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INFLUENCE OF EARLY MATURING
FEMALES ON REPRODUCTIVE
POTENTIAL OF COLUMBIA RIVER
BLUEBACK SALMON (*Oncorhynchus nerka*)

By RICHARD L. MAJOR and DONOVAN R. CRADDOCK



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ABSTRACT

Early maturing fish that have spent only one year in the ocean are common in the spawning escapements of Columbia River blueback salmon (*Oncorhynchus nerka*), particularly in the Okanogan tributary. The unusually high incidence of these 1-year-ocean fish in 1953, however, led to a study to determine the average fecundity of the ocean-age groups composing the runs, and to assess the effect of varying age and sex composition on estimates of reproductive potential.

A fecundity study in 1957-59 revealed that the average egg content of 1-year-ocean females was approximately one-third less than that of 2-year-ocean females. The average egg content of 3-year-ocean females was, in turn, about one-fourth greater than that of 2-year-ocean females.

Analysis of the age group fecundity and sex ratio data showed that the number of spawners or even female spawners does not always accurately portray the reproductive potential of an escapement. Erroneous reproduction estimates seriously distort escapement-return relationships.

INFLUENCE OF EARLY MATURING FEMALES ON REPRODUCTIVE POTENTIAL OF COLUMBIA RIVER BLUEBACK SALMON (*Oncorhynchus nerka*)

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Isolating the causes of variability in escapement-return relationships is among the most urgent problems in the biology and management of the Pacific salmon (*Oncorhynchus* spp.). Of primary concern are the causes of low numbers of fish in the returns. The fresh-water environment is widely thought to be more important than the marine environment in contributing to these subnormal returns.

Age and sex composition of the parent escapement are among the factors of recognized importance. For example, an escapement of normal size, but one containing females that are relatively few in number or small in size (young-ocean-age) will bring to the spawning ground a subnormal number of eggs. Hence, with all other factors affecting the return being similar, this escapement would produce a smaller return than would an escapement of fish normal in size, age, and sex composition.

Salmon runs to many Pacific coast streams contain small fish commonly called "jacks," that have matured after an ocean life shorter than normal for the species and the area. The occurrence of these precocious fish in the runs of Columbia River blueback salmon (*Oncorhynchus nerka*), known also as sockeye or red salmon, is unusual in three respects. First, they are relatively more abundant here than in most other systems, a feature compounded in the escapement because the gill net fishery below Bonneville Dam (fig. 1) is selective for larger fish. Second, they spawn mostly in a single tributary, the Okanogan River, although we occasionally observe individuals in the Wenatchee River system, the other major blueback spawning area in the Columbia River watershed. Finally, precocious blueback salmon (age 3₂'s)¹ in the Okanogan River escapements contain a relatively high proportion of females.¹

NOTE.—Approved for publication May 12, 1961. Fishery Bulletin 194.

The high incidence of 1-year-ocean fish in the escapement of 1953 attracted wide attention. In that year, 52,182 small blueback were counted passing over Rock Island Dam on the main Columbia; this was 34 percent of the total count of 151,747 (table 1). Escapement to the Wenatchee River system reportedly contained few if any 3₂'s in 1953.²

The Columbia River blueback runs include fish that mature at ages 3, 4, and 5 years. Although exact age-composition data are lacking, age 4 fish are known to dominate the runs. As a result, the relatively low return in 1957 revived interest in the 1953 escapement. Furthermore, examination of the escapement-return data (table 2) reveals that this cycle is one of only 2 out of 18 cycles observed, in which the return failed to exceed its parent escapement (1940 and 1953 escapements).

Efforts to explain low returns are ordinarily directed toward the isolation of one or more abnormal conditions which adversely affected production or survival of the progeny in fresh water. Among the factors of potential importance are: (1) unbalanced age and sex composition of the parent stock, (2) unfavorable environmental conditions during the early life history of the young fish and (3) mortalities connected with seaward migration.

¹ This method of designating the age of salmon, developed by Gilbert and Rich (1927), is described by Nelson (1959):

A fish resulting from an egg laid in the spawning gravels in 1950 and that migrated to the ocean in 1952 and returned in 1955 is called a five-two and designated thus, 5₂. Such a fish would have emerged from the gravels of the spawning beds in the spring of 1951 and would have spent 1 growing season or summer in fresh water. In referring to its fresh-water history it is called a two-fresh-water fish, because it migrated seaward in its second year. It would have spent 3 full growing seasons, i.e., 1952, 1953, and 1954, and part of a fourth year in the ocean; but in referring to its ocean history it is called a three-ocean fish, because it returned as an adult in the third year following its seaward migration. A fish that migrated to the ocean in its third year and returned in its sixth is called a six-three and is designated 6₃.

² Personnel communication with Leonard A. Fulton, then project leader of the Columbia River blueback salmon studies, now with the U.S. Fish and Wildlife Service, Washington, D.C., and Alfred C. Gastineau, manager, Leavenworth National Fish Hatchery, Leavenworth, Wash.

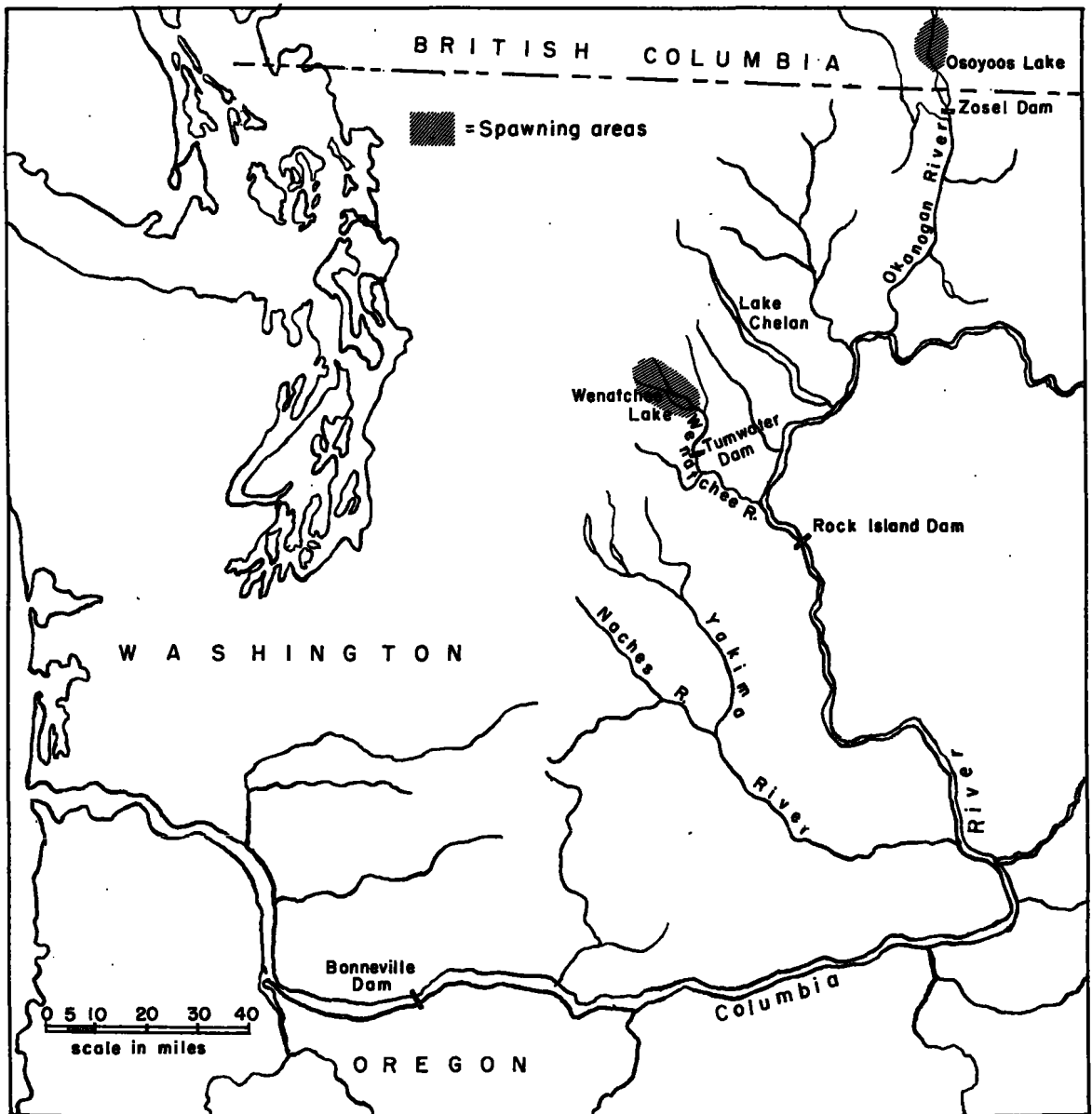


FIGURE 1.—The Columbia River and the major blueback salmon spawning areas and the locations of the dams important to this study.

TABLE 1.—Incidence of small (3₂) blueback in the Columbia River since 1945¹

| Year | Catch below Bonneville Dam | Bonneville Dam fishway count | Total run (catch below Bonneville Dam plus Bonneville Dam fishway count) | Rock Island Dam fishway count | | |
|------|----------------------------|------------------------------|--|-------------------------------|-------------------------|---------------|
| | | | | Total | Small (3 ₂) | Percent small |
| 1945 | 1,325 | 9,501 | 10,826 | 7,148 | 2,319 | 32 |
| 1946 | 25,601 | 74,376 | 99,977 | 44,970 | 6,457 | 14 |
| 1947 | 159,385 | 171,139 | 330,524 | 79,831 | 10,160 | 13 |
| 1948 | 11,647 | 131,541 | 143,188 | 84,184 | 4,912 | 6 |
| 1949 | 1,244 | 51,444 | 52,688 | 18,600 | 1,417 | 8 |
| 1950 | 33,576 | 77,993 | 111,569 | 50,134 | 11,283 | 22 |
| 1951 | 34,941 | 169,428 | 204,369 | 101,826 | 12,093 | 12 |
| 1952 | 135,717 | 184,645 | 320,362 | 114,349 | 9,478 | 8 |
| 1953 | 24,864 | 235,215 | 260,079 | 151,747 | 32,182 | 34 |
| 1954 | 48,474 | 130,107 | 178,581 | 91,234 | 14,486 | 16 |
| 1955 | 7,131 | 237,748 | 244,879 | 155,054 | 9,601 | 6 |
| 1956 | 45,322 | 156,418 | 202,240 | 92,443 | 17,830 | 19 |
| 1957 | 65,261 | 82,915 | 148,176 | 71,261 | 7,528 | 11 |
| 1958 | 190,325 | 122,389 | 312,714 | 98,716 | 18,233 | 18 |
| 1959 | 185,882 | 86,560 | 272,442 | 72,251 | 8,384 | 12 |

¹ Sources of data: Bonneville Dam fishway counts.—From Annual Fish Passage Report, North Pacific Division, Bonneville, The Dalles and McNary Dams, Columbia River, Oregon and Washington, 1958. U.S. Corps of Engineers, Portland and Walla Walla Districts. Also unpublished data, 1959. Catch below Bonneville Dam.—From Oregon Fish Commission, unpublished data. Rock Island Dam fishway counts.—From U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Portland, Oreg.

TABLE 2.—The escapement-return data for the Columbia River blueback runs for the brood years 1938–55

| Year (N) | Rock Island (Year N) (all age groups) | Total run (Year N+4) (all age groups) | Escapement-return ratio |
|----------|---------------------------------------|---------------------------------------|-------------------------|
| 1938 | 17,095 | 94,238 | 5.51 |
| 1939 | 19,591 | 73,484 | 3.75 |
| 1940 | 27,093 | 24,565 | 0.91 |
| 1941 | 963 | 10,826 | 11.24 |
| 1942 | 16,340 | 99,977 | 6.11 |
| 1943 | 17,665 | 330,524 | 18.71 |
| 1944 | 5,035 | 143,188 | 28.43 |
| 1945 | 7,148 | 52,688 | 7.37 |
| 1946 | 45,030 | 111,569 | 2.47 |
| 1947 | 79,831 | 204,369 | 2.56 |
| 1948 | 84,627 | 320,362 | 3.78 |
| 1949 | 18,600 | 260,079 | 13.98 |
| 1950 | 50,134 | 178,581 | 3.56 |
| 1951 | 101,826 | 244,879 | 2.40 |
| 1952 | 114,349 | 202,240 | 1.76 |
| 1953 | 151,747 | 148,176 | 0.98 |
| 1954 | 91,234 | 312,714 | 3.43 |
| 1955 | 155,055 | 272,442 | 1.75 |

Because the lack of more complete data prohibits a comprehensive examination of the latter two items, we shall examine only the first alternative in this report. If age 3₂ females were highly abundant in the 1953 escapement and if these small females contain fewer eggs than normal age 4₂ females, then the egg potential of that escapement may have been much lower than the number of spawners or even female spawners would indicate.

Our main objectives are, therefore: (1) to estimate mean fecundity of the various age groups that spawn in the Okanogan River and (2) to assess the effect of age and sex composition on estimates of egg potential of the Okanogan

River spawning escapements. In the light of our findings, we shall then examine and discuss other aspects of the early maturing fish.

The assistance of the Oregon Fish Commission aided this study materially. The authors are particularly indebted to Lawrence Korn for collecting the ovary samples in 1958.

METHODS AND MATERIALS

Collection and Preservation of Samples

Estimates of age group fecundity are from fish taken both in the tributary spawning streams and in the commercial catch below Bonneville Dam on the main Columbia River. In 1957 the racial sampling program of the International North Pacific Fisheries Commission made available to us 34 females taken at Tumwater Dam on the Wenatchee River and 23 captured at Zosel Dam on the Okanogan River. Samples from this source were not available in 1958; thus we had to find samples elsewhere, preferably from the commercial catch to avoid killing potential spawners in the tributaries. In 1958 sixty-two fish were selected from the commercial catch to represent the length-range of female blueback. Similar sampling provided 27 fish in 1959. Owing to a scarcity of small fish in the catch, the 1959 catch sample was augmented with 10 small fish taken from the fishway at Rock Island Dam.

Members of the 4₂ age group from both the Okanogan and Wenatchee areas are mixed in the catch, and we have no method of classifying catch samples into area of origin. Consequently, it is necessary to assume that fecundity estimates derived from this source accurately represent the Okanogan River spawning population. A statistical test to support this assumption is presented in a later section.

From each fish the fork length was recorded and a scale sample taken for age determination. Ovaries were removed, wrapped in cheesecloth, labeled, and preserved in 10-percent formalin. Total, fresh-water and ocean ages were determined by the age analysis unit at the Bureau of Commercial Fisheries Seattle Biological Laboratory.

Egg Enumeration

Estimation of total egg content for each fish proceeded as follows: Each pair of ovaries was washed of excess formalin, drained of excess moisture, freed of tissue, then weighed to the

nearest hundredth gram. Eggs were weighed and enumerated from cross-sectional samples from each ovary combined to approximate 10 percent of the total egg weight. Total egg count was then computed on a proportional weight-count basis, with the assumption that the sample was representative of the entire ovary.

Spawning Ground Surveys

Spawning grounds of the Okanogan River have been surveyed each year since 1947, except 1950. Gangmark and Fulton (1952) describe the method used to estimate the size of spawning populations.

Estimates of age and sex composition, computed for the years 1953 and 1956 through 1959, are based on standardized collections of fresh dead fish, which were picked up in proportion to their availability at intervals throughout the entire period when spawners are dying.

The sampling methods described herein are not rigorous from a statistical viewpoint. Yet we believe them to be adequate for purposes of this report, which represents the difficult transition from the qualitative to quantitative stages of investigation. Under appropriate headings of the next section are discussed certain preliminary tests which are pertinent to the sampling and to the data thereby derived.

RESULTS

Age Group Fecundity

In the previous section we indicate that because the catch contains 4₂'s from both the Wenatchee and Okanogan populations, we can merely assume that mean fecundity estimates derived from this source are representative of the Okanogan population. The assumption is supported by the following test:

We hypothesize that no fecundity difference exists between the 4₂'s of the two river systems. Comparison of the 1957 sample-means of 16 Okanogan and 17 Wenatchee fish by t-test reveals no significant difference at the 5 percent level ($t=0.15$ with 15 d.f.). On the basis of this evidence the hypothesis is not rejected, and, with reasonable assurance that it holds, we assume that the fecundity difference is not large and that estimates derived from the catch will accurately represent either area.

To determine whether a bias exists in our method of estimating the mean egg content of individual fish, we used a t-test to compare the actual and estimated mean egg content of a randomly selected subsample of 21 fish (table 3). The average difference between the actual and estimated means is 40 eggs, the standard error of the mean, 27 eggs. Although it appears that we are overestimating, the difference is not significant at the 5 percent level ($t=1.49$ with 20 d.f.).

The results of the fecundity study are shown in table 4 and figure 2. Of the statistics shown, the mean and range figures provide the basis for age group comparison, and the standard deviation and the standard error of the mean are presented merely as points of additional interest. Differences between the numbers of fish reported in table 4 or figure 2 and those reported in the original sample are due to the omission of aberrant specimens (2 females, 1 each in 1957 and 1959, had but a single ovary) and those fish whose ages were indeterminable because of scale erosion.

Examination of table 4 or figure 2 discloses that the egg content of individual fish within an age group sample varied by as much as 2,749 eggs. Little between-year variation is evident for the means of a single group. The variation between the means of the 4₂'s and the 5₃'s, different age groups having similar ocean age, is also small.

TABLE 3.—Estimated and actual egg counts of a randomly selected subsample, 1957-59

| Fish No. | Estimated count | Actual count | Difference |
|--------------|-----------------|--------------|------------|
| 1..... | 1,695 | 1,773 | -78 |
| 2..... | 2,007 | 1,958 | 49 |
| 3..... | 2,118 | 2,018 | 100 |
| 4..... | 3,067 | 3,027 | 40 |
| 5..... | 4,272 | 4,088 | 184 |
| 6..... | 2,581 | 2,304 | 277 |
| 7..... | 2,094 | 2,074 | 20 |
| 8..... | 1,611 | 1,697 | -86 |
| 9..... | 3,823 | 3,000 | -177 |
| 10..... | 1,906 | 1,759 | 147 |
| 11..... | 2,038 | 2,000 | 38 |
| 12..... | 1,872 | 1,852 | 20 |
| 13..... | 2,002 | 1,984 | 18 |
| 14..... | 2,840 | 2,706 | 134 |
| 15..... | 3,662 | 3,562 | 100 |
| 16..... | 2,678 | 2,920 | -242 |
| 17..... | 2,488 | 2,608 | -120 |
| 18..... | 2,676 | 2,560 | 116 |
| 19..... | 3,237 | 3,183 | 54 |
| 20..... | 3,437 | 3,300 | 137 |
| 21..... | 3,172 | 3,055 | 117 |
| Total..... | 54,276 | 53,428 | 2,254 |
| Average..... | 2,584.57 | 2,544.19 | 40.38 |

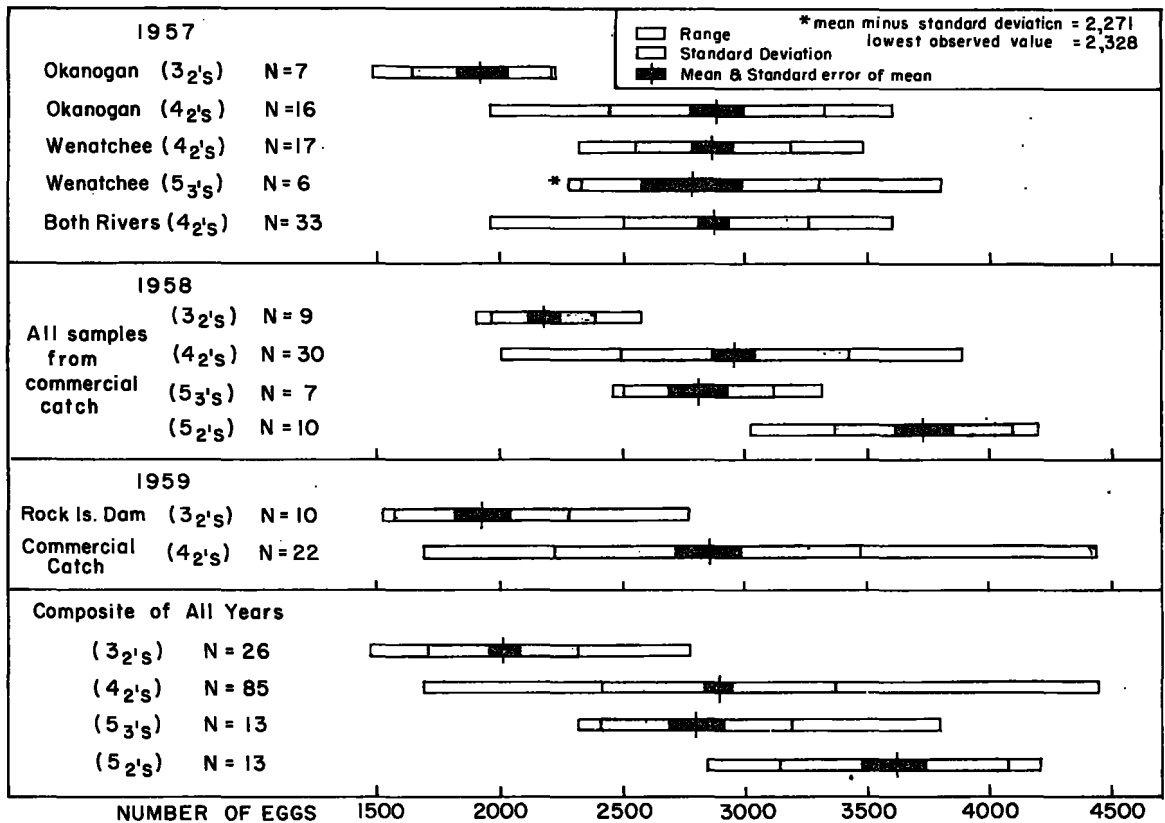


FIGURE 2.—Fecundity statistics of the blueback salmon age group samples.

TABLE 4.—Fecundity statistics of the age-group samples of Columbia River blueback salmon 1957-59

| Sample | | Fecundity information | | | | | |
|-----------|------------------|-----------------------|--------|-------|--------------------|----------------------------|-------------|
| Year | Location | Age group | Number | Mean | Standard deviation | Standard error of the mean | Range |
| 1957 | Okanogan | 3 ₂ | 7 | 1,928 | 283.93 | 107.31 | 1,478-2,216 |
| | Do | 4 ₂ | 16 | 2,887 | 437.03 | 109.26 | 1,959-3,593 |
| | Wenatchee | 4 ₂ | 17 | 2,871 | 317.05 | 76.90 | 2,314-3,481 |
| | Do | 5 ₃ | 6 | 2,890 | 512.89 | 209.43 | 2,328-3,799 |
| 1958 | Both rivers | 3 ₂ | 33 | 2,879 | 374.63 | 65.21 | 1,955-3,593 |
| | | 4 ₂ | 9 | 2,173 | 214.84 | 71.61 | 1,900-2,574 |
| | | 5 ₂ | 7 | 2,952 | 464.42 | 84.79 | 1,990-3,854 |
| 1959 | Rock Island Dam | 3 ₂ | 10 | 3,811 | 302.90 | 114.47 | 2,454-3,319 |
| | | 4 ₂ | 10 | 3,731 | 369.64 | 116.90 | 3,034-4,206 |
| | | 5 ₂ | 7 | 1,931 | 358.57 | 113.40 | 1,526-2,774 |
| All years | Commercial catch | 3 ₂ | 22 | 2,851 | 625.85 | 133.44 | 1,697-4,446 |
| | | 4 ₂ | 26 | 2,014 | 306.71 | 60.15 | 1,478-2,774 |
| | | 5 ₃ | 85 | 2,897 | 477.13 | 51.75 | 1,697-4,446 |
| | | 5 ₂ | 13 | 2,801 | 394.46 | 109.39 | 2,328-3,799 |
| | | 5 ₂ | 13 | 3,609 | 465.96 | 129.22 | 2,847-4,206 |

The most striking feature is the within-year difference in mean fecundity between age groups with different ocean age. The mean fecundity of the 3₂'s was lower than that of the 4₂'s by 33, 26, and 32 percent for the years 1957, 1958, and 1959, in that order. On a similar basis we find that the 1958 3-year-ocean females (5₂'s) averaged 26 percent more eggs than the dominant 4₂ age

group for that year. The 3-year means of fecundity were 2,014, 2,897, 2,801, and 3,609 for the 3₂, 4₂, 5₃, and 5₂ age groups, respectively.

Variations in the measuring techniques and in the sampling sites cast sufficient doubt on the validity of the fork-length data to preclude their extensive use. For that reason we have limited the analysis to comparison of age group means.

We recognize that such comparisons are less sensitive than comparison by analysis of covariance but feel, nevertheless, that the means, usually derived from stratified samples, fairly represent the age groups.

Effect of Age Group Fecundity and Sex Ratio on Egg Potential

Our second specific objective is to assess the effect of age and sex composition on the egg potential of Okanogan River spawning escapements. Using the estimated age and sex composition (table 5)³ and the age group fecundity information, we have calculated the egg potential of the Okanogan River spawning escapements of 1953 and 1956 through 1959 in three ways:

Estimate (A) is based on the number of fish in the escapement and on the assumptions of an even sex ratio and a mean fecundity of 3,000 eggs per female.

Estimate (B) is based on the number of females in the escapement and on the assumption of 3,000 eggs per female.

Estimate (C) is based on the number of females in each age group and the mean fecundity of the age groups present.

It is clearly evident from the results (table 6) that the effect of age and sex composition on the egg potential of the Okanogan River blueback spawning escapements varies widely from year to year. In 1957 and 1959 the individual variables offset one another and resulted in little over-all change in estimated egg potential. In sharp contrast, the combined influence of the two factors

³ Because the 3₂'s are rarely found in streams other than the Okanogan, we believe that the discrepancies between the number of small fish (3₂'s) counted at Rock Island Dam (table 1) and the 3₂'s in the estimated Okanogan population (table 5) are due to (1) errors in the spawning ground estimates, (2) errors in the large-small breakdown at Rock Island Dam, and (3) mortalities that occur between the two sites.

reduced the estimated egg potential by 43, 24, and 60 percent in 1953, 1956, and 1958, respectively.

When we consider the variables separately to determine their relative importance we see that sex ratio was the most important factor in 1956, 1958, and 1959, whereas age group fecundity was the greater source of error in 1953 and 1957.

To illustrate the combined effect of sex ratio and age group fecundity on egg potential and ultimately on escapement-return relationships, let us compare from table 6 the three measures of egg potential for the years 1957 and 1958. Using estimate (A), we note that the egg potential in 1958 was 1.24 times as large as that of 1957. From these data we might expect the return from the 1958 brood to be 1.24 times as great as the return from the 1957 brood, all other factors affecting the return being similar.

Correcting for the numbers of female spawners in each age group and the mean fecundity for each age group (estimate C), we note that the egg potential in 1958 is only about one-half the egg potential in 1957. Other factors affecting the return being similar, we might expect that the return from the 1958 escapement would be only one-half as large rather than 1.24 times as large as the return from the 1957 escapement.

By the same reasoning, we would expect that the 1953 escapement would produce a return only one-half as large as would an escapement of the same size, but normal with respect to age and sex composition.

We fully realize that the escapement-return relationship of 1953-57 would have been poor

TABLE 5.—Estimates of the age and sex composition of the Okanogan River blueback spawning populations 1953, 1956-59

| Year | Spawning ground estimate | Number in sample | Number and percentage— | | | | | | | |
|------|--------------------------|------------------|------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| | | | In each age group | | Of each sex | | | | | |
| | | | 3 ₁ | 4 ₁ | 3 ₂ | | 4 ₂ | | Both | |
| | | | | | Males | Females | Males | Females | Males | Females |
| 1953 | 34,260 | 216 | 29,669 (87) | 4,591 (13) | 16,071 (57) | 12,698 (43) | 3,323 (72) | 1,267 (28) | 20,295 (59) | 13,965 (41) |
| 1956 | 39,256 | 323 | 9,775 (25) | 29,481 (75) | 6,383 (65) | 3,392 (35) | 16,244 (55) | 13,237 (45) | 22,627 (58) | 16,629 (42) |
| 1957 | 25,350 | 695 | 7,630 (30) | 17,720 (70) | 5,074 (67) | 2,556 (33) | 6,751 (38) | 10,969 (62) | 11,825 (47) | 13,525 (53) |
| 1958 | 31,035 | 208 | 26,100 (84) | 4,935 (16) | 21,324 (82) | 4,776 (18) | 1,044 (39) | 2,991 (61) | 23,268 (75) | 7,767 (25) |
| 1959 | 40,650 | 326 | 6,098 (15) | 34,552 (85) | 3,232 (53) | 2,866 (47) | 14,581 (42) | 19,971 (58) | 17,813 (44) | 22,837 (56) |

TABLE 6.—Estimated egg potential of Okanogan blueback salmon escapement using three methods of estimation, 1953 and 1956–59

[In millions of eggs]

| Year | Method | | |
|-----------|--------|----|----|
| | A | B | C |
| 1953..... | 51 | 42 | 29 |
| 1956..... | 59 | 50 | 45 |
| 1957..... | 38 | 41 | 37 |
| 1958..... | 47 | 23 | 19 |
| 1959..... | 61 | 69 | 62 |

compared with other years, regardless of the influence of 1-year-ocean fish. This indicates that other factors also affect the relationship. We have shown specifically, however, that the presence of abnormal numbers of 1-year-ocean females reduced the egg potential of the 1953 Okanogan escapement to a level well below that expected of a run similar in size but normal in age and sex composition. Although the impact of 1-year-ocean females would have been relatively less in terms of the riverwide escapement, we feel that initial overestimation of the egg potential accentuated the poor escapement-return relationship of 1953–57. It is evident that future analyses of the Columbia River blueback escapement-return data can be improved initially by refining the escapement statistic with the added consideration of sex ratio and age group fecundity.

DISCUSSION

Thus far, we have considered the effect of the lower fecundity of 1-year-ocean fish on the egg potential of a spawning stock and have pointed out that, because of fluctuations in relative abundance of 1-year-ocean fish in the escapement, the egg potential is sometimes considerably less than the number of spawners or even female spawners indicates. It is appropriate to examine other aspects of the occurrence of these 1-year-ocean fish in the Columbia River blueback runs, including their direct and indirect importance to the fishery and the cause of their occurrence.

Contribution of 3₂'s to the Fishery

Lack of sustained yearly information about the composition of the escapement at Bonneville Dam hinders efforts to calculate the exploitation rate of the various age groups. The Oregon Fish Com-

mission⁴ reports that in 1957 the fishery took 9 percent of the 3₂ age group as compared to 52 percent of the 4₂ age group. The 3₂'s thus contribute little to the catch but are heavily represented in the escapement. Their relative significance on the Okanogan spawning grounds is further increased by the fact that they return, almost without exception, to that stream. By reason of sheer abundance then, the 3₂'s often contribute heavily to the egg potential of the Okanogan escapement. Utilizing the number of female spawners in each group and the appropriate average fecundity of each age group, we calculate that the 3₂'s contributed 88, 15, 14, 54, and 9 percent of the total egg potential for the years 1953, and 1956 through 1959, respectively.

Because the 3₂'s are relatively invulnerable to the gill net fishery as it is now conducted and, therefore, contribute significantly to the reproductive capacity of the Okanogan escapements, they might be considered as a safety factor in the escapement to that river system. The apparent advantages of such a feature would be nullified, however, if the recurrence of the 3₂'s were genetic in nature. For the 3₂'s to function beneficially as a safety factor, they must be able to produce catchable 4₂'s as well as 3₂'s. Otherwise, the contribution of the Okanogan River blueback populations to the commercial fishery would, in time, be eliminated.

Age at Maturity—Genetic or Environmental?

The question of whether age at maturity of Pacific salmon is the result of environmental or genetic influence or a combination of the two has only recently attracted attention. Godfrey (1958) working with sockeye salmon at Rivers Inlet and Skeena River, B.C. (Canada), concludes that "age at maturity is governed to a great extent by the inheritance of certain genetic components of the parents. Some environmental influence is a possibility but must be proven."

On the Deschutes River in Washington States 3-year-old chinook salmon (*O. tshawytscha*) females were crossed with 2- and 3-year-old males, separately to determine whether or not precocious parents tend to produce precocious offspring

⁴ Westrheim, S. J., and others. 1959. Columbia River investigations progress report October 1957–April 1958. Oregon Fish Commission (Portland), February, 1959, 54 p. Processed.

(Washington Department of Fisheries, 1959). The cross that involved the 2-year-old male produced a significantly larger number (168) of 2-year-old fish than did the cross that involved the 3-year-old male (79).

Ricker⁵ using Adams River, B.C. (Canada) data, found that "observed differences between broods, in age of males at maturity is strongly influenced by the age of their fathers."

Certain evidence, on the other hand, seems to minimize the role of genetics in the recurrence of precocious blueback salmon: (1) the lack of a significant correlation between the 1-year-ocean bluebacks of year n and those of year $n+3$; (2) the scarcity of these small fish in the Wenatchee system. In 1939-43, the years of the Grand Coulee Relocation Program, blueback salmon were intercepted at Rock Island Dam and transported to Lakes Osoyoos and Wenatchee (Fish and Hanavan, 1948). Although exact data are lacking, generally as many small 1-year-ocean fish were placed in the Wenatchee as in the Okanogan system. Were the recurrence of 3₂'s entirely genetic, we could normally expect a continuation of the strain in each system. The absence of 1-year-ocean fish in the Wenatchee runs suggests that the conditions in that system simply did not lend themselves to the production of 1-year-ocean fish. This aspect of the problem is clouded, however, by the lack of knowledge concerning the kokanee-blueback⁶ relationship.

Another question concerned with the function of the 3₂'s as a safety-factor is that of the relative survival of eggs and progeny resulting from small females. The ability of the small females to bury the eggs deep enough to protect them from physical rigors is also subject to speculation.

CONCLUSIONS

Female Columbia River blueback salmon that spawn after spending only one year in the ocean contain roughly one-third fewer eggs than normal 2-year-ocean females.

⁵Ricker, W. E. Evidence for environmental and genetic influence on certain characters which distinguish stocks of the Pacific salmon and steelhead trout. Fisheries Research Board of Canada, Nanaimo, B.C. Unpublished manuscript, 1959.

⁶Individuals of the species that complete their entire life cycle in fresh water.

Escapements to the Okanogan spawning tributary exhibit wide annual fluctuations in age and sex composition. Abnormal numbers of 1-year-ocean females can greatly reduce the egg potential of a particular escapement and, in turn, distort the escapement-return relationship involving that brood.

The unusually high incidence of 1-year-ocean fish in the 1953 Okanogan escapement reduced the egg potential to about one-half that expected of an escapement similar in size but normal in age and sex composition. It appears this initial overestimation of egg potential may have accentuated the relatively poor riverwide escapement-return relationship of 1953-57.

Although the 1-year-ocean fish have a lower fecundity and contribute little directly to the commercial fishery as it is now conducted, they may, by virtue of their contribution to reproduction, have a positive value as a safety factor in the escapement.

Further assessment of the value of 1-year-ocean fish requires more exact knowledge about (a) the role of genetics in the recurrence of the 3₂'s, (b) the relative survival of eggs deposited by large and small females, and (c) the relative viability of progeny produced by 2-year-ocean parents, 1-year-ocean parents, and combinations of both.

SUMMARY

Although 1-year-ocean fish are common in the spawning escapements of the Columbia River blueback salmon, their contribution to the reproductive capacity of an escapement has not previously been assessed.

The need for assessment became evident when the 1953 Rock Island escapement, which contained unprecedented numbers of 1-year-ocean fish, failed to produce a total run in 1957 that exceeded itself.

A fecundity study, conducted from 1957-59, revealed that the 1-year-ocean females contained 33, 26, and 32 percent fewer eggs than the 2-year-ocean fish in those years, respectively. The pooled-means of numbers of eggs per female were 2,014 for 1-year-ocean fish and 2,897 for 2-year-ocean fish.

Three methods were used to estimate the egg potential of 1953 and 1956 through 1959 Okanogan River escapements. The first method was based on the assumptions that one-half of the estimated spawners were females and that the average egg content per female was 3,000 eggs. Method 2 had as its base the observed number of female spawners and an average fecundity of 3,000. The third and most refined method was based on the number of females in each age group and the average fecundity of each age group.

Comparison of the results of the three methods shows that failure to correct for sex ratio and fecundity when estimating the reproductive capacity of an escapement can seriously distort the accuracy of the escapement statistic for use in escapement-return analyses.

The high incidence of small females in the 1953 Rock Island escapement substantially reduced the egg potential normally expected of an escapement of that size. This distortion of the escapement statistic accentuated the poor escapement-return relationship of 1953-57.

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