EFFECT OF THE SPAWNING BED ENVIRONMENT ON REPRODUCTION OF PINK AND CHUM SALMON [1]

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ABSTRACT

Mortality of 5 brood years of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, in spawning beds of three Southeastern Alaska streams was studied. Eggs and larvae were sampled periodically, and mortality was associated with certain environmental factors: The supply of dissolved oxygen, the stability of spawning beds, and freezing.

Total mortality between spawning and fry emergence typically varied between 75 and 99 percent in the study areas. High mortality occurred during low and high stream discharge and freezing air temperatures. Mortalities ranging from 60 to 90 percent of deposited eggs occurred in association with low dissolved oxygen levels during and after the spawning period. Movement of gravel in certain instances was associated with the removal of 50 to 90 percent of eggs and larvae present in spawning beds. Freezing caused up to 65 percent mortality of eggs and larvae in one stream.

Low dissolved oxygen levels occurred once in 5 years. This occurrence was associated with unusually low water during spawning in late summer. Mortality during periods of heavy precipitation was highly variable. In one instance, a 90-percent mortality occurred where wood debris was deposited within the high water channel. Wood debris floating over spawning beds was not damaging to eggs and larvae. There were several instances where mortality estimated at almost 50 percent occurred with no evidence that deposited wood debris shifted position. High mortality from freezing occurred only in the stream having the lowest minimum discharge.

Pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, are the only species of Pacific salmon in North American streams using fresh water [2] solely for spawning. The young of these species, with minor exceptions, migrate to sea soon after emerging from spawning beds, while the young of chinook salmon, *O. tshawytscha;* sockeye, *O. nerka;* and coho, *O. kisutch*, may remain in fresh water for many months.

Adult pink and chum salmon commonly migrate into coastal streams to spawn in summer and early autumn. They excavate pockets in riffle areas and deposit and bury their eggs in the bottom. Surviving embryonic and larval salmon remain in the spawning bed for periods up to 8 months, and fry usually emerge and migrate seaward the spring after spawning.

The spawning bed protects eggs and larvae against predators, light, displacement, and mechanical injury. Despite this protection, mortality from time of egg deposition to fry emergence commonly exceeds 75 percent.

Estimates of total fresh-water mortality of pink and chum salmon have been published for McClinton, Morrison, Nile, and Hook Nose Creeks, British Columbia (Pritchard, 1948; Neave, 1953;

Note.—Approved for publication Nov. 19, 1964.

[1] This research was done while the author was a Research Associate at the Fisheries Research Institute, University of Washington, Seattle, Wash. and was financed by the Bureau of Commercial Fisheries under Contract Nos. 14-17-008-29, 14-17-008-96, 14-17-0005-20, and 14-17-0005-31, with funds made available under the Act of July 1, 1954 (68 Stat. 376), the Saltonstall-Kennedy Act. This report constitutes Contribution No. 198, College of Fisheries, University of Washington, Seattle, Wash.

[2] Includes intertidal areas periodically inundated by salt water or brackish water.

Hunter, 1959); and Sashin Creek, Southeastern Alaska (Merrell, 1962). For the brood years studied, total mortality in these streams ranged from 76 to 99.9 percent. Although these estimates fail to differentiate among mortalities occurring during (1) adult migration, (2) egg and larval development, and (3) fry migration, other evidence indicates that the largest portion of total fresh-water mortality occurs between the time eggs are deposited and fry emerge.

Typical results are seen in mortality studies at Hook Nose Creek (Hunter, 1959). Although Hunter found that total deaths varied considerably from year to year, losses before spawning appeared to be consistently small. The number of fry consumed by predators was fairly constant from year to year and was usually a small fraction of the potential egg deposition. Most deaths occurred between spawning and fry emergence. Hunter's data showed that over a 10-year period, 69–94 percent of the eggs potentially available for deposition were lost before emergence of fry.

Increased utilization of streams and watersheds by logging, mining, and other multiple-use activities has caused concern about the welfare of salmon. A thorough understanding of the factors causing mortality in spawning beds will be required to evaluate the effects of multiple-use activities on pink and chum salmon.

In 1956 the Bureau of Commercial Fisheries gave Saltonstall-Kennedy Act funds to the Fisheries Research Institute (FRI), University of Washington, to study the effects of logging on pink salmon streams in Alaska. These studies concentrated on identifying the time and magnitude of mortality and determining the factors responsible. This paper reviews past work on factors causing mortality in spawning beds and reports findings of field studies in three Southeastern Alaska spawning streams. Field observations on mortality and associated environmental factors thought to cause mortality are described.

REVIEW OF ENVIRONMENTAL REQUIREMENTS OF EGGS AND LARVAE

Given an environment free of mechanical disturbances, the growth, development, and survival of salmon eggs and larvae depend largely upon physical and chemical characteristics of the surrounding water. Properties of water that affect eggs and larvae include temperature, dissolved oxygen content, velocity, mineral and waste metabolite content, and osmotic pressure.

The spawning bed environment is greatly influenced by weather and characteristics of the streambed, stream, and watershed. The quality of intragravel water [3] is influenced in part by the hydrological regimen. Environmental changes within spawning beds can accompany changes in tide level, precipitation, and air temperature. Periods of spawning and development very likely coincide with the seasonal conditions that offer maximum opportunity for survival of the young salmon.

SOURCES OF INTRAGRAVEL WATER

To survive, eggs and larvae must receive an ample supply of oxygenated water suitable in temperature and free of toxic substances. The source of intragravel water may govern to a large extent its physical properties and its suitability for eggs and larvae.

Ground water and surface stream water are the two primary sources of intragravel water. In spawning beds of pink and chum salmon, surface stream water is the primary source of intragravel water (Sheridan, 1962a), while in spring-fed spawning beds commonly used by other salmonid species; e.g., sockeye salmon, ground water may be an important source of intragravel water.

Vaux (1961, 1962) showed that interchange between stream and intragravel water occurred when certain hydraulic requirements of the stream and streambed were satisfied. He formulated models which showed the direction of interchange depends on the curvature of the gravel surface profile. Where the profile was concave, water upwelled; where it was convex, a downdraft occurred. In the absence of curvature, there was no interchange, provided permeability and gravel bed depth did not vary. Vaux verified these relations with field and laboratory experiments. Figure 1 illustrates the direction of interchange with change in curvature of the stream bottom.

WATER TEMPERATURE

Water temperature controls the rate of growth and the developmental and metabolic processes of the salmon embryo. It also affects other water quality characteristics, such as dissolved oxygen concentration.

[3] The term "intragravel water" refers to water occupying interstitial spaces within the streambed.

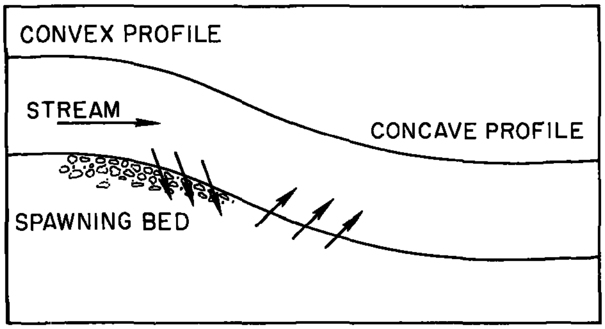

FIGURE 1.—Changes in direction of interchange with changes in curvature of the stream bottom (from Vaux, 1962). Arrows indicate direction of interchange.

The temperature of intragravel water in pink salmon spawning beds is controlled largely by stream water temperature. Sheridan (1961) obtained a linear correlation coefficient of 0.99 when he related intragravel and stream water temperatures.

Pink and chum salmon embryos and larvae survive in streams where water temperatures drop to 0° C. James (1956) reported water temperatures slightly below 0° C. in pink and chum salmon spawning streams. In an experiment with pink salmon embryos, Combs and Burrows (1957) varied water temperature to coincide with variations observed in Sashin Creek, Southeastern Alaska. They found that embryos reared at 5.5° C. for 30 days and then at 0.5° C. to hatching had almost no mortality.

Information is lacking on tolerance of pink and chum salmon eggs and larvae to high temperature, but studies with other salmonid species suggest that temperatures of 15° C. or higher may be tolerated. Chinook salmon embryos exposed to 20° C. water died at all developmental stages, while embryos exposed to 17° C. water died only at hatching (Donaldson, 1955). Larvae of Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*, survived 16 days in 20° C. water (Bishai, 1960).

Pink and chum salmon normally spawn on declining water temperature after maximum summer temperatures. Sheridan (1962b) reported that pink salmon typically spawned in Southeastern Alaska streams after water temperatures declined to 10° C. or less in late summer. Mean water temperature in Hook Nose Creek was reported to be 12° C. or less when pink and chum salmon spawned (Hunter, 1959). It would appear, therefore, that high temperature seldom exerts a direct lethal stress on pink and chum salmon eggs and larvae.

DISSOLVED OXYGEN SUPPLY

Oxygen is transported to the embryo by diffusion. After water hardening, the capsule of a newly fertilized egg is permeable to oxygen molecules but impermeable to water molecules (Krogh and Ussing, 1937).

The oxygen consumption rate per unit mass of embryonic tissue appears fairly constant over most of the developmental period. During the last two-thirds of the period, the oxygen consumption per gram of embryo remained almost constant for Atlantic salmon (Hays, Wilmot, and Livingstone, 1951). The rate of oxygen consumption for chum salmon was highest but variable during the first one-third of the developmental period and fairly constant thereafter (Alderdice, Wickett, and Brett, 1958).

The rate at which oxygen is consumed by salmon embryos decreases with decreasing dissolved oxygen content of the water below a certain "limiting level" while at dissolved oxygen levels higher than the limiting level, the rate is independent of pressure or content of dissolved oxygen. The limiting level corresponds to the dissolved oxygen content or partial pressure below which normal metabolic functions are affected. There is evidence, also, that the limiting level may vary in a complex manner with temperature and stage of development (Lindroth, 1942; Hays, Wilmot, and Livingstone, 1951).

Alderdice, Wickett, and Brett (1958) calculated theoretical values of the limiting dissolved oxygen level for chum salmon embryos by using an equation originated by Harvey (1928) and later modified by Krogh (1941). The equation is

$$C_0 = \frac{SRT}{3U} \qquad (1)$$

where C_0=limiting level of oxygen dissolved in the external medium in atmospheres

R=radius of the egg in cm.

S=ml. of oxygen consumed/g. of embryo/minute.

T=thickness of the capsule in cm.

U=diffusion coefficient of oxygen through the capsule in ml. O_2/cm.^{2} of surface/cm. of thickness/minute.

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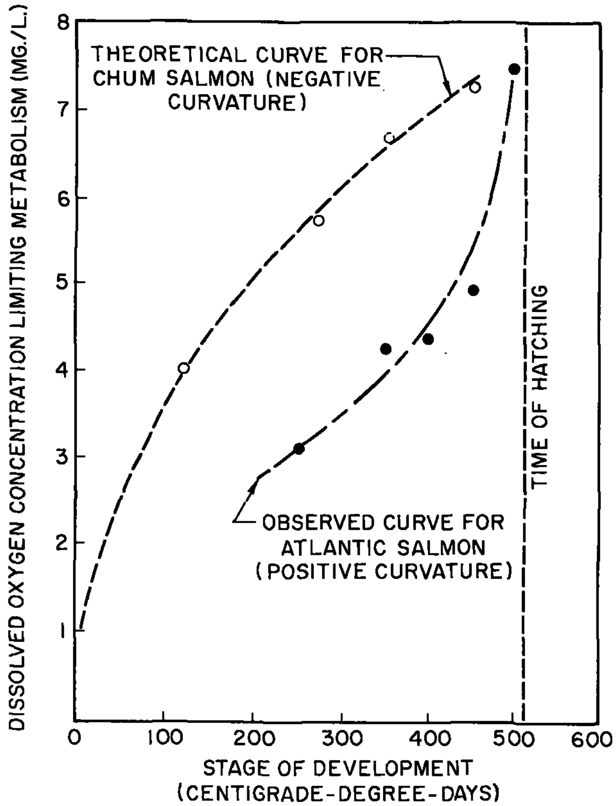

FIGURE 2.—Concentration of dissolved oxygen first reducing rate of oxygen consumption by salmon embryos. Upper curve is from Alderdice et al. (1958). Lower curve is from Hays et al. (1951). Water temperature is taken to be 10° C., and a centigrade-degree-day is equivalent to a constant temperature of 1° C. above 0° C. over a 24-hour period.

In figure 2, the theoretical values of C_0 at 10° C. obtained for chum salmon by Alderdice et al. (1958) (upper curve) are compared with limiting levels determined experimentally for Atlantic salmon by Hays et al. (1951). The most striking difference between theoretical and observed limiting dissolved oxygen concentrations is the sign of curvature of the connected points. It is doubtful if difference in species would account for positive curvature in Atlantic salmon and negative curvature in chum salmon. The validity of equation (1) as it applies to salmonid embryos is, therefore, questioned.

Wickett (1954) pointed out that the delivery rate of oxygen to an egg or a larva is a function of water velocity as well as oxygen content. Others (Coble, 1961; Shumway, 1960; Silver, 1960; Silver, Warren, and Doudoroff, 1963) gave experimental evidence that variations in velocity affected embryonic growth, development, and survival in much the same manner as variations in oxygen content.

According to curves of figure 2, embryos are most susceptible to low dissolved oxygen levels near the time of hatching. Evidence of this was presented by Hays and Armstrong (1942) and Garside (1959), who observed high mortality at hatching. Because mortality increased with slight increases in temperature, these authors attributed death to an inadequate amount of dissolved oxygen diffusing through the egg capsule.

The effect of oxygen supply rate on growth, development, and survival of salmonid embryos has been investigated by several workers. The dissolved oxygen level causing 50-percent mortality of chum salmon embryos increased from about 0.4 mg./1. at fertilization to 1.4 mg./1. at hatching, when apparent velocity [4] and temperature were maintained at 85 cm./hour and 10° C. (Alderdice et al., 1958). Coho salmon eggs incubated at near true velocity of 3 cm./hour, a temperature of 9° C., and an oxygen level of 2.4 mg./1. survived to hatch but produced larvae about one-third the volume of controls (Shumway, 1960). Similar findings were reported by Silver, Warren, and Doudoroff (1963), who experimented with chinook salmon and rainbow trout, *Salmo gairdneri*, embryos. At near true velocity of 6 cm./hour and a dissolved oxygen content of 2.6 mg./1., Silver (1960) observed abnormal development. At similar low levels of dissolved oxygen, Alderdice et al. (1958) and Garside (1959) described abnormal development of caudal regions during somite formation. Garside also found that the development rate was retarded significantly by reduced oxygen level.

Larvae are more tolerant of low dissolved oxygen levels than are embryos. For Atlantic salmon, Hays et al. (1951) found the dissolved oxygen concentration limiting metabolism of embryos to be 7.5 mg./1. at 10° C. After the eggs hatched the limiting concentration decreased to 4.5 mg./1. Initiation of active respiration across gill membranes having vastly increased respiratory areas may have caused the sudden decrease in limiting oxygen concentration.

[4] Apparent velocity is measured by dividing the rate of flow by the cross-sectional area of the bed through which the water had passed. The actual or true velocity is greater than the apparent velocity where part of the cross-sectional area is occupied by eggs or other objects.

Several general conclusions may be drawn regarding the dissolved oxygen requirements of pink and chum salmon embryos and larvae. First, the supply of dissolved oxygen made available to an embryo or larva is both a function of dissolved oxygen content and flow velocity of intragravel water. Second, the rate of oxygen consumption per unit mass of embryonic tissue is little affected by growth over most of the developmental period up to hatching. Hence, the rate of oxygen consumption by a population of embryos is possibly a simple function of the biomass present. Third, oxygen levels limiting metabolic processes and causing mortality approach a maximum shortly before hatching. After hatching, there is a sharp decline in limiting levels of dissolved oxygen. By considering only the requirements of eggs and larvae and neglecting changes in the environment, it would appear that the dissolved oxygen requirements of eggs become most critical at hatching.

METABOLIC WASTE PRODUCTS

Two metabolic waste products excreted by salmon eggs and larvae are free carbon dioxide and ammonia. Both are toxic to aquatic organisms.

The effect of free carbon dioxide on the physiology of blood has been studied exhaustively. Jacobs (1920) showed that molecules of free carbon dioxide passed readily through living cell membranes. The ability of eggs and larvae to respire is influenced by the blood's affinity for oxygen, and there is a loss of affinity for oxygen in the presence of free carbon dioxide (Bohr effect). Salmonid blood in vitro lost half of its oxygen-combining capacity in the presence of 150 mg./l. of free carbon dioxide at 15° C. (Irving, Black, and Safford, 1941). Since the oxygen tension equal to one-half saturation is considered to be the minimum compatible with exchange of oxygen to the tissues, a salmonid having its blood oxygen-combining capacity reduced 50 percent would die theoretically of suffocation.

Only a few investigators have investigated the effect of free carbon dioxide on salmonid eggs and larvae. Bishai (1962) induced a marked metabolic stress on Atlantic salmon and brown trout larvae by subjecting them to high free carbon dioxide levels. High mortality among trout embryos occurred at free carbon dioxide levels between 55 and 80 mg./l. in hatchery water (Surber, 1935). Increased mortality of chum salmon embryos was caused by 125 mg./l. of free carbon dioxide (Alderdice and Wickett, 1958). Additional information on the effect of high free carbon dioxide content in conjunction with low dissolved oxygen levels on growth, development, and survival of salmon eggs and larvae will be required before relationships observed between mortality and quality of intragravel water can be fully evaluated.

Ammonia is the most toxic metabolite. Ammonia excreted by salmon eggs and larvae is removed by the surrounding water, but it is possible that toxic concentrations of ammonia occur where the density of eggs and larvae is high and the circulation of intragravel water is poor.

The toxicity of ammonia is related directly to the concentration of free ammonia (NH_3) or non-ionized ammonium hydroxide ($NH_3 \cdot H_2O$) in solution. Ionization of $NH_3 \cdot H_2O$ occurs according to the equilibrium equation

$$NH_3 \cdot H_2O \rightleftarrows NH_4^+ + OH^-$$

Ionization is nearly complete at pH 7.0 and lower, and ammonia is least toxic in waters having high concentrations of hydrogen ions (pH <7.0). Formation of carbonic acid from respired free carbon dioxide would, therefore, tend to decrease the toxicity of ammonia.

Reviews of influence of ammonia on fish have been given by Doudoroff and Katz (1950) and Doudoroff (1957). These authors concluded that additions of 2 to 7 mg./l. of ammonia to natural waters could kill fish. Experiments by Wuhrmann and Woker (1948) showed that concentrations of only 1.2 mg./l. of NH_3 were lethal to fresh-water fish of the genus *Squalius*. They also found that 1.3 mg./l. of NH_3 killed rainbow trout fry.

According to Wolf (1957a, 1957b), blue-sac disease was induced by subjecting salmonid embryos to high concentrations of ammonia. The incidence of disease was roughly proportional to the contact period and the NH_3 concentration.

SALINITY

Pink and chum salmon spawn in intertidal areas of streams, and in some streams more fry are produced in intertidal areas than in upstream areas (Kirkwood, 1962). From field observation alone, it is apparent that pink and chum salmon eggs and larvae can tolerate intermittent high salinity.

Rockwell (1956) exposed pink and chum salmon eggs and larvae to constant high salinity and found no evidence that fertilization of eggs was affected by salinities up to 18°/₀₀. The tolerance of embryos to sea water was a function of osmotic pressure, time of exposure, and stage of development. Mortality was attributed to dehydration. He found a marked reduction in the rate of early growth of chum salmon embryos at constant salinities of 12°/₀₀ and greater and a total mortality to hatching at a salinity of 12°/₀₀. At 6°/₀₀ salinity, survival to hatching was less than that in the controls.

Larvae are more tolerant of high salinity than eggs. According to Rockwell (1956), salinities as high as 18°/₀₀ killed few pink salmon larvae. Chum salmon larvae were less tolerant, some dying at a salinity of 12°/₀₀.

Salinity of intragravel water in pink and chum salmon intertidal spawning beds is influenced markedly by tidal action. Hanavan and Skud (1954) found salinity of intragravel water of pink salmon spawning beds corresponds closely to salinity of overlying water. Also, they observed high survival of pink salmon eggs and larvae where tidal inundation prevailed during 35 percent of the incubation period. Ahnell (1961) observed that the salinity of intragravel water remained high for a period after the tide had receded and after fresh water had flowed over the streambed. He found also that high salinity of intragravel water was frequently associated with low dissolved oxygen concentration.

The effect of salinity on pink and chum salmon fry production is still poorly understood, although highly productive spawning areas exist in intertidal zones of streams (Kirkwood, 1962). Eggs and larvae of both species can tolerate intermittent high salinity, but tolerance levels have not yet been defined. Also, the retention of salt water by spawning beds and the influence of salt water on temperature, oxygen levels, and water velocity have not been studied in detail. The ultimate need is to determine the relative potential of intertidal and upstream areas to produce fry.

PERMEABILITY OF BOTTOM MATERIALS

It has already been pointed out that the oxygen delivery rate to an egg or larva is a function of both the oxygen content and velocity of intragravel water. Apparent velocity of water flowing within the streambed can be described by the equation.

$$v=\eta i \qquad (2)$$

Where v=apparent velocity,
η=permeability coefficient, and
i=hydraulic gradient.

According to this equation, apparent velocity of intragravel water varies directly with the permeability of materials through which it passes. Other factors being equal, the permeability of bottom materials in spawning beds should be directly related to their potential to produce salmon fry; Wickett (1958) gave evidence that the average survival of pink and chum salmon eggs and larvae in four British Columbia streams was directly related to the permeability of bottom materials (fig. 3).

The permeability of bottom materials is a function of particle compaction, arrangement, and size. McNeil and Ahnell (1964) showed that the permeability of bottom materials in a pink salmon spawning bed is inversely related to the fraction of fine particles composing the total volume of the bed. Thus, the resistance to flow caused by the presence of fine particles in salmon spawning beds must govern, to a large extent, their potential to produce healthy fry.

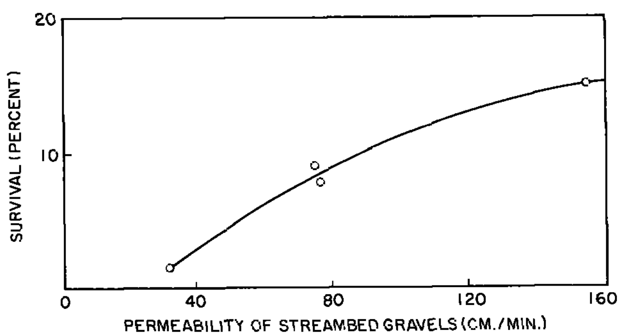

FIGURE 3.—Observed relation reported by Wickett (1958) between permeability and survival of pink and chum salmon to migrant fry.

STABILITY OF SPAWNING BEDS

Dislodgment of salmonid eggs and larvae from spawning beds during high water has been described by a number of workers (Hobbs, 1937; Hutchinson and Shuman, 1942; Davidson and Hutchinson, 1943; Withler, 1952; Needham and Jones, 1959; Wickett, 1959). Estimates of mortality rates from gravel movement have not been made in most instances. Furthermore, little is known about the interactions of factors creating unstable conditions in spawning beds and causing mortality rates to increase.

Changes in surface profile occur where a streambed degrades or aggrades. It is possible, however, for bed movement to occur without an associated change in surface profile or gradient (Mackin, 1948). One important unsolved problem is to determine if bed movement can cause appreciable mortality where there is no associated change in streambed gradient.

The effect of the pool-riffle complex on the capacity of streams to produce pink and chum salmon is not yet well understood. Factors important in generating the pool-riffle complex include debris in the high-flow channel (Bishop and Shapley, 1963) and bends in the channel. Shifts in position of debris create unstable conditions in the spawning bed which could lead to dislodgment of salmon eggs and larvae.

METHODS

STUDY STREAMS

Field studies described in this report were conducted mostly in three streams located in the Kasaan Bay region of Prince of Wales Island, Southeastern Alaska: Harris River, Indian Creek, and Twelvemile Creek (fig. 4). Watersheds of the study streams are precipitous. Soils are shallow and underlaid with impermeable materials. Except for muskegs, which are poorly drained areas, the watersheds have a very low capacity to retain water. Runoff is rapid, and peak discharges occur within a few hours after the beginning of heavy rainfall. These high discharges occur mostly in autumn.

The study streams occasionally freeze over in winter, when water temperatures near 0° C. have been recorded for as long as 6 consecutive days; summer water temperatures rarely exceed 13° C. (James, 1956).

Adult pink and chum salmon usually enter the study streams to spawn between mid-August and late September. Spawning occurs mostly in September. A large percentage of pink salmon spawn in intertidal areas, where the density of spawners is highest in most years.

Harris River is the largest of the three study streams. Salmon have access to about an 8-mile section of the main stream and its North Fork. Chum salmon were observed to spawn mostly in the North Fork, but pink salmon exhibited a marked preference for a ½-mile section of the upper intertidal zone. Discharge during the spawning period commonly fluctuates between 22 and 1,800 cubic feet per second (c.f.s.). During autumn storms, average daily discharge may approach 5,000 c.f.s. Width of intertidal spawning riffles during low flow averages about 60 feet. Spawning beds consist of materials mostly less than 4 inches in diameter.

Indian Creek is the smallest of the study streams but exhibits pronounced fluctuations in discharge. During the spawning period, discharge commonly varies between 4 and 300 c.f.s. Average daily discharge during autumn storms approaches 900 c.f.s. some years, and a peak instantaneous discharge of 6,400 c.f.s. was recorded on one occasion (McNeil, Shapley, and Bevan, 1962). Pink salmon spawn in Indian Creek, primarily in an intertidal section one-fourth mile long beginning at the confluence with Harris River. The average width of Indian Creek spawning beds at low flow is about 25 feet. Spawning beds consist of materials mostly less than 6 inches in diameter.

Twelvemile Creek has a more stable discharge than either Harris River or Indian Creek. During spawning, average daily discharge usually varies between 12 and 300 c.f.s. During autumn storms, average daily discharge rarely exceeds 600 c.f.s. Intertidal spawning areas average about 45 feet wide during low flow, and spawning beds consist mostly of materials less than 4 inches in diameter, and contain a high percentage of sand and silt. About 5 miles are believed accessible to salmon, but the distance has not been measured. Heaviest densities of spawning pink salmon have been observed in the intertidal zone. Chum salmon, less abundant here than pink salmon, commonly spawn in the intertidal zone, too.

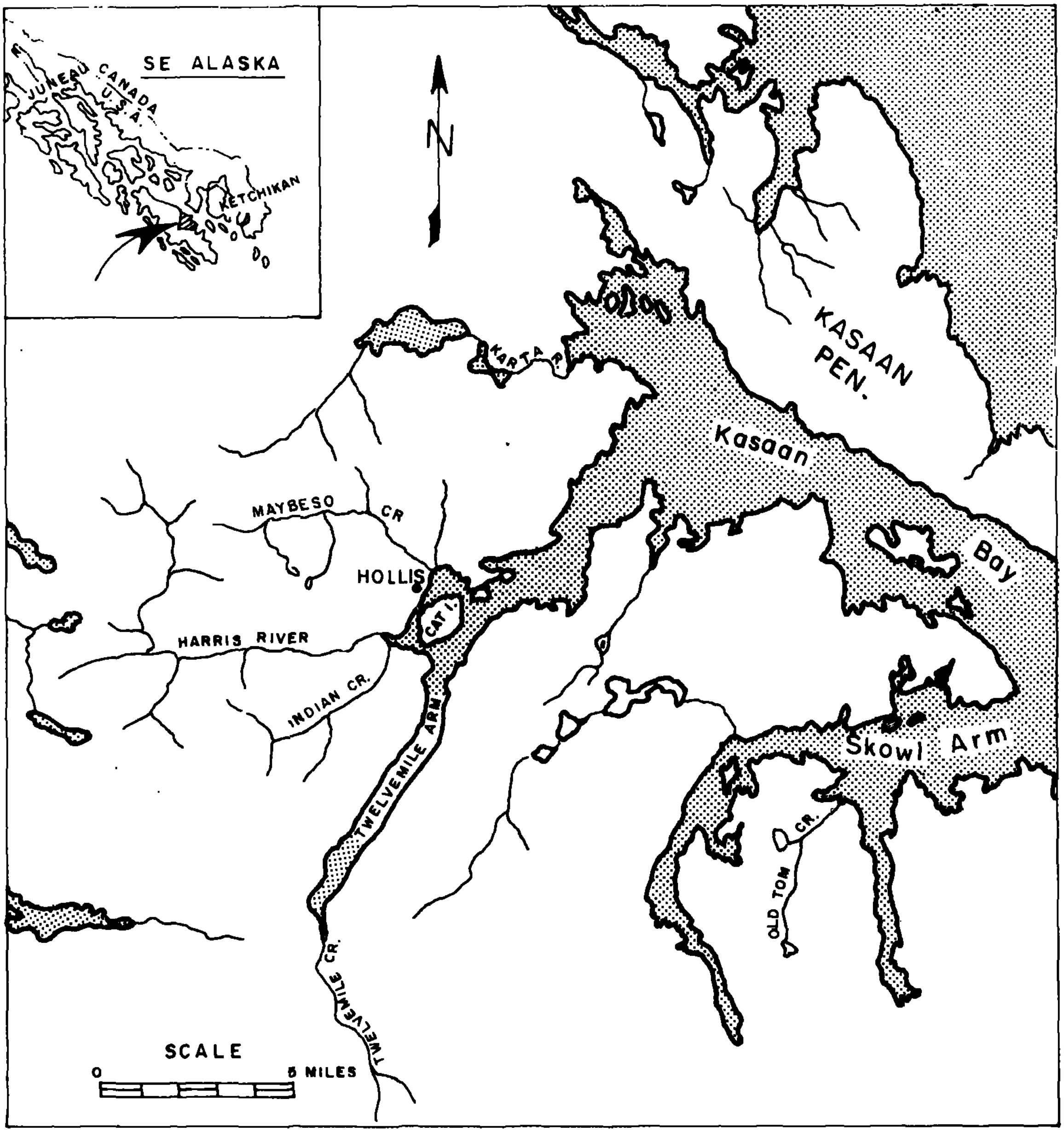

FIGURE 4.—Locations of study streams (Harris River and Indian and Twelvemile Creeks) in the Kasaan Bay region of Prince of Wales Island, Southeastern Alaska.

Field studies began in 1956 when FRI personnel selected six spawning riffles ranging in area from 260 to 650 m.[2] for sampling. Spawning riffles were sampled in 1956, 1957, and 1958 to measure mortality of eggs and larvae and the quality of intragravel water (table 1).

The study areas were enlarged in 1958, when FRI personnel selected five spawning areas ranging in size from 3,400 to 13,400 m.[2] The areas included major spawning grounds of pink and chum salmon in Harris River and Indian and Twelvemile Creeks and incorporated the six spawning riffles previously sampled. The sampling areas were selected to represent both intertidal and upstream areas of the study streams (table 1). Factors measured included density

TABLE 1.—*Size and location of six spawning riffles sampled in 1956, 1957, and 1958 and five spawning areas sampled in 1958, 1959, and 1960*

Study area and years sampled	Tide level	Area
1956, 1957, 1958	*Meters*	*Meters*
Riffle A, Harris River	3.4	305
Riffle B, Indian Creek	4.0	386
Riffle C, Indian Creek	5.2	260
Riffle D, Twelvemile Creek	3.7	648
Riffle E, Twelvemile Creek	4.3	372
Riffle F, Twelvemile Creek	4.9	486
1958, 1959, 1960		
Intertidal Harris River	3.7–4.3	7,800
Upstream Harris River	----	13,400
Intertidal Indian Creek	3.4–5.2	3,400
Intertidal Twelvemile Creek	3.7–4.9	5,580
Upstream Twelvemile Creek	----	6,130

and distribution of spawners, mortality of eggs and larvae, quality of spawning beds, and quality of intragravel water.

To insure random sampling, FRI personnel drew maps of areas sampled to scale on cross-sectional paper having 100 squares per square inch. The scale selected made each square representative of not more than a 0.4 $m.^2$ area in the stream. Co-ordinate axes were established for each map, and sampling points were selected by the following procedure. A pair of random numbers was obtained from a random number table—one number for the abscissa and the other number for the ordinate. Distance of the selected square from a reference point and an angle of the selected square from a reference line were measured on the map and recorded for use in the field. When a sample was to be taken, the angle and distance of the sample area were measured from the base line and reference point.

MEASUREMENT OF ENVIRONMENTAL FACTORS

The Northern Forest Experiment Station, U.S. Forest Service, operated a weather station at Hollis, a logging community located within 3 miles of Harris River and Indian Creek spawning areas and within 12 miles of Twelvemile Creek spawning areas (see fig. 4). Forest Service personnel obtained continuous records of air temperature and precipitation during the study. Instruments installed and operated by the Northern Forest Experiment Station recorded water level and temperature of each study stream. Forest Service personnel also established discharge rating curves for each stream. James (1956) gives further information on hydrological studies made by the Forest Service.

Physical quality of the spawning bed was evaluated in each area where observations were made on egg and larval mortality. Environmental attributes measured included the dissolved oxygen content of intragravel water and the size composition and permeability of bottom materials. McNeil (1962b) described the techniques used to measure dissolved oxygen levels and McNeil and Ahnell (1964) described the methods of measuring size composition and indexing permeability of bottom materials.

ESTIMATION OF SPAWNING DENSITY AND POTENTIAL EGG DEPOSITION

Fisheries Research Institute (FRI) personnel estimated the number of female pink and chum salmon occupying study areas by means of daily foot survey censuses when water conditions permitted. Institute personnel also observed tagged females daily to estimate average life on the spawning ground (redd life). Females were tagged before they entered the spawning ground and FRI workers calculated the total number spawning by summing daily abundance and dividing by average redd life; i.e.,

$$\text{Number spawning} = \frac{\sum \text{daily abundance in female days}}{\text{average redd life in days}}$$

A summation of daily abundance was obtained by constructing an eye-fitted curve of the daily counts of females and determining the area under the curve in female days. In the determination of average redd life, daily observations on tagged females have been adjusted to account for the periodicity of observations. Assuming that each tagged female occupied the spawning bed one-half day before being observed the first time and one-half day beyond the date of the last observation, I added 1 day to the duration each tagged female was observed.

Two observers made most of the survey censuses; periodic comparisons of their counts showed consistently good agreement. Although it was not feasible to determine bias in estimates, a recent unpublished study conducted by the author at Sashin Creek revealed good agreement between the number of spawning female pink salmon estimated by this method and the number counted into the stream.

COLLECTION OF EGGS AND LARVAE

Eggs and larvae were collected with a hydraulic sampler (McNeil, 1962a) from small enclosed quadrat or circular areas (sampling units) of known area. Area of sampling units varied from 0.2 to 0.9 m.^{2}

Samples preserved in the field were examined later to determine the number of live and dead eggs and alevins collected. Eggs were preserved in a clearing solution (Stockard's solution).

ESTIMATION OF MORTALITY

Data on egg and larval populations were analyzed by three methods to obtain information on temporal changes and spatial differences in mortality levels. Although the methods have been described (McNeil, 1962a), they will be reviewed briefly here.

Ratio of Dead to Total Eggs and Larvae

Mortality has commonly been estimated from ratios of dead to total eggs and larvae collected in k samples; i.e.,[5]

$$\hat{M}_r = \frac{\sum_{1}^{k} \frac{\text{dead}}{\text{live}+\text{dead}}}{k} \tag{3}$$

An estimate of mortality based on such ratios underestimates true total mortality where the number of eggs and larvae present in the spawning bed at the time of sampling is less than the number of eggs originally available for deposition. Despite this limitation, estimates of M_r are very helpful in establishing time of mortality where mortality is caused by factors not associated with the direct removal of eggs and larvae from the spawning bed and are sometimes useful in setting lower limits to total mortality.

Actual and Potential Abundance

Total mortality (M_t) can be estimated from statistics on potential egg deposition and abundance of live eggs and larvae at the time of sampling. In this study, estimates of M_t were calculated from the double inequality

$$1-\frac{\bar{a}}{E'} \leq \hat{M}_t \leq 1-\frac{\underline{a}}{E'} \tag{4}$$

[5] The value $\hat{M}_r$ estimates the population parameter M_r. The circumflex sign also will be used to identify estimators of other population parameters.

In double inequality (4), the value $\bar{a}$ and $\underline{a}$ are the upper and lower confidence limits respectively of the estimated number of live eggs and larvae per m.^{2} of spawning bed, and E′ is the expected number per m.^{2} Values for $\bar{a}$ and $\underline{a}$ were calculated with the standard error of the mean obtained from either arithmetic or log-transformed counts of live eggs and larvae. Log-transformed counts are used only if the efficiency of the estimate of M_t is increased without introducing significant bias.

Where the logarithmic transformation is used, each observed count is transformed by the equation

$$b_i = \log_{10} (n_i + \beta) \tag{5}$$

In equation (5), b_i is the transformed variate and n_i is the number of live eggs and larvae collected at the i^{th} point. The term β is a constant which describes the degree of contagion in a negative binomial distribution. A value of β is calculated from the expected frequency of zero observations in a negative binomial distribution. The method, described by Anscombe (1949) and Bliss (1953), requires an iterative solution of the equation

$$\frac{1}{\beta} \log_{10} (1+\beta\bar{n}) = \log_{10} \left(\frac{k}{k'}\right), \tag{6}$$

where k is the total number of observations, k' is the number of zero observations, and $\bar{n}$ is the sample arithmetic mean.

To set confidence limits to estimates of abundance of eggs and larvae with log-transformed data, the mean log values must be corrected so that the arithmetic mean will result from the antilog. A correction term is required because the mean of log-transformed data is geometric rather than arithmetic (Ricker, 1958, ch. 11). Jones (1956) developed the correction term and described the method used here to calculate confidence limits with log-transformed counts. The equation used to obtain an arithmetic mean ($\bar{n}$) from the log-transformed counts is

$$\bar{n} = \text{antilog} (\bar{b} + 1.1518 s_{\bar{b}}^2) - \beta, \tag{7}$$

where $\bar{b}$ is the logarithmic mean value and $s_{\bar{b}}^2$ is the sample variance of the log-transformed counts. The term β is subtracted to correct for its addition to the counts before making the transformation in equation (5).

Provided the estimates $\bar{a}$, $\underline{a}$, and E' are unbiased, double inequality (4) gives an unbiased estimate of the total mortality fraction from the time of spawning to the time of sampling. Absence from the spawning bed of dead eggs and larvae does not introduce bias to estimates of M_t as it does to estimates of M_r based on ratios of dead to total eggs and larvae present.

Potential egg deposition (E) is calculated by multiplying the estimated number of female salmon spawning within each area by average fecundity. The value E' is obtained by multiplying E by a factor correcting for the fraction of eggs and larvae present within the streambed actually collected. In the present study, the relationship

$$E'=\frac{9}{10}E \tag{8}$$

is used. Methods used to obtain the correction term, $\frac{9}{10}$ are described elsewhere (McNeil 1962a).

More recent studies provide evidence that estimates of M_t obtained with a hydraulic sampler are fairly representative of the true total mortality fraction. I used a hydraulic sampler to estimate total mortality of 1961 and 1963 brood year preemergent pink and chum salmon fry in Sashin Creek, where total fresh-water mortality also was calculated from weir counts of adults entering and fry leaving the stream. In Sashin Creek, it was assumed that $E'=\frac{93}{100}E$ for purposes of setting confidence limits to M_t. Based on samples of preemergent fry obtained with a hydraulic sampler, confidence limits of M_t bracketed the total mortality fraction calculated for each species and brood year from weir counts. In each instance, mean estimated mortality from sampling preemergent fry and from counting migrant fry differed by less than 2 percent. The results are summarized in table 2. In Sashin Creek, potential egg deposition was determined by counting adults entering the stream. In Harris River and Indian and Twelvemile Creeks, the methods of estimating potential egg deposition were not as precise, and it is doubtful if estimates of M_t were completely unbiased.

TABLE 2.—*Total mortality of Sashin Creek pink and chum salmon estimated by sampling preemergent fry with hydraulic sampler and by counting migrating fry at weir*

Species and brood year [1]	Mortality estimated by sampling preemergent fry		Mortality estimated by counting migrating fry
	Mean	90-percent confidence limits of the mean	
Pink salmon			
1961	0.777	±0.041	0.790
1963	.800	±.052	.804
Chum salmon			
1961	.928	±.056	.917
1963	.997	±.040	.995

[1] Mortality of the 1962 brood year was not estimated by sampling preemergent fry because populations were very small. Only 4 pink and 42 chum salmon females entered Sashin Creek to spawn in 1962.

Presence or Absence of Eggs and Larvae

Estimates of the population parameters M_r and M_t sometimes fail to differ significantly when other evidence suggests high mortality. A chi-square test helped demonstrate significant mortality in certain of these cases and often proved to be a more sensitive test for detecting time of mortality than the mortality estimates M_t and M_r.

The chi-square test is based on the premise that the proportion of points within a spawning bed occupied by live eggs and larvae varies with total mortality. If no change in mortality occurs, the following conditions will be satisfied: (1) There will be no decrease in the expected fraction of points populated by eggs or larvae (live plus dead); (2) there will be no decrease in the expected fraction of points populated by live eggs and larvae; and (3) there will be no increase in the expected fraction of points populated by dead eggs or larvae.

In this study, each point sampled was classified according to the number of eggs and larvae present, with points containing less than 35 eggs and larvae per m.^{2} (k_0) being classified together. The classes used were (1) less than 35 live plus dead eggs and larvae per m.^{2}, (2) less than 35 live eggs and larvae per m.^{2}, and (3) less than 35 dead eggs and larvae per m.^{2}.

Principal purpose of the classification scheme was to classify jointly all points containing few eggs and larvae and those containing none. The selection of less than 35 per m.^{2} for joint classification was arbitrary, however.

I tested each class independently with chi-square (see Snedecor, 1956), and set confidence limits to the number of points estimated to contain fewer than 35 eggs and larvae per m.^{2} from the normal approximation of the binomial distribution.

The 90-percent confidence limits of k_0 ($\underline{k}_0$ and $\overline{k}_0$) are obtained from the expression

$$(\overline{k}_0, \underline{k}_0) = k\hat{p}_0 \pm 1.645[k\hat{p}_0 (1-\hat{p}_0)]^{1/2} \quad (9)$$

where k is the number of points sampled and $\hat{p}$ is the fraction of points estimated to contain fewer than 35 eggs and larvae per m.²

OBSERVATIONS ON ENVIRONMENT AND MORTALITY

Although numerous workers have postulated factors causing mortality of eggs and larvae, few have presented quantitative estimates of mortality satisfying three essential criteria: (1) Estimates free of bias, (2) estimates representative of natural populations, and (3) estimates related directly to causative factors. It is not surprising that these criteria have not been met entirely in field studies, for there are many difficult problems requiring solution. In the present study, an effort was made to reduce (or at least recognize) bias in mortality estimates. Furthermore, because of the randomization techniques used, the samples were thought to be representative of the populations studied. However, the difficulties in associating observed mortality levels with their causative factors are formidable even with the first two criteria being satisfied in part. The problem of relating observed mortality levels to causative factors is complicated in most instances because of interactions among environmental factors.

I attempted to account for interactions by classifying environmental factors causing mortality into generally inclusive groupings: (1) Oxygen supply and related factors, (2) stability of the spawning bed, and (3) freezing of intragravel water. I did not consider one inclusive grouping—pathogenic agents.

OXYGEN SUPPLY AND MORTALITY

Environmental requirements of salmon eggs and larvae were briefly reviewed in an earlier section. My purpose here will be (1) to describe the physical characteristics of spawning beds where observations on mortality were made, and (2) to describe the relation between environmental quality (as related to oxygen supply) and the observed mortality levels.

Dissolved Oxygen Content of Intragravel Water

The dissolved oxygen content of intragravel water was consistently lower at the beginning than at the end of the spawning period in all study streams. There also were observed spatial differences in mean dissolved oxygen levels among and within the study streams.

In late August, at the beginning of spawning, oxygen levels appeared to be lowest in the intertidal Harris River and the upstream Twelvemile Creek spawning areas and highest in the upstream Harris River and the intertidal Indian Creek and Twelvemile Creek spawning areas. Near the end of spawning, in late September, differences in mean oxygen levels were no longer significant among the spawning areas sampled. The data are summarized in table 3, and mean values obtained in 1959 are shown in figure 5 to illustrate the kind of relation observed.

Differences among years in mean dissolved oxygen levels were considerably greater than differences among streams. Summer 1957 was of particular interest in this regard because unusually low levels of dissolved oxygen were observed. Average values of all dissolved oxygen determinations made in the study streams near the beginning of spawning over the period 1956

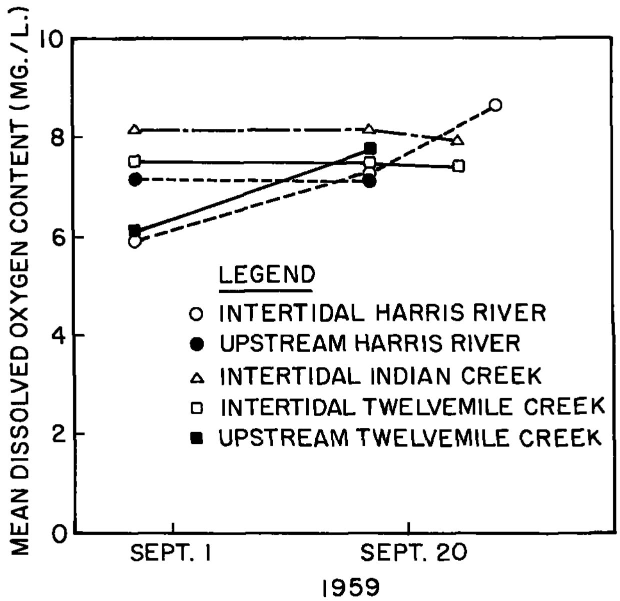

FIGURE 5.—Mean dissolved oxygen content of intragravel water in the study streams over the period of spawning in 1959.

TABLE 3.—*Ninety-five-percent confidence interval estimates of mean dissolved oxygen content of intragravel water in study streams*

[Water samples were collected 7 to 10 inches beneath the streambed surface. All values are given as mg./l.]

Date	Harris River		Indian Creek Intertidal	Twelvemile Creek	
	Intertidal	Upstream		Intertidal	Upstream
1958					
Sept. 1	-----	-----	-----	$6.3<\mu<7.4$	$4.8<\mu<6.1$
Nov. 30	-----	-----	-----	$8.3<\mu<9.5$	$8.0<\mu<9.6$
1959					
Aug. 28	$5.1<\mu<7.0$	$6.4<\mu<8.1$	$7.5<\mu<8.9$	$6.8<\mu<8.3$	$5.3<\mu<6.9$
Sept. 17	$5.6<\mu<9.1$	$6.0<\mu<8.4$	$7.1<\mu<9.3$	$6.5<\mu<8.5$	$6.7<\mu<8.4$
Sept. 24	-----	-----	$7.4<\mu<8.4$	-----	-----
Sept. 27	$8.1<\mu<9.3$	-----	-----	-----	-----
1960					
Aug. 24	-----	-----	-----	$6.8<\mu<8.0$	$5.6<\mu<6.7$
Aug. 25	$5.4<\mu<6.6$	$5.8<\mu<7.0$	$6.3<\mu<7.8$	-----	-----
Sept. 14	$7.1<\mu<9.0$	-----	$7.6<\mu<8.9$	$7.5<\mu<9.0$	$5.4<\mu<7.2$

through 1960 are shown in figure 6. Oxygen levels were severely depressed in 1957, and high mortality of 1957 brood year eggs occurred. The relation between mortality and oxygen levels will be discussed later.

COMPOSITION OF BOTTOM MATERIALS

There were marked differences in size composition of bottom materials among the study streams. The bed of Indian Creek contained greater quantities of coarse materials and smaller quantities of fine materials than the beds of either Harris River or Twelvemile Creek. The bed of Twelvemile Creek contained considerably more silt than the beds of Indian Creek or Harris River. Table 4 lists the average size composition (by volume) of bottom materials in each of the study streams.

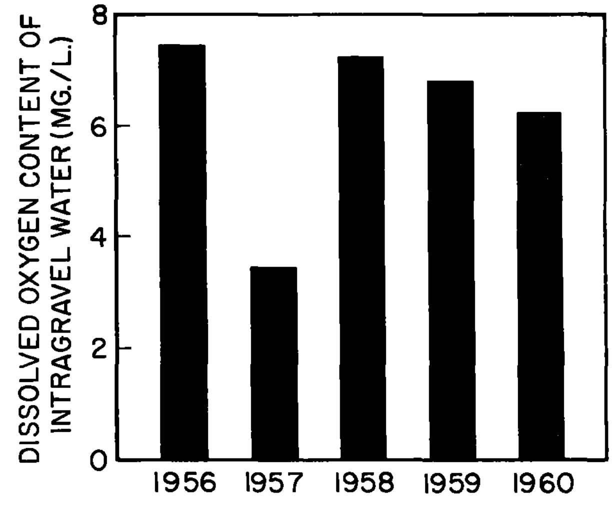

FIGURE 6.—Approximate mean dissolved oxygen content of intragravel water in the three study streams (Harris River, Indian Creek, and Twelvemile Creek) near the beginning of the spawning period (1956–60).

The volume of fine materials in salmon spawning beds is inversely related to the permeability of bottom materials (McNeil and Ahnell, 1964). Figure 7 shows the observed relation between the percentage of bottom materials by volume passing through an 0.833-mm. sieve and the coefficient of permeability.

The observed mean percentages of solids passing through an 0.833-mm. sieve are listed below for the study streams in order of decreasing permeability:

	Percent
1. Intertidal Indian Creek	9
2. Upstream Harris River	14
3. Intertidal Harris River	17
4. Intertidal Twelvemile Creek	18
5. Upstream Twelvemile Creek	19

McNeil and Ahnell (1964) found that the finest fractions contained the highest percentages of organic detritus. It will be assumed, therefore,

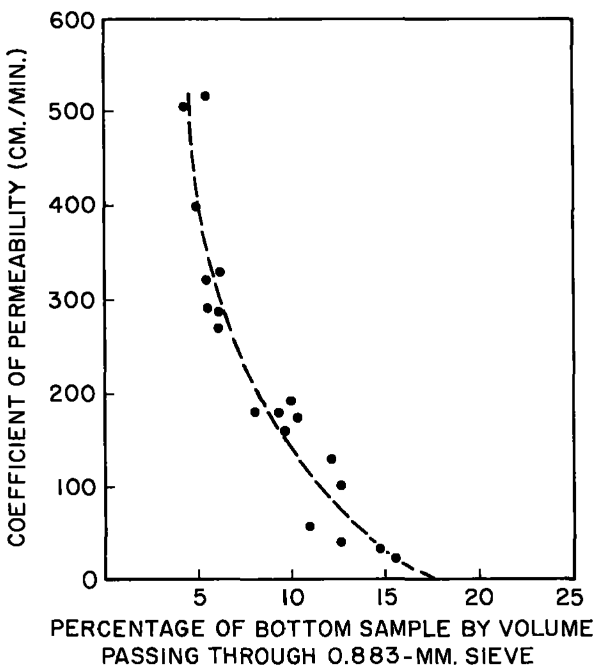

FIGURE 7.—Relation observed between coefficient of permeability and the fraction by volume of a bottom sample passing through an 0.833-mm. sieve (from McNeil and Ahnell, 1964). Curve fitted by eye.

TABLE 4.—*Average size composition of bottom materials in the study streams* [1]

[All rocks larger than 105 mm. diameter have been excluded]

Spawning area	Mean percent of total volume of solids retained by sieves with opening (in mm.) of— [2]									Percent of total volume of solids settling from suspension
	26.26	13.33	6.88	3.33	1.65	0.833	0.417	0.208	0.104	
Harris River (intertidal)	25.1	14.6	13.2	11.0	7.9	11.5	10.5	2.7	0.4	3.1
Harris River (upstream)	24.0	16.2	14.1	11.8	8.4	11.8	9.2	2.4	.4	1.9
Indian Creek (intertidal)	35.2	15.3	12.9	11.3	7.3	8.6	4.9	1.3	.4	2.7
Twelvemile Creek (intertidal)	21.2	15.1	13.9	12.5	8.8	10.7	8.4	2.5	.9	5.9
Twelvemile Creek (upstream)	19.7	13.9	13.0	12.9	9.6	11.6	9.5	3.6	1.2	5.0

[1] For a description of methods of collecting and classifying samples, the reader is referred to McNeil and Ahnell (1964).
[2] Data are taken from table 2 of McNeil and Ahnell (1964).

that the percentage of fine materials obtained from the settling funnel used in the analysis of bottom samples (McNeil and Ahnell, 1964) provides an index of the relative amounts of extraneous organic matter in spawning beds. Percentages of fine materials passing through a 0.104-mm. sieve, observed in the total volume of bottom materials collected from the areas sampled, are listed below in order of increasing values:

	Percent
1. Upstream Harris River	1.9
2. Intertidal Indian Creek	2.7
3. Intertidal Harris River	3.1
4. Upstream Twelvemile Creek	5.0
5. Intertidal Twelvemile Creek	5.9

The rate of interchange between stream and intragravel water is believed to be related to gradient and roughness of the stream bottom. Steep-gradient areas have a greater potential for changes in curvature of the stream bottom than shallow-gradient areas, and coarse materials give greater roughness to the stream bottom than fine materials. To index relative roughness, the study areas are listed below in order of decreasing amounts of solids retained by the largest sieve used in this study (26.26-mm.).

	Percent
1. Intertidal Indian Creek	35
2. Intertidal Harris River	25
3. Upstream Harris River	24
4. Intertidal Twelvemile Creek	21
5. Upstream Twelvemile Creek	20

In addition to having the largest fraction of coarse gravel, Indian Creek also had the steepest gradient (0.7 percent as opposed to 0.2 to 0.4 percent for the other areas). The evidence suggests that the interchange potential of Indian Creek is greater than Harris River or Twelvemile Creek.

Spawning Density

According to the evidence just presented, environmental conditions related to oxygen supply and survival of eggs and larvae would appear to be most favorable in intertidal Indian Creek and least favorable in upstream Twelvemile Creek. The remaining three areas did not appear to vary significantly with regard to the environmental factors evaluated. Observed distributions of spawning female pink and chum salmon appeared to be related to the physical characteristics of the spawning beds studied.

For the years 1958, 1959, and 1960 intertidal Indian Creek had the highest average density of spawners, and upstream Harris River and Twelvemile Creek had the lowest. In order of decreasing average density, the density of spawning females in the sampling areas were estimated to be:

1. Intertidal Indian Creek — mean=35 females per 100 m.^{2} (range 13 to 46 females per 100 m.^{2})
2. Intertidal Harris River — mean=29 females per 100 m.^{2} (range 13 to 48 females per 100 m.^{2})
3. Intertidal Twelvemile Creek — mean=17 females per 100 m.^{2} (range 11 to 25 females per 100 m.^{2})
4. Upstream Harris River — mean=4 females per 100 m.^{2} (range 2 to 6 females per 100 m.^{2})
5. Upstream Twelvemile Creek — mean=4 females per 100 m.^{2} (range 1 to 10 females per 100 m.^{2})

Time and Magnitude of Mortality

The amount of dissolved oxygen required by salmon eggs and larvae for normal metabolism approaches a maximum just before hatching (see fig. 2). After hatching, levels of dissolved oxygen limiting metabolism are greatly reduced, and oxygen requirements are least likely to be satisfied before hatching.

Pink and chum salmon eggs begin to hatch in the study streams in November, and most hatch before mid-December. Figure 8 shows the percentages of live eggs and larvae collected from intertidal Harris River and Indian Creek that had hatched before the date of sampling. Twelvemile Creek is thought to lag 1 or 2 weeks behind Harris River and Indian Creek with regard to time of hatching, because the peak of spawning occurs about 1 week later.

After the spawning period, it is convenient to consider two periods during which mortality occurs—prehatching (autumn) and posthatching (winter). The dissolved oxygen supply and related factors are thought to exert their greatest influence on mortality before hatching, so the discussions here will be limited primarily to mortality of eggs.

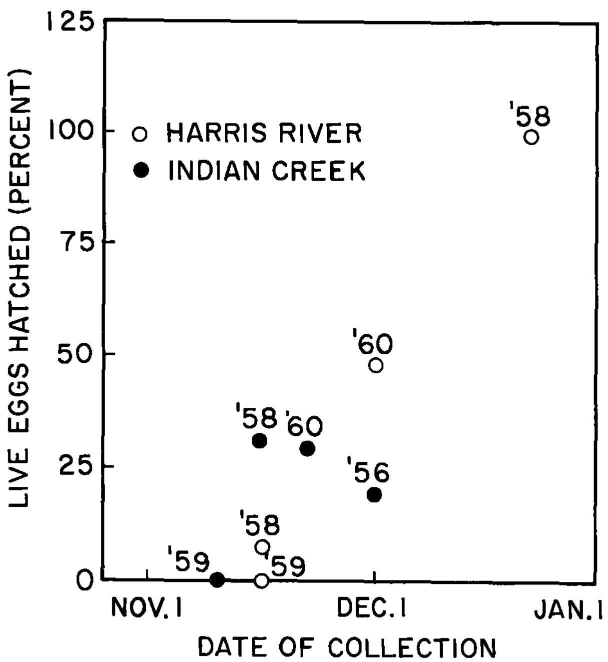

FIGURE 8.—Percentage of live eggs and larvae in collections from intertidal Harris River and Indian Creek hatching before the date of sampling. (Brood years are indicated by numerals.)

In this study, estimates of three population parameters thought to provide evidence of the effect of oxygen supply and related factors on egg mortality were used: (1) Total mortality fraction (M_t), (2) mortality fraction from ratios of dead eggs in samples (M_r), and (3) fraction of points containing fewer than 35 dead eggs per m.^{2} (p_0).

An estimate of M_t includes mortality from all causes, and this estimate includes eggs removed from the spawning bed. Such removal can obscure mortality from causes where there is no direct removal of eggs; therefore, the estimated total mortality ($\hat{M}_t$) was often of limited value in measuring egg mortality from oxygen supply and related factors. Furthermore, estimates of M_t were highly inefficient, and the resulting confidence limits were often broad.

The other two estimates ($\hat{M}_r$ and $\hat{p}_0$) also had limitations imposed by the disappearance of eggs from the spawning bed. Disappearance from gravel shift alone would have little effect on validity of estimates of ratios of dead to total eggs present in the streambed ($\hat{M}_r$), provided live and dead eggs disappear in numbers proportional to their abundance. On the other hand, losses from decomposition and scavenging affect only dead and dying eggs and would cause mortality to be underestimated by $\hat{M}_r$.

Use of the number of points where eggs were present or absent to index occurrence of mortality also would be affected by disappearance because evidence of mortality from factors not related to the direct removal of dead eggs would have been destroyed. Major losses due to gravel shift would tend to invalidate the use of $\hat{p}_0$ to detect significant mortality possibly caused by oxygen supply and related factors.

With these possible limitations in mind, the estimates of M_t, M_r, and p_0 are used to evaluate prehatching mortality of the 1956–60 brood years in the three study streams. Each brood year will be considered separately.

1956 Brood Year

Sampling was confined to spawning riffles A (Harris River), B and C (Indian Creek), and D and E (Twelvemile Creek). Workers sampled the riffles in late November 1956 and in late February

TABLE 5.—*Estimated mortality of 1956 brood year pink and chum salmon eggs and larvae based on ratios of dead to total specimens collected*

Stream [1]	Fraction of dead eggs in late November ($\hat{M}_r$)		Fraction of dead eggs and larvae in late February ($\hat{M}_r$)		Estimated fractions of eggs and larvae dying—		
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Early	Shortly before hatching	After hatching
Harris River	0.27	±0.06	0.50	±0.14	0.27	0.14	0.09
Indian Creek	.10	±.04	.75	±.10	.10	.54	.11
Twelvemile Creek	.27	±.06	.41	±.10	.27	.12	.02

[1] All samples were collected from intertidal riffles.

1957. Since spawning density was not estimated in 1956, no estimates of M_t are given. Also, because of small sample size, it is not possible to give meaningful estimates of p_0. Thus, for the 1956 brood year, only estimates of M_r are given to indicate time and magnitude of mortality (table 5).

In autumn 1956, egg mortality appeared to be highest after embryos had eyed. The February sample included three general categories of dead specimens: (1) Embryos dying early (as evidenced by the opacity and advanced decomposition of the eggs), (2) embryos dying just before hatching (as evidenced by development of body structures), and (3) larvae dying after hatching. Table 5 gives estimates of the fractions of total deaths occurring early, shortly before hatching, and after hatching.

Two features of these data stand out. First, early egg mortality was lowest in intertidal Indian Creek ($\hat{M}_r=0.10$ versus $\hat{M}_r=0.27$ in intertidal Harris River and Twelvemile Creek). Second, this relation had reversed by late February. Other evidence, which will be considered later, strongly suggests that freezing was the major cause of mortality of the 1956 brood shortly before and after hatching.

With regard to early egg mortality possibly associated with oxygen supply and related factors, evidence from 1956 brood year embryos does not contradict the possibility that intertidal Indian Creek provides a more suitable environment than either intertidal Harris River or Twelvemile Creek.

1957 Brood Year

Estimated mortality of the 1957 brood year provided the most striking evidence obtained in the course of these studies on relation between oxygen supply and egg mortality. As shown in figure 6, mean dissolved oxygen levels during the spawning period in 1957 were less than 50 percent of other years. These low levels of dissolved oxygen occurred during a prolonged period of low precipitation and discharge. For example, between August 10 and September 25, discharge of Indian Creek exceeded 20 c.f.s. only 30 percent of the time. Also, over this period very low discharge (4 to 10 c.f.s.) prevailed for 2 weeks during and after spawning. Furthermore, clear skies prevailing over the latter half of September were thought to have contributed to an unusually prolific growth of periphyton observed on the surface of streambeds at the time.

The escapement of adults was the lowest observed during these studies. The density of adult female pink and chum salmon spawning in intertidal areas of the study streams was five or less per 100 m.². The period of spawning lasted only from about September 7–17, the briefest period observed.

There was good evidence that egg mortality was high after spawning in 1957. Eggs were collected from riffles B and C in intertidal Indian Creek and riffles E and F in intertidal Twelvemile Creek during early November 1957 and late March 1958 and from intertidal Harris River in early April 1958.

Because differences in estimated values of M_r were not significant among the study riffles sampled, samples collected from intertidal Indian and Twelvemile Creeks were pooled by date to give the following single estimates of M_r and their 90-percent confidence limits:

November $\hat{M}_r=0.69\pm0.19$

March $\hat{M}_r=0.57\pm0.24$

Difference between the two estimates is not significant. The data indicate that mortality was high before hatching and low after hatching.

Most dead eggs collected in November already had decayed considerably and were classified as fragments, suggesting that mortality occurred shortly after spawning. This finding would not be unexpected because dissolved oxygen levels were unusually low during spawning. Furthermore, there was evidence of high biochemical oxygen demand continuing well into autumn 1957. Although oxygen levels had increased significantly between August and November 1957, they were still lower in November 1957 than in August 1958, even though water temperatures were about 6° C. cooler in November 1957 than in August 1958 (McNeil, 1962b).

The high percentage of fragments among dead specimens collected from intertidal Indian and Twelvemile Creeks in November 1957 remained virtually unchanged through March 1958. The values were:

INDIAN CREEK

Riffle B: 92 percent in November and 96 percent in March.

Riffle C: 70 percent in November and 70 percent in March.

TWELVEMILE CREEK

Riffle E: 66 percent in November and 76 percent in March.

Riffle F: 97 percent in November and 95 percent in March.

This was nearly conclusive evidence that estimates of M_r obtained from egg fragments alone would be little changed over late autumn and winter, and estimates of M_r based on presence of egg fragments and made in early spring 1958 would give essentially the same result as estimates made the previous autumn.

Intertidal Harris River was sampled about April 1, 1958, when egg fragments or live larvae were collected at 34 points. Only egg fragments were found at 31 of the 34 points, giving minimal estimates of

$$M_t \geq M_r = 31/34 = 0.91$$

The available evidence suggested that conditions in 1957 were unfavorable for egg survival, and exceptionally high egg mortality occurred in all study streams. This high mortality was associated with unusually low levels of dissolved oxygen in intragravel water and low density of spawners. Unexpectedly low levels of dissolved oxygen prevailed into November 1957, suggesting that the biochemical oxygen demand was unusually high. There is a possibility that the density of females spawning (five or less per 100 m.^{2}) was too low to remove accumulated organic detritus from spawning beds in quantities sufficient to reduce materially the biochemical oxygen demand (Ricker, 1962; McNeil and Ahnell, 1964).

1958 Brood Year

Adult escapements were moderately low in 1958, though considerably higher than in 1957. Spawning densities ranged from 13 females per 100 m.^{2} in intertidal Harris River and Indian Creek to 1 and 2 females per 100 m.^{2} in upstream Twelvemile Creek and Harris River, respectively. Density of spawning females in intertidal Twelvemile Creek was 11 per 100 m.^{2}

Hydrological conditions during spawning favored a higher egg survival than in 1957. Indian Creek maintained discharges of 10 c.f.s. or more over the spawning period as opposed to a minimum discharge of 4 c.f.s. during spawning in 1957, when high early egg mortality occurred.

Observations on mortality were made in intertidal Harris River, Indian Creek, and Twelvemile Creek. Spawning densities in upstream Harris River and Twelvemile Creek were too light to warrant investigations in these areas. Table 6 summarizes the results of the mortality estimates.

For purposes of the present discussions, intertidal Twelvemile Creek can be dismissed because of extreme high early mortality ($\hat{M}_t = 0.97$ by late November) apparently caused by scouring during floods, which physically removed eggs from the spawning bed.[6] As a consequence, there were insufficient numbers of eggs remaining to relate observations on mortality to observations on factors affecting oxygen supply. Workers resampled the area in December primarily to check the results of the November sampling.

The numbers of eggs collected approached expectation in intertidal Harris River and Indian Creek. Indian Creek was sampled on one

[6] Potential egg deposition in intertidal Twelvemile Creek during September 1958 was estimated to be 175 per m.^{2} By late November, mean density of live plus dead eggs was estimated to be only four per m.^{2}; by late December only one per m.^{2}

TABLE 6.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1958 brood-year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Sept. 18	0.26	[1] ±0.25	0.01	±0.01	1.00	----------
Nov. 15	.51	[1] ±.35	.16	±.23	.96	±0.06
Dec. 20	.84	±.21	.66	±.38	.82	±.12
Intertidal Indian Greek:						
Nov. 15	0	[1] ±.39	.13	±.13	.90	±.07
Intertidal Twelve mile Creek:						
Nov. 30	.97	±.04	----------	----------	1.00	----------
Dec. 28	.99	±.01	----------	----------	1.00	----------

[1] These estimates of M_t were obtained with log-transformed data.

occasion only (mid-November), and comparisons between the two areas will be limited to the mid-November samples.

The expected number of eggs based on potential deposition was 201 per m.^{2} in both intertidal Harris River and Indian Creek. In mid-November the difference between mean estimates of M_r ($\hat{M}_r=0.16$ in intertidal Harris River, and $\hat{M}_r=0.13$ in intertidal Indian Creek) was not statistically significant. Furthermore, a comparison of values of $\hat{p}_0$ in November gave a chi-square value of 0.46 (1 d.f.), indicating no significant difference in the frequency of occurrence of dead eggs in intertidal Harris River and Indian Creek. Hence, for the 1958 brood year, there was no conclusive evidence of higher egg mortality in intertidal Harris River than in intertidal Indian Creek. It is noteworthy, perhaps, that in intertidal Harris River $\hat{M}_r$ increased significantly between mid-November and mid-December. It is not known if a similar increase occurred in intertidal Indian Creek.

1959 Brood Year

Density of spawners was highly variable among and within the study streams in 1959. Estimated densities of females spawning were:

Intertidal Harris River	25 females per 100 m.^{2}
Upstream Harris River	6 females per 100 m.^{2}
Intertidal Indian Creek	46 females per 100 m.^{2}
Intertidal Twelvemile Creek	15 females per 100 m.^{2}
Upstream Twelvemile Creek	1 female per 100 m.^{2}

Because of the very low density of spawning adults, mortality was not studied in upstream Twelvemile Creek, but observations on mortality were made in upstream Harris River. High stream discharge occurred during spawning, providing more favorable conditions for egg survival during spawning than in 1957. Results of studies on mortality of the 1959 brood year are summarized in table 7.

As observed in 1958, mortality in intertidal Twelvemile Creek was very high initially and apparently was associated again with the direct removal of eggs from the spawning bed. Since estimates from upstream Harris River indicated

TABLE 7.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1959 brood year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$ [1]	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Oct. 6	0.27	±0.24	0.08	±0.06	0.97	±0.03
Oct. 20	.35	[2] ±.21	.11	±.09	.89	±.07
Upstream Harris River:						
Nov. 4	.73	±.23	.17	±.33	.99	±.01
Intertidal Indian Creek:						
Oct. 10	.52	±.18	.08	±.07	.96	±.04
Nov. 10	.27	±.29	.02	±.01	.90	±.08
Intertidal Twelve-mile Creek:						
Oct. 27	.95	±.07	----------	----------	1.00	----------

[1] p_0 is the fraction of points containing fewer than 35 dead eggs per square meter.
[2] This estimate of M_t was obtained from log-transformed data.

much the same thing, these areas proved to be of little value in evaluating relations between mortality and oxygen supply.

Differences in mortality level between intertidal Harris River and Indian Creek could not be demonstrated with estimates of M_r and M_t. However, estimates of p_0 made in mid-October showed that samples containing 35 or more dead eggs per m.[2] occurred with almost equal frequency in intertidal Harris River and Indian Creek despite much lower spawning density in intertidal Harris River (about 53 percent of intertidal Indian Creek). This evidence suggested that egg mortality was higher in intertidal Harris River than in intertidal Indian Creek.

1960 Brood Year

Egg mortality was studied in intertidal Twelvemile Creek, Harris River, and Indian Creek (table 8).

High early mortality from causes associated with the direct removal of affected specimens from the spawning bed occurred in intertidal Twelvemile Creek for the third year. In 1960, however, most of this high mortality occurred during spawning ($\hat{M}_t$=0.71 in late September).[7] Since mortality from causes associated with spawning (e.g., redd superimposition) is beyond the scope of this paper, these causes will not be considered further here. By late November there was evidence of increased egg mortality in intertidal Twelvemile Creek, but this mortality was relatively low.

The density of females spawning in intertidal Harris River and Indian Creek was relatively high and nearly equal. Late in September at the conclusion of spawning, estimates of M_r and p_0 were very nearly the same for these two areas. At hatching, however, 35 or more dead eggs per m.[2] were found at 26 percent of the points sampled in intertidal Harris River and at only 10 percent of the points sampled in intertidal Indian Creek. Estimates of $\hat{M}_r$ also indicated that mortality of eggs remaining in the streambed was higher in intertidal Harris River than in intertidal Indian Creek.

[7] This same phenomenon was also observed in 1961 (unpublished data, FRI, University of Washington, Seattle).

STABILITY OF THE SPAWNING BED AND MORTALITY

Two factors causing gravel to shift in spawning beds are flooding and females digging redds. The importance of redd superimposition as a factor limiting production of salmon fry is beyond the scope of this paper and will not be considered. My discussions will be limited to the influence of flooding and debris movement on egg and larval mortality.

Mortality caused by gravel shift would make itself evident by complete disappearance of eggs and larvae from spawning beds. Changes in abundance and distribution of eggs and larvae will be examined to obtain evidence of mortality caused by gravel movement. Three population parameters will be considered in evaluating the stability of spawning beds: (1) Total mortality (M_t), (2) mean abundance of eggs and larvae per m.[2] (live plus dead)($\bar{P}$), (3) fraction of points containing fewer than 35 live plus dead eggs per m.[2] (p_0').

High discharge occurs most frequently in Southeastern Alaska streams during October, November, and December. Autumn storms are often accompanied by heavy rain which sometimes

TABLE 8.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1960 brood year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$ [1]	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Sept. 28	0.29	±0.18	0.03	±0.01	0.92	±0.05
Dec. 2	.69	±.09	.18	±.07	.74	±.07
Intertidal Indian Creek:						
Sept. 22	.44	±.20	.05	±.05	.91	±.05
Nov. 22	.50	±.22	.12	±.08	.90	±.06
Intertidal Twelve-mile Creek:						
Sept. 30	.71	±.17	.02	±.03	.98	±.02
Nov. 30	.75	[2] ±.08	.11	±.11	.92	±.03

[1] p_0 is the fraction of points containing less than 35 dead eggs per square meter.
[2] This estimate of M_t was obtained with log-transformed data.

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TABLE 9.—*Dates on which rain*[1] *at Hollis, Alaska, exceeded 4.0 inches in 72 hours, 1956–60*

Dates precipitation exceeded 4.0 inches in a 72-hour period	Amount
1956	*Inches*
None	
1957	
Nov. 21–23	4.08
1958	
Oct. 19–21	6.79
Oct. 28–31	5.08
Nov. 7–9	4.14
1959	
Nov. 5–7	5.32
Dec. 5–7	7.02
1960	
Oct. 9–11	4.31
Oct. 20–22	4.08

[1] Data provided by Northern Forest Experiment Station, U.S. Forest Service, Juneau, Alaska.

continues over several days. To index periods of heavy precipitation, dates on which total precipitation exceeded 4 inches in 72 hours at Hollis (fig. 4) are given in table 9. Stream discharge records revealed that unusually high discharges accompanied rainfall of this high intensity. The analysis showed that rain was most intense in 1958 and 1959 and least intense in 1956 and 1957.

Although a comprehensive evaluation of mortality of 1956 and 1957 brood year eggs and larvae was not feasible because of limited sampling, estimates of M_t obtained for these brood years (and discussed previously) gave no indication of losses occurring from spawning beds. Observations on subsequent brood years (1958 and 1959 particularly) have shown, however, that gravel movement during high discharge is an important cause of mortality in the study streams.

1958 Brood Year

Rainfall exceeded 4.0 inches in 72 hours three times between October 19 and November 9, 1958 (table 9). Samples of eggs were collected before and after the storms in intertidal Harris River and after the storms in intertidal Indian and Twelvemile Creeks (table 10).

The number of eggs ($\bar{P}$) estimated to be present in intertidal Harris River near the end of spawning agreed with the expected number (E') obtained from the estimated density of females spawning ($\hat{\bar{P}}=189$ and $E'=201$ per m.^{2}). After the three periods of heavy rainfall, the abundance of eggs had decreased significantly, and the fraction of points containing fewer than 35 eggs per m.^{2} had increased significantly ($X^2=5.5$, 1 d.f.). This was good evidence that a significant mortality attributable to gravel movement had occurred.

In Indian Creek, the number of eggs estimated to be present in November after the storms agreed with the expected number ($\hat{\bar{P}}=222$ and $E'=202$ eggs per m.^{2}); hence, there was no evidence of mortality from gravel movement in intertidal Indian Creek.

The number of eggs estimated in intertidal Twelvemile Creek after heavy rainfall was con-

TABLE 10.—*Estimates of the population parameters* E', $\bar{P}$, p'_0, *and* M_t *used to evaluate mortality of 1958 brood year eggs possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per m.^{2} (E' and $\hat{\bar{P}}$)		Fraction of points containing fewer than 35 eggs per m.^{2} ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:							
September 18		[1] 189	[2] ±101	0.71	±0.11	0.26	[2] ±0.25
to	3						
November 15		[1] 104	[2] ±74	.83	±.09	.51	[2] ±.35
Intertidal Indian Creek							
September 20		[3] 201					
to	3						
November 15		[1] 223	[2] ±84				
Intertidal Twelvemile Creek:							
September 25		[3] 174					
to	3						
November 30		4	±6				

[1] Estimated number of live plus dead specimens in the spawning bed ($\hat{\bar{P}}$).
[2] These limits were set with log-transformed data.
[3] Expected number of specimens based on potential egg deposition (E').

siderably less than the expected number. It was thought initially that high discharge caused mortality; however, samples were not collected before heavy precipitation in 1958, and it will be shown subsequently that high mortality of 1960 brood year eggs in Twelvemile Creek occurred in association with spawning before the storms.

1959 Brood Year

Heavy rainfall occurred in early November and December 1959. The evidence indicated that mortality occurred in association with heavy rain in all areas sampled (table 11).

The intertidal Harris River sampling program was modified slightly in 1959 to evaluate egg and larval losses associated with heavy precipitation. Because a sample taken November 16 did not include the entire area sampled on other dates, comparisons were limited to collections made within the area sampled on November 16. It is for this reason that estimates of M_t given in table 11 differ slightly from the estimates given in table 7 for the same dates. The area sampled on November 16 included 75 percent of the intertidal Harris River spawning area described in table 1.

Trees felled by loggers into upstream Harris River and transported through intertidal Harris River on the crests of two mid-October freshets appeared to cause little or no mortality. Nineteen spruce and hemlock trees, some more than 3 feet in diameter at the base of the trunk and more than 100 feet long, and several large alder trees were known to have floated through the intertidal zone. Estimates of $\hat{\bar{P}}$, p'_0, and $\hat{M}_t$ were nearly the same for samples collected before (October 6) and after (October 20) the presence of floating trees.

There was evidence that mortality occurring in intertidal Harris River between October 20 and November 16 was caused by gravel movements during heavy rain. The total population of eggs was estimated to decline about 50 percent between these dates. Associated with this decline were increases in $\hat{p}'_0$ and $\hat{M}_t$. The period of heavy rain

TABLE 11.—*Estimates of the population parameters* E', $\bar{P}$, p'_0, *and* M_t *used to evaluate mortality of 1959 brood year eggs and larvae possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per square meter (E' and $\hat{\bar{P}}$)		Fraction of points containing fewer than 35 eggs per square meter ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River: [1]							
September 26		[3] 393					
to	None						
October 6		[3] 288	±105	0.59	±0.09	0.30	±0.26
to	None						
October 20		[3] 323	±138	.58	±.12	.28	±.33
to	1						
November 16		[3] 159	[4] ±77	.65	±.18	.64	[4] ±.20
to	1						
February 26		[3] 169	[4] ±46	.65	±.09	.73	[4] ±.08
Upstream Harris River:							
September 26		[2] 106					
to	None						
November 4		[3] 31	±26	.93	±.05	.73	±.23
to	2						
March 3		[3] 0				1.00	
Intertidal Indian Creek:							
September 26		[2] 705					
to	None						
October 10		[3] 346	±130	.59	±.09	.52	±.18
to	1						
November 10		[3] 530	±206	.51	±.13	.27	±.29
to	1						
February 29		[3] 24	±18	.91	±.06	.97	±.03
Intertidal Twelvemile Creek:							
October 1		[2] 229					
to	None						
October 27		[3] 11	±17	.99	±.06	.95	±.07
to	2						
February 21		[3] 1	±1	1.00		.99	±.002

[1] Includes 75 percent of the area described in table 1.
[2] Expected number of specimens based on potential egg deposition (E').
[3] Estimated number of live plus dead specimens in the spawning bed ($\hat{\bar{P}}$).
[4] These limits were set with log-transformed data.

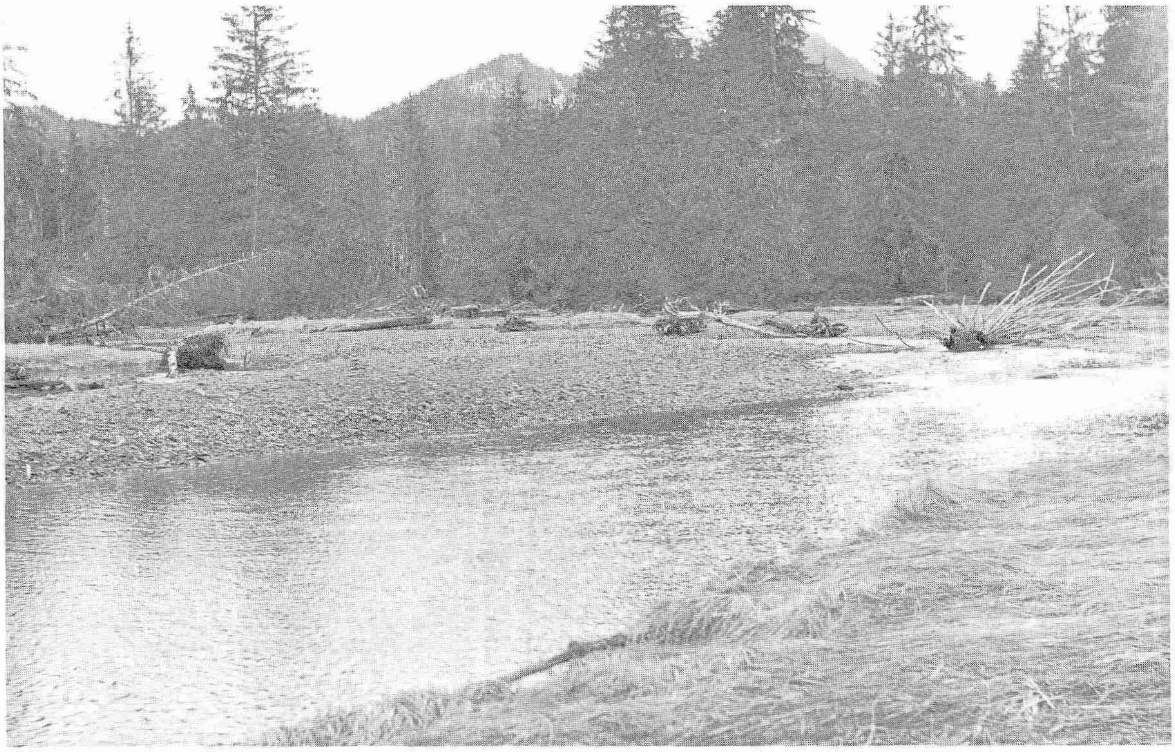

FIGURE 9.—Debris deposited in intertidal Indian Creek by the December 1959 flood.

in early December appeared to result in little additional loss of eggs or larvae from intertidal Harris River.

The period of heavy rain in November was not associated with high egg mortality in intertidal Indian Creek, but the period of heavy rain in December was associated with high mortality of eggs and larvae. After high water had receded in December, large numbers of eggs and larvae scoured from the Indian Creek streambed were observed by workers along the banks. About 90 percent of live eggs and larvae in the intertidal Indian Creek spawning bed at the time of high water in December 1959 were probably destroyed. A factor contributing to this high mortality appeared to be the breaking up of a natural log jam located a short distance above the intertidal Indian Creek spawning area and the subsequent deposition of debris from this jam in the spawning area. Figure 9 shows some of the debris deposited in intertidal Indian Creek. Turbulence created by the stream flowing around this debris was believed to have been mainly responsible for causing the stream to alter its course at several locations, washing out or burying deeply a large percentage of eggs and larvae present.

There was evidence that gravel movement caused high mortality in upstream Harris River. No live or dead eggs or larvae were collected from 68 points sampled in February 1960. Other evidence of widespread gravel movement in upstream Harris River was obtained from studies on size composition of bottom materials. There was a significant reduction in volumes of fine sands and silts in bottom materials during high water in autumn 1959 (McNeil and Ahnell, 1964).

1960 Brood Year

Periods of highest intensity rainfall occurred between October 9 and 22. Intertidal Harris River, Indian Creek, and Twelvemile Creek were sampled in autumn 1960 before and after high water (table 12).

Estimated total abundance of eggs in intertidal Harris River, as in the previous 2 years, declined about 50 percent in association with high water. The mean fraction of points containing fewer than 35 eggs per $m.^2$ increased 0.16 after

TABLE 12.—*Estimates of the population parameters* E′, $\overline{P}$, p′₀, *and* M_t *used to evaluate mortality of 1960 brood year eggs and larvae possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per m.² (E' and $\hat{\overline{P}}$)		Fraction of points containing fewer than 35 eggs per m.² ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:							
September 22		[1] 735					
to	None						
September 28		[2] 538	±132	0.33	±0.08	0.29	±0.18
to	2						
December 2		258	±72	.49	±.08	.69	±.09
Intertidal Indian Creek:							
September 21		[1] 708					
to	None						
September 22		[2] 436	±146	.52	±.09	.44	±.20
to	2						
November 22		[2] 380	±162	.47	±.11	.50	±.20
Intertidal Twelvemile Creek:							
September 28		[1] 381					
to	None						
September 30		114	±66	.68	±.11	.71	±.17
to	2						
November 30		103	[3] ±31	.68	±.11	.75	[3] ±.08

[1] Expected number of specimens based on potential egg deposition (E').
[2] Estimated live plus dead specimens in the spawning bed ($\hat{\overline{P}}$).
[3] These limits were set with log-transformed data.

heavy precipitation in 1960; while in 1958 and 1959 the increase was about 0.10. The difference between an increase of 0.16 and 0.10, however, was not statistically significant in these instances.

As in 1958 and 1959, on occasions when there was no movement of temporarily stationary debris with high water, eggs and larvae in intertidal Indian Creek apparently suffered little mortality. There was also no evidence of mortality associated with flooding in Twelvemile Creek in 1960, although large numbers of eggs had apparently disappeared before high water.

FREEZING OF INTRAGRAVEL WATER AND MORTALITY

The study streams freeze usually in December, January, and February. Hence, mortality attributable to freezing must occur either during or after hatching.

Maximum daytime air temperatures were used as as index of severity of freezing. Periods when daytime temperatures remained below freezing for two or more consecutive days were determined from air temperature records obtained at Hollis by the Northern Forest Experiment Station (table 13). Freezing was most severe in winters 1956–57 (1956 brood year) and 1958–59 (1958 brood year).

1956 Brood Year

There was evidence of high mortality from freezing in winter 1956–57. Estimates of M_r for the 1956 brood year in each of the study streams are summarized in table 5. Mean values of M_r were found to increase between late November 1956 and late February 1957 as follows:

$\hat{M}_r=0.27$ to $\hat{M}_r=0.50$ in intertidal Harris River.

$\hat{M}_r=0.10$ to $\hat{M}_r=0.75$ in intertidal Indian Creek.

$\hat{M}_r=0.27$ to $\hat{M}_r=0.41$ in intertidal Twelvemile Creek.

TABLE 13.—*Periods of daytime freezing and associated precipitation at Hollis, Alaska 1956–61* [1]

Dates when maximum temperature was less than 0° C.	Mean temperature at 5 p.m.	Precipitation
Winter 1956–57:	°C.	*Inches*
Dec. 3–12	−4°	[2] 2.03
Jan. 7–13	−6°	0
Jan. 20–26	−7°	0
Feb. 22–25	−6°	0
Winter 1957–58:		
None		
Winter 1958–59:		
Jan. 1–8	−5°	0
Winter 1959–60:		
None		
Winter 1960–61:		
None		

[1] Data provided by Northern Forest Experiment Station, U.S. Forest Service, Juneau, Alaska.
[2] Fell as snow, given as inches of rain.

Two classes of dead eggs and larvae not present in November samples were found in February samples: dead eggs with well-developed embryos ready to hatch and dead larvae. Death of eggs containing the well-developed embryos occurred after November sampling and before hatching in December.

This prehatching mortality occurred in conjunction with the December 3 to 12 freezeup. The observed posthatching mortality may have been caused, for the most part, by the subsequent more severe periods of freezing in January and February.

I have already summarized in table 5 the estimated fractions of 1956 brood year eggs and larvae dying early, shortly before hatching; and after hatching. Assuming that mortality at and after hatching was caused by freezing, I estimated mortality of the 1956 brood year from freezing to be about 23 percent in Harris River riffle A, 65 percent in Indian Creek riffles B and C, and 14 percent in Twelvemile Creek riffles D and E.

I visited the study streams during the February 22–25 freeze. Except for an occasional exposed riffle, they were coated with ice several inches thick. Freezing appeared to have a greater effect on Indian Creek spawning beds than on Harris River and Twelvemile Creek spawning beds. I attempted to drive metal rods into the Indian Creek streambed at a number of locations. The gravel was often frozen, particularly where exposed by drying of the stream. Anchor ice also had formed at several points examined.

One important conclusion to be drawn from these data is that mortality associated with freezing was highest in the stream having the lowest minimum discharge (4 c.f.s. in Indian Creek as compared with 12 c.f.s. in Twelvemile Creek and 22 c.f.s. in Harris River).

1958 Brood Year

Freezing occurred after hatching in January 1959. Sampling was undertaken in March 1959 (2½ months after freezing), and the possibility that larvae killed by freezing had decayed before sampling could not be ignored. Therefore, the best evidence of winter mortality possibly associated with freezing may be estimates of M_t which are summarized in table 14.

In intertidal Harris River, mortality was high before freezing and there was no evidence of additional mortality over winter. Intertidal Indian Creek, on the other hand, experienced high mortality over winter, thus supporting earlier findings with 1956 brood year eggs and larvae. There was no evidence of winter mortality in intertidal Twelvemile Creek, but because of the scarcity of larvae in the spawning bed, it is highly unlikely that mortality would have been detected here.

TABLE 14.—*Estimated total mortality of 1958 brood year pink and chum salmon eggs and larvae before and after freezing in winter 1958–59*

Spawning area and date	$\hat{M}_t$	
	Mean	90-percent confidence limits of the mean
Intertidal Harris River:		
Dec. 20, 1958	0.84	±0.21
Apr. 5, 1959	.62	±.29
Intertidal Indian Creek:		
Nov. 15, 1958	0	[1] ±.39
March 28, 1959	.64	±.28
Intertidal Twelvemile Creek:		
Dec. 28, 1958	.99	±.01
March 24, 1959	.99	±.01

[1] This limit was set with log-transformed data.

Other Brood Years

According to Hollis air temperatures, there were no prolonged periods of freezing that would affect eggs and larvae of the 1957, 1959, and 1960 brood years. An examination of data on mortality revealed little evidence of mortality possibly caused by freezing.

There was no evidence of winter mortality of the 1957 brood year. Prewinter and postwinter pooled estimates of M_r for riffles B, C, E, and F and their 90-percent confidence limits were:

$$\hat{M}_r \text{ (pooled for November)} = 0.69 \pm 0.19$$
$$\hat{M}_r \text{ (pooled for March)} = 0.57 \pm 0.24$$

With regard to the 1959 brood year, there was a rather high incidence (18 percent) of dead larvae in samples collected from intertidal Harris River on February 26, 1960, but a low incidence (less than 1 percent) of dead larvae collected in samples from intertidal Indian Creek. Factors other than freezing probably were responsible for the mortality observed in intertidal Harris River because temperatures were mostly above freezing in winter 1959–60, and few dead larvae were found in intertidal Indian Creek. Scarcity of eggs and larvae in

Twelvemile Creek spawning areas made it impractical to evaluate winter mortality there.

Only a small number (about 1 percent) of 1960 brood year larvae collected in late winter 1961 from intertidal Harris River and Indian Creek were dead. Of 933 larvae collected in intertidal Twelvemile Creek, 9.4 percent were dead, but most dead larvae were found in one redd. Factors other than freezing were suspected of having caused their death.

An experiment indicated that little or no freezing of intragravel water occurred in winter 1960–61. One-half-dram vials were filled with water and buried 5 and 10 inches in spawning beds during autumn 1960. They were recovered in spring 1961 and examined for breakage caused by water expanding during freezing. The recovery of a broken vial was used to indicate occurrence of freezing at the point of burial. Breakage from causes other than freezing was minimized by enclosing vials in latex tubing. Sixty-three vials were recovered from intertidal Indian Creek, 36 from intertidal Harris River, and 30 from intertidal Twelvemile Creek. There were no broken vials in the lot. This experiment provided further evidence that intragravel water did not freeze in winter 1960–61.

DISCUSSION AND CONCLUSIONS

There is evidence that mortality of pink and chum salmon from egg deposition to fry migration is seldom less than 75 percent and commonly exceeds 90 percent in small coastal streams. Freshwater mortality, therefore, may place more severe restrictions on production of pink and chum salmon than natural salt-water mortality.

A thorough understanding of the ecological and physiological requirements of pink and chum salmon eggs and larvae is necessary for evaluating the potential of spawning beds to produce fry. It has been a goal of these studies to determine the relative importance of certain factors affecting quality of the spawning bed environment and fry production.

OXYGEN SUPPLY AND RELATED FACTORS

It is evident from a review of the literature that the oxygen supply rate to an egg or larva is a function of oxygen content and velocity of flow of intragravel water, both of which are affected by a complex of interacting factors. It would appear that oxygen privation is more critical in embryonic than in larval stages. For evaluating mortality possibly resulting from an oxygen deficiency, observations on mortality were based primarily on the population of eggs present in the spawning bed at the time of sampling. Where large numbers of eggs had disappeared from spawning beds before sampling, or where density of females spawning was light, it was not possible with the sampling scheme used to obtain data adequate to evaluate prehatching mortality possibly associated with the availability of oxygen. Inadequate data for the intertidal Twelvemile Creek and upstream Harris River and Twelvemile Creek spawning areas were of limited value in evaluating mortality possibly due to oxygen privation, and observations were made mostly in intertidal Harris River and Indian Creek.

Data on (1) dissolved oxygen content of intragravel water, (2) streambed gradient, and (3) organic content, size composition, and permeability of bottom materials showed more favorable oxygen supply in intertidal Indian Creek than in intertidal Harris River. Furthermore, results of mortality studies suggested that prehatching mortality not associated with the disappearance of eggs was lower in intertidal Indian Creek than in intertidal Harris River. Hence, there was general agreement between observations on physical quality of the spawning bed environment and egg mortality.

An opportunity arose in 1957 to evaluate the relation between prolonged low streamflow during spawning and egg mortality. In this instance, unusually low levels of dissolved oxygen in intragravel water were observed during the spawning period. The evidence relating an exceptionally high egg mortality to low streamflow corroborated the findings of other workers (Brett, 1951; Neave and Wickett, 1953; Wickett, 1958).

In these studies it was not possible to demonstrate a direct dependence of egg mortality and population size. In 1957, when spawning densities were extremely low and egg mortality was unusually high, there appeared to be some justification for suggesting that a minimum number of spawners is required to reduce the overall biochemical oxygen demand through the removal of organic detritus from spawning beds (Ricker, 1962). Additional research will be required to resolve this question.

STABILITY OF THE SPAWNING BED

Instability of the spawning bed was an important cause of egg and larval mortality in the study streams. There was no apparent relation between gravel composition and stability during flooding, and high mortality occurred in spawning beds composed of coarse and fine materials. Change in position of temporarily stationary debris caused gravel movement, but the presence of floating debris had little or no effect on gravel movement.

The influence of temporarily stationary debris on the stability of bottom materials was studied in Maybeso Creek (fig. 4), a stream located near Hollis (Bishop and Shapley, 1963). The results of this study gave further support to relations observed between movement of wood debris and mortality of eggs and larvae in Harris River, Indian Creek, and Twelvemile Creek.

High discharge may be a common cause of mortality among salmonid eggs and larvae. In New Zealand, Hobbs (1937) concluded that floods seldom destroyed salmon and trout redds, but at times accounted for a partial failure of a brood year. At Sagehen Creek, Calif., a flood in December 1955 destroyed brook trout, *Salvelinus fontinalis*, and brown trout eggs, causing the complete failure of the zero age group of these species in 1956 (Needham and Jones, 1959).

Observations on dislodgment of salmon eggs and larvae from British Columbia and Southeastern Alaska streams during flooding also have been reported. After flooding, Withler (1952) found preemergent sockeye salmon fry washed from a tributary of Babine Lake, British Columbia, and Wickett (1959) reported the observation of coho and chum salmon eggs on banks and in bushes along the Qualicum River, Vancouver Island. Floods at Sashin Creek in 1941 and 1943 were thought to have killed many pink salmon eggs and larvae (Hutchinson and Shuman, 1942; Davidson and Hutchinson, 1943).

FREEZING OF INTRAGRAVEL WATER

Although freezing has been considered an important cause of mortality, except for Neave (1947), Smirnov (1947), and Semko (1954), little direct evidence showing freezing to be an important cause of pink and chum salmon egg and larval mortality has been reported. I found that freezing caused high mortality of 1956 brood year eggs and larvae, particularly in intertidal Indian Creek. There was also an indication that the 1958 brood year experienced similar high mortality in Indian Creek. Winters of 1957–58, 1959–60, and 1960–61 were mild by comparison, and there was little or no evidence of mortality from freezing.

It was apparent that freezing exerted the greatest influence on mortality in the stream having the lowest minimum discharge. Further study may reveal that certain spawning areas are unproductive because of low discharge during periods of freezing. There was no evidence of high mortality from freezing during winters that maximum daytime air temperatures remained above 0° C.

SUMMARY

1. The available evidence indicates that high mortality of eggs and larvae greatly limits the abundance of juvenile pink and chum salmon. Proper management of pink and chum salmon fisheries will depend in part on a thorough understanding of the factors affecting the potential of spawning beds to produce fry. Field studies of egg and larval mortality are important because they provide information on time and magnitude of mortality that can be associated with causative factors.

2. In the study streams, egg mortality after the end of spawning seldom exceeded 20 percent in the absence of low levels of dissolved oxygen, freezing, or high water. There was evidence that mortality attributable to oxygen privation was highest where water circulation within the spawning bed was impaired.

3. Low levels of dissolved oxygen in intragravel water as well as high egg mortality occurred with low flow during and shortly after spawning. The resulting mortality of eggs was estimated to vary between 60 and 90 percent in the spawning areas sampled.

4. Movement of bottom materials during high water was an important cause of mortality, which was most severe where temporarily stationary debris shifted position within the flood plain. Mortality from movement of bottom materials was estimated to exceed 90 percent in one instance.

5. Freezing was an important cause of mortality only when maximum daytime temperatures remained below 0° C. for at least 2 consecutive days. Mortality from freezing was highest in the stream having the lowest minimum discharge, and was estimated to approach 65 percent on one occasion.

ACKNOWLEDGMENTS

Many FRI staff members and personnel at the Northern Forest Experiment Station, U.S. Forest Service, assisted in the planning and field sampling. William L. Sheridan was project leader from 1956 to 1959 and planned much of the early field work. William F. Royce, Donald E. Bevan, and Max Katz of the College of Fisheries, University of Washington, contributed many helpful suggestions during the preparation of the original manuscript. Warren C. Pellett and Jack Cassell of FRI deserve special mention because they endured the harsh autumn and winter weather of Southeastern Alaska to accomplish much of the field work.

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