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Redd Superimposition and Egg Capacity of Pink Salmon Spawning Beds[1]

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ABSTRACT

A study of egg recruitment to pink salmon spawning beds in two southeastern Alaska streams (Indian Creek and Harris River) has shown that egg loss during spawning increases as the density of female spawners increases. Mortality was caused for the most part by superimposition of redds.

A mathematical model of spawning success is derived. The model assumes that the curve describing the recruitment of eggs to a spawning bed is asymptotic and that pink salmon females spawning within any defined spawning ground select the sites of their redds at random. The model is used to estimate the asymptotic limit of the egg recruitment curve for a Harris River spawning bed. Levels of mortality associated with various densities of spawning female pink salmon are predicted for Harris River from the model.

INTRODUCTION

There is evidence that the capacity of a spawning bed to produce fry is impaired by excessive numbers of adults spawning. Ricker (1954, 1958), Neave (1958), and Wickett (1958, 1962) reported that the average yield of fry approached an upper limit as the density of spawners approached an "optimum level". Ricker concluded that maximum fry yield would most likely be realized by allowing spawners to attain a density intermediate between low and high (curve A, Fig. 1). A mathematical model describing an asymptotic relation (curve B, Fig. 1) between egg deposition and recruitment of juvenile fishes has been developed by Beverton and Holt (1957).

Important objectives of research on pink salmon (*Oncorhynchus gorbuscha*) are to understand factors that place an upper limit on the potential of spawning beds to produce fry and to determine the optimum density of adults that should be allowed to spawn. This paper considers one problem pertaining to these questions—mortality from redd superimposition during spawning.

Redd superimposition becomes an important mortality factor for Pacific salmons at high spawning densities (Gilbert and Rich, 1937; Smirnov, 1947; Morgan and Henry, 1959). In one instance, mortality of pink salmon eggs was estimated to be near 90% at high spawning densities (Semko, 1954). The question of competition for spawning space between pink and sockeye (*O. nerka*) salmon in the Karluk River system, Alaska, was considered by Rounsefell (1958), who concluded that large escapements of pink salmon caused a significant reduction in the reproductive potential of sockeye salmon because of crowding on the spawning beds.

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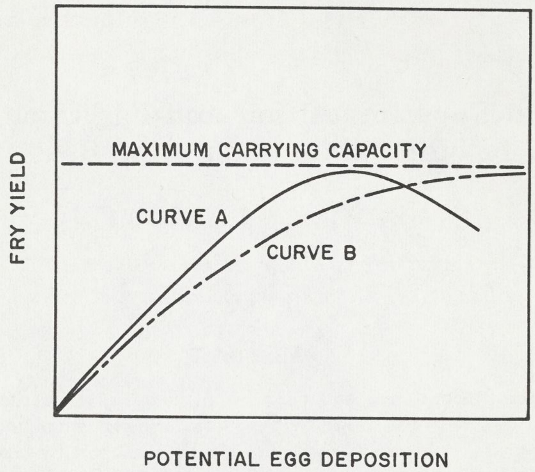

FIG. 1. Postulated relation between potential egg deposition and fry yield of pink salmon. See text for discussion of curves.

The number of fry produced from a spawning bed cannot exceed the number of eggs present at the end of spawning; hence, redd superimposition might place an ultimate upper limit on the potential of spawning beds to produce fry. It is postulated that egg displacement from the spawning bed increases as the density of spawning females increases, ultimately reaching a point where females displace from the spawning bed a number of eggs equal to the number they deposit. In this paper, evidence showing a direct relation between egg loss and density of females spawning is presented; and a mathematical model of spawning success is developed. The model is used to estimate the egg capacity of a pink salmon spawning bed in a southeastern Alaska stream and to predict mortality from redd superimposition.

FIELD STUDY METHODS

The success of pink salmon spawning was evaluated in two southeastern Alaska streams—Harris River and Indian Creek—which are located on Prince of Wales Island about 40 miles west of Ketchikan. Observations were made on intertidal spawning beds utilized almost exclusively by pink salmon. The Harris River study area encompassed 6093 m^2 and the Indian Creek study area 3905 m^2.

A measure of spawning success was obtained from observed differences between two population estimates—(1) the number of pink salmon females estimated to spawn in a study area, and (2) the equivalent number of females required to deposit the number of eggs estimated to be present in the study area after spawning. Methods used to obtain these estimates will be described.

ESTIMATING NUMBER OF FEMALES SPAWNING

The number of pink salmon females spawning in each study area was estimated by counting daily those that were digging and protecting redds and by determining from tagging studies the average length of time a female remained on the spawning ground. The method is illustrated with pink salmon spawning in Harris River in 1960.

The number of pink salmon females counted daily in the Harris River study area is shown by an eye-fitted curve in Fig. 2. The area under the curve represents 31,700 female days. To obtain an estimate of the average duration a pink salmon female occupied the spawning ground, 38 tagged pink salmon

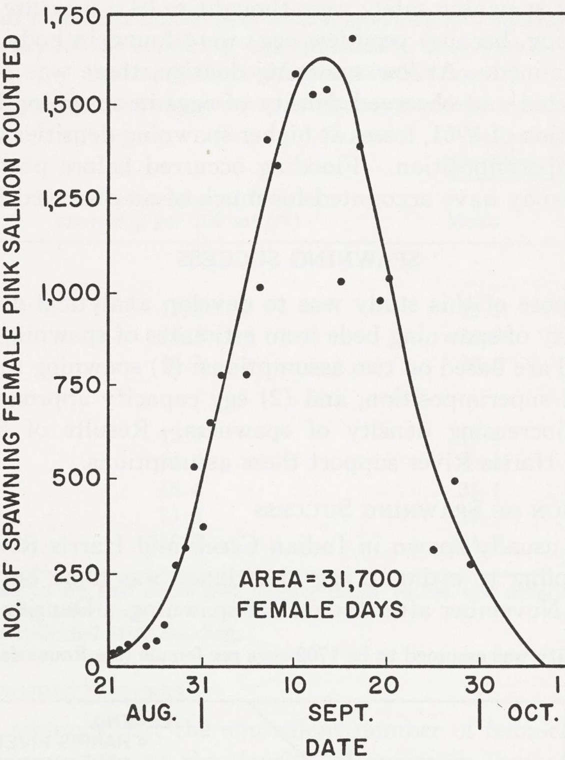

FIG. 2. Daily counts of female pink salmon spawning in the Harris River study area in 1960.

females were observed daily. This gave an average of 9.8 days. One day was added to the total because it was assumed that the average female was present one-half day before the time of the first observation and one-half day after the time of the last. The number of females spawning in the Harris River study area was estimated to be

$$\frac{31{,}700 \text{ female days}}{10.8 \text{ days}} = 2930 \text{ females.}$$

Similar estimates were made for other brood years in Harris River and for Indian Creek. The method and its assumptions are described in more detail by McNeil (1962).

Estimating Equivalent Number of Females Spawning Safely

The abundance of eggs in each study area was estimated by sampling with a hydraulic sampler after spawning (McNeil, 1962). An equivalent number of females spawning safely (i.e. without having their eggs subsequently dislodged) was calculated by dividing the estimated number of eggs in a study area by the assumed average fecundity of pink salmon[2].

Differences between the estimated number of females spawning and the equivalent number spawning safely were thought to be a measure of voided eggs lost during spawning, because very few eggs were found in body cavities of the spent females examined. At low spawning density, there was good agreement between the expected and observed density of eggs in spawning beds; and with the possible exception of 1961, losses at higher spawning densities were attributed mostly to redd superimposition. Flooding occurred before postspawning sampling in 1961 and may have accounted for much of an observed high egg loss.

SPAWNING SUCCESS

A major purpose of this study was to develop analytical methods for predicting egg capacity of spawning beds from estimates of spawning success. The methods described are based on two assumptions: (1) spawning success is limited primarily by redd superimposition, and (2) egg capacity approaches an asymptotic limit with increasing density of spawners. Results of field studies in Indian Creek and Harris River support these assumptions.

Field Observation of Spawning Success

Pink salmon usually spawn in Indian Creek and Harris River during September, and sampling to estimate egg abundance was done between late September and early November after the end of spawning. Density of female pink

[2]Average fecundity was assumed to be 1700 eggs per female (see Rounsefell, 1957).

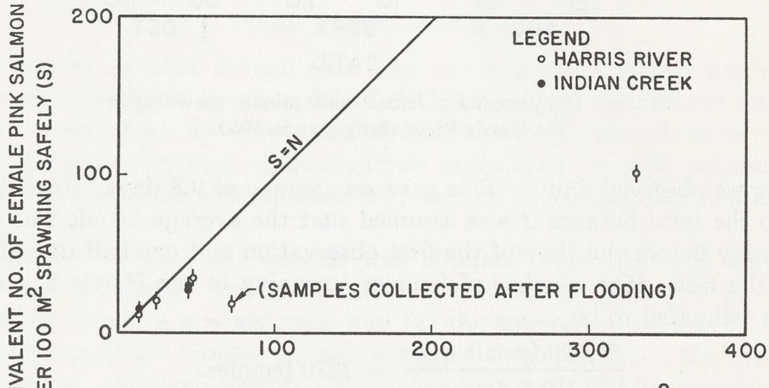

Fig. 3. Observed relation between number of female pink salmon spawning and equivalent number spawning safely. Lengths of vertical bars correspond to 90% confidence interval estimates of population mean.

salmon spawning in the Indian Creek and Harris River study areas and the equivalent number of females estimated to have spawned safely are given in Table I. It is noteworthy that the estimated equivalent number of females spawning safely (S) was consistently less than the estimated total number of females spawning (N), where $N > 24$ females per 100 m^2. Values of S are plotted against their corresponding values of N in Fig. 3 to illustrate the observed relation between these parameters.

TABLE I. Estimated number of female pink salmon spawning and equivalent number required to spawn safely to deposit the number of eggs estimated to be present in the study areas after spawning, Harris River and Indian Creek.

Study area and year	Estimated number of females spawning per 100 m^2 (N)	Estimated equivalent number spawning safely per 100 m^2 (S): Mean	90% confidence limits of mean
Indian Creek			
1958	12.9	15.5	±6.7
1959	46.3	26.9[a]	±7.6
1960	46.3	28.6	±8.6
Harris River			
1958	12.9	12.4	±6.0
1959	24.8	19.6[a]	±4.6
1960	48.4	35.1	±7.8
1961	73.0	18.2[a b]	±6.5
1962	330.0	101.7	±15.9

[a]Samples collected on two dates and having mean values not differing significantly were pooled to obtain a single estimate.
[b]Samples were collected after flooding.

Model of Spawning Success

The model assumes that the equivalent number of females spawning safely approaches an asymptote as the density of spawners increases. Figure 4 illustrates the hypothetical relation between total spawners (N) and the equivalent number laying their eggs safely (S). The asymptotic limit of the equivalent number of spawners that can deposit their eggs safely is designated as "L".

To assist in understanding the model and its assumptions, we will first consider a spawning bed to be represented by a "checkerboard" pattern. Each square of the checkerboard will be equivalent to the average area excavated by a female. The number of squares will equal the number of such sites available for spawning (L), and each female is assumed to select a square at random, i.e. independent of whether or not spawning had previously occurred at the site. Squares receiving more than one female will retain, on the average, a number of eggs equivalent to that deposited by one female.

In a natural spawning bed redds lack the symmetry described by the checkerboard model, and also, redds would in most instances be partially rather than totally superimposed. We will assume that the frequency of occurrence of partially superimposed redds is proportional to the degree of superimposition. Thus the number of eggs lost from superimposition would be equivalent to that of the checkerboard model, and the simplifying assumption that spawning sites are arranged in checkerboard pattern would not affect the model.

The most questionable assumption is that of random distribution of females. Because female pink salmon establish and defend territories during spawning, the assumption that occupation of positions by earlier spawners does not influence the choice of spawning sites by later spawners might not be strictly correct. Questions requiring further investigation include: (1) How long does a female effectively defend her territory? (2) How specific is the location of her territory in relation to the points at which she deposited her eggs? (3) What influence does increasing spawning density have on territorial behaviour?

The equation used to describe spawning success is:

$$S = L(1-e^{-N/L}) \quad \quad . . . (1)$$

Equation 1 can be derived by two methods—from a differential equation and from the Poisson distribution.

Derivation from a differential equation. With each small increment in N (ΔN) there will occur a small increment in S (ΔS) (see Fig. 4). The increments ΔS will decrease in size as N increases and ΔN is held constant. The size

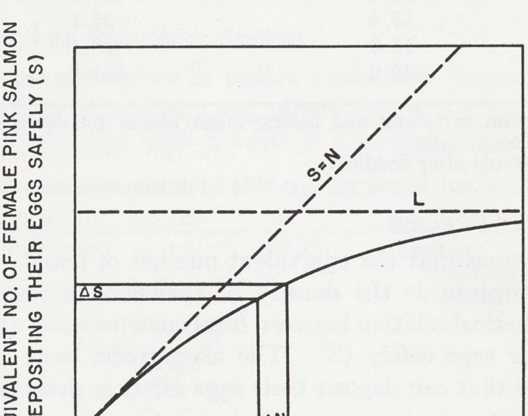

Fig. 4. Relation between number of females spawning in a given area and the equivalent number depositing their eggs safely. ΔS is an increment in S associated with an increment in N(ΔN).

of an increment ΔS will be proportional to the probability that a female entering a spawning ground will select a site which had not already been utilized by another female for spawning. Thus, the increment in S is the increment in N multiplied by the proportion of the area not previously utilized for spawning at the time ΔN occurs, i.e.

$$\Delta S = \frac{(L-S)}{L} \Delta N \qquad . . . (2)$$

Equation 2 is assumed to be independent of time; hence, spawning behaviour is assumed to be constant throughout the spawning period. Dividing by ΔN and taking the limit as $\Delta N \to 0$ gives:

$$\lim_{\Delta N \to 0} \frac{\Delta S}{\Delta N} = \frac{dS}{dN} = \frac{(L-S)}{L} \qquad . . . (3)$$

where the function is continuous, positive, and single valued between $S = 0$ and $S = L$.

Integrating Equation 3 gives:

$$-ln(L-S) = \frac{N}{L} + C \qquad . . . (4)$$

or:

$$L-S = C' (e^{-N/L}) \qquad . . . (5)$$

The value:

$$C' = L \qquad . . . (6)$$

is obtained by letting $N = 0$.

Substitution of Equation 6 in Equation 5 leads directly to Equation 1:

$$S = L(1-e^{-N/L}).$$

Derivation from the Poisson distribution. Let r be the number of females spawning per available site and let λ be the expected mean frequency of females spawning per available site. In this instance, r is assumed to follow the Poisson distribution where the probability of success can be considered to be a continuous, non-negative function of the number of independent trials (Koopman, 1950; Dixon and Massey, 1957). We thus obtain:

$$\text{Prob}(r) = \frac{(\lambda^r)(e^{-\lambda})}{r!} \qquad . . . (7)$$

$$\text{Prob}(r=0) = e^{-\lambda} \qquad . . . (8)$$

$$\text{Prob}(r \neq 0) = (1-e^{-\lambda}) \qquad . . . (9)$$

The proportion of sites utilized by at least one female is $(1-e^{-\lambda})$; hence,

$$\frac{S}{L} = (1-e^{-\lambda}) \qquad . . . (10)$$

The expected mean frequency of females spawning per available site is:

$$\lambda = \frac{N}{L} \qquad . . . (11)$$

It follows from Equations 10 and 11 that the number of females depositing their eggs safely (S) is Equation 1:

$$S = L(1-e^{-N/L}).$$

EGG CAPACITY OF SPAWNING BEDS

Equation 1 can be expressed in linear form, viz.:

$$ln(L-S) = -\frac{1}{L}(N) + lnL \quad \ldots (12)$$

where $-\frac{1}{L}$ is the slope and lnL is the point of intercept on the ordinate. By obtaining estimates of N and S, a graphical technique can be used to estimate L. The method will be illustrated with data from Harris River (Table I). The 1961 estimates are not included because flooding occurred before S was estimated and may have caused the removal of significant numbers of eggs from the spawning bed.

After a trial value of L ($L \geq$ the largest estimated value of S), Equation 12 is drawn with slope $= -\frac{1}{\hat{L}}$ and *y* intercept $= ln\hat{L}$. Values of $ln(\hat{L}-S)$ are calculated for each observed S and are plotted against the corresponding values of N. Different values of $\hat{L}$ are tried until the plotted points exhibit the least deviation from the theoretical line (Equation 12). This is the value accepted as the best estimate of L.

For Harris River, the following numbers of females spawning per 100 m^2 (N) and the numbers spawning safely per 100 m^2 (S) were used to estimate L:

	N	*S*
1958	12.9	12.4
1959	24.8	19.6
1960	48.4	35.1
1962	330.0	101.7

Figure 5 shows the line obtained from Equation 12 where L = 106.4 females per 100 m^2. Larger and smaller trial values of L exhibited greater departure from their theoretical lines, so a value L = 106.4 females per 100 m^2 of spawning ground was accepted for intertidal Harris River.

Provided each female deposits 1700 eggs, the egg capacity of a spawning bed where L = 106.4 females per 100 m^2 is

$$\frac{(106.4)\ (1700)}{100} = 1809 \text{ eggs } m^2.$$

This is approximately equivalent to the potential deposition of one female pink salmon per square meter.

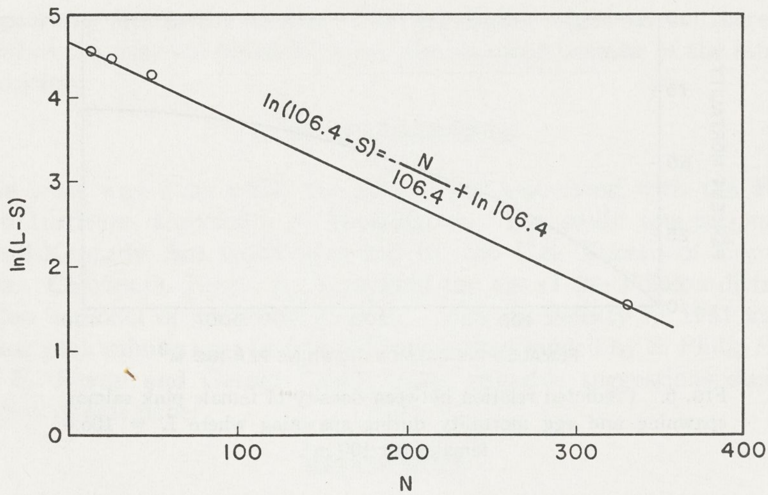

FIG. 5. Line of equation (12) drawn with slope $\left(-\frac{1}{L}\right)$ equal to $-\frac{1}{106.4}$. The plotted points are for Harris River and show the degree of correspondence between the theoretical line and the field observational data.

PREDICTED MORTALITY DURING SPAWNING

If the model adequately describes the dynamics of egg recruitment to the spawning bed and a value of L has been determined with a degree of accuracy commensurate with sampling variations, an estimate of the total mortality percentage (M_t) can be calculated. The number of females required to give any selected number spawning safely can be obtained by solving Equation 12 for N, i.e.

$$N = L(ln L) - L[ln(L-S)] \quad \ldots (13)$$

For example, the number of females required to spawn per 100 m^2 for an equivalent number of 50 to spawn safely (i.e. S = 50), where L = 106.4 is:

$$N = 106.4(ln\ 106.4) - 106.4[ln(106.4-50)] = \frac{68.1 \text{ females}}{100 \text{ m}^2}.$$

The mortality percentage can be calculated from:

$$M_t = \frac{(N-S)}{N}(100) \quad \ldots (14)$$

and in this instance is found to be 27%. Figure 6 shows how the predicted mortality changes with increasing density of females spawning where L = 106.4 females per 100 m^2.

CONCLUSIONS

The development of a successful management program for pink salmon will depend in part on the ability of management biologists to assess fry production potential of spawning beds and optimum escapement of adults to spawning streams. It will be necessary to determine eventually these attributes for each important spawning area and spawning stock.

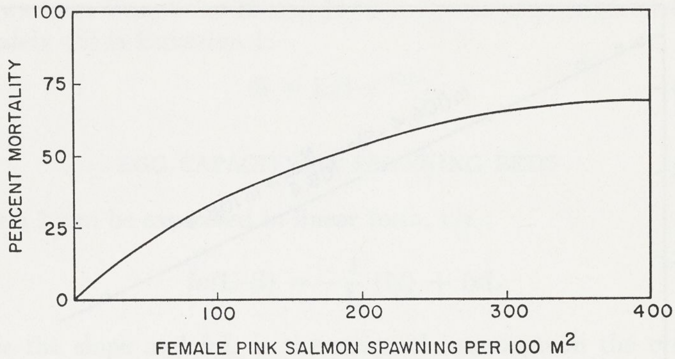

FIG. 6. Predicted relation between density of female pink salmon spawning and egg mortality during spawning where L = 106.4 females per 100 m².

Fry production potential of a spawning bed might ultimately be limited by mortality factors directly related to density of spawning adults. A mathematical model describing the dynamics of mortality from redd superimposition has been advanced in this paper. The model was used to estimate egg capacity of a spawning bed and to predict mortality during spawning. A basic assumption of the model is that females distribute themselves at random over a spawning bed. Further research is required to test the validity of this assumption.

Although redd superimposition is thought to become an important mortality cause at high spawning densities, the potential of a spawning bed to produce fry is possibly limited by additional factors. The oxygen delivery rate, for example, may exert a pronounced influence on carrying capacity. It has been observed, on the other hand, that females remove much extraneous organic matter from spawning beds while excavating redds (Semko, 1954; McNeil and Ahnell, 1964). The removal of eggs through redd superimposition and the cleansing of spawning beds of organic detritus may help the young salmon avoid stresses associated with oxygen privation and help protect them from epidemic outbreaks of pathogenic agents. Redd superimposition may thus be an essential mechanism inhibiting catastrophic mortality due to overcrowding.

In stream areas where spawning occurs over an extended period, mortality from redd superimposition would have its greatest impact on the progeny of early-spawning fish; and in years of large escapement, it is conceivable that late-spawning fish could nearly destroy the progeny of early-spawning fish. The relations between time of spawning and survival potential of young pink salmon are poorly understood. A working hypothesis might be that eggs from a single spawning stock deposited during the middle portion of the run possess a higher survival potential than eggs deposited very early or very late. It is assumed that hereditary differences associated with time of spawning do not exist within the stock. If competition for space on spawning beds becomes critical, as it might in years of great abundance, then the population of embryos surviving at the conclusion of spawning will have originated for the most part from the adults spawning late in the season. The population might arrive, therefore, at a state where its survival potential is greatly impaired because of the lateness of egg deposition.

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REFERENCES

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. *U.K. Min. Agr., Fish. Investig.*, Ser. 2, **19**: 533 pp.

Dixon, W. J., and F. J. Massey, Jr. 1957. Introduction to statistical analysis. 2nd edition. McGraw-Hill Book Co., Inc., New York and London. 488 pp.

Gilbert, C. H., and W. H. Rich. 1927. Investigations concerning the red-salmon runs to the Karluk River, Alaska. *Bull., U.S. Bur. Fish.*, **43**(2): 1–69. (Document No. 1021)

Koopman, B. O. 1950. Necessary and sufficient conditions for Poisson's distribution. *Proc. Am. Math. Soc.*, **1**(6): 813–823.

McNeil, W. J. 1962. Mortality of pink and chum salmon eggs and larvae in southeast Alaska streams. Ph. D. Thesis, Univ. Washington, Seattle, 270 pp.

McNeil, W. J., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. *U.S. Fish and Wildlife Ser., Special Sci. Rept. — Fish.*, No. 469, 15 pp.

Morgan, A. R., and K. A. Henry. 1959. The 1955–1956 silver salmon run into the Tenmile Lakes System. *Oregon Fish Comm., Research Briefs*, **7**(1): 57–77.

Neave, F. 1958. Stream ecology and production of anadromous fish, pp. 43–48. *In* P. A. Larkin, [ed.], The investigations of fish-power problems. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Canada*, **11**(5): 559–623.

1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

Rounsefell, G. A. 1957. Fecundity of North American Salmonidae. *U.S. Fish. and Wildlife Serv., Fish. Bull.*, **57**: 450–468. (Fish. Bull. No. 123.)

1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. *Ibid.*, **58**: 83–169. (Fish. Bull. No. 130.)

Semko, R. S. 1954. [The stocks of West Kamchatka salmon and their commercial utilization.] Zapasy zapadnokamchatskikh lososei i ikh promyslovoe ispolzovanie. *Izv. Tikhookeans. Nauchno-Issled. Inst. Rybn. Khoz. i Okeanogr.*, **41**: 3–109. [Fish. Res. Bd. Canada, Translation Series, No. 288.]

SMIRNOV, A. G. 1947. [Conditions of stocks of the Amur salmon and causes of the fluctuations in their abundance.] Sostoyanie zapasov amurskikh lososei i prichiny ikh chislennykh kolebanii. *Izv. Tikhookeans. Nauchno-Issled. Inst. Rybn. Khoz. i Okeanogr.*, **25**: 33–51. Translation *in* Pacific Salmon, pp. 66–85. Israel Program for Scientific Translations, Jerusalem, 1961.

WICKETT, W. P. 1958. Review of certain environmental factors affecting the production of pink and chum salmon. *J. Fish. Res. Bd. Canada*, **15**(5): 1103–1123.

1962. Environmental variability and reproduction potentials of pink salmon in British Columbia, pp. 73–86. *In* N. J. Wilimovsky, [ed.] Symposium on pink salmon. H. R MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.