstream from the gates to form two rows of concrete baffles that partially dissipate the energy of the water rushing under the gates. The flow through the spillway varies from a few cubic meters per second to several thousand.

Bonneville Dam has little water storage capacity. Differences in the water level between the forebay and the tail water range from 12.1 to 18.3 m., depending on riverflow and power generation requirements. The powerhouse contains 10 Kaplan turbines, each with a maximum discharge capacity of 410 c.m.s. Flow through the powerhouse is nearly constant throughout the year, but flow through the spillway varies greatly.

Facilities for passage of adult salmon upstream over the dam are extensive and complex. Most fish go up two gravity-flow ladders, which have slopes of 0.3 m. in 6 m. The Washington shore (north) ladder has a single entrance adjacent to the north end of the spillway and exits into the forebay about 120 m. upstream from the dam. The Bradford Island (south) ladder has three entrances and a single exit into the forebay about 120 m. above the powerhouse on the south side of Bradford Island. One entrance of the Bradford Island ladder is adjacent to the south end of the spillway; another is at the north end of the powerhouse; and the third, consisting of many small entrances, is across the powerhouse above the draft tubes.

Information on dead fish below Bonneville Dam comes from several sources. The principal sources are Federal and State agencies: the BCF (Bureau of Commercial Fisheries), U.S. Army Corps of Engineers, Oregon Fish Commission, and Washington Department of Fisheries. Some information is also provided by commercial fishermen, who spend much time on the river during the major fish migrations; salmon sport fishermen; and

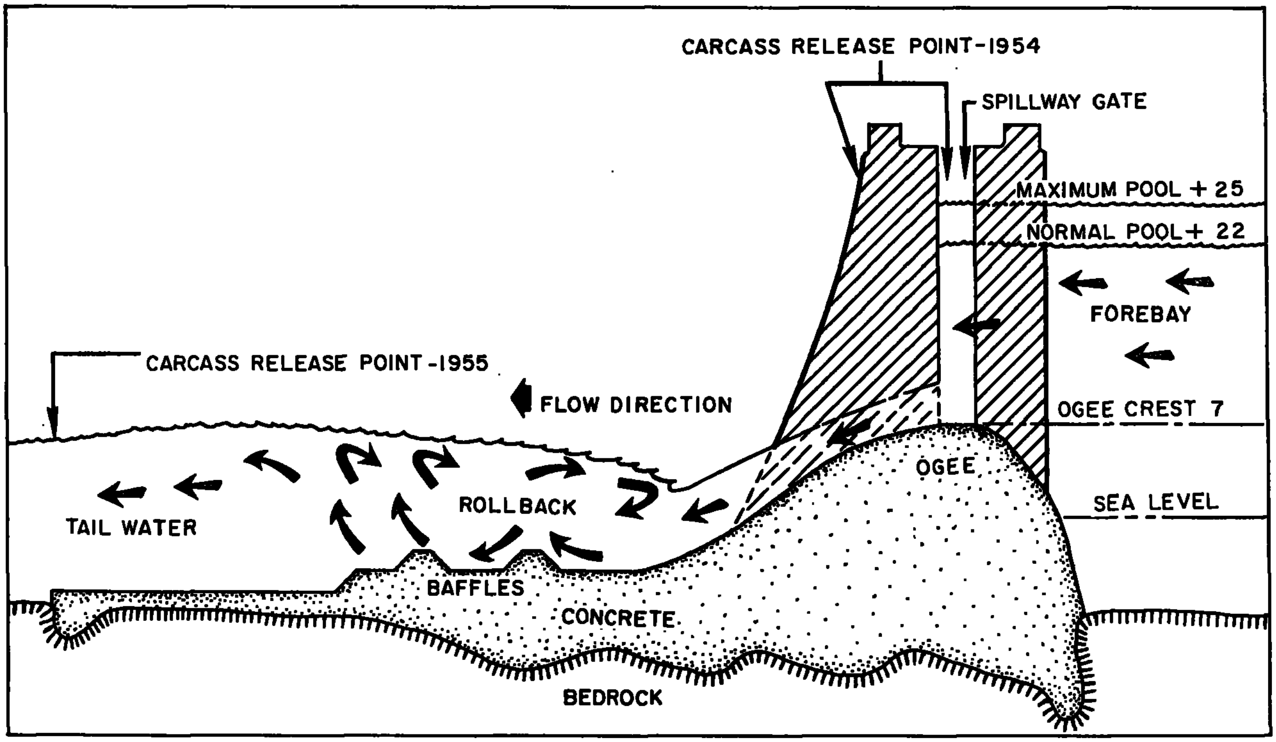

FIGURE 2.—Bonneville Dam spillway construction and flow cross-sectional diagram (from U.S. Army Corps of Engineers drawing). Elevations are in meters above mean sea level.

sturgeon sport fishermen, who seek salmon carcasses for bait.

Until our study, only one extensive effort had been made to evaluate the significance of dead fish near the dam. In 1946 FWS (U.S. Fish and Wildlife Service) and the U.S. Army Corps of Engineers investigated the causes of injuries and deaths of fish (Hanson et al., 1950). The major emphasis of that study was on counting, from boats, the floating dead fish near the dam during the main part of the chinook salmon fall migration. The study did not provide the information needed to determine the relation between numbers of floating dead salmon, numbers of dead salmon not observed, and numbers of salmon surviving to continue their upstream spawning migration.

Sporadic observations in other years by biologists and fishermen also failed to provide information that could be used to evaluate the significance of floating dead salmon. To illustrate the difficulty of interpreting such information, we cite two examples of observations made at a time when unusually large numbers of floating dead salmon were in the Columbia River.

The first observation was on September 9, 1943. Arnie J. Suomela, Fishery Biologist with the Washington State Department of Fisheries, spent 8 hours searching from a boat for dead salmon between Bonneville Dam and Multnomah Falls. He found 146 floating chinook salmon, nine steelhead trout, and one sockeye salmon; the following statement is from his report. "Checked Oregon shore and river on trip down to Multnomah Falls. Only two salmon were found on this part of trip. The first floating dead fish were found at Butler's Eddy, at 3:05 p.m.; and floaters were found from that point to below the spillway at the dam. This observation definitely traces the mortality to the north spillway channel and it is reasonable to believe that the mortality is occurring at the spillway."[4]

The second observation was in the spring of 1952. The Oregonian newspaper for June 12, 1952, reported: "A commercial fisherman . . . recently . . . found 'thousands' of dead chinook salmon between Martins Slough [102 km. downstream from Bonneville Dam] and the mouth of the Lewis River. [He] said the beaches were littered with spring chinook. 'You could find more as you get closer to the Dam.' "

[4]Unpublished field notes, Washington State Department of Fisheries.

The inadequacy of the simple observational method in assessing the true magnitude of mortality is exemplified further in a classic study by the International Pacific Salmon Fisheries Commission. At Hell's Gate on the Fraser River, salmon were blocked by turbulent water at certain riverflows, and an annual loss of thousands (even millions) of salmon there has been well documented (Thompson, 1945; Talbot, 1950; Jackson, 1950). Although a great mortality was suspected, only a relatively small number of moribund or dead fish were sighted on extensive searches downstream from Hell's Gate over a period of many years. Thompson (1945: 96) described the situation at Hell's Gate in 1941: "It could be said that numbers of them [sockeye salmon] were observed approaching death, having reached a condition which obviously precluded their passage through any difficult currents; yet simple observation could not prove that death actually occurred nor that the percentage dying was very high. To find even hundreds of fish near death along the riffles in the river, or in the creeks did not necessarily prove that a great part of the run perished below. Some form of evidence more conclusive was necessary."

Thus, on neither the Columbia nor Fraser Rivers did simple observations of dead fish provide a basis for estimating the true mortality. For this reason, we devised a different method.

Our aims were (1) to estimate the mortality of adult chinook salmon near Bonneville Dam during a period when large numbers of salmon were passing the dam and (2) to evaluate factors contributing to or associated with these deaths, such as streamflow, temperature, turbidity, commercial fishing, fish passage facilities, and disease. Throughout this paper, data on counts of fish at Bonneville Dam and on flow, turbidity, and temperature of the Columbia River are from U.S. Army Corps of Engineers (1943–56).

We first examined records of observations of dead fish and counts of chinook salmon through the ladders at the dam to determine when maximum mortality had occurred. Biologists, commercial fishermen, and boat moorage operators near the dam generally reported that the number of floating dead salmon was greatest in the spring, coincident with high riverflows and large numbers of chinook salmon in the river. We, therefore, selected the spring period of high riverflows for intensive investigation. (We subsequently found that summer is usually the period of maximum mortality.)

The method we used to estimate the total numbers of dead fish was based on a mark-and-recovery technique. Preparatory to making the estimates, we determined the relative floating qualities of tagged experimental (killed, frozen, and thawed) and "natural" river-killed salmon, located points where salmon lodge downstream from the dam before they float, and made systematic surveys from boats and airplanes to determine the best sites for observing dead fish near the dam. Searchers in boats below Bonneville Dam recovered all the tagged and untagged floating salmon used for the population estimate.

BCF contracted with the Oregon Fish Commission to make this study.

ABUNDANCE AND LOCATION OF FLOATING SALMON CARCASSES

Dead salmon in the Columbia River are most evident as "floaters" (partially decomposed floating carcasses); hereafter in this paper this term refers to any floating dead salmonid. Floaters are carried downstream by the current and can usually be seen from a considerable distance. We searched systematically from boats and aircraft in 1954 and 1955 and also tagged and recovered floaters to learn how they disperse in the Columbia River. We also introduced tagged dead chinook salmon into the river at Bonneville Dam in both years to provide a basis for estimating total numbers of dead fish; in 1955 the observations from boats were used to estimate the mortality of summer chinook salmon.

SEARCHES FROM BOATS

1954

In 1954 we searched for floaters downstream from Bonneville Dam during three periods (table 1). Five boats were used; four were 4.9 to 5.5-m. skiffs propelled by outboard motors, and the fifth was a 7.9-m. inboard Columbia River gill-netter. The skiffs were usually manned by one person and the large boat by two. Efficiency of observations was assumed to be equal for all boats. Each observer was equipped with Petersen disk tags, Polaroid[5] glasses, and a dip net to recover floating carcasses. Search time was recorded in hours and minutes. Table 1 shows the numbers of floaters (by species).

TABLE 1.—*Floaters observed during three search periods on Columbia River downstream from Bonneville Dam, July 12 to September 12, 1954, and numbers of chinook salmon floaters observed per hour of search*

Period of search	Floaters observed				Chinook floaters observed per hour of search
	Chinook salmon	Steelhead trout	Sockeye salmon	Unidentified salmonids	
	Number	*Number*	*Number*	*Number*	*Number*
July 12 to Aug. 5	30	7	8	1	1.1
Aug. 9–20	6	14	1	1	0.2
Sept. 4–12	99	54	2	4	0.8

The searches were all made relatively close to the dam. During the first search period (July 12 to August 5), observers in the five boats searched midstream and shoreline sections from the dam to the mouth of the Willamette River. In the early part of this period an additional observer was stationed on shore on a high dock at Ellsworth, Wash., where he could scan the main river channel with binoculars. The second search period (August 9–20) included the same areas. During the final search period (September 4–12), effort was reduced to a roving search from two boats between Ellsworth and the dam and observations from the Ellsworth dock. One of the two boats patrolled the 31 km. of river from Ellsworth to Cape Horn, and the other the 23 km. of river from Cape Horn to the dam (fig. 3).

1955

Searches by boat for floaters in 1955 were limited mainly to the main current in midstream on transects across the river channel at eight locations. The boats and equipment used by observers were the same as those used in 1954, and search time was again recorded in hours and minutes. The eight stations and their locations (fig. 3) were (1) St. Helens—93 km. below the dam, and 1.6 km. upstream from St. Helens, Oreg.; (2) Willamette—70 km. below the dam, immediately upstream from the confluence of the Willamette and Columbia Rivers; (3) Ellsworth—53 km. below the dam at Ellsworth, Wash.; (4) Reed Island—35 km. below the dam, immediately downstream from Reed Island; (5) Cape Horn—23 km. below the dam; (6) McGowan

[5] Trade name referred to in this publication does not imply endorsement of commercial product.

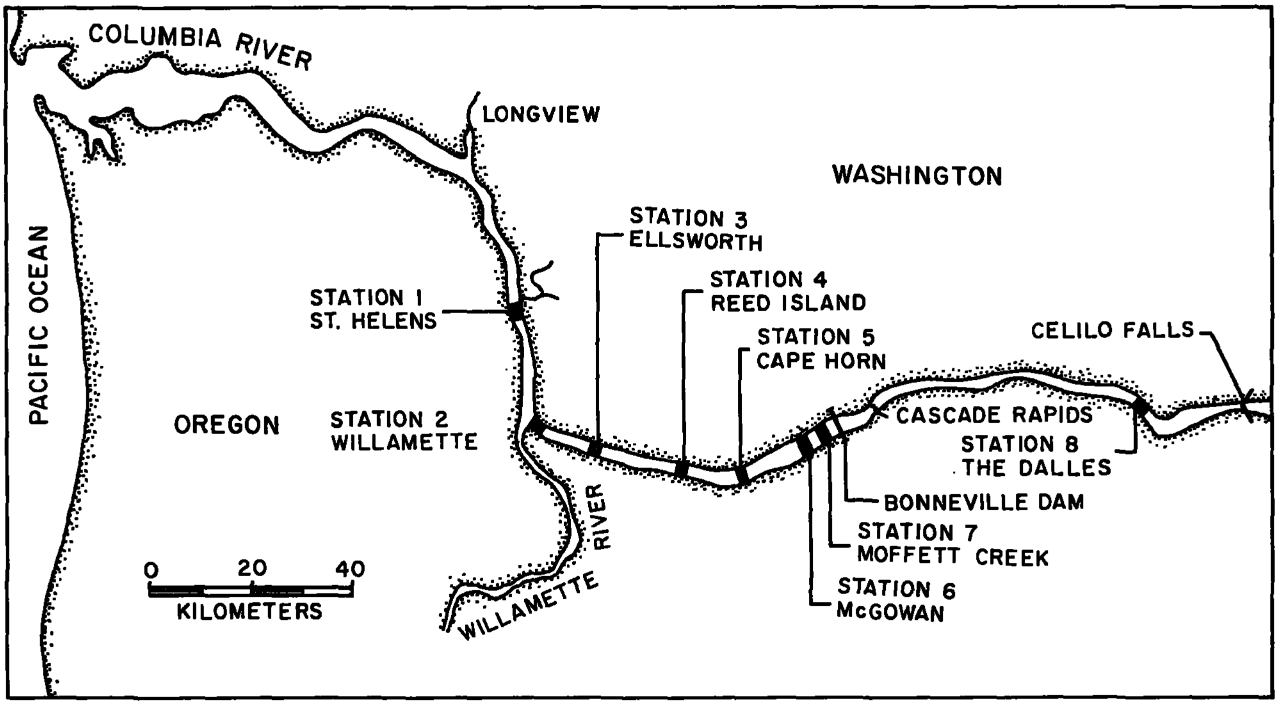

FIGURE 3.—Locations of search stations on Columbia River near Bonneville Dam where floaters were observed in 1954 and 1955.

—7 km. below the dam; (7) Moffett Creek—3 km. below the dam opposite the mouth of Moffett Creek; and (8) The Dalles—72 km. above the dam, 0.8 km. downstream from The Dalles, Oreg.

At each station, an observer in a boat roved back and forth across the river 8 hours a day on a transect perpendicular to the riverflow. All observations were recorded in one of three categories: river site—midstream search at a station; river vicinity—midstream search at other than an established station (usually en route to and from a station at the beginning and end of the day); and shore—search on foot alongshore (table 2). Eighty-two percent of the total search time was at river sites, 15 percent at river vicinities, and 3 percent on shore. Stations 6 and 7 were alternately manned by the same boat crew at different times, depending on visibility. Observations began on April 4 at stations 2, 4, 6, and 7 and on May 3 at station 8. The observer at station 1 was moved to station 5 at the end of June, and on July 12 the observer at station 4 was moved to station 3. A total of 1,666 hours and 50 minutes were spent on all searches in 1955 (table 2).

By the time the observations began in April, appreciable numbers of spring chinook salmon had passed Bonneville Dam. The numbers passing through the ladders increased rapidly in late April and reached a peak on May 2, when 13,763 fish were recorded. Only four chinook salmon floaters, or 0.02 per hour of search, were found in April at search stations, and only eight—again 0.02 per hour—were found in May (table 3). Thus, in April and May, when a record run of 170,205 spring chinook salmon passed the dam, the observers found only a few chinook salmon floaters at the four stations between St. Helens and the dam.

During the first half of June, only 11,551 chinook salmon passed the dam, but 13 chinook salmon floaters (0.07 per hour) were found downstream from the dam. In the second half of June, most of the summer chinook salmon run (33, 951) passed the dam, and searchers found an increasing number as floaters below the dam—0.23 per hour of search (table 3).

TABLE 2.—*Time observers spent searching in boats for floating salmon carcasses at eight stations on the Columbia River near Bonneville Dam, April 4 to July 22, 1955*

[See text for definition of search areas]

Station and month (station number in parentheses)	River site		River vicinity		Shore		Total	
	Hr.	*Min.*	*Hr.*	*Min.*	*Hr.*	*Min.*	*Hr.*	*Min.*
The Dalles (8)								
May	72	10	1	40		35	74	25
June	55	15			1	45	57	0
July	88	15					88	15
Total	215	40	1	40	2	20	219	40
Moffett Creek (7)								
April	12	35					12	35
June	11	10					11	10
Total	23	45					23	45
McGowan (6)								
April	17	40	12	25			30	5
May	53	50	25	5	1	10	80	5
June	44	20	26	50	1	50	73	0
July	59	30	23	50	24	15	107	35
Total	175	20	88	10	27	15	290	45
Cape Horn (5)								
June	1	40	1	0			2	40
July	79	50	28	50	1	20	110	0
Total	81	30	29	50	1	20	112	40
Reed Island (4)								
April	68	15	13	5			81	20
May	78	5	12	10		25	90	40
June	96	40	28	15	7	5	132	0
July	47	25	33	15	8	25	89	5
Total	290	25	86	45	15	55	393	5
Ellsworth (3)								
July	56	45	15	15	4	40	76	40
Total	56	45	15	15	4	40	76	40
Willamette (2)								
April	85	30					85	30
May	101	45					101	45
June	94	55	1	30		45	97	10
July	92	35	2	35	7	30	102	40
Total	374	45	4	5	8	15	387	5
St. Helens (1)								
May	75	40	9	0			84	40
June	67	40	10	50			78	30
Total	143	20	19	50			163	10
Grand total	1,361	30	245	35	59	45	1,666	50

The greatest numbers of floaters were found below the dam in July: between the dam and station 2, 182 chinook and 53 sockeye salmon floaters were recovered (0.40 chinook and 0.12 sockeye salmon per hour of search). Between July 1 and 15, 23,034 chinook and 199,095 sockeye salmon were counted over the dam. Thus, although counts of chinook salmon were declining, the rate of recovery of floaters in early July was much greater than in earlier periods—nearly double the next highest rate in June. Counts of salmon at the dam and floaters in the river were both declining by July 22 when the study ended.

Searches above the dam were limited to station 8 from May 3 to July 22. Chinook salmon floaters found per hour of search were: May, 0.0; June, 0.04; and July, 0.17.

Our experience in 1954 and 1955 demonstrated that floaters could be effectively counted by observers in boats.

TABLE 3.—*Chinook and sockeye salmon counted over Bonneville Dam, April 1 to July 15, 1955, and number found as floaters per search hour at stations below dam, April 4 to July 22, 1955*

Time period	Salmon counted: Chinook salmon	Salmon counted: Sockeye salmon	Floaters found [1]: Chinook salmon	Floaters found [1]: Sockeye salmon	Floaters per hour: Chinook salmon	Floaters per hour: Sockeye salmon
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
April 1–30	84,436	0	4	0	0.02	
May 1–31	85,769	77	8	0	.02	
June 1–15	11,551	68	13	0	.07	
June 16–30	33,951	21,855	45	0	.23	
July 1–15	23,034	199,095	182	53	.40	0.12

[1] Floaters found and search time spent on shore search area (table 2) not included.

SEARCHES FROM AIRCRAFT IN 1954 AND 1955

Synoptic observations of floaters in the Columbia River were needed to determine if at any given time the numbers of floaters were greater below dams on the river than above. The aerial survey method was chosen because Merrell had seen carcasses of chinook salmon on low-altitude spawning survey flights on the Columbia River and the upper Snake River in Idaho—a distance too great to cover with boat searches. At the time of our study the Columbia River had only two dams, Bonneville and McNary (237 km. up the Columbia River from Bonneville Dam).

A chartered two-place single-engine, high-wing monoplane with a cruising speed of about 120 km. per hour was used for all flights. The pilot sat in the rear seat, and a biologist in the front seat, from which point the visibility was excellent. A blind spot directly below the aircraft when it was in level flight did not significantly hamper observations. Merrell and Collins made all observations. Altitude varied between 15 and 100 m. The river was searched on both the upstream and downstream flights. Over sections where the river was wide, observations were confined to one side of the river on the first trip and to the opposite side on the return trip; less than half the total river surface could be observed in these sections. In narrower sections, particularly between The Dalles and McNary Dams, a greater portion of the river surface, and at times the entire width of the river, could be seen clearly. Because all flights were made in the same manner, it is not important whether we saw all floaters; the significant point is that we determined the relative abundance of floaters.

Floaters could be seen easily at the low altitude at which observations were made. Although chinook salmon could usually be distinguished from other species by their relatively large size, all floaters were combined in interpreting the observations. Adverse light conditions and waves occasionally reduced the efficiency of the observations. To compensate for the glare on the water surface, the plane was flown on the side of the river toward the sun and the observers wore Polaroid glasses. Waves and whitecaps were the most serious problems because they reduced the distance at which carcasses could be seen. Fortunately, visibility was generally good on all flights. We recorded all floaters except in the rare instance when on the return trip we definitely recognized a carcass that we had counted before. We may have counted some twice but believe this seldom occurred.

We assumed that we saw a nearly constant proportion of the floaters present on each flight. Granting this assumption, the variations in numbers and distribution of floaters on different flights reflect real differences. In 1954, between July 16 and September 17, floaters were counted on 10 flights over the Columbia River between Longview, Wash., and the McNary Dam (320 km.). Figure 4 shows the numbers of floaters in 8-km. sections of the river on each flight. In 1955, between May 6 and September 13, floaters were counted on seven flights from the mouth of the Columbia River at Astoria, Oreg., to its confluence with the Snake River and up the Snake River to Lewiston, Idaho—a total distance of 720 km. Figure 5 shows the numbers of floaters in 8-km. sections of the area surveyed. The survey between Astoria, Oreg., and Lewiston, Idaho, extended over 2 days, July 14 and 15.

Floaters in both years were not uniformly distributed throughout the river but were consistently concentrated at certain locations. The greatest density was downstream from Bonneville Dam when riverflows were high or when relatively large numbers of migrating salmon were present. Floaters were present, but at much lower densities, throughout the river between Longview and McNary Dam in July of both years—probably as a result of rapid downstream dispersion from points of occurrence of high mortality during this high-flow period.

Most flights were at times when no experimental dead chinook salmon (released by us) were in the river. Only on the flights of September 9, 1954, and July 9, 1955, could experimental fish have been present; six were seen below Bonneville Dam on the first date and four on the second.

The observations on the flights of July 14 and 15, 1955 (fig. 5), were of particular significance because they included the greatest length of river of any surveys and were made during the period of our experiment to estimate chinook salmon mortality. Visibility was good on both days, and we believed our observations revealed typical distribution of floaters at high riverflows. The fact that floaters were most numerous below Bonneville Dam suggests that dead fish were originating near the dam. In the lowest 225 km. of the Snake River, where there were no dams, only three floaters were seen, despite the presence of large numbers of live sockeye and chinook salmon that were migrating up the river.

The aerial surveys were useful in showing that floaters were usually more numerous below Bonneville Dam than in other areas and in indicating the times when the greatest numbers of floaters were present.

MARK-AND-RECOVERY EXPERIMENTS TO ESTIMATE ABUNDANCE OF DEAD CHINOOK SALMON

In the mark-and-recovery technique we used to measure mortality of chinook salmon near Bonneville Dam during periods of high flow, carcasses were tagged and introduced into the river at the dam in 1954 and 1955. The recovery sample consisted of the floaters found on boat searches downstream from the dam at the search stations shown in figure 3. The sample contained the tagged carcasses as well as the carcasses of chinook salmon that died naturally in the river. Only the 1955 experiment had enough recoveries for us to estimate the numbers of dead chinook salmon.

Our experiments differed from an experiment that would lead to a standard Petersen-type of population estimate in one important respect: Instead of removing carcasses from the river, tagging them, and returning them to the river, we acquired carcasses from other sources, tagged them, and added them to the population of carcasses already in the river.

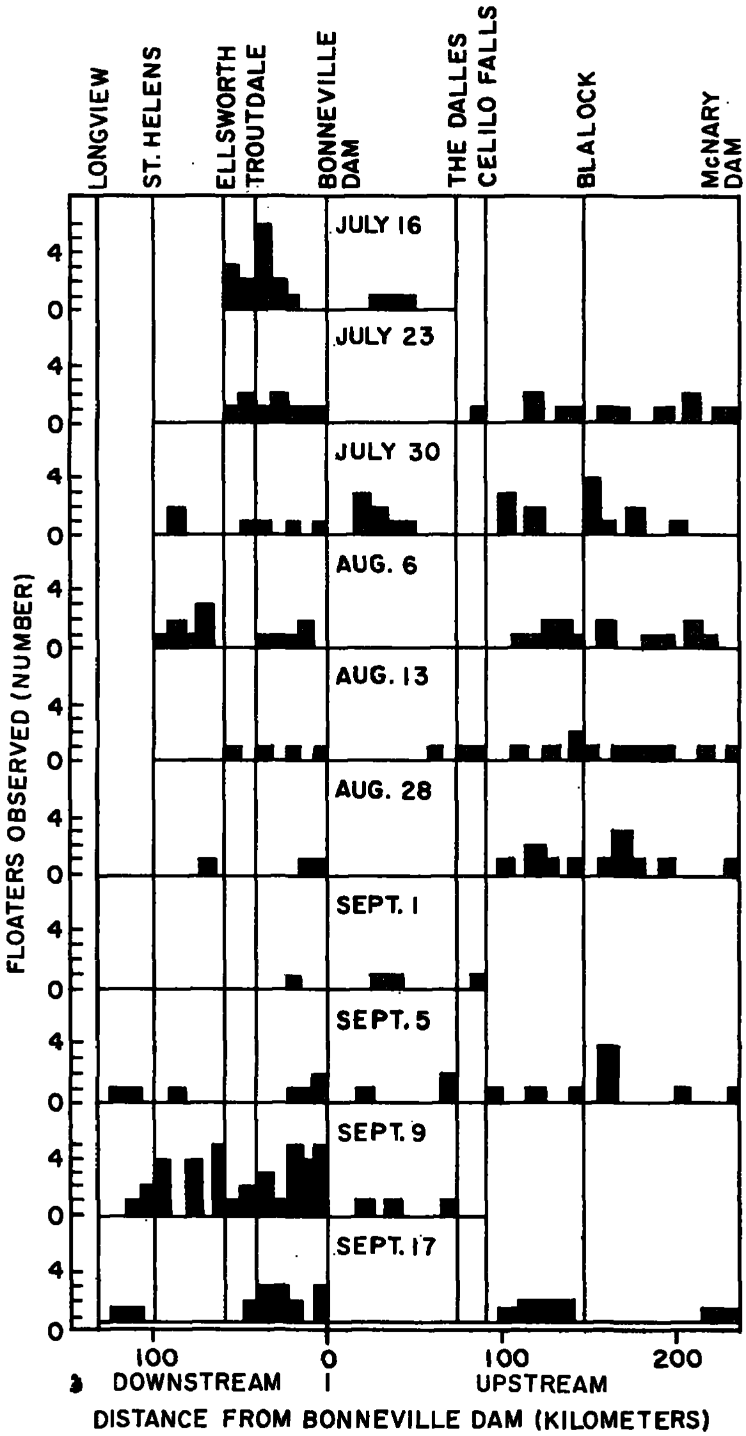

FIGURE 4.—Distribution of floaters observed in 8-km. sections of Columbia River between Longview, Wash., and McNary Dam (320 km.), July 16 to September 17, 1954.

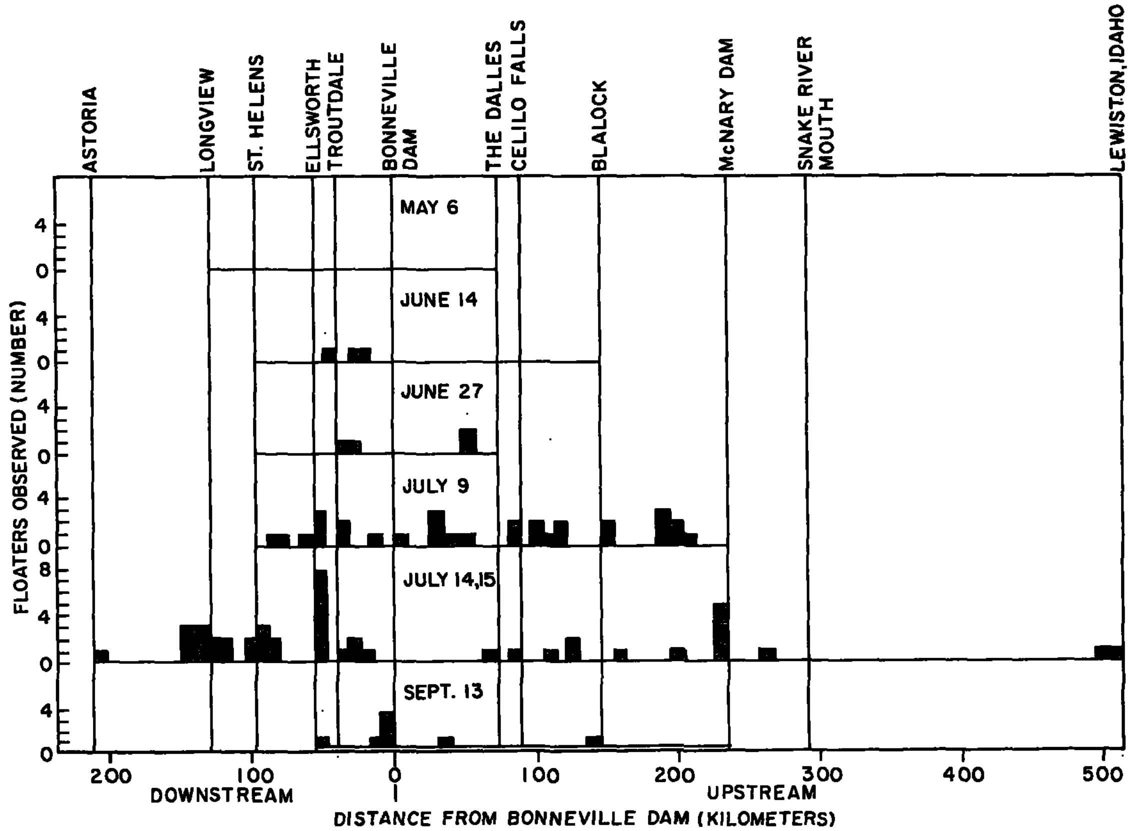

FIGURE 5.—Distribution of floaters observed in 8-km. sections from the mouth of Columbia River, Astoria, Oreg., to its confluence with the Snake River and up the Snake River to Lewiston, Idaho (720 km.), May 6 to September 13, 1955.

It is a simple matter to modify the standard Petersen-type of estimate to fit the circumstances of our experiment, as is shown below. But first, it is instructive to identify our experiment as a typical example of a much larger class of CIR (change-in-ratio) experimental techniques (Paulik and Robson, 1969).

CIR experiments are designed to estimate population characteristics, such as abundance, productivity, rate of exploitation, and survival and mortality rates. Any CIR estimate is based on the observed differences in the relative numbers of two distinguishable types of individuals at two points in time when the population is observed. In our experiment the two types of carcasses are those that are marked (x-type individuals) and those that are unmarked (y-type individuals); the first observation of the population is made immediately before tagging (time 1), and the second observation is made at time of recovery (time 2).

Throughout the following analysis an important distinction is made between carcasses (both tagged and untagged) that are potentially recoverable at the time of death and carcasses that are unrecoverable at the time of death. These two classes of carcasses are mutually exclusive. A potentially recoverable carcass is a more or less unmutilated carcass of a fish that sinks to the bottom of the river after it dies. After several days, it may or may not float to the surface and drift through the area in which recovery crews are searching. Some recoverable carcasses do not float because they are buried or wedged on the bottom, eaten by scavengers, stranded on the bank, or otherwise prevented from floating (these carcasses are still considered recoverable). An unrecoverable carcass is the carcass of a fish so severely mutilated at the time of death that it cannot float to the surface and be recovered. Thus, a recoverable carcass has a fixed chance of floating to the surface where it can be recovered, whereas an unrecoverable carcass has no chance of floating to the surface. (All floating salmonid carcasses are considered here as floaters.)

We follow Paulik and Robson (1969) in introducing the following notation:

Y_1 = number of untagged recoverable carcasses at time 1. (We wish to estimate Y_1. In our estimate based on 1955 data, this quantity is interpreted as the number of recoverable carcasses below Bonneville Dam resulting from earlier mortalities that could possibly be recovered during our sampling period.)

N_1 = number of tagged and untagged recoverable carcasses combined at time 1.

p_1 = fraction of marked recoverable carcasses at time 1.

p_2 = fraction of marked recoverable carcasses at time 2.

R_x = change in population of marked recoverable carcasses between time 1 and time 2 (i.e., the number of tagged carcasses introduced into the river because it is reasonably assumed that all marked carcasses are recoverable).

R = change in total population of marked and unmarked recoverable carcasses between time 1 and time 2.

n_2 = number of carcasses observed in a sample at time 2.

x_2 = number of marked carcasses observed in a sample at time 2.

$\hat{p}_2$ = x_2/n_2 = estimate of p_2.

The fraction of marked recoverable carcasses at time 2 can be written as the ratio of the number of these carcasses at time 1 corrected for changes that have taken place between times 1 and 2 to the total number of tagged and untagged recoverable carcasses at time 2. That is,

$$\hat{p}_2 = \frac{p_1 N_1 + R_x}{N_1 + R} \quad (1)$$

Solving (1) for N_1 gives

$$N_1 = \frac{R_x - p_2 R}{p_2 - p_1} \quad (2)$$

Because in our experiment there was no change in the population of unmarked recoverable carcasses, $R = R_x$, and because the population consisted entirely of unmarked recoverable carcasses at time 1, $N_1 = Y_1$ and $p_1 = 0$. Substituting these quantities and replacing unknown quantities with their estimates, we arrive at an equation for estimating the number of recoverable chinook salmon carcasses that were killed near Bonneville Dam:

$$\hat{Y}_1 = R_x\left(\frac{1}{\hat{p}_2} - 1\right) \quad (3)$$

If all recoverable carcasses, marked and unmarked, are equally likely to be included in the recovery sample and if the recovery sampling is with replacement (as it was), then it is appropriate to make use of binomial sampling theory to set a confidence interval about $\hat{Y}_1$. To do this, upper and lower limits are set on p_2 (the proportion of marked carcasses in the recovery sample (Pearson and Hartley, 1966)), and these limits are then converted to upper and lower limits for $\hat{Y}_1$ by substituting in equation (3).

As was noted above, this same result can be developed from a Petersen-type estimate by noting that the total number of recoverable carcasses at time of release is $\hat{Y}_1 + R_x$; the number tagged is R_x; the size of the recovery sample is n_2; and the number of recoveries is x_2. Hence,

$$\hat{Y}_1 + R_x = \frac{R_x n_2}{x_2} \quad (4)$$

When solved for $\hat{Y}_1$, this yields expression (3) above.

The validity of this method for estimating the number of recoverable carcasses in the river below Bonneville Dam depends on several basic assumptions. First, we assume that carcasses of untagged chinook salmon float and are similar in all other significant respects to the tagged carcasses we introduced into the river. With regard to floating qualities, we demonstrated the validity of this assumption experimentally by using fresh and frozen chinook salmon carcasses. (These experiments are described in the appendix.) Differences in floating characteristics were insignificant at water temperatures similar to those at the time of our 1955 experiment.

Broadly interpreted, the above assumption implies that all of the untagged carcasses were of fish that had died near the dam; our extensive observations substantiate this implication. In the fall of 1954, when riverflow was low and carcasses were unlikely to be swept far downstream after death before becoming sufficiently buoyant to float, most carcasses were found within a few miles downstream from the dam. In the summer of 1955, many fresh dead salmon were found on the bottom in shallow water on gravel bars immediately below the dam. Finally, very few floating carcasses were observed during aerial surveys of the forebay above the dam. (See also the data on p. 15, last paragraph.)

Another assumption is that no tags were lost from recoverable carcasses. This assumption is supported by the fact that there was no evidence of missing tags on untagged chinook salmon floaters. The tags were fastened to the jaw in 1954 and to the caudal peduncle in 1955; both locations are exceptionally secure anchoring points for tags on dead salmon.

1954 EXPERIMENT

To secure carcasses for releases in 1954, 1,095 chinook salmon were placed in frozen storage in the summer and fall of 1953. All were ice glazed to retard dehydration and oxidation. About 245 of these fish were spring chinook salmon of both sexes that had been killed during construction of Lookout Point Dam on the Middle Fork of the Willamette River; the rest were fall male chinook salmon from Bonneville and Oxbow Hatcheries on the Columbia River.

Frozen chinook salmon float when placed in water; to ensure that they would sink like a naturally killed salmon, the frozen carcasses were thawed in air for 24 hours before being tagged and released. The tags were sequentially numbered, bright-colored nylon or plastic ribbons fastened to the jaw. The tagged carcasses were released during two periods: The first group (280 carcasses) was released August 4 to 6 when spillway flows averaged 3,300 c.m.s. and powerhouse flows 4,100 c.m.s.; the second group (815 carcasses) was released September 2 to 3 when spillway flows averaged 1,300 c.m.s. and powerhouse flows 3,700 c.m.s.

Earlier evidence suggested that the spillway channel was the source of most dead salmon near the dam. Therefore, most of the tagged carcasses (240 in August and 635 in September) were released into the spillway channel either by dropping them from the dam immediately above the gates or into the rollback below the gates (fig. 2). Another 150 carcasses (20 in August and 130 in September) were dropped into the draft tube discharge at the downstream face of the powerhouse. Finally, 50 were dropped into the river in September from the Bridge of The Gods, 8 km. above the dam, and 20 were released in August from a boat at Oneonta, 11 km. below the dam.

Less than 1 percent of the 1,095 carcasses were recovered. Only one of the 280 carcasses released in August was recovered; it was found at Oneonta on August 10 at the same location where it had been released on August 5. Eight carcasses were recovered from the 815 released in September—six from the powerhouse and two from the spillway releases. No carcasses were recovered from the group dropped from the Bridge of The Gods.

The significance of the apparent difference in the rates of recovery of the carcasses released at the two sites in September can be evaluated by a chi-square test for homogeneity. The null hypothesis is that the probability of a carcass being recovered does not depend on release location. To test this hypothesis, we constructed the following fourfold contingency table:

	Powerhouse release site	Spillway release site	Total
Recovered	6	2	8
Unrecovered	124	633	757
Total releases	130	635	765

For these data, $\chi^2 = 15.35$ with 1 d.f., and the hypothesis of homogeneity is strongly rejected. (The observed frequency for recoveries from spillway releases is smaller than is generally considered desirable for this statistical treatment, but in this experiment the conclusion is so clear-cut that we need not be greatly concerned over this fact.) The conclusion is that carcasses released in the spillway are less likely to be recovered than carcasses released at the powerhouse.

The small number of carcasses recovered from the spillway release indicated that many of them had probably disintegrated in the extremely turbulent flow of the spillway rollback (fig. 2). Such carcasses would have a reduced chance of floating and being recovered. The less turbulent flow of the powerhouse discharge probably contributed to the higher recovery rate of carcasses released there.

Although the 1954 experiment did not produce adequate data to estimate precisely the number of recoverable carcasses, we can, if we assume that all carcasses released in the powerhouse channel were recoverable, make a crude estimate of the fraction of recoverable carcasses from the spillway releases.

If none of the carcasses released at the spillway had been rendered unrecoverable, the proportion of recoveries from the spillway releases should have equaled the proportion of recoveries from the powerhouse releases. On this assumption, the expected number of recoveries from spillway releases is $\frac{(635)(6)}{130} = 29.3$. Because only two carcasses were actually recovered, we can estimate that the proportion of recoverable carcasses for fish dying by being swept over the spillway is only $\frac{2}{29.3} = 0.0683$ and that the proportion of unrecoverable carcasses is 0.9317. Because this estimate is based on small numbers of recoveries, however, sampling error could be large.

1955 EXPERIMENT

In 1955, 1,169 carcasses were released. They were all male fall chinook salmon collected in 1954 from Bonneville, OxBow, and Spring Creek Hatcheries. They were killed by a blow on the head and placed in frozen storage a few hours later; as in 1953, the carcasses were ice glazed to retard dehydration and oxidation during overwinter storage.

When the carcasses were removed from storage for the 1955 experiment, they were handled in the same manner as the carcasses for the 1954 experiment except that they were tagged with sequentially numbered cellulose-acetate Petersen disks fastened by nickel pins through the caudal peduncle.

Figure 6 demonstrates the rationale on which our entire 1955 study was based: the number of chinook salmon floaters is an indication of the total number of dead chinook salmon in the river. Few floaters were recovered until late June, when

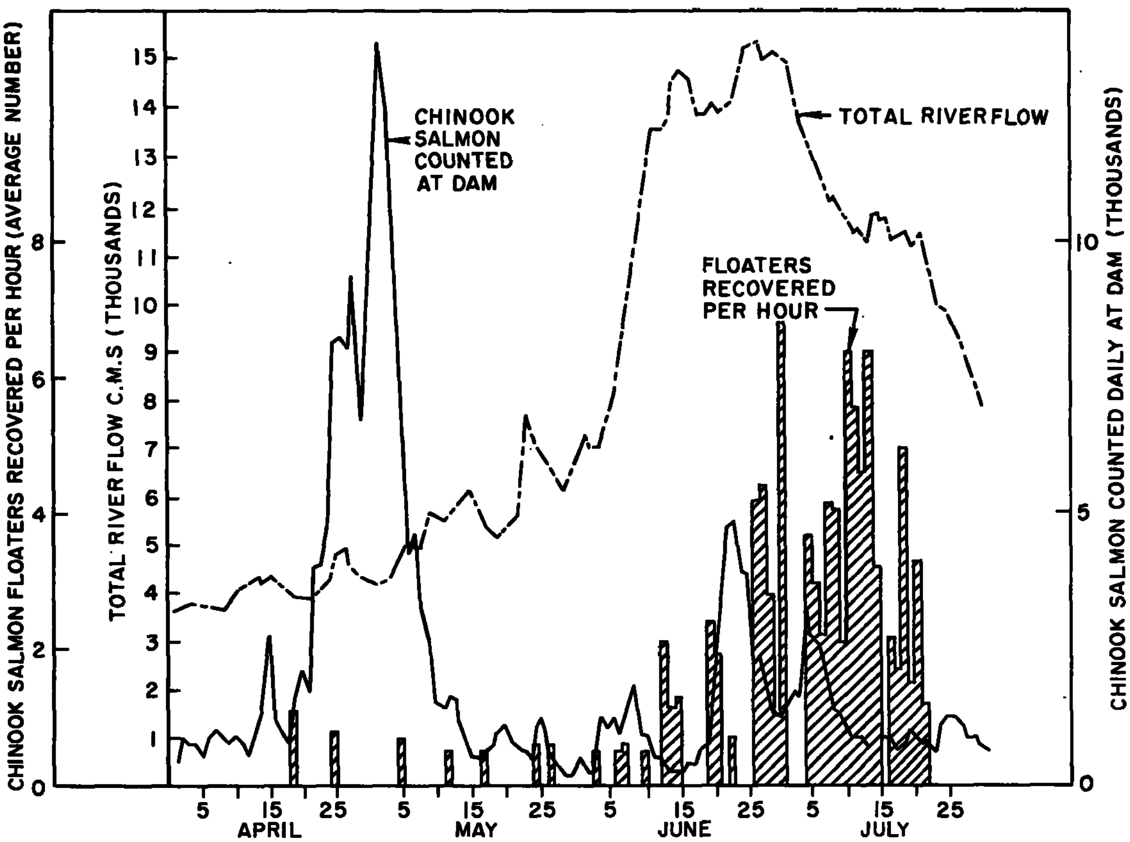

FIGURE 6.—Daily counts of chinook salmon and total riverflow at Bonneville Dam and number of untagged chinook salmon floaters recovered per hour, Bonneville Dam to St. Helens, 1955.

the rate of recovery rose rapidly. We then released our entire supply of carcasses over a 2-day period, June 30 and July 1, so that our estimate of mortality would include a period during which large numbers of salmon were dying. The counts of chinook salmon migrating over the dam and the riverflows were also near their summer maximums. Thus, large numbers of live fish were present, coinciding with inimical high flows.

Because of our experience in 1954 with disintegration of carcasses in the extremely turbulent flow in the spillway rollback, we released the tagged carcasses in 1955 into the spillway channel from a boat downstream from the rollback. In that area high velocities and extreme turbulences shunt migrating salmon toward the fish ladder entrances at either end of the spillway (figs. 1 and 2). At the release points, which were distributed across the river, one man kept the boat in position under power while a second pitched the tagged carcasses overboard—1,068 were released in the spillway channel (183 m. below the dam) and 101 in the powerhouse channel (64 m. below the dam).

The 2-day release period coincided with a temporary slackening of chinook salmon passage over the dam; the count dropped from a peak of 4,912 fish on June 23 to slightly more than 1,000 per day near the end of June. At this time, many live fish were below the dam and were liable to be killed, as shown by a second peak count of 3,434 on July 4 and large numbers of chinook salmon floaters through the first half of July (fig. 6).

The search by boats for floaters downstream from Bonneville Dam was not begun until July 5 because we knew from previous experiments on the floating characteristics of chinook salmon carcasses that the tagged carcasses would not float in fewer than 5 days at the existing water temperature of 13.9° to 14.4° C. (see appendix). Daily searches for floaters continued until July 22. Table 4 gives the release and recovery data on which we base our estimate of the number of recoverable chinook salmon carcasses from mortalities at the dam from June 21 through July 10, 1955. No tagged carcasses were recovered from July 18 through July 22. Table 4 includes only data actually used in computing the estimate.

The level of recovery effort throughout the recovery period was essentially constant—an observer in a boat recovered floaters for 8 hours a day at each of the seven stations below the dam (fig. 3). The only exception was July 16, when no searches were made. This was the 16th day after the releases on June 30 and the 15th day after the releases on July 1; for this reason estimates of fractions of recoverable carcasses available for recovery a given number of days after release (discussed on p. 16) are slightly biased.

The absence of recovery effort on July 16 also affects the estimate of Y_1, the number of recoverable untagged carcasses in the river. However, trial calculations made by using plausible values for the numbers of tagged and untagged carcasses that might have been recovered on July 16 suggest that the likely error is slight. For example, if we assume that one tagged carcass and six untagged carcasses would have been recovered—a probable event in the light of the data of table 4—our estimate of Y_1 (given on p. 17) would change by only 1.8 percent.

TABLE 4.—*Data for computing mortality of the summer chinook salmon run near Bonneville Dam, 1955*

[Only data actually used in computations are included]

Date	Chinook salmon counted at Bonneville Dam ladders	Tagged carcasses released	Tagged floaters recovered from releases of		Untagged floaters recovered
			June 30	July 1	
	Number	*Number*	*Number*	*Number*	*Number*
June:					
21	3,567				
22	4,798				
23	4,912				
24	3,890				
25	3,868				
26	2,220				
27	2,343				
28	1,680				
29	1,291				
30	1,185	338			
July:					
1	1,411	831			
2	1,713				
3	1,667				
4	3,434				
5	2,729		0	0	
6	2,576		0	0	
7	1,940		0	0	8
8	1,339		3	4	15
9	1,241		5	7	13
10	962		0	0	7
11			1	0	13
12			4	4	19
13			0	0	15
14			0	1	16
15			0	1	9
16					
17			0	1	2
18			0	0	
19			0	0	
20			0	0	
21			0	0	
22			0	0	
Total	48,766	1,169	13	18	117

Another minor problem was the removal of untagged carcasses (either floating or stranded in shallow water alongshore) from the river by sturgeon fishermen. Putrefied salmon flesh is regarded by many sturgeon fishermen as superior bait, and one of the most productive locations on the Columbia River for sturgeon fishing and for finding putrefied salmon is just below Bonneville Dam.

Beacon Rock Moorage, 6.4 km. below the dam, is the principal base of operations for sturgeon fishermen in the area. Lee Motley, a moorage operator, recorded carcasses found by his employees and customers near the dam during the spring and summer of 1955. His data are as follows:

Search period	Chinook salmon		Sockeye salmon	Steelhead trout
	Untagged	Tagged		
April	1			
May	3			
June	29			4
July	48	3	39	3

Of the carcasses found by sturgeon fishermen in July, a relatively large number were found during the sampling period, July 7 to 17 (23 untagged and three tagged chinook salmon and 24 sockeye salmon). This record probably includes most of the carcasses removed by fishermen in the study area.

The numbers of carcasses found by sturgeon fishermen increased steadily during the summer. The relatively large number of carcasses of both chinook and sockeye salmon in July is of particular significance in relation to mortality at the dam. Many of these were not floating but were freshly killed fish that had collected on a shallow submerged bar near the upper end of Hamilton Island, close to the spillway. Each year Lee Motley retrieves many fish on this bar.

Some carcasses recovered by sturgeon fishermen probably would have been found at our regular search stations had they not been intercepted. The fishermen returned the three tagged carcasses to the river because they knew of our study and did not want to interfere with it; two tagged chinook salmon floaters were subsequently recovered at station 6 (fig. 3). The removal of 23 untagged chinook salmon carcasses by moorage personnel during the period of the experiment results in a slightly smaller estimate of mortality than would have been obtained if a few of the removed untagged carcasses had been recovered at search stations. If these were typical recoverable carcasses, a correction for the resulting bias could readily be made by the method suggested by Paulik and Robson (1969). However, carcasses removed by fishermen probably have a higher probability of floating than typical recoverable carcasses, so that a bias correction is not possible. In any event, the bias is very slight and does not significantly affect our conclusions.

The removal of carcasses by scavengers was also considered. Scavengers near Bonneville Dam that feed on dead salmon both before and after they float include sturgeon, squawfish, gulls, crows, raccoons, and skunks. Sometimes almost every floater was accompanied by one gull or more, but at other times, only a few were accompanied by gulls. The effect (if any) of gull scavenging on the length of time carcasses remain at the surface was not determined. Floaters that go aground probably disappear more quickly than those that remain afloat because they are more accessible to terrestrial or avian scavengers. Gulls and crows were frequently seen feeding on dead salmon that had drifted ashore. Nocturnal feeding by raccoons and skunks, which are numerous in the area, may be even more important in the rate of disappearance of carcasses along the riverbanks.

Hence, scavengers reduce to an unknown extent the number of dead salmon available to be observed. Whatever effect scavengers might have had, there was no evidence that it was different for tagged and untagged carcasses in the search area. Therefore, scavenging was assumed to have no significant effect on the estimate of mortality.

Floaters originating above the dam could also affect our mortality estimate, but we believe that few, if any, such chinook salmon floaters drifted into the recovery area during the estimate period. The best and most direct way to evaluate the possibility of recruitment of floaters originating above the dam into the search area below the dam would be to observe the river from above the dam. We looked for floaters on two dates from the Bridge of The Gods, which spans the river 4.8 km. above the dam, where the entire surface can easily be seen. No chinook salmon floaters were observed passing under the bridge on July 10, 1955, whereas seven were sighted below the dam. Again, on July 3, 1956, observers were stationed at station 5 (Cape Horn), and on the Bridge of The Gods. In 6 hours and 35 minutes no chinook salmon floaters were seen from the bridge, but five were found in 1 hour and 50 minutes at station 5 below the dam. Furthermore, during the period of our study in both 1954 and 1955, greater numbers of floaters were usually found in the 48 km. of river below Bonneville Dam than in any other section of river. No adjustment in the calculated mortality appears necessary for recruitment of untagged floaters into the sample area from above the dam.

The 31 tagged floaters used in the mortality estimates were recovered by our search crews below the dam from July 8 to 17 (table 4). The first tagged floater was found by a fisherman on July 7, the 7th day after the first date carcasses were released (June 30); but it, as well as three other carcasses found by fishermen, was not used in computing the mortality estimate. Our searchers actually recovered 32 tagged floaters, but one was eliminated from the computations because it was on shore.

No tagged floaters were recovered by search crews after July 17, although sampling continued through July 22 (table 4). Because no tagged fish were recovered before July 7 or after July 17, we assume that tagged carcasses were available for recovery only during the period July 7 to 17. During this 11-day period, 117 untagged chinook salmon floaters were recovered at search stations.

The tagged chinook salmon floaters were recovered from 7 to 16 days after they were released (table 5). Because tagged and untagged carcasses behave in a similar fashion, the smoothed daily percentages of total tags recovered given in table 5 can be interpreted to mean that 21.99 percent of the recoverable carcasses of chinook salmon dying on a given day will have a chance of floating and becoming available for recovery on the 7th day after death (of this 21.99 percent, some will actually float and others will not); 19.87 percent will have a chance of becoming available for recovery on the 8th day; 15.71 percent on the 9th day; and so forth. Note that an additional assumption is being made here: An individual floating carcass is available for recovery only on the day that it floats because it drifts out of the recovery area in less than 1 day. This assumption is supported by experiments in which chinook salmon floaters were tagged and later recovered (see appendix). These experiments showed that floaters rapidly passed through the entire recovery area within a few hours during high riverflows.

Table 5.—*Number and percentage of 31 tagged chinook salmon floaters recovered below Bonneville Dam on each day after release, 1955*

Days after release	Tagged floaters recovered	Total tagged floaters recovered on each day after release	
Number	*Number*	*Percent*	*Percent smoothed by threes*
7	4	12.90	21.99
8	[1] 10	32.26	19.87
9	[1] 5	16.13	15.71
10	0	0.00	10.46
11	5	16.13	9.43
12	4	12.90	10.46
13	1	3.23	6.28
14	1	3.23	2.10
15	0	0.00	2.10
16	1	3.23	1.57

[1] Two recoveries on July 9 were arbitrarily assigned to releases of June 30 and July 1 because the release dates were unknown.

Knowledge of the estimated percentage of recoverable carcasses that have a chance of floating and becoming available for recovery any given number of days after death (table 5) enables us to estimate the percentage of recoverable carcasses of fish dying on any given date that have a chance of floating and becoming available for recovery at some time during the July 7 to 17 recovery period. The method for calculation of these estimates is shown in figure 7 which, together with table 4, indicates the structure of the 1955 experiment. The figure shows that, of the recoverable carcasses of chinook salmon dying on June 21, an estimated 1.57 percent were recoverable 16 days later on July 7, the first day of the recovery period. Similarly, considering recoverable carcasses from mortalities on June 22, 2.10 percent were recoverable 15 days later on July 7 and 1.57 percent 16 days later on July 8; consequently, a total of 3.67 percent of the carcasses from June 22 mortalities were recoverable during the recovery period. Computations for other days through July 10 follow the same pattern.

We are now ready to estimate Y_1, the number of untagged recoverable carcasses in the river during the July 7 to 17 recovery period. As has been noted, of 1,169 carcasses tagged and released on June 30 and July 1, 31 were recovered floating during the recovery period. At the same time, 117 untagged floating chinook salmon carcasses were observed (table 4). Assuming that all tagged carcasses are recoverable, R_x = 1,169,

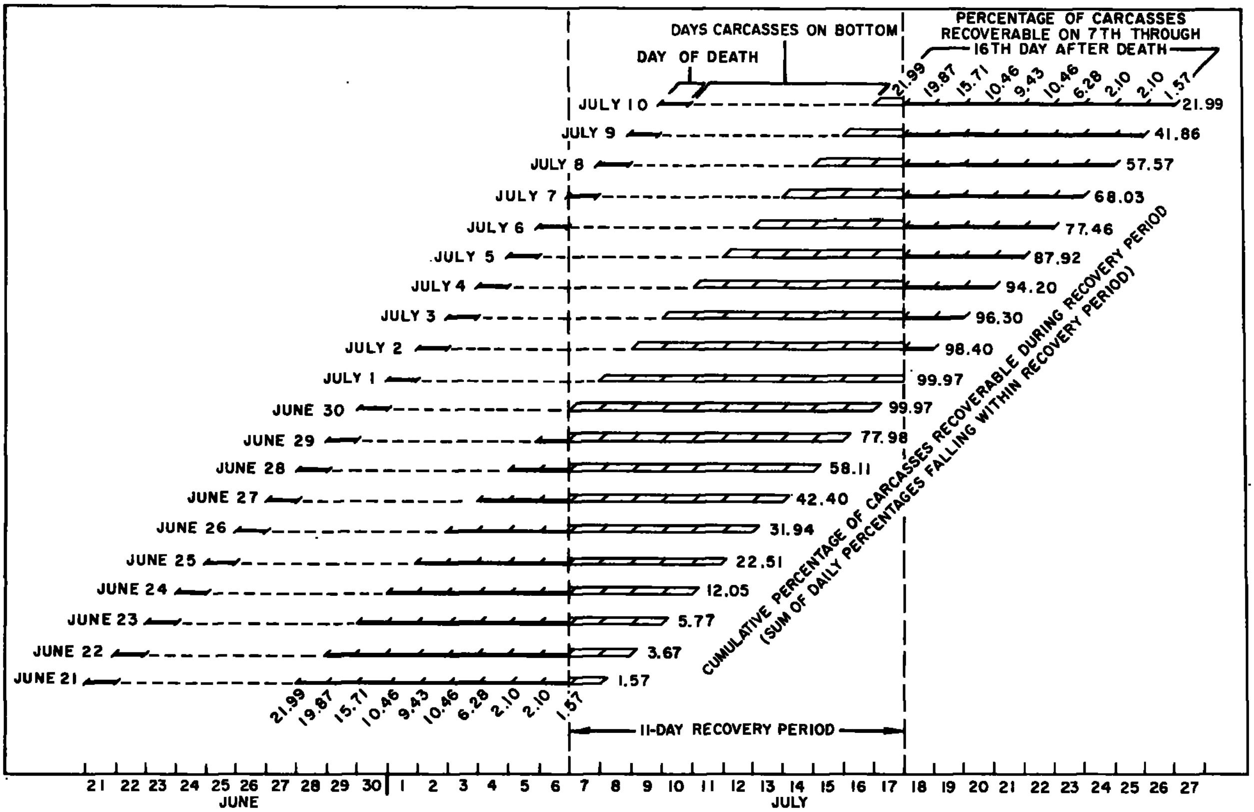

FIGURE 7.—Availability of carcasses for recovery. When chinook salmon die, the carcasses sink to the bottom. Recoverable carcasses may or may not float to the surface between 7 and 16 days after death. When a carcass floats, it can be recovered only on the day it floats. Percentages of recoverable carcasses that become recoverable on the 7th through 16th days after death are given at the top of the figure, and the sums of these percentages falling within the 11-day recovery period are given on the right diagonal edge for each date of mortality.

$x_2 = 31$, $n_2 = 117 + 31 = 148$, and $\hat{p}_2 = 31/148 = 0.2095$. Substituting in equation (3) gives an estimate of Y_1:

$$\hat{Y}_1 = R_x\left(\frac{1}{\hat{p}_2} - 1\right) = 1{,}169\left(\frac{1}{0.2905} - 1\right) = 4{,}412$$

untagged recoverable carcasses. An approximate 95-percent confidence interval on $\hat{p}_2$ is $0.12 \leq 0.2095 \leq 0.33$. The corresponding 95-percent confidence interval on $\hat{Y}_1$ is $2{,}373 \leq 4{,}412 \leq 8{,}572$ untagged recoverable carcasses.

It is clear from the preceding discussion and from figure 7 that this estimate of 4,412 untagged recoverable chinook salmon carcasses represents:

(1.57 percent of the recoverable carcasses from June 21 mortality)
+ (3.67 percent of the recoverable carcasses from June 22 mortality)
+ . . . + (21.99 percent of the recoverable carcasses from July 10 mortality).

PROPORTION OF CHINOOK SALMON RUN KILLED

To estimate the proportion of the chinook salmon run killed near Bonneville Dam during our experiment in 1955, we relate our estimate of the number of recoverable carcasses in the river below the dam (i.e., $\hat{Y}_1 = 4{,}412$ recoverable carcasses) to the size of the run producing these carcasses.

Two additional factors should be taken into account. In our 1955 experiment, all tagged carcasses were released immediately below the dam. This situation would correspond to one in which all chinook salmon mortality at the dam occurs before the fish are counted over the dam. However, earlier tagging experiments in which salmon were tagged as they emerged from the ladders above the dam showed that some salmon are swept down over the dam and are caught by fishermen below or counted as they reascend the ladders (Schoning and Johnson, 1956). Some of the salmon that are swept over the dam probably do not survive, although we have no direct evidence of what portion is killed. The mortality model that we have developed provides for the possibility that some of the salmon counted over the dam are subsequently killed by being swept back over the dam.

We have evidence from our 1954 experiments (previously described) that carcasses of fish killed by being swept over the spillway may be so severely mutilated by the extreme turbulence that they are rendered unrecoverable. Thus, the second additional factor taken into account in our mortality model is the possible presence of unrecoverable carcasses from mortality occurring after counting.

To derive the mortality model, some additional symbolism is required. In these symbols, the subscript i refers to days on which mortality occurs that could possibly produce floating carcasses for recovery during the recovery period. (Recall that recoverable carcasses may float and be available for recovery 7, 8, . . . , or 16 days after death.) Thus, $i = 1$ corresponds to June 21 because this is the first day which could have produced floating carcasses for recovery during the recovery period. (The first day of the recovery period, July 7, is the 16th day after June 21.) Similarly, $i = 20$ corresponds to July 10, the last day which could have produced floating carcasses for recovery during the recovery period. (The last day of the recovery period, July 17, is the 7th day after July 10.) Reference to figure 7 will help to clarify this subscripting scheme.

M = proportion of the chinook salmon run dying near Bonneville Dam. (M is the quantity to be estimated. If the proportion of the run dying at Bonneville Dam remained constant from June 21 through July 10, then M is this quantity. However, if the proportion dying varied during this period, M can be thought of as a weighted average of the daily proportions dying, with the weighting being related to the extent to which carcasses from a given day's mortality become available for recovery during the July 7 to 17 recovery period.)

C_i = count over fish ladders on day i.

D_i = mortalities on day i below the dam.

q_i = proportion of total mortality on day i producing carcasses which, if recoverable, could be recovered during the July 7 to 17 recovery period.

Note that $C_i + D_i$ is the total run on day i and that $M(C_i + D_i)q_i$ is the total number of mortalities on day i producing carcasses, which, if recoverable, could be recovered during the recovery period. Therefore,

$$\sum_{i=1}^{20} M(C_i + D_i)q_i = M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \quad (5)$$

is an expression for the total number of mortalities producing carcasses (both recoverable and unrecoverable) which, if recoverable, could be recovered during the recovery period. For 1955, the term $\sum_{i=1}^{20} C_iq_i$ can be estimated from our experimental data and the observed fish ladder counts at Bonneville Dam. Table 6 shows this calculation.

TABLE 6.—*Estimation of* $\sum_{i=1}^{20} C_iq_i$ *for 1955 experiment at Bonneville Dam*

Date	i	C_i (see table 4)	q_i (see table 5)	C_iq_i
June:				
21	1	3,567	0.0157	56.0
22	2	4,798	.0367	176.1
23	3	4,912	.0577	283.4
24	4	3,890	.1205	468.7
25	5	3,868	.2251	870.7
26	6	2,220	.3194	709.1
27	7	2,343	.4240	993.4
28	8	1,680	.5811	976.2
29	9	1,291	.7798	1,006.7
30	10	1,185	.9997	1,184.6
July:				
1	11	1,411	.9997	1,410.6
2	12	1,713	.9840	1,685.6
3	13	1,667	.9630	1,605.3
4	14	3,434	.9420	3,234.8
5	15	2,729	.8792	2,399.3
6	16	2,576	.7746	1,995.4
7	17	1,940	.6803	1,319.8
8	18	1,339	.5757	770.9
9	19	1,241	.4186	519.5
10	20	962	.2199	211.5
			Estimate of $\sum_{i=1}^{20} C_iq_i$ =	21,877.6

We now define the quantities required to take account of (1) deaths that occur after counting and (2) the possibility that some of the carcasses of fish dying after counting are mutilated and rendered unrecoverable.

- f_a = fraction of all deaths occurring after counting.
- r_a = fraction of carcasses of fish dying after counting that are recoverable (i.e., not mutilated and rendered unrecoverable).
- D_o = number of carcasses of fish dying after counting that are unrecoverable.
- M_a = proportion of those fish that are counted over the dam that die near the dam.

The quantity D_o can be expressed as

$$D_o = (1 - r_a)f_a M\left(\sum_{i=1}^{20} C_i q_i + \sum_{i=1}^{20} D_i q_i\right) \qquad (6)$$

Because Y_1 is the number of untagged recoverable carcasses in the river, it is clear that Y_1 is the difference between the total number of untagged carcasses and the number of unrecoverable untagged carcasses:

$$Y_1 = M\left(\sum_{i=1}^{20} C_i q_i + \sum_{i=1}^{20} D_i q_i\right) - D_o$$
$$= [1 - f_a(1 - r_a)]M\left(\sum_{i=1}^{20} C_i q_i + \sum_{i=1}^{20} D_i q_i\right) \qquad (7)$$

The quantity $\sum_{i=1}^{20} D_i q_i$ represents the number of mortalities occurring below the dam before counting and can be expressed as the difference between the number of untagged recoverable carcasses and the number of untagged recoverable carcasses dying after counting:

$$\sum_{i=1}^{20} D_i q_i = Y_1 - M_a r_a \sum_{i=1}^{20} C_i q_i \qquad (8)$$

(Note that at this point, we are assuming all untagged carcasses originating below the dam are recoverable.) Finally, the total number of mortalities after counting can be expressed as follows:

$$M_a \sum_{i=1}^{20} C_i q_i = f_a(Y_1 + D_o)$$
$$= f_a\left[Y_1 + (1 - r_a)f_a M\left(\sum_{i=1}^{20} C_i q_i + \sum_{i=1}^{20} D_i q_i\right)\right] \qquad (9)$$

To derive an expression for M, (9) is solved for M_a, and this result is substituted into (8). Then (8) is solved for $\sum_{i=1}^{20} D_i q_i$, and the result is substituted into (7). An expression for M is then derived by solving (7). The final result is:

$$M = \frac{Y_1}{\left(\sum_{i=1}^{20} C_i q_i + Y_1\right)\left(1 - f_a\right) + f_a r_a \sum_{i=1}^{20} C_i q_i} \qquad (10)$$

If all mortality occurs below the dam ($f_a = 0$), then (10) becomes

$$M = \frac{Y_1}{\sum_{i=1}^{20} C_i q_i + Y_1} \qquad (11)$$

This situation corresponds to the manner in which we performed our experiment in 1955 when we released all tagged carcasses below the dam. Recalling that $\hat{Y}_1 = 4{,}412$ untagged recoverable carcasses and that $\sum_{i=1}^{20} C_i q_i$ was estimated to be 21,877.8 fish, we use (11) to calculate $\hat{M} = 0.1678$. In other words, on the assumption that all mortality occurs below the dam, we estimate that 16.78 percent of the chinook salmon run was killed near Bonneville Dam in 1955 at the time of our experiment.

It would be desirable to set a confidence interval about the estimate of mortality level given by equation (11). Unfortunately, this does not seem to be possible. All quantities appearing in equation (11) are subject to sampling error. The variances of the q_i's and the variance of Y_1 could be approximately estimated from our experimental data for 1955, but no estimates are available for the variances of the C_i's—the daily chinook salmon counts over the dam. These counts are known to be inexact and may also be biased. Some of the causes of counting errors are: fish are counted more than once as a result of being swept over the spillway; fish are not counted through the ship navigation lock; and fish are misidentified, especially the smaller salmon with similar appearances such as sockeye salmon and chinook salmon jacks. For example, in 1957, only 9,879 chinook jack salmon were counted over Bonneville Dam, but 13,415 were counted over McNary Dam and 8,402 into Spring Creek Hatchery, between Bonneville and McNary Dams (Junge and Phinney, 1963). Thus, more than twice as many jack salmon were tabulated above Bonneville Dam as were counted in that year at Bonneville.

In developing the model of chinook salmon mortality at Bonneville Dam expressed in equation (10), we assumed that the carcasses of all fish dying below the dam were recoverable. We also assumed that all tagged carcasses introduced into the river below the dam were recoverable. In the event that these assumptions are unjustified, a somewhat more general mortality model can be used. This more general model provides for the possibility that a certain percentage of carcasses released or dying below the dam become unrecoverable.

To derive this model, we define the following quantities:

r_b = fraction of carcasses of fish dying before counting or released below the dam that are recoverable.

T = number of tagged carcasses introduced into the river below the dam.

D'_o = number of carcasses of fish dying before counting that are unrecoverable.

Note that $R_x = r_bT$ so that a more general equation for estimating Y_1 than equation (3) is

$$\hat{Y}_1 = r_bT\left(\frac{1}{\hat{p}_2} - 1\right) \qquad (12)$$

An equation for D'_o that is analogous to equation (6) for D_o can be written

$$D'_o = (1 - r_b)(1 - f_a)M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \qquad (13)$$

Three relationships analogous to those given in equations (7), (8), and (9), respectively, can then be written as follows:

$$Y_1 = M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) - D_o - D'_o$$

$$= (f_ar_a - f_ar_b + r_b)M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \qquad (14)$$

$$r_b\sum_{i=1}^{20} D_iq_i = Y_1 - M_ar_a\sum_{i=1}^{20} C_iq_i \qquad (15)$$

$$M_a\sum_{i=1}^{20} C_iq_i = f_a(Y_1 + D_o + D'_o)$$

$$= f_a\left[Y_1 + (1 - f_ar_a + f_ar_b - r_b) M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right)\right] \qquad (16)$$

Equations (14), (15), and (16) may be used to derive a general expression for M in the same way that equations (7), (8), and (9) were used to derive the expression for M given in equation (10). The result, which allows for the possibility of carcasses of fish dying or being introduced into the river below the dam becoming unrecoverable, is as follows:

$$M = \frac{Y_1}{\left(r_b\sum_{i=1}^{20} C_iq_i + Y_1\right)(1 - f_a) + f_ar_a\sum_{i=1}^{20} C_iq_i} \qquad (17)$$

where the value of $\hat{Y}_1$ from (12) is used. Note that equations (12) and (17) reduce to equations (3) and (10), respectively, when $r_b = 1$.

In estimating that 16.78 percent of the chinook salmon run was destroyed near Bonneville Dam, we assumed that all mortalities occurred below the dam (i.e., that $f_a = 0$). As has already been pointed out, it is likely that some mortality occurs as a result of fish being swept back over the spillway after they have been counted. Therefore, it is of considerable interest to explore the effect that this mortality of counted fish would have on our estimate of M. Because some of the carcasses of fish that die by being swept back over the spillway could be so severely mutilated as to be rendered unrecoverable (i.e., have no chance of floating and being recovered), this factor must also be considered.

To explore the various possibilities, f_a (fraction of deaths occurring after counting) and r_a (fraction of carcasses of fish dying after counting that are recoverable) were assumed to take on various pairs of values, and $\hat{M}$ was calculated for each assumed pair of values by using equation (10).

For f_a the following values were assumed: 0.0, 0.125, 0.250, 0.375, 0.500, 0.625, 0.750, 0.875, and 1.0. The same values were assumed for r_a, and $\hat{M}$ was calculated for all possible pairwise combinations of these values. From these results, we constructed an isopleth diagram giving values of M corresponding to values of f_a and r_a (fig. 8).

Figure 8 shows that our estimate, $\hat{M} = 0.1678$ (based on the assumption that $f_a = 0$) is a mini-

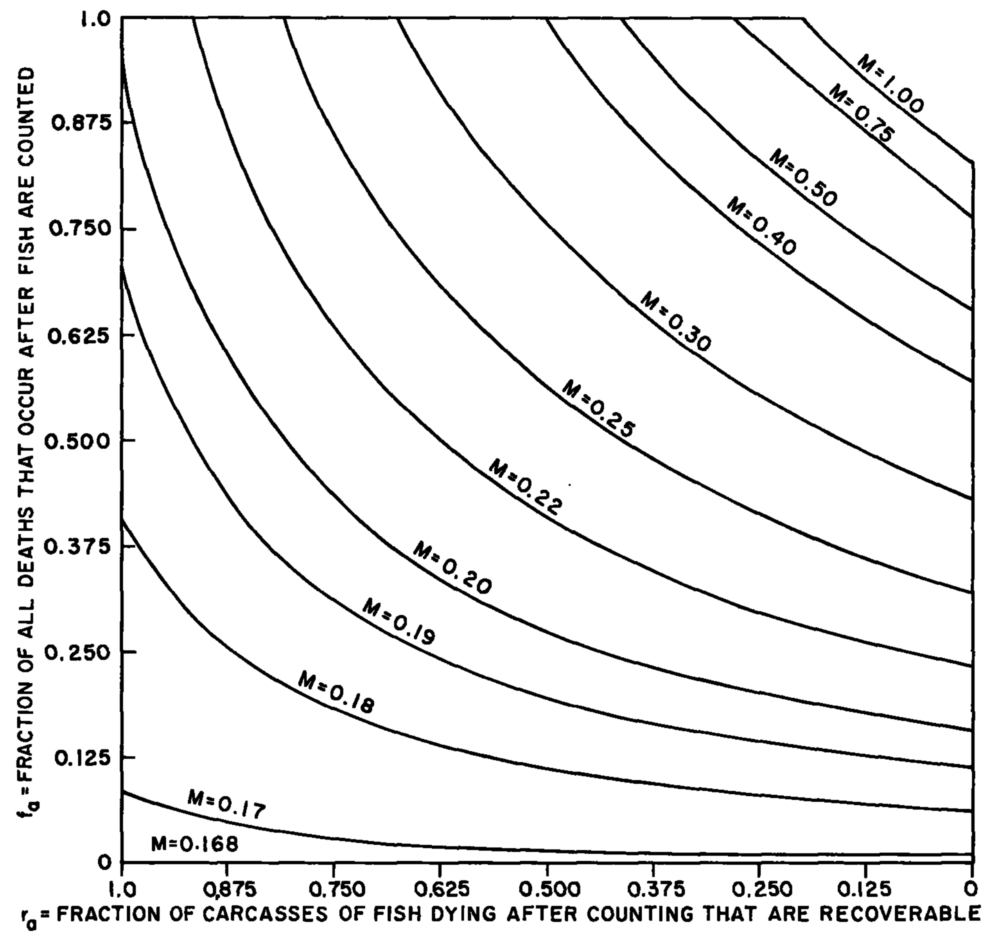

FIGURE 8.—Values of $\hat{M}$, the fraction of the chinook salmon run dying near Bonneville Dam at the time of the 1955 experiments, corresponding to pairs of values for f_a and r_a.

mum point estimate of the level of chinook salmon mortality at Bonneville Dam. As f_a increases, $\hat{M}$ also increases; the rate at which $\hat{M}$ increases depends strongly on the value of r_a. For large values of r_a, corresponding to an assumption that only a small percentage of the carcasses of fish that die by being swept over the spillway are rendered unrecoverable, values of $\hat{M}$ increase only slightly as f_a increases. On the other hand, if a large percentage of these carcasses are rendered unrecoverable, r_a is small and $\hat{M}$ increases rapidly as f_a increases. (Note in figure 8 that points in the region above and to the right of the line for $\hat{M}$ = 1.00 correspond to values of f_a and r_a that are incompatible with data collected in our 1955 experiment.)

FACTORS ASSOCIATED WITH MORTALITY AND THEIR SIGNIFICANCE

We have established in preceding sections that many chinook salmon died near Bonneville Dam at the time of our 1955 experiment. The next logical step is to examine factors associated with these deaths to determine the actual cause or causes.

In addition to the 1955 period, we also examined available information for other periods between 1943 and 1956 when high or low mortality was apparent (table 7). The seven periods of apparently high mortality were September 1943, September 1950, May 1952, July 1954, September 1954, June-July 1955, and June-July 1956. Low mortality periods were September 1946 and April-May 1955.

TABLE 7.—*Comparative mortality of chinook salmon at Bonneville Dam in spring, summer, and fall periods between 1943 and 1956*

Season and date	Average daily spillway flow	Water temperature range	Average count of chinook salmon at dam	Search time	Chinook salmon floaters	Chinook salmon floaters per hour of search	Chinook salmon floaters per hour per 10,000 fish	Mortality rating
	C.m.s.	*° C.*	*Number*	*Hours*	*Number*	*Number*	*Number*	
Spring:								
May 1–31, 1952	8,700	11.1–13.9	3,478	----	(1)	----	----	High
April 20 to May 10, 1955	1,050	7.8–11.1	6,481	212.6	2	0.009	0.015	Low
Summer:								
July 1–31, 1954	7,900	14.4–17.8	1,051	26.5	30	1.132	10.771	High
June 20 to July 22, 1955	9,020	13.9–17.2	1,836	603.4	194	0.322	1.751	Do.
June 20–29, 1956	10,500	13.3–15.6	4,317	6.5	19	2.923	6.771	Do.
Fall:								
Sept. 1–15, 1943	620	18.3–18.9	12,543	8.0	146	18.250	14.550	Do.
Sept. 1–30, 1946	140	16.1–20.6	9,235	116.6	21	0.180	0.195	Low
Sept. 1–20, 1950	480	18.9–20.6	10,054	----	54	----	----	High
Sept. 1–15, 1954	1,160	17.8–18.3	5,001	125.5	99	0.789	1.577	Do.

[1] A commercial fisherman reported "thousands" of dead chinook salmon below the dam.

The "high" and "low" mortality ratings are subjective classifications based on the number of chinook salmon floaters relative to the average daily chinook salmon counts at Bonneville Dam. Major differences in search techniques and in the lengths of search periods make detailed comparison between most of the periods of dubious value. Only for our study in 1955, and for a brief followup study in 1956, can we be certain that search techniques were comparable. We, therefore, gave the greatest weight to data for these years in reaching our conclusions. Data for earlier years were useful, however, in lending support to the conclusions.

In spring 1955, when spillway flows and water temperatures were low and numbers of salmon were high, only 0.009 chinook salmon floater was found per hour of search. Later the same year (midsummer), when spillway flows averaged 9,000 c.m.s., water temperatures were higher, and numbers of salmon were low, 0.322 chinook salmon floater was found per hour of search.

A pattern of characteristic circumstances accompanying high mortality periods was evident: floating dead salmon were likely to be especially numerous below the dam when either high spillway flows or exceptionally large numbers of salmon occurred. If high flows and large numbers of salmon occurred simultaneously, even greater numbers of floating dead salmon could be predicted downstream from the dam. The data in table 7 generally substantiate this conclusion.

After completing our study in 1955, we wished to test the hypothesis that large numbers of chinook salmon would die and float near Bonneville Dam whenever large numbers of fish and high spillway flows coincided. Late June 1956 had such a coincidence.

From June 20 to 29, spillway flow at the dam averaged 10,500 c.m.s. and coincided with chinook salmon counts over the dam averaging over 4,300 per day. We predicted that at the prevailing water temperatures of 13.3° to 15.6° C., floaters from a given day's mortality would appear downriver about 7 days later and a large number of floaters would be evident below the dam by about July 3. On July 3, during 1 hour and 50 minutes of search at the Cape Horn station, five chinook salmon carcasses were observed; on July 5, 14 carcasses were seen during 4 hours and 40 minutes of observation. In terms of numbers of chinook salmon floaters recovered per hour these numbers were greater than for any previous observation period (except September 1943), indicating, as predicted, that serious mortality had occurred. The cause of the high mortality of September 1943 is unknown.

FLOW

We were unable to determine which specific conditions at Bonneville Dam contribute to salmon deaths, but evidence is strong from our study and from observations in earlier years that high mortality in spring and summer occurs during high flows. The annual peak flow of the Columbia River at Bonneville Dam is in May or June, depending on the time of maximum snowmelt in the upper watershed; the peak flow dates from 1938 to 1955 fell between May 11 and June 28. Flows of more than 8,500 c.m.s. may occur for up to 3 months.

The maximum combined flow capacity of the 10 power turbines at Bonneville Dam is about 4,100 c.m.s. when the Columbia River is at flood stage. At low riverflows, maximum turbine capacity is about 3,400 c.m.s. This means that flows above 4,100 c.m.s. during high water and above 3,400 c.m.s. during low water are discharged through the spillway (flows through the fish ladders are an insignificant portion of the total flow).

Columbia River chinook salmon migrations may be separated into spring, summer, and fall runs by their time of appearance at Bonneville Dam. For the purpose of this discussion, the spring run is defined as occurring in April and May, the summer run in June and July, and the fall run in August and September. Only a few chinook salmon migrate past Bonneville Dam before April or after September.

The three runs are characteristically exposed to different river discharges at the dam. The summer chinook salmon run, the smallest of the three, usually migrates upstream during the period of peak river discharge. Less frequently the spring run passes the dam during annual peak flows, although both spring and summer runs are always subjected to relatively high flows. During the fall run, flows are relatively low and little water is discharged through the spillway.

Figure 9 shows the daily flows at the dam in 1946–55 for the periods when the central 75 percent of the spring, summer, and fall chinook salmon runs were counted. The 75-percent figure was arbitrarily selected to include the major part of each run; 12.5 percent was subtracted from each end of the run to determine the 75-percent period. The dashed line indicates the 7,000-c.m.s. flow level.

The 7,000-c.m.s. figure was arbitrarily selected as the point above which heavy mortalities occur, based primarily on 1955 information—the year for which the most extensive data are available (fig. 6). The reasons for establishing 7,000 c.m.s. as the critical level are: In 1955, 75 percent of the spring run passed the dam when total river flow was low—between 4,200 and 5,100 c.m.s.; few floating chinook salmon were observed on an intensive search of the river during a large spring chinook salmon run (172,000); the maximum daily count past the dam was more than 13,000 fish. Therefore, flows under 5,100 c.m.s. were not associated with a high mortality. Increasing numbers of floating chinook salmon became apparent downriver from the dam by June 12, 1955, after a period when the chinook salmon count was

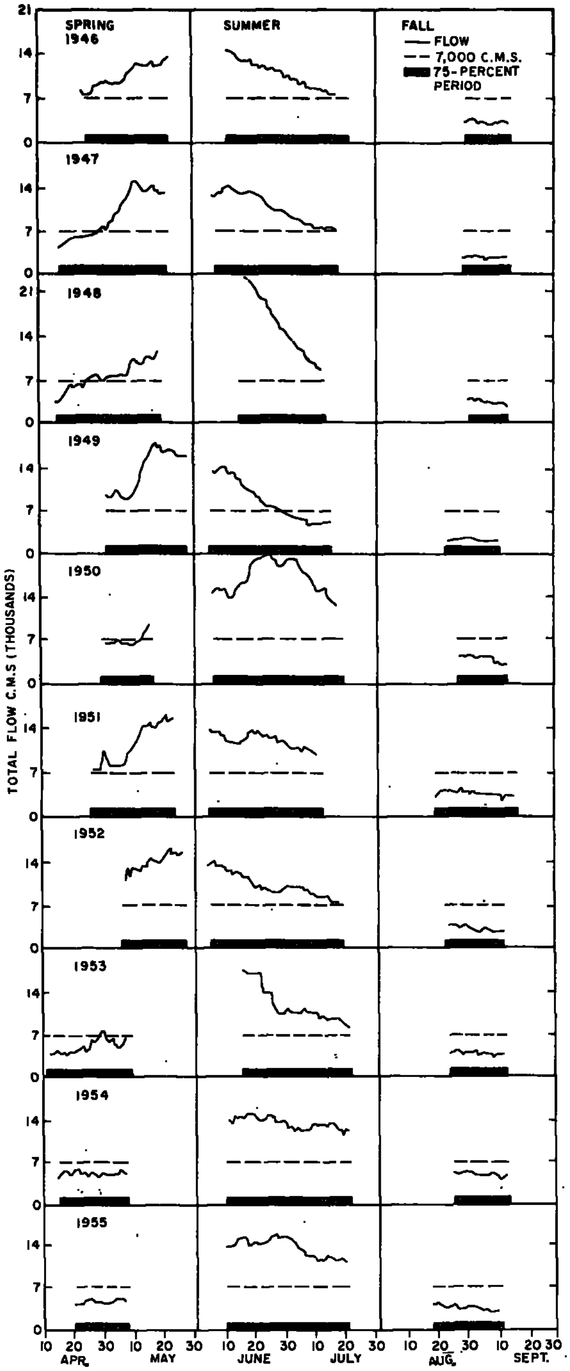

FIGURE 9.—Columbia River flows (solid lines) at Bonneville Dam during periods (horizontal bars) when 75 percent of the spring, summer, and fall chinook salmon runs passed the dam, 1946–55. Dashed line at 7,000 c.m.s. indicates flow above which serious mortality occurs.

about 1,100 fish per day for several days and flow had increased to between 7,000 and 9,900 c.m.s.

To understand better the relation of numbers of chinook salmon counted at the dam and numbers floating below the dam, it should be noted that at a water temperature of 14.4° C., salmon carcasses float in about 7 days after death (appendix table 1). Because water temperature averaged 13.3° C. during the first 10 days of June 1955, 8 or 9 days would elapse between death and the time carcasses first floated. The increase in floaters observed after mid-June was an indicator that after June 3, when total riverflow approximated 7,000 c.m.s., the numbers of chinook salmon dying suddenly increased. We conclude on the basis of these observations that mortality may be expected to be high whenever total riverflow rises above 7,000 c.m.s., and low whenever total flow is less than 5,100 c.m.s.

In some years (1943, 1946, 1950, and 1954) floating chinook salmon were recovered below the dam when total flow was less than 5,100 c.m.s. Although data for these periods are limited, the relatively large numbers of floating chinook salmon in September 1943 and 1950 probably represented a low rate of mortality because very large numbers of chinook salmon were migrating through the area. The search by A. Suomela in 1943 (discussed in an earlier section), which resulted in the recovery of a large number of carcasses, is not comparable with later searches because he searched in midstream, on shore, in eddies, and any place that fish could be expected to accumulate, whereas in our later searches, floaters were observed only from fixed locations. Fall chinook salmon runs in these 4 years of apparently high mortality were large—peak daily counts at Bonneville Dam were 20,000 to 30,000 chinook salmon. Water temperatures were about 21.1° C., and riverflows were low. Under these conditions, floating chinook salmon were more apparent because they floated in a shorter time, thereby reducing their dispersion downstream from the area of death both before and after they became buoyant.

The many floaters below the dam in September 1954 may have represented a higher rate of loss of chinook salmon than is usual in the fall. Daily counts were relatively low; the peak was only about 8,000. During the 75-percent period of passage of the 1954 fall run, total riverflow was the highest in the 10-year period 1946–55, ranging from about 4,700 to 5,500 c.m.s. This higher-than-normal flow may have resulted in a somewhat higher-than-average fall mortality rate.

Because a total flow of 7,000 c.m.s. or greater is associated with high mortality rates, figure 9 may be interpreted as follows: (1) The flow over Bonneville Dam has never reached 7,000 c.m.s. during the fall run of chinook salmon. Observations have substantiated that fall runs generally have experienced relatively low mortality rates. (2) Most of the summer chinook salmon run in every year has been subjected to flows exceeding 7,000 c.m.s., which are associated with a high level of mortality. (3) In 4 of the 10 years (1946, 1949, 1951, and 1952) the entire 75-percent periods of spring runs were subjected to flows greater than 7,000 c.m.s., and in 2 of the remaining 6 years (1947 and 1948) flows exceeded 7,000 c.m.s. for about two-thirds of the 75-percent period. The remaining four spring runs (1950, 1953, 1954, and 1955) passed the dam when flows were less than 7,000 c.m.s.

In summary, fall runs of chinook salmon were never subjected to killing flows; spring runs were exposed to killing flows in some years; and summer runs always encountered killing flows.

WATER TEMPERATURE

River water temperatures affect the floating qualities of carcasses and thereby make carcasses more or less evident to observers. Warm water makes carcasses more apparent and cold water makes them less apparent.

Flotation experiments described in the appendix showed that carcasses require more time to float in cold water than in warm. As a result, in the interval between death and floating, carcasses may be swept farther downstream during periods of low water temperatures than during periods of high temperatures. Furthermore, during the longer interval between death and floating in cold water, scavengers have more opportunity to consume carcasses.

With this in mind, we examined the relation of water temperatures and numbers of chinook salmon counted at the dam. In 1946–55 the range of temperatures during spring runs (April and May) was 7.8° to 13.9° C.; during summer runs (June and July), 10.0° to 19.4° C.; and during fall runs (August and September), 17.8° to 21.1°

C. (fig. 10). Thus, dead salmon are least likely to be evident as floaters in the spring and most likely to be evident in the fall. Figure 10 shows that in the spring of 1955 average water temperatures were the lowest for the 10 years shown (8.9° C.). Unusually cold water probably contributed to the almost complete absence of floaters during the spring run in 1955. In 1952, a period of apparently high mortality (table 7, fig. 10), water temperatures during the spring chinook salmon migration were highest of the 10-year period.

TURBIDITY

Turbid water, as measured by Secchi disk visibility, was investigated as a possible factor contributing to chinook salmon deaths. We hypothesized that fish rely partially on sight to locate and negotiate the fish ladders, and reduction of visibility might handicap them.

High flows in the Columbia River are characterized by turbid water, and low flows by relatively clear water. During low flows the water may be turbid for short periods when a tributary floods from heavy rains or rapid snowmelt. For example, in mid-January 1953 after a flash flood on a tributary, a Secchi disk visibility reading of 0.06 m. was recorded at Bonneville Dam when flow was only 2,700 c.m.s.

Secchi disk visibility at the dam has seldom been less than 0.3 m. during periods of major salmon migrations (fig. 11). From 1950 to 1955, visibility was 0.3 m. or less for only short, infrequent periods from April to September, except in 1952, when it remained about 0.3 m. or less from April 1 through May 30, throughout the spring migration. The 1952 spring run suffered a heavy mortality, but because the high turbidity was accompanied by high flows and relatively high water temperatures, it was impossible to evaluate the separate effects of flow, temperature, and turbidity.

In 1955, from April 10 to June 30, Secchi disk visibility varied between 0.3 and 0.8 m.; it was 0.6 m. at the peak of the spring chinook salmon run (May 2) and 0.45 m. at the peak of the summer run (June 23). Few floating chinook salmon were observed in May, but large numbers were seen in June and July. Because turbidity differed little between the two periods, we concluded that it was not a major factor in mortality at the dam in 1955.

Because high turbidity and high flow usually coincide, we could not evaluate the separate effect of turbidity, if any.

COMMERCIAL FISHING

The Columbia River gill net fishery has sometimes been blamed for dead salmon in the river because some fish escape from nets after becoming enmeshed. An escaped fish usually has characteristic net marks—encircling bands where scales have been scraped off and cuts on the anterior edges of fins. Hanson et al. (1950: 24) concluded from observations in the fish ladders at Bonneville Dam and at hatcheries above and below the dam that "Most injuries to the fish observed are traceables (sic) to fishermen's gill nets; none of the injuries were directly traceable to conditions at Bonneville Dam. Most net injuries were not fatal to fall-run chinook salmon at hatcheries above and below Bonneville Dam in 1946." The conclusion is questionable because only the fish that survived after being injured were available for observation—those that may have died could not, of course, be sampled at the hatcheries.

Most significant in discounting gill nets as a major cause of mortality in our study is the fact that 85,769 spring chinook salmon passed the dam in May 1955 with little apparent mortality, despite an intensive commercial gill net fishery from April 30 to May 27. The spring chinook salmon run during this period was the largest since 1939 (the first year runs were counted at Bonneville Dam). The catch was 80 percent of the total run; the catch below the dam was the second largest since 1939. Four stations below the dam and one station near The Dalles were searched intensively for floaters throughout this period, but few were found and none of these bore characteristic net marks. This is strong evidence against attributing the death of floating chinook salmon to the gill net fishery.

We concluded that gill net injuries are not a major cause of death of chinook salmon found floating near the dam.

FISH PASSAGE FACILITIES AT BONNEVILLE DAM

Great effort has been made by fishery agencies and especially by the U.S. Army Corps of Engineers to discover any structure or operation at the dam that might delay, injure, or kill migrating adult fish. Mechanical failures or routine

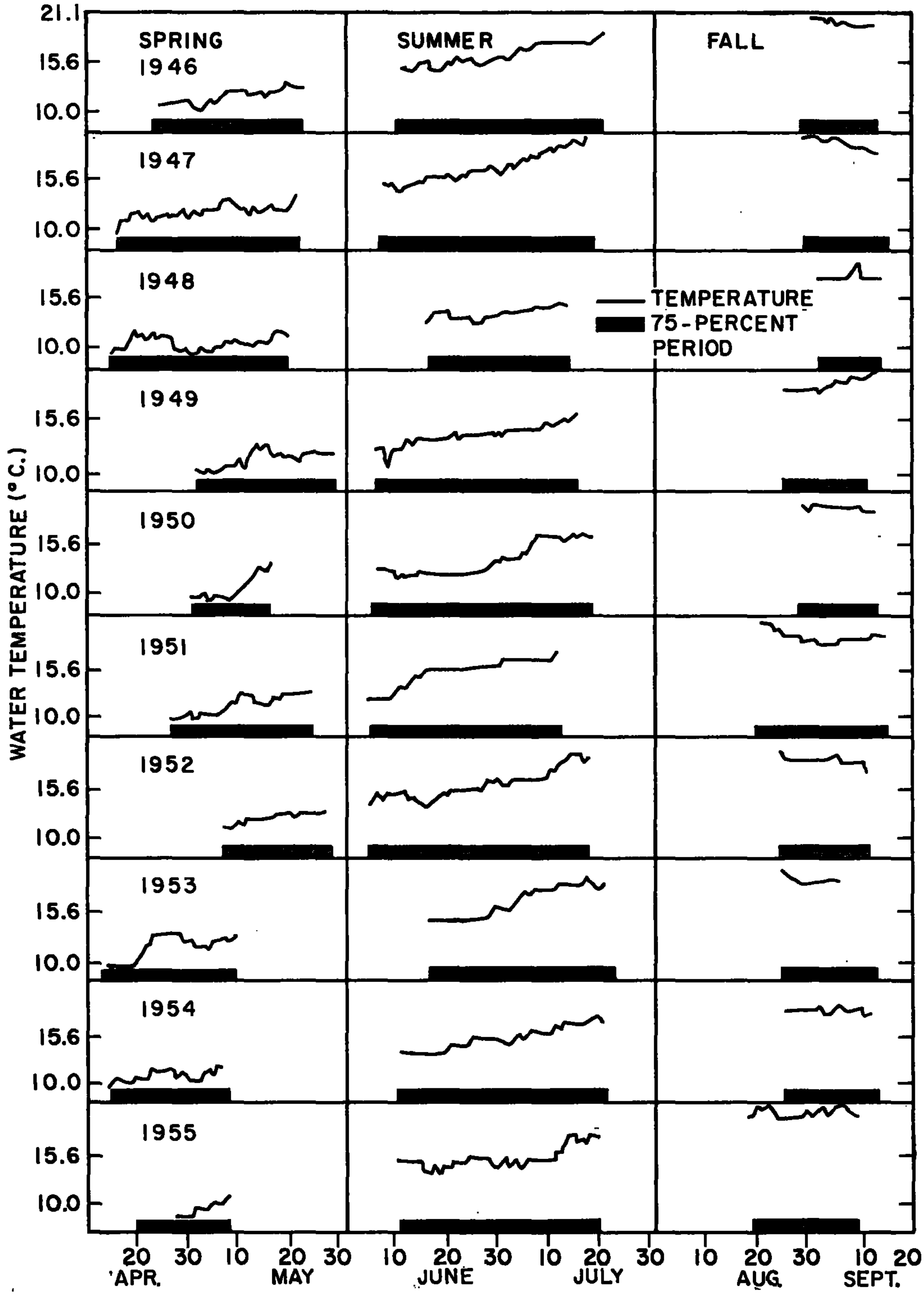

FIGURE 10.—Columbia River water temperatures at Bonneville Dam during periods when 75 percent of the spring, summer, and fall chinook salmon runs passed the dam, 1946–55.

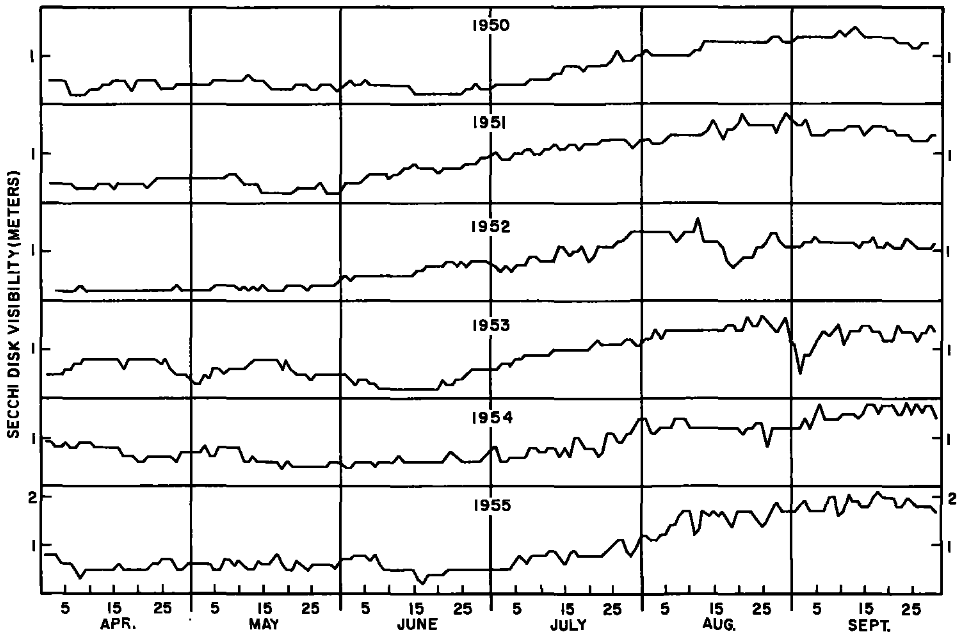

FIGURE 11.—Secchi disk visibility in the Columbia River at Bonneville Dam, 1950–55.

maintenance operations have sometimes necessitated shutting down portions of the fish-passage facilities, but these have rarely affected passage for long.

Many improvements have been made in the fish passage facilities at Bonneville Dam over the years. Among them are alteration of the powerhouse collection system, addition of auxiliary attraction flows at the entrance to the ladders, installation of flow baffles below the ladder entrances, and installation of barrier screens below the spillway bays adjacent to the ladder entrances.

In 1946 a submarine viewing chamber made of a section of large steel pipe with the ends sealed off and with two watertight windows, was used by the U.S. Army Corps of Engineers and FWS. A series of observations of migrating fish were made by an observer inside the chamber, which was lowered into a fish ladder. Fish within the ladder experienced no difficulty in moving through the ladder (Hanson et al., 1950). Other observations through the years have shown that once fish have entered the ladders they generally pass through with little or no injury or delay.

Because there is no evidence that fish are injured in the ladders, we eliminated this possible source of mortality from further consideration.

DISEASE

Another possible cause of salmon mortality is disease. In 1954 and 1955, to determine the causes of death we collected all of the recently killed fish we could find below the dam.

None of the fish collected in 1954 were sufficiently fresh to warrant a detailed examination, although gross injuries of external origin were obvious in some instances (table 8).

In 1955, we recovered three chinook and six sockeye salmon, four white sturgeon, one shad, and two carp in fresh condition (table 8). Seven of the fish (two chinook and five sockeye salmon) were immediately frozen and later autopsied by Edward M. Wood, fish pathologist at the FWS Fish Nutrition Laboratory, Carson, Wash. In summarizing the results of his examinations, Wood said:

> "In some cases these fish had severe injuries which clearly caused death. In these instances we have attempted to determine if there were any contributing factors which might have made the fish more susceptible to injury such as disease. At other times, however, there was no gross evidence of injury other than slight internal hemorrhage, congestion of various organs with blood, or

slight edema over the brain. In these cases we do not know the cause of death and little of the nature of the injury. All of these fish were sexually immature and death was presumably not related to the reproductive cycle."

TABLE 8.—*Observations at time of recovery of 8 moribund and recently dead fish found within 5 miles of Bonneville Dam, 1954–55*

Date found	Species	Condition at time of recovery
1954:		
September 9	Chinook salmon	Fresh; jaw reflexes; right eye turned backward into socket; gills bleeding; slight bloody bruises on pectoral fins, isthmus, right opercle, and caudal peduncle.
September 11	White sturgeon	Fresh; fin reflexes; abrasions on pectoral girdle and side.
1955:		
May 3	do	Alive; deep gash near left ventral fin.
May 12	do	Alive; peduncle severed.
Do	Carp	Alive, deep dorsal gash.
Do	do	Fresh; decapitated.
May 18	White sturgeon	Severed at midbody.
June 7	Chinook salmon	Fresh; torn premaxillary, isthmus, and first gill arch; clotted blood in heart cavity.
June 10	Chinook salmon [1]	Moribund; abrasions on head and dorsal fin; blood clot between first and second left gill arches.
June 17	American shad	Fresh; head severed; caudal peduncle severed.
June 21	White sturgeon	Fresh; body severed.
July 9	Sockeye salmon	Fresh; abrasion on left opercle.
July 12	Sockeye salmon [1]	Fungused gashes on right side.
Do	do	Fresh; no apparent injuries.
Do	do	Do.
July 14	do	Fresh; massive wound into body cavity.
July 15	do	Alive; floating.
July 21	Chinook salmon [1]	Large gash on peduncle.

[1] Autopsy performed.

Since the conclusion of our study of mortality, other investigators have discovered that supersaturation of nitrogen in Columbia River water at times of high flow may be a significant cause of fish mortalities. Some of the physiological symptoms described by Wood when he autopsied the fresh dead salmon are characteristic of nitrogen poisoning (such as internal hemorrhaging and congestion of spleen), which could well have been a direct cause of mortality that we did not recognize.

Ebel (1969) found that nitrogen saturation levels potentially dangerous to fish always occurred at Bonneville Dam when water was discharged through the spillway. Nitrogen supersaturation may occur when atmospheric nitrogen is entrained and dissolved in the plunging turbulent spillway flow. Therefore, highest nitrogen saturation values coincide with peak spillway flows. Nitrogen levels in tail waters below Bonneville Dam were substantially higher than levels below seven other Columbia River dams. High nitrogen levels, coinciding with high flows and a delay of chinook salmon below Bonneville Dam (Schoning and Johnson, 1956) could have been the immediate cause of death of at least a portion of the chinook salmon included in our estimate of mortality.

An epidemic of the bacterial disease columnaris, *Chondrococcus columnaris*, among salmon (particularly sockeye) was reported in the Columbia River system in late July and August 1955.[6] Sockeye salmon in the latter part of the run seemed more heavily infected than those in earlier segments, probably because water temperature increased during the summer. We do not believe that columnaris was an important contributing factor to death of chinook salmon in June and early July 1955 because our study was completed before the outbreak of the disease. Because columnaris epidemics are associated with relatively warm water, mortalities reported during spring cold-temperature periods in previous years were probably not caused by this disease.

In summary, although we were able to recover only a small number of freshly killed fish immediately below Bonneville Dam, there was no indication that disease contributed to death in 1954 and 1955. Many of the fish had severe recent external injuries. Some of the dead fish without massive injuries probably died as a result of nitrogen poisoning, a potential cause of death not recognized by us at the time of our study.

SUMMARY

1. In most years since the completion of Bonneville Dam in 1938, floating dead fish—particularly chinook salmon—have been observed downstream from the dam.

2. In 1954 and 1955 the Oregon Fish Commission, under a contract with FWS, studied salmon mortality at Bonneville Dam.

3. The main aims of the studies were to estimate the chinook salmon mortality at Bonneville Dam and to determine the causes of death.

4. From ratios of tagged to untagged floating carcasses, we estimated that 4,412 recoverable carcasses of chinook salmon that had died near Bonneville Dam were in the river at the time of our 1955 experiment.

5. The chinook salmon mortality at Bonneville

[6] Erling J. Ordal. 1955. Progress Report No. 13, U.S. Fish and Wildlife Service, Contract No. 14-19-008-2418, 7 pp. On file Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash. 98102.

Dam was estimated to be 16.8 percent of the total run during the period of our 1955 experiment (June 21 through July 10).

6. If a substantial proportion of the fish died after they were counted (by being swept back over the spillway) and if a substantial number of these carcasses were mutilated and rendered unrecoverable, actual mortality was substantially higher than our estimate.

7. Our experiment probably included the period of maximum mortality in 1955.

8. The numbers of floating carcasses are related to the amount of flow of the Columbia River. The mortality of salmon is highest when flows exceed 7,000 c.m.s.

9. Fall chinook salmon runs have never been subjected to flows above 7,000 c.m.s. (killing flows); spring runs were exposed to such flows in some years; and summer runs nearly always encountered such flows.

10. Water temperature, turbidity, disease, and injuries from gill nets had little influence on the number of carcasses in the river.

11. The specific causes of death and the precise areas at Bonneville Dam where death occurred were undetermined, but the major source of chinook salmon mortality is associated with the spillway during high flows.

12. We did not consider nitrogen poisoning resulting from high flow turbulence as a possible cause of mortality at the time of our experiment, but evidence subsequently developed by other investigators indicates that this may be a major specific mortality factor.

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Lee Motley, operator of Beacon Rock Moorage, supplied information on the use of salmon carcasses by fishermen for sturgeon bait. Finally, Edward M. Wood, former pathologist of the U.S. Fish and Wildlife Service, performed the histological examinations of freshly killed salmon to determine causes of death.

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APPENDIX

EXPERIMENTS ON FLOATING QUALITIES OF CHINOOK SALMON CARCASSES

This appendix describes experiments designed to test two key assumptions: (1) that experimental tagged carcasses and carcasses of natural river-killed fish have similar floating characteristics; (2) that floating carcasses pass rapidly through the recovery area and are available for recovery on only 1 day.

Floating Qualities of Fresh and Experimental Carcasses

Salmon sink after death, but decomposition gases cause them to float after a period of time. In the mark-and-recovery method that we used to estimate the population of dead fish, it was essential to ascertain whether tagged experimental carcasses had floating qualities similar to those of other salmon that die in the Columbia River. Differences between the two kinds of carcasses could influence results. We made a series of experiments at various water temperatures with fresh and frozen experimental chinook salmon carcasses to determine whether there are differences in elapsed time between death and rise of the carcass to the surface.

Some information was already available from experiments by Hanson et al. (1950). They determined the elapsed time between death and floating for 21 fresh salmonids at water temperatures of 13.9° to 20.6° C. We performed similar experiments over a wider range of temperatures with 24 frozen and 14 fresh chinook salmon. Cold-water experiments were done in a spring-fed pond at the Oregon Fish Commission Laboratory, Clackamas, Oreg.; warm-water experiments were done in the Columbia River near Bonneville Dam. Frozen fish were thawed in air for 24 hours before submersion for testing; they were from the same lots as those that were later tagged and released to estimate the population of dead salmon. Fresh fish were purchased from commercial fishermen and were submerged within a few hours after death. The time required to float was calculated from the time the fish was placed in the water until some part was visible at the water surface.

In the cold-water temperature range (7.2°-11.1° C.) frozen salmon took 2.3 days longer to float than fresh salmon (appendix table 1), whereas in the warm range (12.8°-17.2° C.) the difference was reduced to 1.7 days (appendix table 2). We tested the significance of these differences by using Wilcoxon rank sum tests for comparison of group means. This nonparametric test does not require that any assumption be made concerning the distributions of floating times in the populations from which our samples are drawn. When fresh and frozen carcasses were compared under cold-water conditions (appendix table 1), the null hypothesis that there is no difference in floating times between the two types of carcasses was accepted at the 90-percent level of significance. A similar result was obtained for warm-water conditions (appendix table 2). Appendix figure 1 shows the similarity of floating characteristics of fresh and frozen carcasses, especially at relatively warm water temperatures of over 10° C. The temperature of the Columbia River was 14.4° C. during the experiment to estimate the population of dead salmon.

Next we compared floating times of carcasses in warm and cold water, again using the Wilcoxon rank sum test. Because no differences had been found between fresh and frozen carcasses, both types of carcasses were included in the comparison between water temperatures. We rejected (at the 99-percent significance level) the null hypothesis

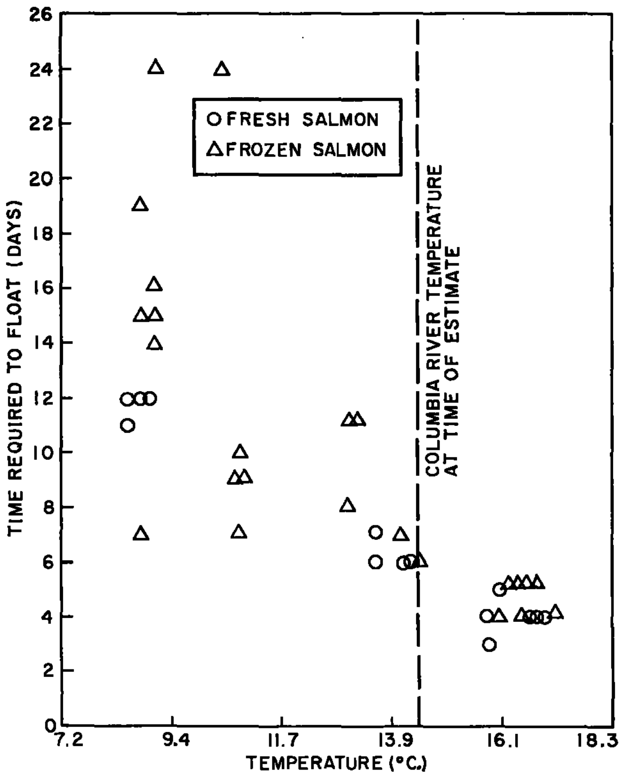
APPENDIX TABLE 1.—*Days required for fresh and frozen chinook salmon to float in cold water (7.2°–11.1° C.)*

Fresh chinook salmon			Frozen chinook salmon		
Water temperature	Days required to float	Average days required to float	Water temperature	Days required to float	Average days required to float
° *C.*	*Number*	*Number*	° *C.*	*Number*	*Number*
7.2–10.0	11		7.2–10.6	15	
7.2–10.0	12	11.8	7.2–10.6	7	
8.3–10.6	12		7.2–10.6	19	
8.3–10.6	12		7.2–11.1	24	
			8.3–10.0	16	
			8.3–10.0	14	14.1
			8.3–10.0	15	
			10.0–11.1	24	
			10.6–11.1	10	
			10.6–11.1	7	
			10.6–11.1	9	
			10.6–11.1	9	

APPENDIX TABLE 2.—*Days required for fresh and frozen chinook salmon to float in warm water (12.8°–17.2° C.)*

Fresh chinook salmon			Frozen chinook salmon		
Water temperature	Days required to float	Average days required to float	Water temperature	Days required to float	Average days required to float
° *C.*	*Number*	*Number*	° *C.*	*Number*	*Number*
13.3–13.9	7		12.8–13.3	11	
13.3–13.9	6		12.8–13.3	11	
13.3–14.4	[1] <6		12.8–13.3	8	
13.3–14.4	[1] <6		13.3–14.4	[1] <6	
15.6–16.1	3	4.6	13.3–14.4	7	
15.6–16.1	4		15.6–16.7	4	6.3
15.6–16.7	5		15.6–16.7	5	
16.7–17.2	4		15.6–16.7	5	
16.7–17.2	4		15.6–16.7	5	
16.7–17.2	4		16.7–17.2	5	
			16.7–17.2	4	
			16.7–17.2	4	

[1] These observations omitted from calculations of means and statistical comparisons of floating times.



APPENDIX FIGURE 1.—Days required for fresh and frozen chinook salmon to float at water temperatures of 7.2° to 17.2° C.

that floating time is unaffected by water temperature.

To determine whether massive tissue damage such as ruptured body cavities might affect the time required to float, we made another experiment with 15 frozen carcasses. Slits of 2.5 to 7.5 cm. were made in the body wall of eight carcasses, and full-length slits (from vent to isthmus) were made in seven.

Three fish, two with full length slits and one with a 7.5-cm. slit, took only 4 or 5 days to float at temperatures of 15.6° to 18.3° C. Of the remaining 12 fish, tested at water temperatures of 9.4° to 11.1° C., all but two floated—one of these had a 2.5-cm. slit and the other had a full-length slit. Except for the two that did not float, the time required for slit fish to float was about the same as for intact fish: in the warm-water range, slit fish required an average of 4.3 days to float compared with 4.6 days for intact fish; in the cold-water range, slit fish required an average of 12.8 days to float compared with 11.8 days for intact fish.

All the tagged experimental carcasses used for the population estimates were intact. Some of the natural population of killed fish had massive wounds, and part of these could not float and be recovered as floaters. Therefore, in the main body of this report we have referred to such fish as being unrecoverable, and in our basic model we allow for the possibility that a fraction of the fish that die are rendered unrecoverable.

Pertinent results of the flotation experiment are summarized as follows:

1. All intact dead chinook salmon, fresh or frozen, floated.
2. The relation between water temperature and time required to float was inverse, i.e., the colder the water the greater the time required for the carcass to float.
3. No statistically significant or practical differences were found between floating times of fresh and frozen fish over the range of temperatures tested.
4. A slit or puncture of the abdominal wall usually did not greatly affect the floating qualities of the fish.
5. Fresh and frozen chinook salmon carcasses have similar floating properties; therefore, frozen carcasses can be used to simulate fresh carcasses.

Disappearance of Floaters from Recovery Area

We conducted another experiment to estimate the rapidity of disappearance of floaters from the surface of the Columbia River within the recovery area and to trace their dispersion from the point of first appearance. From April 4 to July 22, 1955, all floaters in reasonably good condition were tagged with Petersen disks and released where they were found (appendix table 3). Of 289 chinook salmon floaters tagged, 11 percent were recovered; 26 were recovered again after the first release, and five after a second release. The single recovery from the 17 chinook salmon released above the dam at station 8 (The Dalles) was by a fisherman about 4.8 km. downstream from the release point. Nineteen percent of the 11 steelhead floaters were recovered. The greatest distance traveled by any tagged floater before recovery below the dam was 74 km.

APPENDIX TABLE 3.—*Number of floaters tagged at search stations near Bonneville Dam and percentage recovered, April 4 to 22, 1955*

Tagging location	Chinook salmon		Sockeye salmon		Steelhead trout	
	Tagged	Recovered	Tagged	Recovered	Tagged	Recovered
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
The Dalles	17	1	4	0	0	0
Bonneville [1]	32	0	5	0	2	0
Cape Horn	75	6	21	0	0	0
Reed Island	92	13	3	1	3	0
Ellsworth	17	4	15	1	2	0
Willamette	63	4	13	1	4	1
St. Helens	3	3	0	0	0	1
Total	[2] 299	[3] 31	61	3	11	2
Percent recovered		11		5		19

[1] McGowan and Moffett Creek stations combined.
[2] Including 26 released twice and five released a third time.
[3] Including five second recoveries.

Tags from eight of the 272 chinook and three of the 57 sockeye salmon released downstream from the dam were returned by fishermen; the rest were recovered at search stations.

Forty-four chinook and 12 sockeye salmon were released at stations 1 (St. Helens) and 2 (Willamette) when there was no search effort farther downriver. These fish, therefore, had no chance for recovery at search stations. In both years, carcasses released at stations farther downstream had less chance of recovery than those released farther upriver because the number of search stations was smaller downstream from the dam.

Only five of the 22 chinook salmon floaters recovered at search stations in 1955 traveled more than 16 km., and all but one were found the same day they were released. Thus, the small number of second recoveries of tagged floaters was indicative of their rapid disappearance.

Tagging and recovery of floaters also provided useful information on their rate of travel: during our experiment in July 1955, when river flow was high, the rate below Bonneville Dam was from 3.4 to 5.1 km.p.h. (average 4.2 km.p.h.).

Thus, during the period of recovery of tagged floaters for the mortality estimate, a floater required a maximum of only 16 hours to pass through the entire search area between the dam and the mouth of the Willamette River, a distance of 70 km.

From these facts, the following conclusions may be drawn regarding disappearance and rate of travel of floaters:

1. Floaters appearing at the surface near Bonneville Dam would pass through the 70-km. search area between the dam and the mouth of the Willamette River in less than 16 hours, provided they remained in the current.

2. Floaters would pass through the entire search area during the night between successive days of sampling, eliminating any possibility of being observed.

3. Floaters originating near the dam would reach the mouth of the Columbia River in 3 or 4 days.