PROBABLE CASE OF STREAMBED OVERSEEDING—1967 PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, SPAWNERS AND SURVIVAL OF THEIR PROGENY IN SASHIN CREEK, SOUTHEASTERN ALASKA

WILLIAM R. HEARD[1]

ABSTRACT

The 1967 escapement of 38,067 pink salmon, *Oncorhynchus gorbuscha,* to Sashin Creek, southeastern Alaska, was the largest since 1942. Studies on distribution and density of spawners and freshwater survival of their progeny indicated that deposition of excessive numbers of eggs caused a severe compensatory mortality of alevins during winter. Spawner density was 1.7, 1.6, and 1.2 females/m^2 in upper, middle, and lower study areas respectively. The greater density of spawners in the upper area in the odd-numbered years may be determined by genetic factors like timing of escapements and by greater marine survival of fry from the upper area. Based on the previously consistent relation between timing of adult entry and resulting freshwater survival, 1967 spawners should have produced 8 million fry rather than the 3 million that were produced.

Mortality of eggs and alevins was high during spawning, low between spawning and hatching, and high between hatching and emergence. Between 1 December 1967 and 25 March 1968, 11.1 million eggs or alevins, 10.7 million of which were alive on 1 December, disappeared within the streambed. Initial mortality of these progeny probably occurred in the early alevin stage from oxygen privation, whereas disappearance was probably related to rapid decomposition and invertebrate scavenging. A "snowball effect" is postulated whereby alevins that die shortly after hatching place increasing demands on available oxygen, causing accelerated mortality. A review of historical patterns of fry production in Sashin Creek indicates that streambed overseeding occurred in 1967.

Studies of pink salmon, *Oncorhynchus gorbuscha,* in Sashin Creek, Baranof Island, southeastern Alaska, have shown that certain factors markedly affect freshwater survival. These factors include: 1) seasonal timing of spawning (Skud 1958); 2) density and distribution of adults on the spawning grounds relative to ecological characteristics of the stream, especially gradient (Merrell 1962); and 3) quality of the intragravel environment, including oxygen content of intragravel water and amount of silt and fine particulate material in streambed gravels (McNeil 1966, 1968). Other factors of significance, but believed to be of less influence on freshwater survival in Sashin Creek, include predation on eggs and alevins (McLarney 1967), stream discharge during spawning (Ellis 1969), and incubation (McNeil 1968).

The spawning ground of Sashin Creek extends from the head of tidewater to an impassable falls 1,200 m upstream and includes 13,629 m^2 of streambed. Ninety-six percent (13,084 m^2) of this ground comprises three distinct ecological areas that differ in gradient and size of particles in the substrate. McNeil (1966) called the areas upper, middle, and lower and described them briefly as follows: upper (2,945 m^2)—relatively steep gradient (0.7%) and coarse streambed gravel; middle (4,067 m^2)—intermediate gradient (0.3%) and medium-sized streambed gravel; and lower (6,072 m^2)—low gradient (0.1%) and relatively fine streambed gravel. The remaining 4% (545 m^2) of spawning ground is located in a short section of stream between the counting weir and the lower area and is not treated in this paper.

Pink salmon spawners entering Sashin Creek (the escapement) have been counted at a weir at the mouth of the creek since 1934, and the resulting numbers of fry from these escapements have been determined since 1940. During this time, the number of spawners varied from as few as 8 to more than 90,000 and the number of fry produced varied from 50 to almost 6 million. The percentage of freshwater survival, based on the estimated potential egg deposition, ranged from 0.06 to 21.75% (Table 1).

The high escapement of 38,067 pink salmon spawners in 1967, following a long series of relatively low escapements, gave me an opportunity to

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

Manuscript accepted February 1978.
FISHERY BULLETIN: VOL. 76, NO. 3, 1978.

TABLE 1.—Number of adult pink salmon, potential egg deposition, number of fry produced, and freshwater survival in Sashin Creek, 1934-67. (Modified from McNeil 1968.)

Brood year	Number of adults	Potential egg deposition[1]	Number of fry produced	Percentage freshwater survival
1934	7,917	—	—	—
1935	6,323	—	—	—
1936	5,364	—	—	—
1937	9,085	—	—	—
1938	6,467	—	—	—
1939	16,830	—	—	—
1940	53,594	52,858,000	3,399,900	6.43
1941	84,303	88,678,000	1,024,300	1.16
1942	92,085	78,894,000	674,000	0.85
1943	14,883	14,980,000	227,800	1.52
1944	4,050	3,904,000	105,600	2.71
1945	5,465	5,062,000	43,100	0.85
1946	933	736,000	1,200	0.16
1947	1,486	1,330,000	27,600	2.07
1948	597	516,000	9,100	1.76
1949	4,902	4,800,000	176,200	3.67
1950	112	86,000	50	0.06
1951	4,366	4,062,000	412,500	10.15
1952[2]	45	—	740	—
1953	1,164	1,284,000	95,400	7.43
1954	21	12,000	660	5.48
1955	9,267	10,286,000	266,200	12.31
1956	933	1,018,000	5,040	0.50
1957	2,834	2,588,000	562,900	21.75
1958	217	174,000	10,700	6.13
1959	35,391	40,379,000	5,332,400	13.21
1960[2]	162	—	480	—
1961	28,759	29,425,000	5,940,300	20.19
1962[2]	8	8,000	100	1.20
1963	16,757	16,640,000	3,256,300	19.57
1964	[3]2,193	2,230,000	[4]310,000	13.91
1965	14,833	12,668,000	[4]2,235,000	17.92
1966	5,761	6,255,000	[4]744,000	11.99
1967	38,067	44,384,000	3,007,200	6.78

[1]Based on 2,000 eggs/female except when actual fecundity was calculated.
[2]An attempt was made to destroy the spawners or their progeny.
[3]Natural returning adults (327) were supplemented by the introduction of 1,866 adults taken from Bear Harbor, Kuiu Island.
[4]Fry weir not operated; figures are estimates of live alevins in the gravel just before start of emergence.

study the effects of a large spawning population on freshwater survival. For the 1967 escapement I studied 1) timing of entry into the stream and the distribution and density of pink salmon on the spawning grounds, and 2) survival of progeny by time periods in the three ecological areas of the stream and the overwinter disappearance of eggs and alevins from streambed gravels. In this paper I present all the available data on escapament size and production of fry in Sashin Creek and develop the hypothesis that streambed overseeding occurred in 1967. As Ricker (1962:186) pointed out, detailed knowledge on the effects of overseeding is important in understanding why pink salmon populations fluctuate. He stated, "Because it [overseeding] happens rarely nowadays, no chance should be lost to make such a study if one occurs." Simply stated, overseeding can be defined as an egg density in spawning bed gravels that leads to a significantly greater freshwater mortality than a lesser density would cause. As discussed more fully later, it is a complex and dynamic interaction between egg density, streambed ecology, and specific climatic conditions.

TIMING OF ENTRY AND DISTRIBUTION AND DENSITY OF SPAWNERS

The timing of stream entry was determined from daily counts of the adults at the Sashin Creek weir. This timing apparently influences the freshwater survival of the progeny. An inverse relation between time of stream entry of spawners and survival of progeny is usual in Sashin Creek (Skud 1958; Merrell 1962; McNeil 1968; Ellis 1969): high survival has been associated with early spawning and low survival with late spawning. Merrell (1962) further pointed out that pink salmon spawn in Sashin Creek an average of 12 days earlier during odd years than even years.[2] As a result, freshwater survival is usually higher among progeny of spawners from odd years than among those from even years (Table 1).

In 1967, 50% of the spawners had entered Sashin Creek by 20 August, the second earliest date on record. The early entry indicated that survival of eggs and alevins would be high, but this did not prove to be the case.

Throughout the run, random lots of females were tagged at the weir, and the distribution and density of spawners were determined from daily counts of both tagged and untagged females on the spawning grounds. This technique, described by McNeil (1968) and used by Ellis (1969), provides two methods of estimating the numbers of females spawning in the upper, middle, and lower areas. One method assumes that tagged females distribute themselves among the three sections the same as untagged females. In the other method, the summed daily count of all females in each area is divided by the average longevity on the spawning grounds. The results from the two methods were generally in agreement, except for the upper area where estimates based on distribution of tagged females were considerably higher than those based on total females. The difference may reflect the difficulty in making accurate counts on spawning riffles where densities of spawners are high; in such a situation an observer might count small

[2]The date when 50% of the escapement to Sashin Creek had entered the stream has been commonly used as an index of time of spawning.

numbers of tagged females more accurately than large numbers of untagged females. Because the relative accuracy of the two methods is unknown, I averaged them to arrive at mean estimates of densities of females in the three areas (Table 2).

Spawner density in Sashin Creek is usually unequal in the three study areas, depending in part on the total number of spawners. Densities in 1967 were the highest recorded for specific areas[3] of the stream (Table 3). Merrell (1962) noted that in years when many spawners were present, they utilized all of the available spawning grounds, and in years when few were present, they spawned mostly in the lower portion of the stream. When the upper area was used, survival of eggs and alevins in that area was higher and the number of fry produced was proportionally much greater than in the middle and lower areas (Merrell 1962). In addition, the sediment content and water quality of the stream in the upper area were better than in the other two areas (McNeil 1966, 1968). Sashin Creek thus presents an apparent paradox—the least favorable areas are used in years of relatively few spawners, and the best areas are used only during years of great numbers of spawners.

Merrell (1962) thought that the greater use of the upper area was related primarily to density-dependent spawner interactions. In 1967, however, the heavy use of the upper area was apparently not the result of high densities downstream forcing spawners into upstream areas: spawner densities in the upper area built up rapidly before spawning reached significant levels in the middle and lower areas. Although the upper area contains only 22% of the combined spawning grounds of the three areas, in 1967, 62% of the first group of female pink salmon tagged at the weir spawned in the upper area (Table 4). In general, the intensity of spawning in 1967 progressed to downstream areas from the upper area rather than the reverse. McNeil (1966, 1968) noted similar downstream shifts in spawning in Sashin Creek in 1963 and 1965. Although McNeil (1966) felt that the shift occurred because of heavy rainfall during the spawning period, he later noted (McNeil 1968) the same phenomenon during an unusually dry year.

It appears that the upper area in Sashin Creek is not necessarily used because of spawner overflow but because of more complex factors. Two interrelated factors could account for the spawner distributions observed in recent years: 1) migratory behavior associated with timing of the escapement, and 2) a genetic tendency for odd-year spawners to use upstream areas. Odd-year spawners enter the stream earlier than even-year spawners. A characteristic of early stream entry in anadromous fishes may be a tendency to migrate farther upstream than spawners associated with late stream entry (Briggs 1955). In addition to early entry and use of the upper area, odd-year spawners for the past 9 or 10 generations have consistently had higher escapements and, except for 1967, higher freshwater survival of progeny than even-year spawners (Table 1). Natural selection may be operating, in recent odd-year generations, to encourage progeny produced in the upper area to spawn in that area. Wells and McNeil (1970) showed that fry produced in the upper area of Sashin Creek were larger and presumably of better quality than those produced in the downstream areas. Differential marine survival

[3]Although the total number of spawners entering the stream has been recorded since 1934 (Table 1), detailed studies on the distribution of spawners in the upper, middle, and lower areas of the stream have been available only since 1961.

TABLE 2.—Estimated densities of female pink salmon spawning in three areas of Sashin Creek, 1967.

	Females per square meter		
Area	Based on counts of tagged females only	Based on counts of tagged and untagged females	Mean
Upper	1.90	1.59	1.74
Middle	1.49	1.76	1.62
Lower	1.19	1.15	1.17

TABLE 3.—Estimated densities of female pink salmon spawning in three areas of Sashin Creek, 1961-67.

	Females per square meter					
Area	1961[1]	1963[2]	1964[3]	1965[4]	1966[5]	1967
Upper	1.00	0.59	0.01	0.58	0.04	1.74
Middle	1.00	0.89	0.09	0.62	0.27	1.62
Lower	1.00	0.59	0.13	0.44	0.28	1.17

[1]Extrapolated from subjective estimate (McNeil et al. 1964).
[2]Adjusted from McNeil (1966).
[3]McNeil et al. (1969).
[4]McNeil (1968).
[5]Ellis (1969).

TABLE 4.—Dates of tagging and percentage of total escapement counted through weir, numbers of female pink salmon tagged, and spawning distribution of tagged females in three areas of Sashin Creek, 1967.

Date of tagging[1]	Percentage of total escapement counted through weir	Females tagged	Tagged females observed spawning	Percentage of tagged fish accounted for: Upper area	Middle area	Lower area
10 Aug.	3	49	40	62	25	12
12 Aug.	13	50	40	22	37	40
17 Aug.	26	50	42	21	23	55
20 Aug.	54	50	50	22	42	36
5 Sept.	98	50	40	22	30	48

[1]Females tagged on each date received color-coded tags that differentiated them from females tagged on other dates.

that favored fry produced in the upper area over those produced in the downstream areas could account for the greater escapements of odd-year spawners in recent years.

SURVIVAL OF EGGS AND ALEVINS

Survival of eggs and alevins from the 1967 brood year was estimated in Sashin Creek for four time periods: 1) from stream entry to end of spawning, 2) from end of spawning to hatching, 3) from hatching to shortly before fry emergence, and 4) from shortly before emergence to emergence and downstream migration of fry.

The estimates of survival were based on estimates of the potential egg deposition of female spawners and estimates of the surviving eggs and alevins in the three study areas. Potential egg deposition was estimated by multiplying the number of females by average fecundity. Densities of eggs and alevins were determined after spawning, during hatching, and before fry emergence by sampling randomly selected 0.1-m^2 points in the streambed with a hydraulic sampling technique described by McNeil (1964a). The number of fry migrating from the stream were estimated on the basis of daily counts of fry migrating through a weir at the stream mouth.

Numbers of females entering the stream and average fecundity were derived from counts and samples taken at the weir. Of the 38,067 pink salmon spawners entering Sashin Creek in 1967, 19,639 (52%) were females. Total counts of mature eggs from each of 35 females selected at random from the run ranged from 810 to 2,954 (average 2,260) eggs/female (90% confidence limit of mean fecundity was ±115 eggs).

The percentage of eggs available for deposition that are actually buried in the streambed is partly dependent on the density of spawners. McNeil (1964b) discussed the role of redd superimposition and showed that at spawner densities approaching 3 to 4 females/m^2 of spawning ground, an upper asymptotic limit on the density of eggs in the streambed is reached. Factors other than spawner density that may influence egg deposition include loss of adults in the stream before spawning and retention of eggs in the female's body (Neave 1953), type and characteristics of the spawning substrate (McNeil 1966), streamflow during spawning (Ellis 1969), and loss of eggs to vertebrate predators during the spawning process (Moyle 1966; McLarney 1967; Reed 1967).

The efficiency of egg deposition of pink salmon spawners in Sashin Creek is highly variable, from 37 to 82% of the potential egg deposition (Ellis 1969). In 1967 the number of pink salmon eggs potentially available for deposition was 44.4 million, with 19.9 million of these (45% of the potential) estimated to be in the streambed after spawning. The efficiency of egg deposition was 47% in the upper area, 50% in the middle area, and 38% in the lower area.

Although spawner densities were high in 1967 (Table 3), the ability of pink salmon to void most of their eggs during spawning did not seem to be affected. Egg retention is characteristically low in Sashin Creek, usually less than 5% of fecundity (McNeil 1966; Ellis 1969). In 1967, I examined the body cavities of 402 spent female pink salmon (about 2% of the total) and found that average egg retention was 1.5% of average fecundity.

The proportion of eggs actually deposited that were alive at the end of the spawning period in 1967 was highest (93%) in the upper area, intermediate (83%) in the middle area, and lowest (74%) in the lower area (Table 5). This high survival in the upper area is consistent with that of previous years. The ratio of live to combined live and dead eggs and alevins was usually higher in the upper and middle areas than in the lower area through hatching to the beginning of fry emergence (Table 5).

Survival of eggs and alevins varied among the three time periods (during spawning, between end of spawning and hatching, and between end of hatching and emergence). Survival within each time period for each area was higher between spawning and hatching than during spawning or between hatching and emergence (Table 6). As previously discussed, survival during spawning was related primarily to the ability of females to successfully deposit their eggs because a high percentage of the eggs buried were alive shortly after spawning. Survival between spawning and hatching and between hatching and emergence pertains to survival of eggs and alevins within the streambed.

The densities of live preemerged fry in the streambed of Sashin Creek in late March 1968 were 382, 260, and 108/m^2 in the upper, middle, and lower areas, respectively. From these densities I estimated a population of 2.9 million fry in the entire stream. Operation of the fry weir began just after the late March streambed sampling was

TABLE 5.—Potential egg deposition, number of live and dead eggs and alevins, ratio of live to combined live and dead eggs and alevins, and estimated survival of 1967 brood year pink salmon in three areas of Sashin Creek.

Area	Potential egg deposition per square meter: Mean	90% confidence limits of mean	Period beginning 10 Aug. and ending	Combined live and dead eggs and alevins per square meter: Mean	90% confidence limits of mean	Percentage of live to combined live and dead eggs and alevins: Mean	90% confidence limits of mean	Percentage calculated survival
Upper	3,947	±201	1 Oct.	1,863	±254	93	± 1	43
			1 Dec.	1,714	±295	86	± 4	37
			25 Mar.	647	±138	59	±13	10
Middle	3,672	±187	1 Oct.	1,826	±218	83	±12	41
			1 Dec.	1,591	±226	70	± 7	30
			25 Mar.	702	±147	37	± 2	7
Lower	2,644	±136	1 Oct.	1,015	±120	74	±17	28
			1 Dec.	989	±116	72	± 2	27
			25 Mar.	350	±70	31	±10	4

TABLE 6.—Percentage of estimated survival of 1967 brood year pink salmon eggs and alevins for three time periods in three areas of Sashin Creek and for the entire stream, 1967.

Area	Percentage survival: During spawning	Between end of spawning and hatching	Between end of hatching and emergence	Total
Upper	43	85	26	10
Middle	41	73	23	7
Lower	28	95	15	4
Entire stream[1]	37	83	22	6.8

[1]Data weighted and adjusted to include spawning grounds not included in the three study areas.

completed. Relatively few fry migrated downstream through the weir until mid-April; the daily fry migrations increased steadily through late April, reached a peak in early May, then declined rapidly, and were essentially completed by early June (Figure 1). The total number of pink salmon fry estimated to migrate from Sashin Creek from the 1967 brood year spawners was 3 million. Similar close agreements between estimates based on densities of preemerged fry and those based on number of fry counted at the weir have occurred in previous years (McNeil 1968).

The 3 million fry migrating from Sashin Creek in the spring of 1968 represent a total freshwater survival of 6.8% of the 44.4 million potential egg deposition. This is the lowest freshwater survival in the odd-year line of pink salmon spawners in Sashin Creek since 1949 (Table 1). I will subsequently attempt to show that this reduced survival was primarily due to excessive seeding of the streambed during spawning.

DISAPPEARANCE OF EGGS AND ALEVINS

To determine the number of eggs and alevins that disappeared from the streambed, I compared the potential egg deposition with the numbers of live and dead eggs at the end of spawning and the number of eggs and alevins at the time of hatching and just before emergence. In 1967, 55% of the potential egg deposition disappeared during spawning. The fate of these eggs is unknown, but they were probably removed from the stream during the spawning period by predators, scavengers, or turbulent streamflow. McLarney (1967) and McNeil (1968) discussed the roles of fish predators (especially sculpins) and water turbulence in removing eggs from Sashin Creek during spawning and between spawning and hatching.

McNeil (1968) found that eggs and alevins of the 1963 and 1965 brood years disappeared at different rates in the upper, middle, and lower study areas of Sashin Creek. Most of the 1963 brood year progeny disappeared during spawning, and most of the 1965 brood year progeny disappeared between hatching and emergence (over the winter). I will examine closely the possible fate of eggs and alevins during this period (December to March) because the factors that caused a reduced freshwater survival of 1967 brood year progeny prevailed during this period.

The estimated percentages of the potential egg deposition that disappeared in the upper, middle, and lower areas of Sashin Creek were similar within each of the three periods. This disappearance varied greatly between periods: 55% of the progeny (eggs or alevins) had disappeared by 1 October, 4% between October and December, and 25% between December and March (Table 7). The disappearance between hatching and emergence (December and March) appears more significant when expressed in terms of numbers present in December; 56-65% of the eggs and alevins in the upper, middle, and lower areas of Sashin Creek on 1 December had disappeared by 25 March (Table 8).

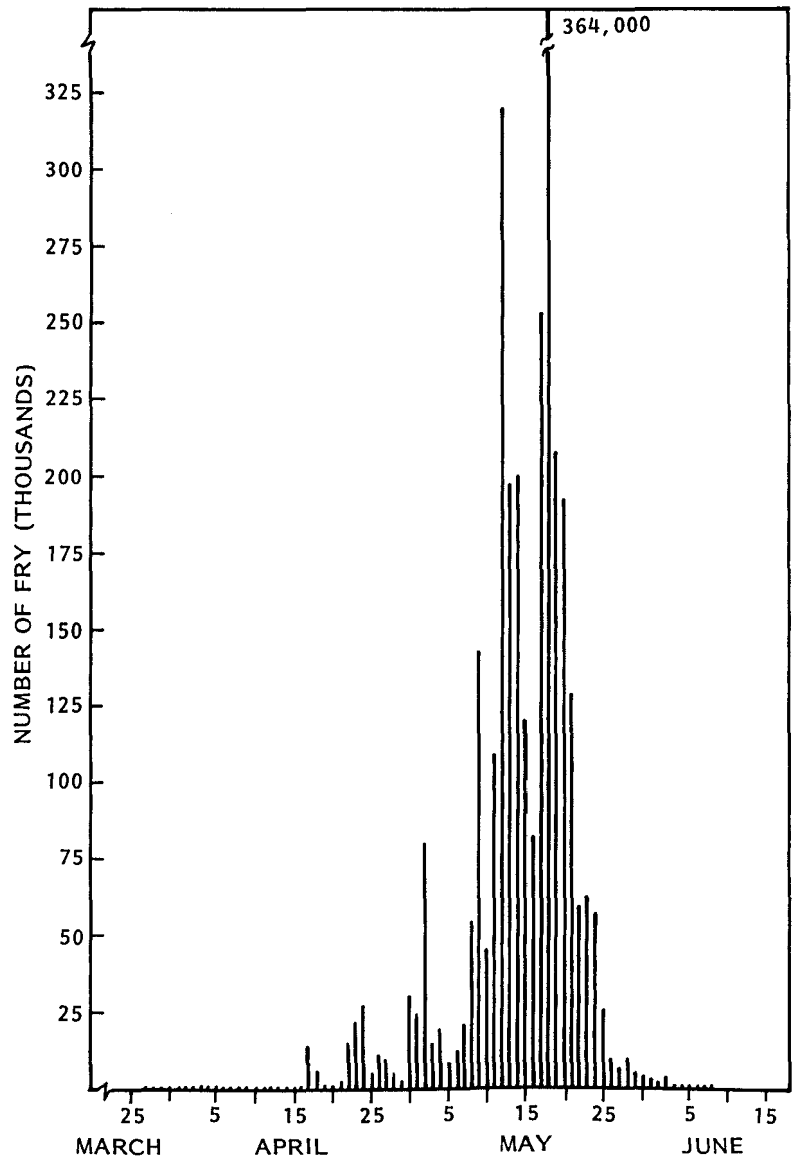

FIGURE 1.—Daily number of 1967 brood year pink salmon fry counted through Sashin Creek weir in spring 1968.

Mortality Patterns in the Streambed

Mortality of eggs and alevins within the streambed at Sashin Creek is evident in two ways: 1) as a reduction in the total population of eggs and alevins within the streambed, i.e., they disappear, and 2) as an increase in the number of dead eggs and alevins in the streambed and a decrease in the number of live eggs and alevins. In the first instance, some factors that can cause eggs and alevins to disappear are turbulent streamflow, streambed scouring, predation, and scavenging. Excluding predation, these same factors can also cause dead eggs and alevins that may have died for other reasons to disappear from the streambed. In the second instance, factors causing an increase in the number of dead eggs and alevins within the streambed are generally relatable to desiccation, freezing, and the quality of intragravel water.

In addition, dead eggs and alevins may disappear because of at least two factors that do not affect live eggs and alevins: biochemical decomposition and consumption by intragravel invertebrate scavengers. Thus, factors that cause eggs

TABLE 7.—Percentage of potential egg deposition of 1967 brood year pink salmon that disappeared from three areas of Sashin Creek and from the entire stream by 1 October 1967, 1 December 1967, and 25 March 1968.

Area	Estimated percentage of potential egg deposition disappearing		
	By 1 Oct.	1 Oct. to 1 Dec.	1 Dec. to 25 Mar.
Upper	53	4	27
Middle	50	6	24
Lower	62	1	24
Entire stream[1]	55	4	25

[1]Data weighted and adjusted to include spawning grounds not included in the three study areas.

TABLE 8.—Estimated densities of all eggs and alevins (live and dead) in three areas of Sashin Creek on 1 December 1967 and 25 March 1968, and percentage that disappeared between the two dates.

Area	Number of eggs and alevins per square meter on		Percentage that disappeared between dates
	1 Dec.	25 Mar.	
Upper	1,714	647	62
Middle	1,591	702	56
Lower	989	350	65

or alevins to disappear from streambed gravels may or may not have been the initial cause of death.

It is unlikely that turbulent streamflow, streambed shifting, or predation were the reasons that 1967 brood year eggs or alevins disappeared between early December and late March. Streamflows were generally low, and although an intermittent ice cover was present on Sashin Creek during January, February, and March, there was no indication of streambed shifting because of ice scouring. A series of short metal stakes driven into the streambed throughout the stream in November to mark coho salmon, *O. kisutch,* redds was still in place in March, indicating that no streambed shifting had occurred.

Most fish in Sashin Creek that could eat pink salmon eggs and alevins (juvenile coho salmon; rainbow trout, *Salmo gairdneri*; Dolly Varden, *Salvelinus malma*; and coastrange sculpin, *Cottus aleuticus*) are essentially dormant during the winter when water temperatures are low. Chapman and Bjornn (1969) have shown that resident stream salmonids may disappear into the substrate when water temperatures fall below 4.4 °-5.5 °C. I have observed similar behavior in Sashin Creek. Stream temperatures in Sashin Creek were below 4.4 °C from 13 December 1967 to 20 April 1968.

Water ouzels, *Cinclus mexicanus,* and mergansers, *Mergus merganser,* are occasionally present on Sashin Creek during the winter and could account for the disappearance of some eggs and alevins during open water periods. In considering the magnitude of the disappearance of 1967 brood year eggs and alevins in Sashin Creek between December and March, it is unlikely that the maximum possible loss to these sources is significant. This conclusion is based on the small numbers of mergansers and ouzels present, the amount of time the stream was covered with ice, and the large number of eggs or alevins that disappeared. Between two and five mergansers were noted in the vicinity periodically. When present, these birds spent much of their time in the intertidal portion of Sashin Creek or in the adjacent estuary. Only four of the smaller and territorial ouzels normally occur along the upper, middle, and lower areas of Sashin Creek in winter, and during periods of ice cover these birds go elsewhere. Based on periodic observations and temperature records, I estimate the stream was covered with ice approximately half the 1967-68 winter.

The estimated population of live and dead pink salmon eggs and alevins in Sashin Creek was 18.3 million on 1 December 1967 and 7.2 million on 25 March 1968 (Table 9), making a loss of 11.1 million eggs and alevins between the two dates. Because there is little evidence that the loss was caused by external factors that physically removed eggs or alevins from the streambed, the loss was likely due to factors within the intragravel environment.

The disappearance of 11.1 million eggs and alevins from the streambed between hatching and emergence led me to examine the relation between live eggs and alevins and dead eggs and alevins in the streambed. The densities of dead eggs and alevins in the upper, middle, and lower areas (Table 10) indicated that the numbers of dead eggs and alevins remained relatively stable between the time periods. This does not necessarily indicate that dead eggs in the streambed during one sampling period were still there during a later sampling period. Dead eggs can disappear at any time for many reasons, but can persist in a

TABLE 9.—Estimated population of live and dead pink salmon eggs and alevins in Sashin Creek on 1 October 1967, 1 December 1967, and 25 March 1968.

Sample date	Millions of eggs and alevins in streambed		
	Live	Dead	Total
1 Oct. 1967	16.5	3.4	19.9
1 Dec. 1967	13.7	4.6	18.3
25 Mar. 1968	3.0	4.2	7.2

streambed for as long as 18 mo (McNeil et al. 1964). Once hatching is completed, no new dead eggs can be added to the streambed. Because hatching of live eggs was well underway on 1 December (about 35% completed), many of the dead eggs present in March had already died by 1 December (Table 10).

Most of the eggs and alevins that disappeared over the winter (about 11 million; Tables 7, 8, 9) were individuals that had been alive on 1 December because the number of dead eggs and alevins was essentially unchanged from December (4.6 million) to March (4.2 million) (Table 9). Mortality (in the form of disappearance) of live eggs and alevins in the streambed between 1 December and 25 March was 74% in the upper area, 77% in the middle area, and 85% in the lower area (Table 11). Of the 11.1 million pink salmon eggs and alevins that disappeared within the streambed between 1 December and 25 March, 10.7 million were alive on 1 December.

As previously mentioned, the cause of the disappearance of dead eggs and alevins in the streambed may differ from the cause of their deaths. This apparently occurred with the 1967 brood year pink salmon progeny in Sashin Creek, and I offer the following theoretical sequence to explain the major overwinter disappearance of eggs and alevins.

The greatest number of fry produced in Sashin Creek since 1940 was 5.9 million (Table 1). On 1 December 1967, 13.7 million live pink salmon eggs and alevins were in the Sashin Creek streambed (Table 9), a number that appears to exceed the capacity of the streambed for pink salmon fry production. I postulate that the high initial density of eggs led to a severe mortality of embryos in the early alevin stage, probably because of widespread oxygen privation or a combination of oxygen privation and a buildup of toxic metabolites. The rate of oxygen consumption by embryos increases steadily with development (Wickett 1954, 1962) and coincides with the general lowering of streamflows during the late fall, followed by stabilization of streamflows at near the normal winter levels.[4] This combination of conditions permitted the embryo population to survive up to, but not much beyond, the hatching period. These recently hatched dead alevins then apparently disappeared rapidly within the streambed through the combined action of biochemical decomposition and intragravel invertebrate scavenging. As I will show later, the rapid disappearance of recently hatched dead alevins in the streambed seems consistent with this hypothesis.

Although no intragravel water quality data are available from Sashin Creek during or shortly after hatching to support the above theory, a comparison of the rates of oxygen consumption by pink salmon embryos of various ages indicates that oxygen requirements do steadily increase during the hatching period. The rates of oxygen consumption reported for early stage eggs (7-26 days old) have ranged from 0.0003 mg O_2/egg per h (Wickett 1954) to 0.0005 mg O_2/egg per h (Brickell 1971). Brickell found that the rate of oxygen consumption by 35-day-old pink salmon eggs was 0.0018 mg O_2/egg per h, almost four times the rate he measured for 7-day-old eggs. Faintly eyed 38-day-old eggs had an oxygen consumption rate of 0.002 mg O_2/egg per h (Wickett 1962) while 7-day-old alevins had a consumption rate of 0.01 mg O_2/alevin per h (Wickett 1954).

TABLE 10.—Estimated densities of dead pink salmon eggs and alevins in three areas of Sashin Creek on 1 October 1967, 1 December 1967, and 25 March 1968.

	Dead eggs and alevins per square meter					
	Upper area		Middle area		Lower area	
Date	Eggs	Alevins	Eggs	Alevins	Eggs	Alevins
1 Oct. 1967	129	0	310	0	264	0
1 Dec. 1967	223	7	459	18	266	11
25 Mar. 1968	196	69	334	108	199	43

TABLE 11.—Estimated densities of live pink salmon eggs and alevins in three areas of Sashin Creek on 1 December 1967 and 25 March 1968 and disappearance of live eggs or alevins between the two dates.

	Live eggs and alevins per square meter				Percentage of live eggs or alevins that disappeared between dates
	1 Dec. 1967		25 Mar. 1968		
Area	Eggs	Alevins	Eggs	Alevins	
Upper	899	575	0	382	74
Middle	769	345	0	260	77
Lower	463	249	0	108	85

[4]Seasonally, stream discharge in Sashin Creek is usually highest in fall and lowest in summer. Discharge in winter months may also be low, but is normally above summer levels. Because unseasonably low winter discharge could reduce oxygen delivery to embryos below the normal seasonal pattern, I compared the low monthly discharge during December, January, February, and March for 1967-68 with low discharge patterns in the same months for the period 1951-52 to 1966-67. The low mean monthly discharge from Sashin Creek during December, January, February, and March ranged from 18 to 62 ft^3/s and averaged 33 ft^3/s for the 16-yr period. The mean minimum monthly discharge during these same 4 mo in 1967-68 was 30 ft^3/s (U.S. Geological Survey 1969), suggesting that low streamflow levels during these months in 1967-68 were near normal.

In addition to the increasing oxygen requirements due to growth and development of live embryos, Brickell (1971) found that rates of oxygen consumption by dead intact pink salmon eggs exceeded those of early stage live eggs fourfold: 0.0018 mg O_2/whole dead egg per h versus 0.0004-0.0005 mg O_2/7-day-old live egg per h. He noted even greater oxygen consumption for dead eggs when the chorion was pierced or slit or the egg was fragmented: mean oxygen consumption of fragmented dead eggs in constant-flow cylinders was 0.017 mg O_2/egg per h, which exceeds the rate Wickett (1954) found for 7-day-old live alevins. It follows that alevins that die shortly after hatching, because of their soft, exposed, and readily oxidizable tissue, would have higher rates of oxygen consumption than whole intact dead eggs, live eggs, or early stage live alevins.

These increases in oxygen consumption upon death of developing pink salmon embryos are the rationale for suggesting a "snowball effect"—rapidly increasing deaths of embryos once lethal oxygen concentrations were approached. With high densities of live embryos already placing excessive demands on the oxygen and each death increasing the demand, the resulting heavy mortality could have caused fry production to plunge below that expected from lower initial egg densities—an excellent example of Neave's (1953) theory of compensatory mortality.

Disappearance of Dead Eggs Versus Disappearance of Dead Alevins

To test the hypothesis that dead alevins disappear within the streambed more rapidly than dead eggs, I conducted a small study in Sashin Creek in the winter of 1968-69 to consider the relative persistence of dead eggs and alevins in the streambed. A series of Vibert boxes (small plastic perforated containers), each containing a mixture of streambed gravel, 10 dead eggs, and 10 dead alevins (all from 1968 brood year pink salmon) were buried in Sashin Creek on 14 December 1968. The boxes were buried about 20.3 cm deep across a riffle in the middle study area. At irregular intervals, pairs of the boxes were removed from the streambed and the contents were preserved for examination.

Alevins disappeared from the Vibert boxes at a much faster rate than eggs (Table 12). Fewer than half of the original number of alevins were still recognizable at the end of 2 wk; after 37 days only one box contained identifiable alevins. Although the dead alevins disappeared rapidly, only a few of the dead eggs disappeared. In a study to determine whether certain stonefly numphs were predators or scavengers on salmon eggs and alevins, Ellis (1970) found in one experiment that dead pink salmon alevins buried in Vibert boxes in a stream essentially disappeared within a 2-wk period.

TABLE 12.—Contents of Vibert boxes with dead pink salmon eggs and alevins buried in Sashin Creek streambed between 14 December 1968 and 14 April 1969.[1]

No. of days buried	Eggs recovered	Alevins recovered	Invertebrates recovered: Insect larvae[2]	Invertebrates recovered: Planarian worms[3]
0	20	20	0	0
9	20	10	14	4
16	20	4	37	20
24	20	2	40	34
30	20	1	27	144
37	20	4	36	11
44	20	0	55	5
51	19	0	70	3
71	19	0	196	4
86	20	2	72	9
96	20	0	135	6
109	20	0	149	29
121	19	0	102	36

[1]Each box originally contained 10 dead eggs and 10 dead alevins. Two boxes were removed on each sample date and the contents combined for reporting.
[2]Of all insect larvae recovered, 80% were Plecoptera, 16% Diptera, 3% Trichoptera, and 1% Ephemeroptera.
[3]Tentatively identified as *Polycelis borealis*, a species that Kenk (1953) commonly found in clear cold streams in southern parts of Alaska.

Concurrently with the rapid disappearance of dead alevins from the buried boxes was a rapid buildup of invertebrates in the boxes. Although invertebrates are commonly found with salmon embryos (Briggs 1953; McDonald 1960; Nicola 1968), it is frequently impossible to determine if predation or scavenging is occurring. Although some groups of stonefly nymphs are known to attack live salmon embryos (Stuart 1953; Claire and Phillips 1968), Ellis (1970) concluded that nymphs of the carnivorous genus *Alloperla* were basically scavengers rather than predators.

In addition to various insect larvae, a planarian worm tentatively identified as *Polycelis borealis* was commonly found in the boxes buried in Sashin Creek (Table 12). Little is known on the biology or life history of this planarian, but under favorable conditions it appears to rapidly increase its numbers in the streambed, and thus may be particularly important in removing dead alevins. I have observed successive seasonal increases in the relative abundance of planarians in samples taken from the Sashin Creek streambed with the hydraulic sampler in the fall, winter, and spring. Total counts of planarians removed from the streambed with the hydraulic sampler are not possible,[5] but partial counts indicated that by March the densities of planarians in some parts of Sashin Creek commonly reached several thousand per square meter. A similar seasonal increase in streambed populations of planarians concomitant with the seasonal occurrence of sockeye salmon, *O. nerka,* embryos has been noted elsewhere.[6]

In Sashin Creek there is little doubt that high planarian populations are related to the presence of salmon eggs and alevins, because planarians are scarce in streambed gravels above the impassable falls where salmon do not spawn. However, the precise role of these organisms in the ecology of spawning beds is unknown. To learn something about the role of planarians, I conducted tests with various combinations of planarians and live and dead salmon eggs and alevins in experimental containers. In these tests planarians did not prey on and were not toxic to live embryos, nor did they feed on dead eggs unless the chorion was broken and the egg contents exposed.

EVIDENCE OF OVERSEEDING

In assessing the probability of streambed overseeding in Sashin Creek in the 1967 brood year, it is most useful to compare fry production in 1967-68 with production in other years. Since 1940, production has varied from 50 fry to almost 6 million fry; corresponding parent escapements varied from 8 to 92,085 (Table 1). Only three escapements exceeded that of 1967, and only one of these (1940) produced more fry (about 0.4 million more) (Table 1). When the numbers of fry are plotted against potential egg deposition, a dome-shaped fry production curve is derived for Sashin Creek (McNeil 1969). The relative position of fry production for the 1967 brood year falls near the descending limb of the curve; fry production from the 1941 and 1942 brood years indicates a continuing decrease in fry production as escapements increased (Figure 2).

Data collected since 1961 on the density of eggs in the three study areas at the end of spawning provide a means of more precisely defining the fry production potential of the stream. Plotting fry production as a function of actual egg deposition for each area produces curves that suggest the potential maximum fry production in the upper and middle areas is around 500 fry/m^2 and the potential in the lower area is about half that number (Figure 3). In 1967 the actual density of eggs deposited considerably exceeded twice the theoretical maximum fry production in all three areas and the fry production was considerably below the maximum; it appears that overseeding occurred in 1967.

Until 1967 the timing of entry of adults into Sashin Creek had usually been an accurate indicator of the freshwater survival of progeny (Merrell 1962; McNeil 1968; Ellis 1969). The presumed biological basis for the correlation between early spawning and high survival was that embryos de-

[5]When large numbers of planarians are excavated with the hydraulic sampler, many elongate their bodies and pass through the meshes of the collecting net.

[6]W. L. Hartman, W. R. Heard, and C. W. Strickland. 1962. Red salmon studies at Brooks Lake biological field station, 1961. Unpubl. manuscr. on file, NWAFC Auke Bay Lab. NMFS, NOAA, P.O. Box 155, Auke Bay, Alaska.

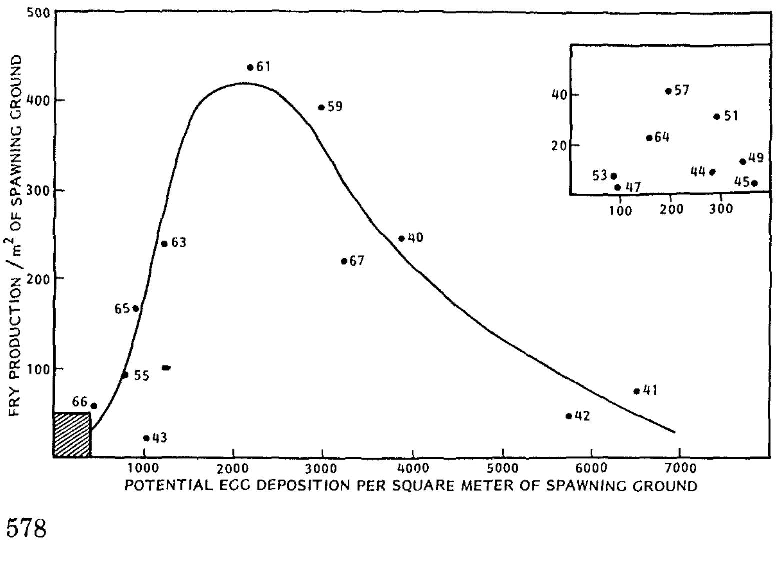

FIGURE 2.—Production of pink salmon in Sashin Creek, 1940-67. The shaded area in the lower left is shown on a larger scale in the upper right corner. Nine generations of the even-year line 1946-62 were excluded because fry productions were all <1/m^2. Adult escapement in these years was correspondingly low. The curve (modified from McNeil 1969) is fitted by eye.

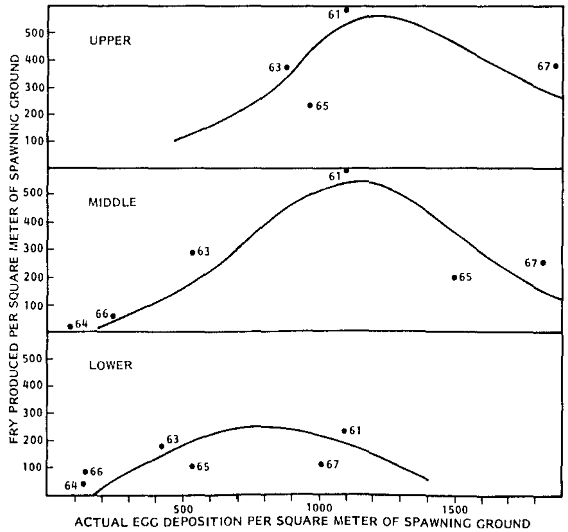

FIGURE 3.—Production curves for pink salmon in three study areas of Sashin Creek, 1961-67, showing relation between number of eggs in the streambed at the end of spawning and number of fry produced. Spawning did not occur in all areas in all years. Location of the 1961 point on the abscissal axis is not precise: success of spawning that year was based on subjective estimates (see McNeil et al. 1964). Curves are fitted by eye.

veloping initially at warmer temperatures had a survival advantage over those developing initially at cooler temperatures (Merrell 1962). In Sashin Creek, spawning closely follows the time of entry into the stream, so that early entry implies early spawning. Although the 1967 spawners entered Sashin Creek on the second earliest date on record, freshwater survival fell well below the predicted level (Figure 4). From the predicted freshwater survival of about 18% shown in Figure 4, the 1967 spawners should have produced 8 million fry.

On the basis of the relation of survival to time of spawning, McNeil (1969) suggested the dome-shaped freshwater production curve for Sashin Creek (Figure 2) may be the result of large escapements, more superimposition, and replacement of the more viable eggs from early spawning by less viable eggs from later spawning. From evidence available, there is little doubt that in Sashin Creek, progeny from early spawners have survival advantages over progeny from late spawners. I suggest, however, that when escapements are large, a point is reached where the number of eggs in the streambed determines ultimate survival, regardless of when spawning occurs.

The local climate and its resulting effects in the stream are extremely variable and have a marked influence on what actually constitutes an overseeded spawning bed at a specific time. Climate influences efficiency of spawning through variations in streamflows, so that overseeding does not occur at a fixed number of spawners. Similarly, streambed overseeding results from a dynamic interaction between the density of eggs in the gravel, certain ecological characteristics that define the fry production capability of the streambed, and prevailing climatic influences on the intragravel environment during the 6 to 8 mo eggs and alevins are in the streambed. Overseeding of streambed gravels will occur at lower egg densities when climatic influences (rainfall, stream discharge, ice cover, etc.) are more adverse to the intragravel environment.

Perhaps the most convincing evidence of streambed overseeding in Sashin Creek is the seasonal change in instantaneous (monthly) mortality coefficients of the 1963, 1965, and 1967 brood

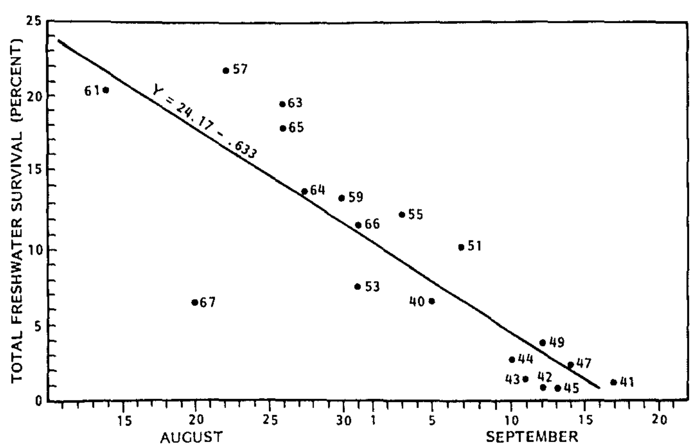

FIGURE 4.—Relation of freshwater survival of pink salmon in Sashin Creek to date when 50% of spawners had entered the stream. Data are from period 1940 to 1967; escapements<1,000 adults are excluded. The curve $Y = 24.17 - 0.633X$ fitted by least squares, where $X = 0$ corresponds to 10 August. Numbered points identify brood years (modified from McNeil 1968).

year progeny (Figure 5). Mortality coefficients for 1963 and 1965, the only years besides 1967 when estimates of live eggs and alevins were made after spawning, at hatching, and before emergence, are from McNeil (1968); the equation and notation for computing the instantaneous mortality coefficients for the 1967 brood year follow McNeil (1966). Time intervals assigned the three periods were 1.4 mo (from potential egg deposition through spawning), 2.0 mo (from spawning to hatching), and 3.7 mo (from hatching to emergence). The survival percentages by time periods are given in Table 6.

The impact of the heavy mortality between hatching and emergence in 1967 brood year progeny is evident in Figure 5. Monthly mortality coefficients during spawning were also high in

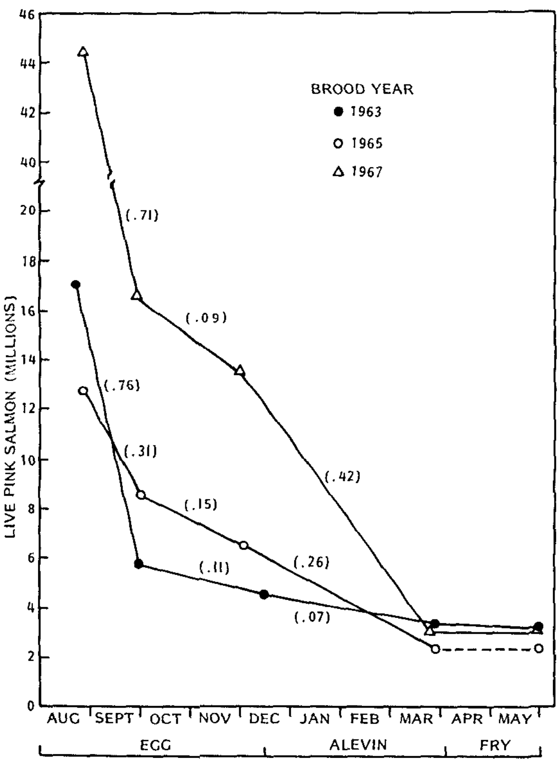

FIGURE 5.—Number of live pink salmon in Sashin Creek at the beginning and end of three periods in freshwater for 1963, 1965, and 1967 brood years. Numbers in parentheses show instantaneous monthly mortality coefficients from the egg through alevin stages. Mortality during fry migration (April and May) for the 1963 and 1967 brood years was negligible when measured as the difference between streambed and weir estimates of total fry production. The dotted extension of the 1965 brood year assumes no mortality during this period.

1963 and 1967 (0.76 and 0.71); the lower mortality during spawning in 1965 (0.31) probably reflects efficient spawning during the low streamflow condition prevailing that year (McNeil 1968). Mortality from spawning to hatching was similar, but mortality from hatching to emergence was strikingly different in each of the 3 yr (Figure 5). McNeil (1968) suggested the increase in overwinter mortality of 1965 brood year progeny (0.26) over 1963 brood year progeny (0.07) might have been related to a delayed mortality from low concentrations of dissolved oxygen in early embryo development during drought conditions in late summer and early fall in 1965. The number of spawners in 1967 was more than double the number in 1963 and 1965 (Table 1). The overwinter mortality of 1967 brood year progeny (0.42) was considerably higher than the high mortality of the 1965 brood year (0.26). The heavy overwinter mortality experienced by the 1967 brood year progeny may also have been caused by low dissolved oxygen concentrations. However, because no drought conditions existed while the progeny were in the gravel, these poor oxygen conditions probably resulted from the high density of eggs and alevins in the streambed.

SUMMARY

1. In 1967, 38,067 pink salmon spawned in Sashin Creek on Baranof Island, Alaska. Fifty-two percent of the spawners (19,639) were females; mean fecundity was 2,260 eggs/female and the potential number of eggs available for deposition totaled 44.4 million.

2. Entry of spawners into the stream was the second earliest on record; based on the previously consistent relation between time of entry and freshwater survival, the production of fry should have been greater than any previously recorded, but the 3 million fry produced were less than half the predicted number.

3. Mean female densities on the spawning grounds were $1.74/m^2$ in the upper area, $1.62/m^2$ in the middle area, and $1.17/m^2$ in the lower area. Densities were higher in the upper area at the beginning of spawning before significant levels of spawning occurred in the middle or lower areas. The tendency for spawners in the odd-year line to utilize the upper area of Sashin Creek may be due to genetic factors, including timing of escapements, and possibly differential marine survival favoring fry produced in the upper area.

4. Survival of progeny of the 1967 spawners was determined a) from stream entry to end of spawning, b) from end of spawning to hatching, c) from hatching to shortly before fry emergence, and d) from shortly before emergence to emergence and downstream migration of fry. In general, survival in each of these time periods was greatest in the upper area, lowest in the lower area, and intermediate in the middle area, a pattern consistent with previous survival studies at Sashin Creek. Total freshwater survival from potential egg deposition to preemerged fry was 10%, 7%, and 4% in the upper, middle, and lower areas, respectively, and 6.8% for the entire stream. The total number of migrating fry agreed closely with the estimates of preemerged fry in the streambed in late March.

5. Mortality of eggs and alevins was high during spawning, low between spawning and hatching, and high between hatching and emergence. Between 1 December 1967 and 25 March 1968, 11.1 million eggs or alevins disappeared within Sashin Creek streambed; 10.7 million of these were alive on 1 December. The high densities of eggs and alevins in the streambed after spawning and at hatching are believed to exceed the streambed capacity for fry production. High overwinter mortalities appear to have occurred shortly after hatching, probably from critical levels of dissolved oxygen in intragravel water. Critical oxygen levels apparently developed under average winter streamflow conditions due to the high biochemical oxygen demand placed on the streambed by high egg and alevin densities.

6. Recently hatched dead alevins disappear rapidly within the streambed because of biochemical decomposition and invertebrate scavenging. In comparison with dead alevins, dead eggs disappear slowly. In Sashin Creek, insect larvae and a planarian, probably *Polycelis borealis*, may be particularly important in removing dead salmon eggs and alevins from the streambed.

7. Several aspects of the historical patterns of pink salmon fry production in Sashin Creek suggest that streambed overseeding occurred in 1967. Fry production from the 1967 spawners falls on the descending limb of the fry production curves, both for the stream as a whole (since 1940) and for the individual stream areas (since 1961). From the historical pattern of time of adult entry and resulting freshwater survival, freshwater survival of 1967 brood year progeny should have been around 18% (or a production of 8 million fry). Survival of progeny during spawning and between spawning and hatching was adequate to reach these predicted levels. Overwinter mortalities (between hatching and emergence), however, were higher than any previously recorded. Compensatory losses during this period were probably due to the presence of too many eggs and alevins in the gravel for existing environmental conditions—streambed overseeding.

8. Overseeding does not invariably occur at some precise density of eggs, but rather is a dynamic interaction between densities of eggs and alevins in the gravel, certain ecological characteristics that define the fry production capability of the streambed, and the prevailing climatological features during the 6- to 8-mo period eggs and alevins reside in the streambed.

ACKNOWLEDGMENTS

The following people assisted with field studies on the 1967 spawners and freshwater survival of the progeny: David Brickell, Robert Coats, Richard Crone, Calvin Fong, Henry Kopperman, Derek Poon, and Roger Winchester.

LITERATURE CITED

BRICKELL, D. C.
1971. Oxygen consumption by dead pink salmon eggs in salmon spawning beds. M.S. Thesis, Univ. Alaska, College, 53 p.

BRIGGS, J. C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. Calif. Dep. Fish Game, Fish Bull. 94, 62 p.
1955. Behavior pattern in migratory fishes. Science (Wash., D.C.) 122:240.

CHAPMAN, D. W., AND T. C. BJORNN.
1969. Distribution of salmonids in streams, with special reference to food and feeding. *In* T. G. Northcote (editor), Symposium on salmon and trout in streams, p. 153-176. H. R. MacMillan Lect. Fish. Inst. Fish. Univ. B.C., Vancouver.

CLAIRE, E. W., AND R. W. PHILLIPS.
1968. The stonefly *Acroneuria pacifica* as a potential predator on salmonid embryos. Trans. Am. Fish. Soc. 97:50-52.

ELLIS, R. J.
1969. Return and behavior of adults of the first filial generation of transplanted pink salmon, and survival of their progeny, Sashin Creek, Baranof Island, Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 589, 13 p.
1970. *Alloperla* stonefly nymphs: Predators or scavengers on salmon eggs and alevins? Trans. Am. Fish. Soc. 99:677-683.

KENK, R.
1953. The fresh-water triclads (Turbellaria) of Alaska. Proc. U.S. Natl. Mus. 103:163-186.
MCDONALD, J. G.
1960. A possible source of error in assessing the survival of Pacific salmon eggs by redd sampling. Can. Fish Cult. 26:27-30.
MCLARNEY, W. O.
1967. Intra-stream movement, feeding habits, and population of the coastrange sculpin, *Cottus aleuticus*, in relation to eggs of the pink salmon, *Oncorhynchus gorbuscha*, in Alaska. Ph.D. Thesis, Univ. Michigan, Ann Arbor, 131 p.
MCNEIL, W. J.
1964a. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish Wildl. Serv., Fish. Bull. 63:575-588.
1964b. Redd superimposition and egg capacity of pink salmon spawning beds. J. Fish. Res. Board Can. 21:1385-1396.
1966. Distribution of spawning pink salmon in Sashin Creek, southeastern Alaska, and survival of their progeny. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 538, 12 p.
1968. Migration and distribution of pink salmon spawners in Sashin Creek in 1965, and survival of their progeny. U.S. Fish Wildl. Serv., Fish. Bull. 66:575-586.
1969. Survival of pink and chum salmon eggs and alevins. *In* T. G. Northcote (editor), Symposium on salmon and trout in streams, p. 101-117. H. R. MacMillan Lect. Fish. Inst. Fish. Univ. B.C., Vancouver.
MCNEIL, W. J., S. C. SMEDLEY, AND R. J. ELLIS.
1969. Transplanting adult pink salmon to Sashin Creek, Baranof Island, Alaska, and survival of their progeny. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 587, 9 p.
MCNEIL, W. J., R. A. WELLS, AND D. C. BRICKELL.
1964. Disappearance of dead pink salmon eggs and larvae from Sashin Creek, Baranof Island, Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 485, 13 p.
MERRELL, T. R., JR.
1962. Freshwater survival of pink salmon at Sashin Creek, Alaska. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 59-72. H. R. MacMillan Lect. Fish. Inst. Fish. Univ. B.C., Vancouver.
MOYLE, P.
1966. Feeding behavior of the Glaucous-winged Gull on an Alaskan salmon stream. Wilson Bull. 78:175-190.
NEAVE, F.
1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9:450-491.
NICOLA, S. J.
1968. Scavenging by *Alloperla* (Plecoptera: Chloroperlidae) nymphs on dead pink *(Oncorhynchus gorbuscha)* and chum *(O. keta)* salmon embryos. Can. J. Zool. 46:787-796.
REED, R. J.
1967. Observation of fishes associated with spawning salmon. Trans. Am. Fish. Soc. 96:62-67.
RICKER, W. E.
1962. Regulation of the abundance of pink salmon populations. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 155-201. H. R. MacMillan Lect. Fish. Inst. Fish. Univ. B.C., Vancouver.
SKUD, B. E.
1958. Relation of adult pink salmon size to time of migration and freshwater survival. Copeia 1958:170-176.
STUART, T. A.
1953. Spawning migration, reproduction and young stages of loch trout *(Salmo trutta L.)*. Scott. Home Dep., Freshwater Salmon Fish. Res. 5, 39 p.
U.S. GEOLOGICAL SURVEY.
1969. Water resources data for Alaska 1968. Part 1. Surface water records. U.S. Geol. Surv., Water Resour. Div., 155 p.
WELLS, R. A., AND W. J. MCNEIL.
1970. Effect of quality of the spawning bed on growth and development of pink salmon embryos and alevins. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 616, 6 p.
WICKETT, W. P.
1954. The oxygen supply to salmon eggs in spawning beds. J. Fish. Res. Board Can. 11:933-953.
1962. Environmental variability and reproduction potentials of pink salmon in British Columbia. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 73-86. H.R. MacMillan Lect. Fish. Inst. Fish. Univ. B.C., Vancouver.