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# FECUNDITY OF NORTH AMERICAN SALMONIDAE

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## ABSTRACT

Data on fecundity of North American Salmonidae are scarce, but analysis of available material shows that use of the total number of females as a measure of reproductive potential may introduce considerable error. Fecundity varies between populations of the same species, so that data from one locality cannot be safely applied to another. Annual differences in fecundity in the same population may be caused by differences in average size, or by differences in age at maturity.

Fecundity in the sockeye does not appear to vary between fish remaining for 3 or 4 years in the lake before seaward migration, but fish spending 2 years at sea have a higher fecundity than fish of the same size spending 3 years at sea.

Data are needed to answer two questions: (1) What is the relation between egg size and egg number in the same species; and (2) Does reproductive potential depend chiefly on number of eggs or on total volume of eggs.

## CONTENTS

# FECUNDITY OF NORTH AMERICAN SALMONIDAE

By George A. Rounsefell, *Fishery Research Biologist*

This paper is the first in a projected series in which the author proposes to compile and evaluate the published information on various phases of the life history and conservation of North American salmonids. The available information is so widely scattered that merely bringing it together will facilitate the expanding research. Furthermore, even a hasty perusal of the literature reveals large gaps in our knowledge. Once these gaps are clearly seen, there is a much better chance of their being filled.

The primary purpose, however, is to discover through comparison of the same life phases of the different species and genera, the relation between the fish and the ecological factors in their environment. Since emphasis has been placed on material that would aid in developing principles, and as I am making the study as complete as possible without assistance, I am not including minor items of information. Original data are presented for Karluk River sockeye.

Although not indigenous, the brown trout, *Salmo trutta*, is included in this study as a thoroughly naturalized species. European and Asiatic literature is used sparingly, either to aid where knowledge of the North American stock is deficient, or to corroborate the North American findings.

Fecundity is an especially interesting topic in the Salmonidae because the comparatively small number of large eggs suggests (as other researchers have proved, e. g., Rounsefell and Kelez, 1938, Rounsefell, 1949 and in ms.[1]) a demonstrable relation between the reproductive potential of the spawning stocks and the numbers of young surviving. Neave (1948) has also pointed out that the variation in egg number between species of *Oncorhynchus* is related to the varying vicissitudes of their life history.

The relation between size of spawning stock and number of young produced is fundamental to studies of changes in population size. The survival from spawnings cannot always be determined at an early stage, but is more usually measured at some later stage of the life history. In this paper we are concerned with quantitative measurement of the reproductive potential of the spawning stock. Such measurements are usually gross estimates derived from one of the following bases:

1. Relative abundance of the adult population. This will usually be in pounds of fish caught by some standard amount of fishing effort (a standardized unit of gear fishing a certain period of time).

2. Relative abundance of the eggs or larvae. This usually is a summation of the density of eggs (in the case of pelagic eggs) per cubic meter over the water area inhabited by the particular population under consideration. Estimates of abundance of species spawning in the littoral zone, e. g., Pacific herring (*Clupea pallasi*), may be based on miles of shoreline utilized for spawning.

3. Actual numbers of mature adults. These numbers may be an actual count of the individuals or may be statistical estimates of population size.

These measures of reproductive potential are each based on one or more of the following assumptions:

1. That the number of eggs spawned is in direct proportion to the number of mature adults and their mean weight (or length). For this to be true, the relation between size of fish and fecundity must be linear. Moreover, if the size composition of the adult population varies from year to year, then the theorem is true only if the regression of eggs on size passes through the origin, i. e., the regression formula must be of the form $y=bx$.

[1] Factors causing decline in sockeye salmon of Karluk River, Alaska. U. S. Department of the Interior, Fish and Wildlife Service, Washington, D. C.

Approved for publication, February 8, 1957.

2. That the annual sex ratio remains constant.
3. That the regression of number of eggs on size of fish does not vary between years.
4. That the size and/or age at maturity does not vary between years.
5. That the number of eggs is a function of fish size independent of age.
6. That there is no annual variation in the proportion of the eggs retained by the females in spawning.

The foregoing assumptions are usually not fully satisfied so that the variability of an approximate measure of reproductive potential in critical experiments may be so large as to obscure the very factors, the effects of which the biologist is seeking to measure.

This variability between numbers of mature adults and actual reproductive potential has long been recognized, and biologists have attempted to discount it by substituting an estimation of the total annual egg deposition for number of adults as being a better measure of reproductive potential. This paper is confined to an analysis of the factors causing variation in the relation between number of eggs and number of mature adults.

After making the necessary allowance for differences in size of fish, a wide range in fecundity still exists between races of the same species from different localities. For instance, McGregor (1922, 1923a) found that the king salmon of the Sacramento River have a far higher fecundity than those of the Klamath River. Thus, if $y$ is number of eggs and $x$ is length of the fish in centimeters, the formulae for the regressions of number of eggs on length are—

| | |
|---|---|
| Klamath River | $\text{Log } Y = .00682\ X + 3.01116$ |
| Sacramento River | $\text{Log } Y = .00319\ X + 3.56836$ |

The Klamath River fish (65 specimens) ranged from 61 to 107 centimeters in length (average, 82.6), with a geometric mean of 3,754 eggs. The Sacramento River fish (50 specimens) ranged from 59 to 110 cm. (average, 92.4) and had a geometric mean of 7,298 eggs. At 85 cm., the calculated geometric means for the two populations are 3,894 and 6,912 eggs, an increase of 78 percent in number of eggs for the Sacramento River fish when compared with king salmon from the Klamath River.

The question arises as to the causes and the biological significance of such a great difference in fecundity between populations of the same species. It is recognized that harsher ecological situations impose lower survival rates on some races. Assuming that the number of eggs can be increased by selection (as seems to have been done for domesticated strains of trout), then the number of eggs may well differ genetically between various wild races of salmonids. In the case in point there is good reason to believe that the variation in egg number is not caused by variation in the marine environment since, as McGregor pointed out (1923b), Sacramento River and Klamath River king salmon occur together in the ocean troll catches.

That the fecundity of fish of the same length may even differ widely between populations spawning in different portions of the same river system is shown by Aro and Broadhead (1950) for the sockeye salmon of the Skeena River. For 3 years, 1939, 1948, and 1949, the female sockeye of small Lakelse Lake (5.5 sq. mi.) averaged 58.9 cm. in length (58.1–59.6) with an average of 3,816 eggs (3,699–3,888); while for the 3 years of 1946, 1947, and 1949, the female sockeye of the large upriver Babine Lake (171.8 sq. mi.) averaged 58.5 cm. (57.1–60.1) in length with an average of only 3,181 eggs (3,056–3,389).

In assessing the significance of differences in fecundity between fish of various localities, it becomes important to measure the variation within localities. Some of the important factors within localities to be considered are—

1. Size of the fish in relation to number of eggs.
2. Age at maturity.
3. Size of the eggs.
4. Seasonal trends in fecundity in the same locality.
5. Annual variation in fecundity.

## RELATION OF SIZE OF FISH TO NUMBER OF EGGS

Combining his own observations with those of Titcomb (1897), Ricker (1932) states that the relation between number of eggs and length of fish is curvilinear for the eastern charr, or brook trout, *Salvelinus fontinalis*. The number of eggs varied from 80 in a 5.1-inch charr to 5,630 in a 22-inch charr. However, Allen (1956) points out that Titcomb's data are of limited value since Titcomb stated that some of the charr had apparently dropped part of their eggs before being captured. Osgood Smith (1947) obtained a linear relation between the logarithm of the number of eggs and the body length of 29 eastern charr, but inasmuch as his specimens were from such diverse localities as California, Ontario, and North Carolina, the results cannot be regarded as conclusive.

The number of eggs of eastern charr from four localities is shown according to size of fish in table 1 and figure 1. These data show that the differences in egg number between localities are too great to permit combining localities in studying the egg number–fish size relation. When the curves for the separate localities are examined, it becomes apparent that the number of eggs increases approximately as the weight of the fish, since the logarithm of egg number plotted against the logarithm of fish length approximates a straight line, as does the logarithm of fish weight against the logarithm of fish length.

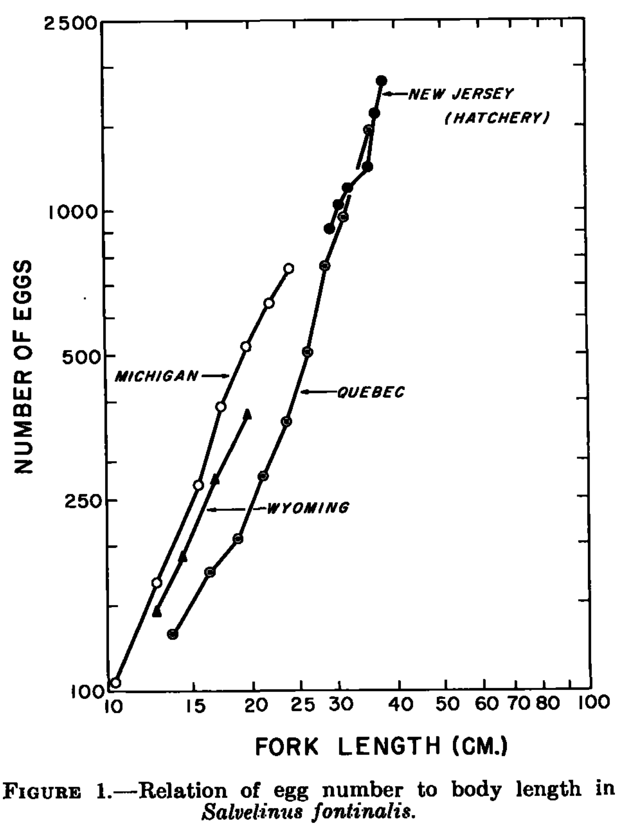


FIGURE 1.—Relation of egg number to body length in *Salvelinus fontinalis*.

TABLE 1.—*Fecundity of eastern charr*, Salvelinus fontinalis

| Locality and fork length | Number of fish | Average number of eggs | Authority |
|---|---|---|---|
| Wyoming (beaver pond): | | | |
| 12.70 cm | 2 | 148 | Allen (1956). |
| 14.44 cm | 5 | 191 | |
| 16.82 cm | 5 | 275 | |
| 19.65 cm | 2 | 376 | |
| New Jersey (hatchery stock): | | | |
| 29.69 cm [1] | 5 | 916 | Hayford and Embody (1930). |
| 31.00 cm | 4 | 1,028 | |
| 32.13 cm | 30 | 1,114 | |
| 35.21 cm | 22 | 1,249 | |
| 36.50 cm | 4 | 1,611 | |
| 38.00 cm | 8 | 1,867 | |
| Michigan (streams): | | | |
| 10.40 cm [2] | 38 | 104 | Cooper (1953). |
| 12.73 cm | 91 | 169 | |
| 15.07 cm | 59 | 268 | |
| 17.41 cm | 24 | 395 | |
| 19.74 cm | 15 | 525 | |
| 22.08 cm | 8 | 643 | |
| 24.42 cm | 4 | 753 | |
| Quebec (Laurentides Park): | | | |
| 13.75 cm | 4 | 131 | Vladykov and Legendre (1940). |
| 16.25 cm | 14 | 177 | |
| 18.75 cm | 10 | 206 | |
| 21.25 cm | 11 | 280 | |
| 23.75 cm | 14 | 362 | |
| 26.25 cm | 13 | 505 | |
| 28.75 cm | 3 | 732 | |
| 31.45 cm | 6 | 970 | |
| 35.50 cm | 2 | 1,469 | |

[1] Converted from standard length by factor 1.1.
[2] Converted from total length by factor 0.92.

The logarithm of the number of eggs shows a closer linear relation to length than does the actual number of eggs when specimens are available over a wide range of length. However, over the rather narrow ranges of length at maturity found in *Oncorhynchus*, the difference is usually trifling and can be disregarded in computing.

Extensive data on the relations between number of eggs and length and weight of the fish are given by Foerster and Pritchard (1941). Correlations between egg number and fish length and between egg number and fish weight are shown for Cultus Lake sockeye for each of 6 years (1932–35, 1937, and 1938) and for pink salmon from McClinton Creek, Masset Inlet, for each of 6 even-numbered years from 1930 to 1940, inclusive.

In order to compare the values of the two series of correlations, we have combined the correlation coefficients for the various years by transforming the $r$ values into $z$ values (Fisher 1930, p. 171). The value of $r$ for the combined samples is obtained from the weighted average value of $z$. The results are as follows:

| | *Value of correlation of egg number with—* | |
|---|---|---|
| | *Fish length* | *Fish weight* |
| Sockeye salmon (Cultus Lake) | 0.57 | 0.56 |
| Pink salmon (McClinton Creek) | 0.35 | 0.40 |

This means that in the sockeye about 31 to 32 percent of the variation in number of eggs is associated with change in length of the fish; but in the pink salmon this association is much weaker, only about 12 to 16 percent.

The two combined regression lines for number of eggs on length and on weight of the fish in figures 3 and 4 of Foerster and Pritchard (1941, pp. 58, 59) obviously have much steeper slopes than the regressions for the individual years, showing that these lines do not represent the regressions within years. Since the mean annual lengths of the fish varied in the same direction as the average number of eggs, these combined lines represent chiefly regression between years and are therefore of no utility in predicting egg number for various fish lengths within any individual year.

As the relation between egg number and fish length within any year appears to be so weak in pink salmon, it is of interest to determine what factor is controlling egg number. One factor for which measurements are available is sea temperature at Ketchikan, Alaska, which is just across Dixon Entrance from Masset Inlet and slightly east of it. To determine the role of sea temperature we have made a covariance analysis using the pink salmon data from McClinton Creek, Masset Inlet, B. C., prepared by Foerster and Pritchard (1941), as follows:

| Year | Mean length ($X_1$) | Mean sea temperature in degrees Fahrenheit at Ketchikan, July to Sept. ($X_2$) | Mean number of eggs ($Y$) |
|---|---|---|---|
| | *Cm.* | | |
| 1930 | 51.1 | 56.7 | 1,535 |
| 1940 | 51.6 | 57.0 | 1,619 |
| 1938 | 52.7 | 55.3 | 1,698 |
| 1934 | 53.0 | 55.4 | 1,804 |
| 1936 | 53.0 | 54.8 | 1,899 |
| 1932 | 54.0 | 54.9 | 1,758 |
| Average | 52.67 | 55.68 | 1,719 |

The results of the test are as follows:

| Number of eggs ($Y$) | Fish length ($X_1$) | Sea temperature ($X_2$) |
|---|---|---|
| Correlations of $Y$ with $X$'s | 0.7801 | −0.8592* |
| Standard regressions of $Y$ on $X$'s | 0.0310 | −0.8314* |

$R$=0.8593 (N. S.)
$Y=3.834X_1-115.616X_2+7,954$
Standard error of $\beta$'s=0.21536

$t$ for $\beta_{y2.1}$=0.83138/0.21536=3.860
$P$ of .05 =3.182.

The relation between the average number of eggs in McClinton Creek pink-salmon females and the summer sea temperature at Ketchikan, with fish length held constant, is shown in figure 2. The correlation, $r_{12}$, of $X_1$ with $X_2$ is −0.9011 and is statistically significant. Obviously, both annual mean fish length and annual mean egg number are negatively correlated with sea temperature. The annual differences in mean egg count in pink salmon are a function of sea temperature, because it is the principal factor controlling average fish length.

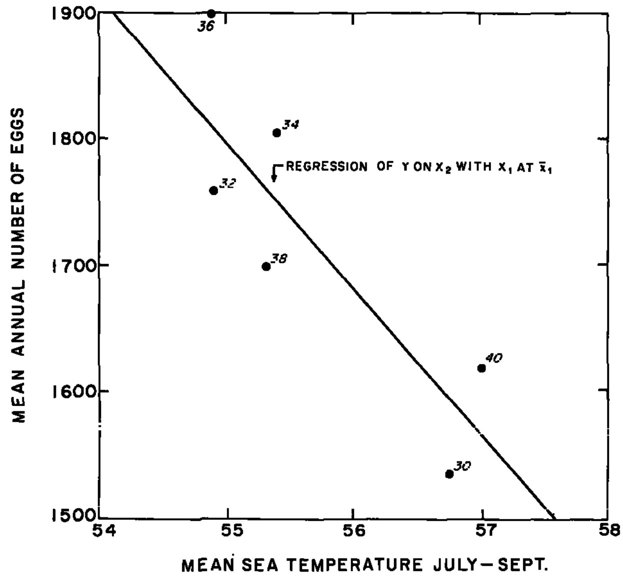


FIGURE 2.—Relation of annual mean egg number of McClinton Creek pink salmon, *O. gorbuscha*, (body length held constant) to mean July–September sea temperature at Ketchikan.

The above analysis does not mean that the regression between egg number and fish length within years is invalid, but that the within-years regression for the combined samples can only be obtained by reanalysis of the original data to eliminate the portion of the total regression accounted for by regression between years.

The problem of the relative effects of mean annual size and sea temperature on egg number for the sockeye salmon is complicated by the effect of varying age at maturity which will be discussed later.

In addition to the between-years difference in egg number at any particular length, there is also the difference between rivers mentioned previously in the case of the king salmon populations of the Klamath and Sacramento Rivers. A better illustration of this is perhaps afforded by the data from Eguchi, Hikita, and Nishida (1954) on chum salmon, *Oncorhynchus keta*, in Japanese waters. They point out that chum salmon from Hokkaido rivers have a larger number of eggs than chum salmon from rivers in South Kurile; however, analysis of their data shows that in both areas there is a significant difference between individual rivers. The analysis, based on data from 7 rivers in Hokkaido and 109 specimens of chum salmon, is as follows, using data for the left ovary only to simplify the tabulations:

| Source of variation | D. F. | Sums of squares and products | | | Errors of estimate | | |
|---|---|---|---|---|---|---|---|
| | | $Sx^2$ | $Sxy$ | $Sy^2$ | Sums of squares | D. F. | Mean square |
| Total | 108 | 2250.0300 | 64603.0 | 6,992,007 | 5,137,112 | 107 | ---------- |
| Between rivers | 6 | 666.0752 | 28678.8 | 2,369,067 | ---------- | ---------- | ---------- |
| Within rivers | 102 | 1583.9548 | 35924.2 | 4,622,940 | 3,808,177 | 101 | 37,704.7 |
| For test of significance of adjusted means | | | | | 1,328,935 | 6 | 221,489.2 |

$F=221{,}489.2/37{,}704.7=5.87$. For $P$ of .01, $F=2.99$

Similarly for South Kurile rivers, $F=3.50$ with $F$ for $P$ of .01 of 3.17. For the combined data (243 specimens) which come from 13 rivers, $F=13.74$ with $F$ for $P$ of .01 of 2.27. This shows that there is a tendency for each river to have its own regression line for egg number on fish length.

The fact of differences between the regressions for chum salmon from different rivers results in three regression lines (three center curves of figure 3). The total regression (dotted line)

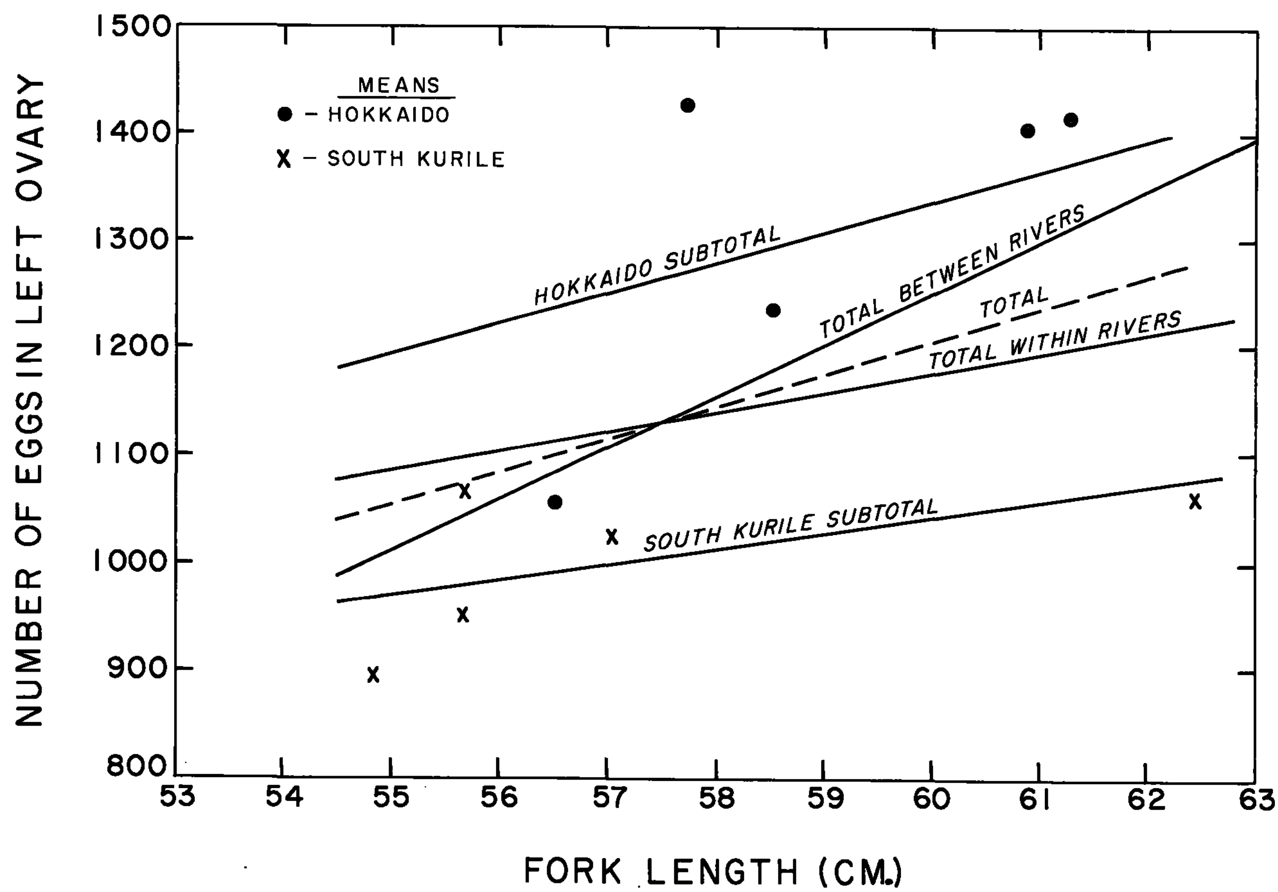


FIGURE 3.—Relation of egg number (left ovary) of Japanese chum salmon, *O. keta*, to body length to illustrate total, between-rivers, and within-rivers regressions.

includes both the within- and the between-rivers regressions. The within- and the between-rivers regressions each has a useful connotation. If one wishes to estimate from the lengths of the fish, the number of eggs contained in a sample of chum salmon from a particular river, then from the between-rivers regression one obtains an estimate of the average number of eggs per female (left ovary) in accordance with the average length of the entire sample. If, however, one wishes to determine the difference in egg number (left ovary) between fish of different lengths within the same sample, then the slope of the regression would follow the within-rivers slope.

## RELATION OF AGE AT MATURITY TO NUMBER OF EGGS

The best material available on the effect of age at maturity on egg count is in unpublished data for the sockeye salmon of Karluk River, Alaska, as follows:

| Year | Number of specimens | Ages available | Lengths taken | Method of enumeration of eggs [1] | Dates sampled |
|---|---|---|---|---|---|
| 1926 [2] | 40 | No | Yes | Number in 5 gm. | Sept. 15, 1926. |
| 1938 | 65 | Yes | Yes | Weight of a counted sample. | Aug. 1–6, 1938. |
| 1939 | 220 | Yes | Yes | Actual count | June 9–July 6, 1939; no dates for individuals. |
| 1940 | 155 | Yes | All 60 cm | Volume—200 eggs. | June 2–Sept. 13, 1940. |
| 1941 | 114 | Yes | All 60 cm | Volume—200 eggs. | June 9–Sept. 8, 1941; no sampling July 3–Aug. 11. |
| 1943 | 182 | No | Daily average. | No information | June 29–Aug. 18, 1943. |

[1] Left and right ovaries estimated separately.
[2] Summary published in Gilbert and Rich (1927).

Some measure of the reliability of these data is contained in figure 4, which shows for 1938 the average weight in grams for 1 egg of the right ovary plotted against the weight of 1 egg of the left ovary for 41 Karluk River sockeye of ages $5_3$, $6_3$, and $6_4$. The samples were taken from salmon captured at the mouth of the river so that there is great variation in the stage of maturity of the ova, but the figure shows that the eggs in the two ovaries are maturing at the same rate. Since the data from the two ovaries form two independent estimates from the same fish, their close agreement gives confidence in the consistency of this method of calculating the number of eggs.

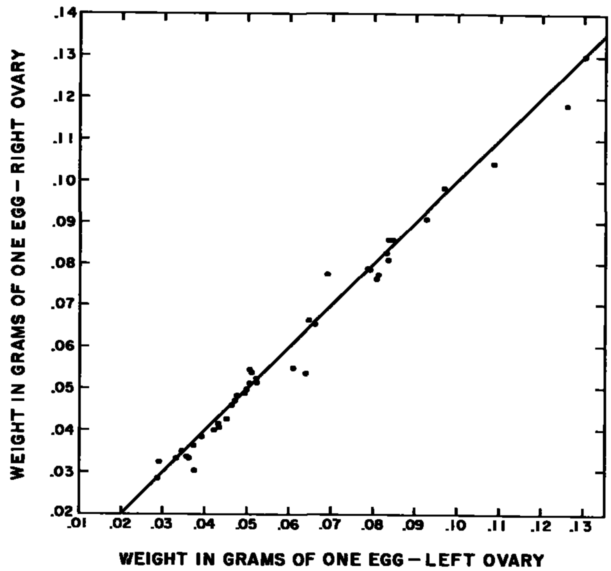


FIGURE 4.—Paired observations of egg weights in right and left ovaries of sockeye salmon, *O. nerka*, of ages $5_3$, $6_3$, and $6_4$, of Karluk River in 1938.

It is interesting to note that although the eggs in the left and right ovaries maintain the same rate of egg maturation the total number of eggs in the two differ noticeably. Figure 5 shows that for low total number of eggs the right ovary contains as many eggs as the left or more; however, as the total number of eggs rises the proportion in the left ovary becomes increasingly greater than in the right.

Kendall (1921, pp. 195, 197) says,

> As the ova approach maturity, the left ovary is nearly or quite always the longer, and it extends, tapering, to the posterior end of the abdominal cavity.

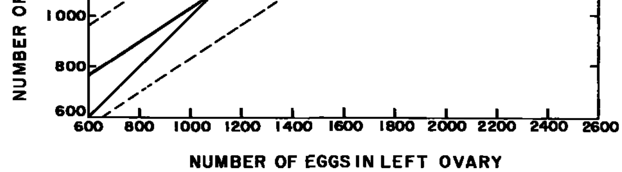


FIGURE 5.—Relation between the egg number in the right and the left ovaries of the sockeye, *O. nerka*, of Karluk River in 1939.

These backward extensions of the ovaries are formed by the maturing and enlarging ova filling the previously crowded interlamina spaces at the posterior end of the ovary, thus stretching it longitudinally.

This increasing disproportion between the left and right ovaries in fish with larger numbers of eggs is logical since in a fish with few eggs the posterior portion of the body cavity would be relatively empty. Fish of the same size with more eggs would have to utilize this space and the left ovary, which is usually longer than the right, would thus be proportionately larger. However, for the chum salmon in Japanese waters, the data of Eguchi et al. (1954) show no significant differences in egg number between the two ovaries. For 243 chum salmon the averages are 1,134 in the left ovary and 1,146 in the right ovary. Sockeye salmon from little Bare Lake in the Red River system of Kodiak Island contain more eggs in the right than in the left ovaries (personal communication from Philip R. Nelson). It is interesting to speculate whether this is a genetic difference or induced by the great environmental difference between Bare and Karluk Lakes.

Probably the best explanation of this disproportion in the size of the two ovaries is given by Brown and Kamp (1942, p. 196). In discussing the brown trout, *Salmo trutta*, they say—

In the brown trout, the posterior portion of the intestine usually bends strongly to the right, thus crowding the right ovary at its caudal end. The length of the ovary is inversely proportional to the degree of crowding. However, the left ovary is not always the longer. One fish was observed to have a longer right ovary and it was interesting to note that this specimen had an intestine which bent to the left instead of the right. In one or two fish the ovaries were of approximately equal length, with the intestine bending neither to the right nor the left.

They found in 8 brown trout averaging 36 cm. in standard length that the right ovary was 133 mm. long and weighed 32.4 grams, while the left ovary averaged 169.5 mm. and weighed 42.6 grams.

In discussing the effect of age at maturity on number of eggs in *Oncorhynchus* there are two questions: (1) Is the number of eggs determined by length of residence in fresh water or length of residence in the sea? (2) Does the number of eggs for any given length of fish increase or decrease with age? These questions cannot be answered by the pink salmon data because they leave fresh water immediately after emerging from the gravel, and because they invariably mature in their second year.

The following tabulation has been made for the Karluk River sockeye salmon, showing the average number of eggs in relation to the period of residence of the salmon in fresh water and in the ocean.

| Ocean age and year sampled [1] | Summers in ocean | Fresh-water age [2] | | | | | |
|---|---|---|---|---|---|---|---|
| | | In third year | | | In fourth year | | |
| | | Summers in fresh water | Number of fish | Average number of eggs | Summers in fresh water | Number of fish | Average number of eggs |
| 2-year ocean age: | | | | | | | |
| 1938 | 1936–37 | 1934–35 | 24 | 3,430 | 1933–35 | 10 | 2,972 |
| 1939 | 1937–38 | 1935–36 | 36 | 3,055 | 1934–36 | 7 | 2,674 |
| 1940 | 1938–39 | 1936–37 | 80 | 3,421 | 1935–37 | 25 | 3,549 |
| 1941 | 1939–40 | 1937–38 | 45 | 3,708 | 1936–38 | 36 | 3,668 |
| 3-year ocean age: | | | | | | | |
| 1938 | 1935–37 | 1933–34 | 9 | 2,631 | 1932–34 | [3] 2 | 3,610 |
| 1939 | 1936–38 | 1934–35 | 58 | 2,973 | 1933–35 | 13 | 2,866 |
| 1940 | 1937–39 | 1935–36 | 23 | 2,926 | 1934–36 | 1 | 3,459 |
| 1941 | 1938–40 | 1936–37 | 20 | 3,011 | 1935–37 | 11 | 3,160 |

[1] Since smolts enter the sea from early to late spring and reenter the rivers as adults from spring to early fall the ocean age gives number of ocean summers, but 2 years at sea may vary from about 23 to 27 months. The growing seasons are of paramount importance to this discussion.
[2] Fresh-water age is from the time the eggs are deposited (from late June to November) until smolts enter the sea (from May to July), so that a fresh-water age of 3 can vary from about 29 to 36 months in fresh water, but the summers spent in the lake after hatching are the periods important to this discussion.
[3] Not corrected for length of fish.

The data for 1940 and 1941 are for 60-cm. fish, so to make the data for 1938 and 1939 comparable to data for the other years it was necessary to obtain the number of eggs for 60-cm. fish from the regressions of eggs on length of fish. These regressions were computed separately for the left and the right ovaries and the counts for each, calculated from these regressions, were then combined.

In order to discount environmental effects the

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averages were compared according to seasons spent in each environment as follows:

| Summers in lake | Ocean age | | | | Difference |
|---|---|---|---|---|---|
| | 2-year | | 3-year | | |
| | Number of fish | Average number of eggs | Number of fish | Average number of eggs | |
| 1934–35 | 24 | 3,430 | 58 | 2,973 | 457 |
| 1935–36 | 36 | 3,055 | 23 | 2,926 | 129 |
| 1936–37 | 80 | 3,421 | 20 | 3,011 | 410 |
| 1933–34–35 | 10 | 2,927 | 13 | 2,866 | 106 |
| 1935–36–37 | 25 | 3,549 | 11 | 3,160 | 389 |
| Average | | 3,285 | | 2,987 | [1] 298±74.7 |

| Summers in ocean | Fresh-water age | | | | Difference |
|---|---|---|---|---|---|
| | 3-year | | 4-year | | |
| | Number of fish | Average number of eggs | Number of fish | Average number of eggs | |
| 1936–37 | 24 | 3,430 | 10 | 2,972 | 458 |
| 1937–38 | 36 | 3,055 | 7 | 2,674 | 381 |
| 1938–39 | 80 | 3,421 | 25 | 3,549 | −128 |
| 1939–40 | 45 | 3,708 | 36 | 3,668 | 40 |
| 1936–37–38 | 58 | 2,973 | 13 | 2,866 | 107 |
| 1938–39–40 | 20 | 3,011 | 11 | 3,160 | −140 |
| Average | | 3,266 | | 3,148 | 118±103.7 |

[1] $t$—3.99, $P$ for 0.05=3.75, 4 d. f.

The significant difference of 298 eggs between fish spending 2 summers at sea and those spending 3 summers, but with similar lake histories, is fairly clear evidence that younger ocean-age fish have higher fecundity than older ocean-age sockeye of the same size. The rather consistent difference between 2- and 3-ocean-age fish would also indicate that the ocean environment is relatively stable as the two groups were not at sea during identical years.

If we now turn the analysis around and note the egg counts for 3- and 4-fresh-water-age fish with identical ocean histories that spend 2 and 3 summers in fresh water, the difference in fecundity is neither consistent nor significant. This could be interpreted to mean that fecundity does not differ between fish of 3 and 4 fresh-water ages, but since there are obvious differences between year classes, owing probably to lake conditions, such a conclusion is not fully warranted by these data. What is required are data over a sufficiently long period to discount these fresh-water environmental effects.

## RELATION OF EGG SIZE TO EGG NUMBER

Surprisingly few records have been published on actual size of ova of Salmonidae, investigators being content to speak of size in a purely comparative sense. For instance, Belding et al. (1932, p. 214) say—

> In general the size of the egg depends upon the size of the parent salmon, the larger specimens producing the larger egg. Also, the size of the egg varies with the salmon of the different rivers. The material used in this study permits its division into two classes, large and small eggs. There is no relationship between the size of the egg and the length of the incubation period.

Gilbert (1915, p. 57) also used only a comparative measure of size. He says in speaking of British Columbia sockeye,

> A similar difference, but even more pronounced, is found among certain lots of eggs collected by Mr. Stone in Smith Inlet, those from Quey Creek being markedly smaller than those from the Gelulch and Delelah Rivers. It required 74 Quey Creek eggs to fill a tube which would hold only 38 from the Gelulch and the Delelah.

Perhaps the chief reason for this lack of data on size of ova is that the salmon taken by the commercial fishery are in various stages of egg maturation. Thus, at Karluk River many of the sockeye taken in the fishery may not spawn for at least another month. This is reflected in the weight of sockeye eggs at Karluk ranging from .03 to .095 grams (fig. 4).

The same late maturation is found in the Atlantic salmon. Speaking of *S. salar* in Norway, Dahl and Sømme (1944, p. 39) say—

> In the grilse, which have spent more than a year in the sea, the GW/TW [ratio of gonad weight to total weight] is still practically in the same undeveloped stage in the early part of the season. A gradual development in the relative size of the sexual organs asserts itself as the fishing season advances, but the main growth towards maturity takes place after the fish have entered the rivers.

They agree with Belding et al. that the individual egg size is partially dependent on fish size, saying (op. cit., p. 22), "It is a well known fact that in large salmon the ovaria as well as the single ova are larger than in salmon of small size."

Egg size is regarded by Svärdson (1949, p. 120) as resulting from natural selection. He states—

> Summing up it can be said that the evidence now at hand shows that competition among fry gives the larger

fry better survival chances. A selection pressure in favour of large eggs therefore certainly exists and this selection must work until the eggs are so few that no noteworthy competition for food exists among the fry.

While we must agree that larger fry generally have better survival rates, the reason given by Svärdson—intraspecific competition—may sometimes have little bearing on the matter; undoubtedly, there are other important factors. For instance, Robertson (1922) has pointed out that the race of small-sized sockeye salmon that spawns in Harrison Rapids, a tributary of the Fraser River, produces larger eggs than the other races of sockeye in the Fraser. This may be related to the fact that this is one of the few races of sockeye in which the young go to sea as fry, since large, vigorous fry would be required to survive in sufficient numbers to maintain the population.

It should be noted, moreover, that among the Pacific salmons (table 2) the smallest eggs are found in the sockeye which normally spend the longest time in fresh water. Size can be attained only by the sacrifice of number. In each ecological situation there is some point at which, on the average, the forces favoring size are exactly balanced by those favoring number. This point must vary between river systems, tending to produce genetic variation between populations for egg size and number.

TABLE 2.—*Size and weight of eggs and fry of certain North American Salmonidae*

[Asterisk (*) indicates diameter calculated from volumetric measure by Von Bayer conversion table]

| Species and area | Eggs | | Sac fry | | Fry after yolk is absorbed | | Authority |
|---|---|---|---|---|---|---|---|
| | Diameter | Weight | Length | Weight | Length | Weight | |
| *Oncorhynchus*: | | | | | | | |
| *tshawytscha*: | *Mm.* | *Gm.* | *Mm.* | *Gm.* | *Mm.* | *Gm.* | |
| Washington | | | | 0.520 | | 0.509 | Chapman (1938). |
| Columbia R | | | | | 35–40 | | Rich (1920). |
| Oregon | *6.3 | | | | | | Brice (1898). |
| Area not recorded | *7.8 | | | | | | Bower (1910). |
| Sacramento R., Calif | *7.9 | | | | | | Stone (1897). |
| Do | | | | | 35–40 | | Rich (1920). |
| *keta*: | | | | | | | |
| Area not recorded | | | | | 30–40 | 0.24–.62 | Kobayashi (1953). |
| Hokkaido, Japan | *7.4 | 0.232 | | | | | Watanabe (1956). |
| *kisutch*: | | | | | | | |
| Green R., Wash | | | | | | 0.284 | Chapman (1938). |
| Lakes in Montana | *8.4 | | | | | | Beal (1955). |
| Scott Creek, Calif | *7.2 | | | | | | Shapovalov and Taft (1954). |
| *gorbuscha*: | | | | | | | |
| Sashin Creek, S. E. Alaska | | | | | 971–1800 | per pint | Skud (1955). |
| McClinton Cr., B. C | | | | | 32–38 | ca 0.3 | Pritchard (1944). |
| *nerka*: | | | | | | | |
| Yes Bay, Alaska | *6.3 | | | | | | Bower (1910). |
| Baker R., Wash | | | | | | 0.192 | Chapman (1938). |
| *Salmo*: | | | | | | | |
| *salar*: | | | | | | | |
| Rivers in Norway | 5.3–7.0 | 0.1–.2 | | | | | Dahl (1917). |
| Gaspe, P. Q | 6.8 | 0.200 | 17.4 | 0.180 | | | Vladykov (1954). |
| Morell R., P. E. I | | | 17.7 | 0.141 | 27.5 | 0.057 | Belding and Hyde (1932). |
| Nova Scotia | | | 18.1 | 0.133 | 26.7 | 0.124 | Do. |
| New Brunswick | | | 18.8 | 0.146 | 27.9 | 0.144 | Do. |
| Pollitt R., N. B | 5.4 | 0.090 | 16.0 | 0.110 | | | Vladykov (1954). |
| Area not recorded | *6.1 | | | | | | Brice (1898). |
| *s. sebago*: Area not recorded | *6.6 | | | | | | Do. |
| *gairdneri*: | | | | | | | |
| Area not recorded | 5.1 | | | | | | Do. |
| Scott Cr., Calif | *5.5 | | | | | | Shapovalov and Taft (1954). |
| *g. aqua-bonita*: Cottonwood L., Calif | | | 15.0 | | | | Curtis (1935). |
| *trutta*: | | | | | | | |
| Area not recorded | *4.2 | | | | | | Brice (1898). |
| Madison R., Mont | 4.94 | | | | | | Brown and Kamp (1942). |
| *clarki*: Henrys L., Idaho | 4.3–5.1 | | | | | | Irving (1955). |
| *c. lewisi*: Yellowstone R | *4.5 | | | | | | Lord (1930). |
| *Cristivomer*: | | | | | | | |
| *namaycush*: | | | | | | | |
| Baldwins Mills, P. Q | 5.8 | 0.125 | 16.2 | 0.080 | | | Vladykov (1954). |
| Twin Mountain, N. H | 5.7 | 0.125 | 19.1 | 0.075 | | | Do. |
| Lake Superior | 4.9–5.4 | | | | | | Eschmeyer (1955). |
| Seneca L., N. Y | *5.2 | | | | | | Royce (1951). |
| Adirondack Lakes, N. Y | *5.5–5.6 | | | | | | Do. |
| Northville, Mich | *5.4 | | | | | | Bower (1910). |
| Area not recorded | *5.8 | | | | | | Brice (1898). |
| *Salvelinus*: | | | | | | | |
| *alpinus*: Area not recorded | 5.0 | | | | | | Vladykov (1933). |
| *aureolus*: New Hampton, N. H | 4.7 | 0.050 | 17.1 | 0.055 | | | Vladykov (1954). |
| *fontinalis*: | | | | | | | |
| L. Jacques-Cartier, P. Q | 4.4 | 0.040 | 15.0 | 0.033 | | | Do. |
| New Hampton, N. H | 4.0 | 0.040 | 13.9 | 0.040 | | | Do. |
| Vermont | *4.6 | | | | | | Bower (1910). |
| Area not recorded | *4.2 | | | | | | Brice (1898). |

The data given in table 2 are from several sources. Undoubtedly exhaustive search of the literature would reveal more data on the subject; however, these suffice to give a general picture. Because data on ova size are missing or very scanty for several species we have included length and weight of sac fry and free-swimming fry.

Egg size, in general, is correlated with the average size of the species. Thus *Oncorhynchus tshawytscha,* the largest species, has the largest ova. This is, however, only a generalization. It may be noted that the fry of the small pink salmon, *O. gorbuscha,* are larger than those of the Atlantic salmon, *Salmo salar.* That is, the tendency toward large eggs and fry appears to be a characteristic of the genus *Oncorhynchus.* Because of the scarcity of data from actual measurement of diameters of mature eggs, it is felt that the scattered material brought together in table 2 cannot be wholly relied on to give a true picture of egg size. However, corroborative evidence can be obtained by an indirect method.

In figure 6 (data from appendix table 4), the average number of eggs is plotted against the average weight of the females for each species. (See also appendix tables 1, 2, and 3 for detailed information on egg numbers, by species and locality.) Obviously the data fall into two general groups: fluvial anadromous *Oncorhynchus,* which show a low number of eggs for their weight, and lacustrine anadromous sockeye and members of the other 3 genera, which show a large number of eggs for their weight. That this difference in egg number for comparable weights is not due to a difference in the shape of the fish is indicated by the very close correspondence between the length-weight relation for all of the genera (fig. 7, data from appendix table 5).

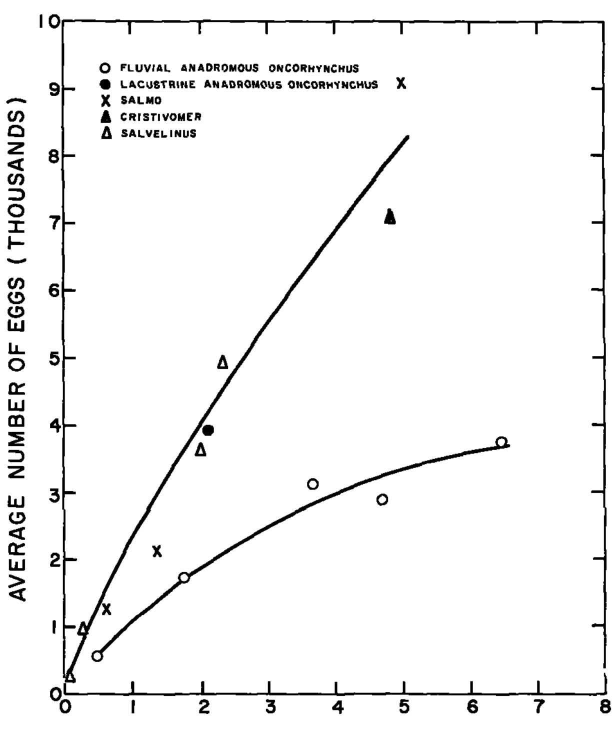


FIGURE 6.—Relation, by species, of average egg number to average weight. (Data from appendix table 4.)

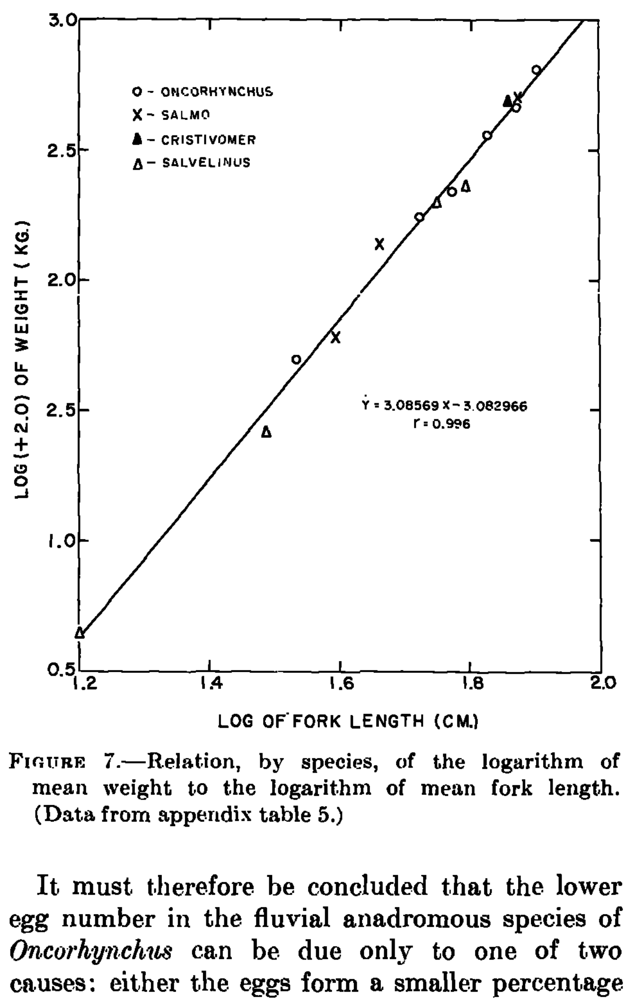


FIGURE 7.—Relation, by species, of the logarithm of mean weight to the logarithm of mean fork length. (Data from appendix table 5.)

It must therefore be concluded that the lower egg number in the fluvial anadromous species of *Oncorhynchus* can be due only to one of two causes: either the eggs form a smaller percentage of the total weight of the fish or the eggs are considerably larger. Despite the paucity of available information, the true cause of the lower egg number in these species can be confidently ascribed to egg size if we consider the data on weight of fry in conjunction with that of egg diameter (see appendix table 6). Thus, the sac fry of *O. tshawytscha* weighed 2.9 times the upper limit given for *Salmo salar*.

There is general agreement that, within the genus *Oncorhynchus*, the largest eggs are found in *tshawytscha* and the smallest in *nerka*. O'Malley (1920) gives the following number of eggs of each species required to fill a hatchery basket:

| Species: | *Thousands of eggs* |
|---|---|
| *O. tshawytscha* | 20–30 |
| *O. kisutch* | 30–35 |
| *C. keta* | 33–38 |
| *O. gorbuscha* | 40–50 |
| *O. nerka* | 50–60 |

Bean (1893, p. 30) says of the pink salmon, *O. gorbuscha*, "The eggs are larger than those of the red salmon [*O. nerka*], but smaller than king salmon [*O. tshawytscha*] eggs and not so bright red."

It is not surprising that there is some disagreement concerning the relative size of the eggs of *kisutch*, *keta*, and *gorbuscha* since, as we have seen, there is considerable difference between localities in regard to average number within the same species. Only accurate measurements of fully mature eggs from several localities, preserved in the same manner, can be relied upon to show the size ranges in eggs of the various species.

## RELATION OF EGG NUMBER TO LATITUDE

In order to determine whether there is any relation between fecundity and latitude we have constructed table 3, showing the average fork length and egg number for species of *Oncorhynchus* arranged geographically from south to north. The averages are shown in figure 8 with the southernmost locality for each species in black. The egg number of four of the species is higher than expected for the average length in the most southern locality.

If further research should prove that there is a valid tendency for higher fecundity toward the south, this may possibly be ascribed to the difference in growth rates. This follows because the average age at maturity of all of the species (except *gorbuscha*) tends to increase toward the north. We have already shown that at Karluk the sockeye spending 2 years at sea have a higher fecundity than sockeye of the same length spending 3 years at sea.

TABLE 3.—*Egg number and fork length in species of* Oncorhynchus, *arranged geographically from south to north*

[Includes only samples of more than 20 fish]

| Species and area | Average number of eggs | Fork length | Number of fish |
|---|---|---|---|
| | | *Cm.* | |
| *nerka*: | | | |
| Fraser R., B. C | 4,048 | 58.33 | 463 |
| Namu, B. C | 3,264 | 57.2 | 33 |
| Skeena R., B. C | 3,432 | 59.50 | 276 |
| Nass R., B. C | 3,461 | 66.5 | 35 |
| Karluk R., Alaska | 3,277 | 59.59 | 451 |
| *kisutch*:[1] | | | |
| Fraser R., B. C | 3,152 | 65.3 | 48 |
| Namu, B. C | 3,002 | 69.85 | 21 |
| *gorbuscha*: | | | |
| Fraser R., B. C | 1,755 | 51.8 | 48 |
| Namu, B. C | 1,841 | 53.6 | 41 |
| McClinton Cr., B. C | 1,733 | 52.6 | 536 |
| Sashin Cr., S. E. Alaska | 2,074 | 54.6 | 77 |
| *keta*: | | | |
| Fraser R., B. C | 2,943 | 73.9 | 51 |
| Namu, B. C | 2,760 | 73.9 | 21 |
| *tshawytscha*: | | | |
| Sacramento R., Calif | 5,449 | 83.71 | 108 |
| Klamath R., Calif | 3,753 | 81.35 | 105 |
| Cowichan R., B. C | 3,885 | 86.4 | 25 |

[1] Scott Creek omitted, as averages (appendix table 1) were read from regression curve.

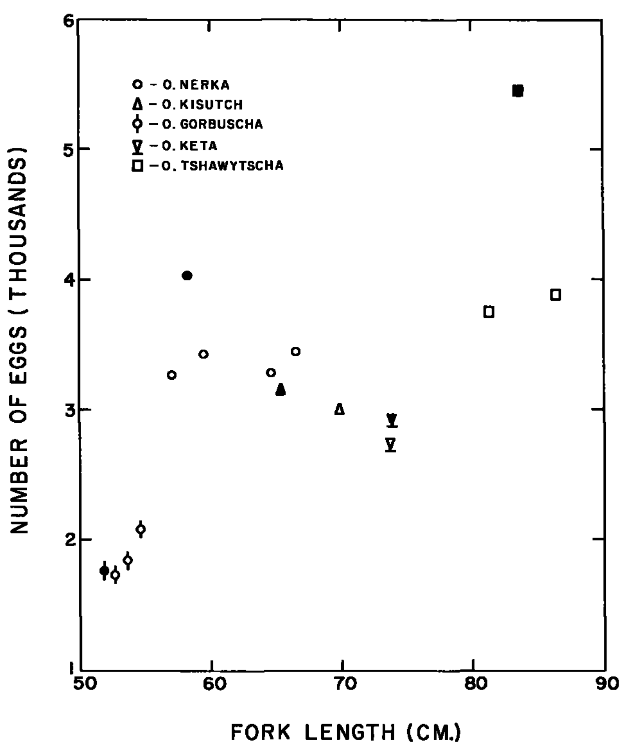


FIGURE 8.—Relation of mean egg number to mean fork length in species of *Oncorhynchus*, by locality. Southernmost localities are shown in solid black for each species.

## SUMMARY

The data show differences in fecundity between populations of the same species of salmon for different localities—the best examples being the king salmon, *Oncorhynchus tshawytscha*, of the Sacramento and Klamath Rivers; the sockeye salmon, *O. nerka*, of the Skeena River system; and the chum salmon, *O. keta*, of Japan.

The number of eggs shows a linear relation with the logarithm of fork length; but for *Oncorhynchus*, in which the size range of the mature adults is slight, the regression of egg number on fork length may more conveniently be treated as linear.

There is an annual variation in fecundity. Owing possibly to the short life history of the pink salmon, this variation is pronounced in that species. The annual differences in fecundity of pink salmon are shown by covariance analysis to be negatively associated with sea temperature for a Queen Charlotte Island population.

The number of eggs in the left and in the right ovary differs in some species, the left ovary usually having the larger number; but this will vary with the individual fish. This disparity between the two ovaries in egg number is apparently due to one ovary exceeding the other in length because of crowding of the small posterior end of the body cavity by the intestine.

Fecundity in sockeye salmon was not shown to be affected by length of sojourn in fresh water prior to entering the sea. However, sockeye spending 2 years at sea mature more eggs than sockeye of the same size with 3 years of sea life.

The four species of fluvial anadromous *Oncorhynchus* have larger eggs than the sockeye, *O. nerka*, or species of the other genera.

There is a suggestion of lower fecundity from south to north in *Oncorhynchus* (except in *O. gorbuscha*). This may be caused by a higher age at maturity, and therefore slower growth rates, from south to north.

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# APPENDIX

Appendix Table 1.—*Number of eggs at maturity in North American Salmonidae of the genus* Oncorhynchus

| Species and area | Average number of eggs | Sampling | | | | | Number of eggs per kilogram | Authority |
|---|---|---|---|---|---|---|---|---|
| | | Number in sample | Year | Age | Average fork length | Average weight of fish | | |
| *tshawytscha:* | | | | | *Cm.* | *Kg.* | | |
| Sacramento R., Calif. | 7,422 | 50 | 1922 | | 92.4 | | | McGregor (1923a). |
| Do. | 3,423 | 20 | 1950 | | 75.4 | 4.72 | 725 | Wales and Coots (1955). |
| Do. | 3,948 | 20 | 1951 | | 80.0 | 6.40 | 617 | Do. |
| Do. | 3,888 | 18 | 1952 | | 72.9 | 4.58 | 849 | Do. |
| Fort Bragg, Calif. | 5,034 | 53 | 1922 | | 80.8 | | | McGregor (1923b). |
| Klamath R., Calif. | 3,419 | 24 | 1920 | 4 | 78.5 | 6.175 | 554 | Snyder (1921). |
| Do. | 4,297 | 5 | 1920 | 5 | 88.0 | 8.664 | 496 | Do. |
| Do. | 2,648 | 3 | 1921 | 3 | 64.7 | | | McGregor (1922). |
| Do. | 3,504 | 29 | 1921 | 4 | 75.2 | | | Do. |
| Do. | 4,364 | 27 | 1921 | 5 | 89.8 | | | Do. |
| Do. | 4,270 | 6 | 1921 | 6 | 95.5 | | | Do. |
| Do. | 3,570 | [1] 29 | 1920 | | 80.1 | 6.604 | 541 | Snyder (1921). |
| Do. | 3,892 | [1] 65 | 1921 | | 82.7 | | | McGregor (1922). |
| Do. | 3,413 | 11 | 1922 | | 76.7 | | | McGregor (1923b). |
| Fraser R., B. C. | 4,944 | 12 | 1934 | | 87.1 | 9.843 | 502 | Foerster and Pritchard (1936). |
| Cowichan R., B. C. | 3,885 | 25 | 1935 | | 86.4 | 8.346 | 465 | Do. |
| Namu, B. C. | 8,426 | 11 | 1934 | | 103.4 | 16.148 | 522 | Do. |
| Kamchatka | 8,154 | | | | | | | Kuznetzow (1928). |
| *keta:* | | | | | | | | |
| Fraser R., B. C. | 2,943 | 51 | 1934 | | 73.9 | 4.58 | 643 | Foerster and Pritchard (1936). |
| Nile Cr., B. C. | 2,726 | 47 | | | | | | Neave (1953). |
| Namu, B. C. | 2,760 | 21 | 1934 | | 73.9 | 4.94 | 559 | Foerster and Pritchard (1936). |
| Hooknose Cr., B. C. | 2,254 | 114 | | | | | | Neave (1953). |
| Port John Cr. | 2,107 | 94 | 1947–48 | | | | | Hunter (1948, 1949). |
| Hokkaido, Japan | 2,625 | 109 | | | 58.8 | | | Eguchi et al. (1954). |
| Do. | 3,153 | 40 | 1940–43 | 3.5 | 61.0 | 3.84 | 821 | Watanabe (1956). |
| South Kurile, Japan | 2,000 | 134 | | | 56.6 | | | Eguchi et al. (1954). |
| Siberia (summer) | 2,498 | | | | | | | Kuznetzow (1928). |
| Siberia (autumn) | 4,302 | | | | | | | Do. |
| Kamchatka | 2,544 | | | | | | | Do. |
| *kisutch:* | | | | | | | | |
| Scott Cr., Calif. | [2] 2,500 | 65 | 1935–36 | | 65.3 | | | Shapovalov and Taft (1954). |
| Montana lakes | 567 | 37 | | | 34.0 | 0.50 | 1,136 | Beal (1955). |
| Fraser R., B. C. | 3,152 | 48 | 1934 | | 65.3 | 3.45 | 914 | Foerster and Pritchard (1936). |
| Cowichan R., B. C. | 2,329 | | | | | | | Neave (1948). |
| Port John Cr., B. C. | 2,313 | 3 | 1947 | | | | | Hunter (1949). |
| Namu, B. C. | 3,002 | 21 | 1934 | | 69.8 | 4.13 | 727 | Foerster and Pritchard (1936). |
| Nile Cr., B. C. | 2,310 | (3) | 1945–49 | | | | | Wickett (1951). |
| Kamchatka | 4,883 | | | | | | | Kuznetzow (1928). |
| *gorbuscha:* | | | | | | | | |
| Fraser R., B. C. | 1,755 | 48 | 1934 | 2 | 51.8 | 1.72 | 1,020 | Foerster and Pritchard (1936). |
| Morrison Cr., B. C. | 1,779 | 38 | 1943 | 2 | | | | Neave (1953). |
| Do. | 1,862 | 27 | 1945 | 2 | | | | Do. |
| Port John Cr., B. C. | 1,520 | 38 | 1947 | 2 | | | | Do. |
| Do. | 1,320 | 57 | 1947–48 | 2 | | | | Hunter (1948, 1949). |
| Do. | 1,593 | 20 | 1950 | 2 | | | | Neave (1953). |
| Namu, B. C. | 1,841 | 41 | 1934 | 2 | 53.6 | 1.86 | 990 | Foerster and Pritchard (1936). |
| McClinton Cr., B. C. | 1,535 | 97 | 1930 | 2 | 51.1 | | | Foerster and Pritchard (1941). |
| Do. | 1,538 | [4] 91 | 1930 | 2 | | 1.64 | 938 | Do. |
| Do. | 1,758 | 73 | 1932 | 2 | 54.0 | | | Do. |
| Do. | 1,804 | 165 | 1934 | 2 | 53.0 | 1.76 | 1,025 | Do. |
| Do. | 1,899 | 91 | 1936 | 2 | 53.0 | | | Do. |
| Do. | 1,899 | [4] 90 | 1936 | 2 | | 1.70 | 1,117 | Do. |
| Do. | 1,698 | 40 | 1938 | 2 | 52.7 | 1.81 | 938 | Do. |
| Do. | 1,619 | 70 | 1940 | 2 | 51.6 | 1.63 | 993 | Do. |
| Do. | 1,733 | [1] 536 | 1930–40 | 2 | 52.6 | | | Do. |
| Do. | 1,599 | [1,4] 456 | 1930–40 | 2 | | 1.71 | 935 | Do. |
| Sashin Cr., S. E. Alaska | 2,074 | 77 | 1951 | 2 | 54.6 | | | Hanavan and Skud (1954). |
| Siberia | 1,192 | 52 | Even | 2 | | 1.12 | 1,069 | Kuznetzow (1928). |
| Do. | 1,913 | 73 | Odd | 2 | | 1.82 | 1,054 | Do. |
| *nerka:* | | | | | | | | |
| Cultus L., B. C. | 4,310 | 46 | 1932 | | 58.5 | | | Foerster and Pritchard (1941). |
| Do. | 4,267 | [4] 43 | 1932 | | | 1.95 | 2,188 | Do. |
| Do. | 3,796 | 47 | 1933 | | 56.5 | 1.70 | 2,233 | Do. |
| Do. | 4,282 | 75 | 1934 | | 59.0 | 2.00 | 2,141 | Do. |
| Do. | 4,067 | 55 | 1935 | | 59.0 | 2.05 | 1,984 | Do. |
| Do. | 3,864 | 35 | 1937 | | 56.0 | | | Do. |
| Do. | 3,864 | [4] 36 | 1937 | | | 1.75 | 2,208 | Do. |
| Do. | 4,246 | 47 | 1938 | | 58.5 | | | Do. |
| Do. | 4,248 | [4] 32 | 1938 | | | 2.05 | 2,072 | Do. |
| Do.[5] | 3,800 | 112 | 1933 | | 57.0 | 1.95 | 1,949 | Do. |
| Fraser R., B. C. | 4,180 | 46 | 1934 | | 63.0 | 3.04 | 1,375 | Foerster and Pritchard (1936). |
| Namu, B. C. | 3,264 | 33 | 1934 | | 57.2 | 2.09 | 1,562 | Do. |
| Port John Cr., B. C. | 2,511 | 3 | 1948 | | | | | Hunter (1949). |
| Lakelse L., Skeena R. | 3,888 | 24 | 1939 | | 59.6 | | | Aro and Broadhead (1950). |
| Do. | 3,860 | 22 | 1948 | | 59.0 | | | Do. |
| Do. | 3,699 | 41 | 1949 | | 58.1 | | | Do. |
| Babine L., Skeena R., B. C. | 3,281 | 59 | 1946 | | 60.9 | | | Withler (1950). |
| Do. | 3,187 | 73 | 1947 | | 59.1 | | | Do. |
| Do. | 3,353 | 57 | 1949 | | 59.7 | | | Do. |
| Nass R., B. C. | 3,461 | 35 | 1934 | | 66.5 | 3.08 | 1,124 | Foerster and Pritchard (1936). |

See footnotes at end of table.

APPENDIX TABLE 1.—*Number of eggs at maturity in North American Salmonidae of the genus* Oncorhynchus—Continued

| Species and area | Average number of eggs | Sampling | | | | | Number of eggs per kilogram | Authority |
|---|---|---|---|---|---|---|---|---|
| | | Number in sample | Year | Age | Average fork length | Average weight of fish | | |
| *nerka:*—Continued | | | | | *Cm.* | *Kg.* | | |
| Karluk R., Alaska | 3,691 | 40 | 1926 | | 60.8 | | | Gilbert and Rich (1927). |
| Do | 3,305 | 24 | 1938 | $5_3$ | 58.7 | | | This report. |
| Do | 3,082 | 9 | 1938 | $6_3$ | 63.2 | | | Do. |
| Do | 2,909 | 10 | 1938 | $6_4$ | 57.6 | | | Do. |
| Do | 3,190 | [14] 46 | 1938 | 5–7 | 59.6 | | | Do. |
| Do | 2,548 | 36 | 1939 | $5_3$ | 54.8 | | | Do. |
| Do | 3,049 | 58 | 1939 | $6_3$ | 60.7 | | | Do. |
| Do | 2,805 | 13 | 1939 | $7_4$ | 59.5 | | | Do. |
| Do | 2,842 | [14] 117 | 1939 | 4–7 | 58.3 | | | Do. |
| Do | 3,421 | 80 | 1940 | $5_3$ | 60.0 | | | Do. |
| Do | 2,926 | 23 | 1940 | $6_3$ | 60.0 | | | Do. |
| Do | 3,549 | 25 | 1940 | $6_4$ | 60.0 | | | Do. |
| Do | 3,357 | [14] 135 | 1940 | 4–7 | 60.0 | | | Do. |
| Do | 3,708 | 45 | 1941 | $5_3$ | 60.0 | | | Do. |
| Do | 3,006 | 20 | 1941 | $6_3$ | 60.0 | | | Do. |
| Do | 3,668 | 36 | 1941 | $6_4$ | 60.0 | | | Do. |
| Do | 3,160 | 11 | 1941 | $7_4$ | 60.0 | | | Do. |
| Do | 3,521 | [14] 113 | 1941 | 4–7 | 60.0 | | | Do. |
| Kamchatka | 3,763 | | | | | | | Kuznetzow (1928). |
| *n. kennerlyi:* | | | | | | | | |
| L. Washington, Wash | 452±51 | 23 | 1938 | | [6] 27.3 | | | Scattergood (1949). |
| Kootenay L., B. C | 368 | 2 | 1898 | | [7] 22.9 | | | Do. |
| California reservoir | 479 | 626 | 1943 | | | | | Curtis and Fraser (1948). |

[1] Summary.
[2] Values read from published regression curve.
[3] 3 to 8 specimens per year.
[4] Partial duplication of fish in previous total or totals.
[5] Marked Cultus Lake *O. nerka* caught outside of Fraser River.
[6] Standard length of 103 females converted to fork length by factor 1.1.
[7] Standard length of 5 females converted to fork length by factor 1.1.

APPENDIX TABLE 2.—*Number of eggs at maturity in North American Salmonidae of the genus* Salmo

| Species and area | Average number of eggs | Sampling | | | | | Number of eggs per kilogram | Authority |
|---|---|---|---|---|---|---|---|---|
| | | Number in sample | Year | Age | Average fork length | Average weight of fish | | |
| *salar:* | | | | | *Cm.* | *Kg.* | | |
| Miramichi R., Canada | 7,678 | 163 | | 2 sea | [1] 71.4 | 4.26 | 1,802 | Belding (1940). |
| Gulf of St. Lawrence | 9,409 | 340 | | 2 sea | [1] 74.8 | 5.07 | 1,856 | Do. |
| Do | 13,883 | 15 | | 3 sea | [1] 86.7 | 8.68 | 1,594 | Do. |
| Do | 12,313 | 16 | | ([2]) | [1] 83.6 | 7.57 | 1,627 | Do. |
| *gairdneri:* | | | | | | | | |
| Scott Cr., Calif.[3] | 2,400 | 537 | 1932–33 | | 40.0 | | | Shapovalov and Taft (1954). |
| Do | 3,900 | | | | 50.0 | | | Do. |
| Do | 5,600 | | | | 60.0 | | | Do. |
| Do | 7,600 | | | | 70.0 | | | Do. |
| *g. aqua-bonita:* | | | | | | | | |
| Cottonwood Lakes, Calif | 326 | 450 | | | 20.0 | | | Curtis (1935). |
| Do | 765 | | | | 30.0 | | | Do. |
| Do | 1,102 | | | | 37.5 | | | Do. |
| *clarki:* | | | | | | | | |
| Henrys L., Idaho | 1,577 | 10 | 1953 | | [4] 31.9 | 0.573 | 2,752 | Irving (1955). |
| Do | 1,914 | 10 | 1953 | | [4] 40.8 | 1.180 | 1,622 | Do. |
| Do | 2,930 | 10 | 1953 | | [4] 51.8 | 2.394 | 1,224 | Do. |
| *c. lewisi:* Yellowstone R | 1,113 | 104 | | | | | | Lord (1930). |
| *c. henshawi:* | | | | | | | | |
| Blue L., Calif.[3] | 1,100 | 55 | 1941 | ([5]) | 35.0 | 0.33 | 3,333 | Calhoun (1944). |
| Do | 1,750 | | 1941 | ([5]) | 40.0 | 0.50 | 3,500 | Do. |
| Do.[3] | 750 | 38 | 1941 | ([2]) | 35.0 | 0.30 | 2,500 | Do. |
| Do | 900 | | 1941 | ([2]) | 40.0 | 0.44 | 2,045 | Do. |
| Heenan L., Calif | [6] 3,560 | 214 | 1940 | | | | | Smith, O. (1947). |
| Do | [6] 2,594 | 310 | 1941 | | | | | Do. |
| Do | [6] 2,508 | 320 | 1942 | | | | | Do. |
| *trutta:* | | | | | | | | |
| Madison R., Mont | 1,238 | 1 | 1936 | 2 | [4] 37.1 | 0.51 | 2,427 | Brown and Kamp (1942). |
| Do | 1,383 | 18 | 1936 | 3 | [4] 37.6 | 0.55 | 2,515 | Do. |
| Do | 1,164 | 14 | 1936 | 4 | [4] 40.7 | 0.66 | 1,764 | Do. |
| Do | 1,279 | 4 | 1936 | 5 | [4] 41.4 | 0.68 | 1,881 | Do. |
| Convict L., Calif | 1,061 | 14 | 1952 | | | | | Nielson (1953). |
| Michigan streams | 1,208 | 78 | | | 34.0 | | | Cooper (1953). |

[1] These values from weight-length regression of fig. 6.
[2] Previously spawned.
[3] Readings from published regression curves.
[4] Standard length converted to fork length by factor 1.1.
[5] First spawning.
[6] Eggs stripped by hatchery.

APPENDIX TABLE 3.—*Number of eggs at maturity in North American Salmonidae of the genera* Cristivomer *and* Salvelinus

| Species and area | Average number of eggs | Sampling | | | | | Number of eggs per kilogram | Authority |
|---|---|---|---|---|---|---|---|---|
| | | Number in sample | Year | Age | Average fork length | Average weight of fish | | |
| *Cristivomer:* | | | | | | | | |
| *namaycush:* | | | | | *Cm.* | *Kg.* | | |
| Lake Ontario | 7,943 | 25 | 1927 | | 72.7 | 5.00 | 1,589 | Dymond (1928). |
| Lake Superior | 3,383 | 9 | 1951–53 | | [1] 60.7 | 2.81 | 1,204 | Eschmeyer (1955). |
| Do | 4,253 | 15 | 1951–53 | | [1] 65.4 | 3.36 | 1,266 | Do. |
| Do | 4,995 | 13 | 1951–53 | | [1] 70.4 | 4.26 | 1,173 | Do. |
| Do | 8,667 | 17 | 1951–53 | | [1] 75.3 | 5.26 | 1,648 | Do. |
| Do | 8,881 | 8 | 1951–53 | | [1] 78.5 | 6.31 | 1,408 | Do. |
| Do | 11,603 | 6 | 1951–53 | | [1] 83.2 | 7.48 | 1,551 | Do. |
| Do | 13,836 | 2 | 1951–53 | | [1] 87.9 | 8.75 | 1,581 | Do. |
| Do | 11,789 | 2 | 1951–53 | | [1] 93.9 | | | Do. |
| Do | | [2] 72 | | | | | 1,424 | Do. |
| *n. siscowet:* Lake Superior | 4,387 | 12 | 1950–54 | | [1] 59.2 | 4.34 | 1,011 | Do. |
| *Salvelinus:* | | | | | | | | |
| *alpinus:* | | | | | | | | |
| Baffin Island | 3,589 | 23 | 1950–51 | 13–22 | 56.0 | | | Grainger (1953). |
| Do | 3,645 | [3] 21 | 1950–51 | 13–22 | | 2.00 | 1,822 | Do. |
| Ungava Bay | 2,726 | 6 | 1951 | 7–9 | 41.2 | | | Do. |
| Lakes in Sweden | 909 | 211 | 1945–48 | | 30.6 | 0.26 | | Määr (1949). |
| Do | 1,313 | 51 | 1949 | | 31.4 | | | Määr (1950). |
| Do | 1,443 | [3] 42 | 1949 | | | 0.26 | | Do. |
| *malma:* Clark's Fork R., Mont | 4,927 | 28 | 1950 | | 61.9 | 2.31 | 2,133 | Brunson (1952). |
| *fontinalis:* | | | | | | | | |
| New Jersey (domestic) | 1,183 | 53 | | ([4]) | 29.9 | | | Hayford and Embody (1930). |
| Do | 1,414 | 20 | | ([5]) | 31.4 | | | Do. |
| Michigan streams | 254 | 239 | | | [1] 14.4 | | | Cooper (1953). |
| Wyoming beaver pond | 148 | 2 | 1952 | | 12.70 | 0.0215 | 6,907 | Allen (1956). |
| Do | 191 | 5 | 1952 | | 14.44 | 0.0316 | 6,032 | Do. |
| Do | 275 | 5 | 1952 | | 16.82 | 0.0506 | 5,435 | Do. |
| Do | 376 | 2 | 1952 | | 19.65 | 0.0835 | 4,509 | Do. |
| Laurentides Park, P. Q | 399 | 77 | | | 22.3 | | | Vladykov and Legendre (1940). |
| Various (wild) | [6] 410 | 29 | | | 20.3 | | | Smith (1947). |
| Do | [6] 640 | | | | 25.4 | | | Do. |
| Do | [6] 950 | | | | 27.9 | | | Do. |
| Do | [6] 1,400 | | | | 35.6 | | | Do. |

[1] Total length converted to fork length by factor 0.92.
[2] Summary.
[3] Partial duplication of fish in previous total or totals.
[4] First spawning.
[5] Previously spawned.
[6] Values read from published regression curve.

APPENDIX TABLE 4.—*Summary of number of eggs by size of fish for North American Salmonidae*

| Species | All specimens | | Specimens with length data | | | | Specimens with weight and length data | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Average number of eggs | Number of fish | Average fork length | Mean number of eggs | Average number of eggs per centimeter | Number of fish | Average weight of fish | Average number of eggs | Average number of eggs per kilogram | Number of fish |
| *Oncorhynchus:* | | | *Cm.* | | | | *Kg.* | | | |
| *tshawytscha* | 4,772 | 314 | 83.46 | 4,772 | 57.2 | 314 | | | | |
| | | | 79.26 | 3,759 | 47.4 | 207 | 6.465 | 3,759 | 581 | 207 |
| *keta* | 2,546 | 233 | 73.90 | 2,890 | 39.1 | 72 | 4.685 | 2,890 | 617 | 72 |
| *kisutch* | 2,801 | 137 | 66.01 | 2,812 | 42.6 | 134 | | | | |
| | | | 66.68 | 3,106 | 46.6 | 69 | 3.657 | 3,106 | 849 | 69 |
| *kisutch* [1] | 567 | 37 | 34.00 | 567 | 17.7 | 37 | 0.499 | 567 | 1,136 | 37 |
| *gorbuscha* | 1,765 | 825 | 52.82 | 1,778 | 33.7 | 702 | | | | |
| | | | 52.61 | 1,754 | 33.3 | 364 | 1.746 | 1,754 | 1,005 | 364 |
| *nerka* | 3,597 | 1,262 | 59.24 | 3,600 | 60.8 | 1,258 | 2.121 | 3,946 | 1,860 | 514 |
| | | | 59.11 | 3,896 | 65.9 | 403 | 2.178 | 3,896 | 1,789 | 403 |
| *n. kennerlyi* | [1] 478 | 651 | 26.95 | 445 | 16.5 | 25 | | | | |
| *Salmo:* | | | | | | | | | | |
| *salar* | 9,092 | 534 | 74.36 | 9,092 | 122.3 | 534 | 4.999 | 9,092 | 1,819 | 534 |
| *gairdneri* [2] | [3] 5,541 | 537 | [4] 59.00 | (5,541) | 93.9 | 562 | | | | |
| *clarki* [1] | 2,140 | 30 | 45.65 | 2,140 | 46.9 | 30 | 1.382 | 2,140 | 1,548 | 30 |
| *c. lewisi* | 1,113 | 104 | | | | | | | | |
| *c. henshawi* | 2,806 | 844 | | | | | | | | |
| *trutta* | 1,233 | 115 | 35.66 | 1,233 | 34.6 | 115 | | | | |
| | | | 39.17 | 1,258 | 32.8 | 37 | 0.605 | 1,285 | 2,124 | 37 |
| *Cristivomer: namaycush* | 7,186 | 97 | 72.03 | 7,089 | 98.4 | 95 | 4.825 | 7,089 | 1,469 | 95 |
| *Salvelinus:* | | | | | | | | | | |
| *alpinus* [2] | 3,410 | 29 | 52.94 | 3,410 | 64.4 | 29 | | | | |
| | | | 56.00 | 3,589 | 64.1 | 23 | 2.000 | 3,645 | 1,822 | 21 |
| *alpinus* [5] | 988 | 262 | 30.76 | 988 | 32.1 | 262 | 0.260 | 998 | 3,838 | 253 |
| *malma* [1] | 4,927 | 28 | 61.90 | 4,927 | 79.6 | 28 | 2.310 | 4,927 | 2,133 | 28 |
| *fontinalis* [1] | 461 | 403 | 18.84 | 461 | 24.5 | 403 | | | | |
| | | | 15.79 | 241 | 15.3 | 14 | 0.044 | 241 | 5,477 | 14 |

[1] In fresh water.
[2] Anadromous.
[3] Calculated from egg volumes (Shapovalov and Taft, 1954, table A-17).
[4] Values from regression curve.
[5] In Swedish lakes.

APPENDIX TABLE 5.—*Summary of length-weight data on North American Salmonidae*

[A=anadromous; F=fresh water]

| Species | Habitat | Average weight | Average fork length | Number in sample | Logarithm | |
|---|---|---|---|---|---|---|
| | | | | | Average weight+2.0 Y | Average length X |
| *Oncorhynchus:* | | *Kg.* | *Cm.* | | | |
| *tshawytscha* | A | 6.465 | 79.26 | 207 | 2.8106 | 1.8991 |
| *keta* | A | 4.685 | 73.90 | 72 | 2.6707 | 1.8686 |
| *kisutch* | A | 3.657 | 66.68 | 69 | 2.5631 | 1.8240 |
| *kisutch* | F | 0.499 | 34.00 | 37 | 1.6981 | 1.5315 |
| *gorbuscha* | A | 1.746 | 52.61 | 364 | 2.2420 | 1.7211 |
| *nerka* | A | 2.178 | 59.11 | 403 | 2.3381 | 1.7717 |
| *Salmo:* | | | | | | |
| *salar* | A | 4.999 | 74.36 | 534 | 2.6989 | 1.8713 |
| *clarki* | F | 1.382 | 45.65 | 30 | 2.1405 | 1.6594 |
| *trutta* | F | 0.605 | 39.17 | 37 | 1.7818 | 1.5930 |
| *Cristivomer: namaycush* | F | 4.825 | 72.03 | 95 | 2.6835 | 1.8575 |
| *Salvelinus:* | | | | | | |
| *alpinus* | A | 2.000 | 56.00 | 21 | 2.3010 | 1.7482 |
| *alpinus* | F | 0.260 | 30.76 | 253 | 1.4150 | 1.4880 |
| *malma* | F | 2.310 | 61.90 | 28 | 2.3636 | 1.7917 |
| *fontinalis* | F | 0.044 | 15.79 | 14 | 0.6435 | 1.1984 |

APPENDIX TABLE 6.—*Summary of various measures of egg size in North American Salmonidae*

| Group and species | Eggs per cm. of fish | Eggs per kg. of fish | Egg diameter | | Weight of sac fry | Weight of fry with yolk absorbed |
|---|---|---|---|---|---|---|
| | | | Measured | Calculated | | |
| *Oncorhynchus:* | | | | | | |
| Fluvial anadromous: | | | *Mm.* | *Mm.* | *Gm.* | *Gm.* |
| *tshawytscha* | 47 | 581 | | 6.3–7.9 | 0.520 | 0.509 |
| *keta* | 39 | 617 | | 7.4 | | 0.24–0.62 |
| *kisutch* | 47 | 849 | | 7.2 | | 0.284 |
| *gorbuscha* | 33 | 1,005 | | | | Ca. 0.30 |
| Lacustrine anadromous: *nerka* | 66 | 1,789 | | 6.3 | | 0.192 |
| Fresh water: *kisutch* | 18 | 1,136 | | 8.4 | | |
| *Salmo:* | | | | | | |
| Fluvial anadromous: | | | | | | |
| *salar* | 122 | 1,819 | 5.4–6.8 | 6.1 | 0.110–0.180 | 0.057–0.144 |
| *gairdneri* | 94 | | 5.1 | 5.5 | | |
| Fresh water: | | | | | | |
| *salar sebago* | | | | 6.6 | | |
| *clarki* | 47 | 1,548 | 4.3–5.1 | | | |
| *clarki lewisi* | | | | 4.5 | | |
| *trutta* | 33 | 2,124 | 4.9 | 4.2 | | |
| *Cristivomer:* | | | | | | |
| Fresh water: *namaycush* | 98 | 1,469 | 4.9–5.8 | 5.2–5.8 | 0.075–0.080 | |
| *Salvelinus:* | | | | | | |
| Anadromous: *alpinus* | 64 | 1,822 | 5.0 | | | |
| Fresh water: | | | | | | |
| *alpinus* (Sweden) | 32 | 3,838 | | | | |
| *aureolus* | | | 4.7 | | 0.055 | |
| *malma* | 80 | 2,133 | | | | |
| *fontinalis* [1] | 15 | 5,477 | 4.0–4.4 | 4.2–4.6 | 0.033–0.040 | |

[1] The small sample available contained only small fish so that these figures are not believed to be representative for eggs per centimeter or per kilogram.

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