INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION

BULLETIN IV

A STUDY OF THE SPAWNING POPULATIONS OF SOCKEYE SALMON IN THE HARRISON RIVER SYSTEM, WITH SPECIAL REFERENCE TO THE PROBLEM OF ENUMERATION BY MEANS OF MARKED MEMBERS.

BY

MILNER B. SCHAEFER

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INTRODUCTION

The Sockeye Salmon Fisheries Convention, ratified by the United States and Canada in 1937, established the International Pacific Salmon Fisheries Commission for the purpose of restoring and maintaining the greatly reduced sockeye salmon fisheries of the Fraser River system. Pursuant to the authority of the treaty, the Commission's scientific staff commenced, in 1938, detailed studies of the natural history and population dynamics of the sockeye salmon runs upon which the fishery operates. Although much valuable information regarding these runs had been accumulated through the years by the scientists and fishery administrators of the Canadian Provincial and Dominion fisheries departments, and of the fisheries agencies of the United States and the State of Washington, the requisite knowledge for adequate management of the fishery was far from complete. It was anticipated by the treaty that two complete cycles (8 years) of study would be required before regulation could even be commenced by the Commission.

The Commission has the direct responsibility to manage the sockeye salmon resources of the Fraser River so as to restore them to something approaching their former productiveness. To this end it is imperative that methods be devised for estimating the abundance of the stock, since the productivity and level of abundance must be known in order to judge the effects of any regulatory or other rehabilitation measures. It has long been known that the Fraser River sockeye stock is composed of a number of separate races, each of which returns upon reaching maturity to that spawning area which constitutes the home of the particular race. This is demonstrable from the evidence of scale markings, from statistical analysis of morphometric data, and from marking experiments on downstream migrants. Furthermore, the various races have been quite unevenly reduced in numbers. Certain formerly abundant racial groups, such as those of the Quesnel and Horsefly Rivers, have been very nearly exterminated, while others, such as that of the Birkenhead River, have suffered a far lesser degree of diminution (Thompson, 1939, 1945). Because the total stock is composed of a number of genetically separate groups, which, because of their differences in regard to location of spawning areas, times of passage through the fishery, and other factors, may be expected to exhibit more or less independent variations in abundance, the measurement methods employed must be designed to give the desired information for each racial group separately. Indices of abundance, such as those of Rounsefell and Kelez (1938) or of Thompson (1945) measure the average condition of all the independent component stocks making up the whole. Yet the rehabilitation of the separate components is a requisite condition of the optimum development of the fishery. As Thompson (1939) stated, "Foremost among the necessities is an

accurate system of estimating the runs, and the numbers which escape to the spawning grounds of each race."

The estimation of size of spawning populations of salmon has been primarily of two types. The most accurate method is to construct a counting fence below the spawning area and enumerate the migrants as they pass through a gate in the fence. This is of limited applicability on the Fraser because of the many localities where such fences cannot be maintained because of the navigability of the streams in question, or because of extreme flood conditions, which would necessitate an extremely large and costly structure to withstand the high water. The second commonly employed method depends upon the comparison from year to year of estimates made by observers during the spawning season. These estimates may be made to depend upon counts of adult salmon observed on the spawning ground or on a fixed part thereof, or may be merely the results of a general impression of a trained observer. The Commission has carried out extensive researches toward standardizing such methods for the various spawning grounds of the Fraser, and the estimates published in its annual reports are largely based on such methods. These methods suffer from the drawback of containing a large subjective factor. The result depends partly upon the judgment of the observer, and it is not often evident what degree of confidence can be placed in it. Realizing the drawbacks of such methods, the Commission early undertook experiments toward developing the applications of other, more objective, methods to the problem. Among these is the method of estimating a population by means of marked members. If a number of members in a population have some distinctive characteristic, say a mark or tag, by which they may be recognized, and this number is known, and if the proportion of members so marked in the population may be estimated from a sample, the total members of the population may be then estimated from this information.

In 1938 and 1939 experiments were conducted at Cultus Lake under the direction of Dr. J. L. Kask to examine the feasibility of employing marked members for estimating the adult sockeye population. At Cultus Lake all the fish were counted past a fence below the spawning grounds, and the known total population thus formed the basis for determining the correctness of the results arrived at by the marking method. Of the 1938 experiments, the report of the Director for 1937 and 1938 (Thompson, 1939) said:

> "The method is simple and direct. The adult migrants lifted over the weir were 13,000 in number. Of these a third were tagged. The ratio of tagged to untagged thus established reappeared wherever the spawners could be obtained, even though in small number. It was shown that if the ratio was ascertained from even a small fraction of the run, dead or alive, the total number of migrants could be determined. This was true even when the ratio was reduced to 3 in 100."

In 1939 the experiment at Cultus Lake was repeated on a large run of 73,189 fish.

The data from the two Cultus Lake experiments were examined by Kask and Howard (M.S.). They found that when *all* the recovery data were considered, the average ratios of tagged to untagged fish among the samples of the population

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were very close to those expected in both years, and therefore the calculated populations agree very closely with the actual. However, closer examination of the data leads to somewhat modified conclusions (Howard, 1948). When the data are broken down, there are some evidences of differential mortality related to the tagging, and evidences of differences in tag ratios among different segments of the population, which affect the accuracy of computations based on samples of such different sub-divisions.

The design of experiments to measure populations by marking methods, in particular the sampling, and the computations necessary to obtain a reliable estimate from the data obtained, depend to a very great degree on the nature of the populations being studied. In order to gain information on the structure and behaviour of populations of migrating adult salmon, to examine into the validity of marking methods for making population estimates, and to lay a foundation for employing these methods in larger stream systems than Cultus Lake, and under more nearly "average" conditions than obtained there, experiments were conducted by the author, with the aid of a number of assistants, in 1939, 1940 and 1941 in the Harrison River System. This paper is an analysis, by no means exhaustive, however, of some of the data thus obtained, with the following objects:

1. To trace the migrations of the important spawning populations within the Harrison River System.

2. To examine the nature of the spawning migration of representative runs, with particular regard to the amount of mixing enroute to and on the spawning grounds, and the degree to which the populations are stratified.

3. To study the design of sampling procedure and statistical analysis in the determination of population numbers by means of marked members.

4. To detect, and if possible to measure, harmful effects of the marking procedure which would cause the marked fish to behave differently from the unmarked, and so give erroneous results in the population computations.

5. To determine whether estimation of spawning sockeye salmon populations by means of marked members is practicable in the Harrison River System, and presumably, therefore, in other similar systems, and to discover limitations of the applicability of the method.

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THE EMPLOYMENT OF MARKED MEMBERS IN THE ESTIMATION OF ANIMAL POPULATIONS, WITH SOME CONSIDERATIONS OF SAMPLING THEORY

Simple Case

The problem

The simplest case with which we have to deal, and which we will see can be applied to most of our salmon problems, is where we have a population containing N members (unknown) which is known to contain T marked members and $U = N - T$ unmarked, and where we have drawn a single representative sample of n members containing t marked and $u = n - t$ unmarked. The term "representative" is here used to mean such that the character estimated from repeated samples will have a mean value equal to the population value. This corresponds with the commonly accepted sense of the term, and also with its usage by Neyman (1934). A simple random sample of the population is representative, but so also may be various others.

The problem of estimating N consists in making such an estimate given T and the sample values n, t and u. The usual basis of procedure is to accept $\frac{N}{T} = \frac{n}{t}$ intuitively and to estimate N by the equation

$$N = \frac{nT}{t} \qquad \ldots \ldots \ldots \ldots \ldots \ldots \quad (1)$$

This estimate has been employed by a considerable number of investigators during the last two decades to estimate the populations of various organisms. The method is much older than this, however, having been employed as early as 1783 by the famous French mathematician and scientist, La Place, in estimating the human population of France. La Place gave considerable attention to the theoretical problem of the error involved in employing the above estimate. This problem attracted the attention of another famous statistician, Karl Pearson, who published an analysis of it in 1928. Later workers in various branches of zoology seem to have overlooked Pearson's work and also that of their zoological contemporaries. They have apparently often "rediscovered" the same method, but have in the main given little or no attention to the problem of the accuracy of the resulting estimate.

In the following discussion I will, except where specifically stated to the contrary, take the liberty of changing the symbols employed by the various authors to a uniform set of symbols throughout, so that the notation in this thesis shall be uniform to as great an extent as is practicable, and therefore be more easily understandable.

La Place determined from a sample the ratio of births in a year to the population producing those births, and then ascertained the number of births in a year in each urban and rural district of France; by multiplying the number of births by the ratio of population to births determined from the sample he arrived at an estimate of the total population. La Place was led to consider also the error inherent in his estimate. This problem, as restated by Pearson (1928), but using

my notation, is as follows: "A population of unknown size N is known to contain T affected or marked members. It is desired to ascertain—on the hypothesis of inverse probabilities—a measure of the error introduced by estimating N to be $n\dfrac{T}{t}$, where t is the number of marked individuals in a sample of size n. La Place treated this problem as an urn problem, with an infinite number of black and white balls representing marked and unmarked members. On the basis of an extension of Bayes' theorem he predicted from a first sample of t and n observed what a second sample with known T but unknown N might produce. He found that the mean value of N would be equal to $\dfrac{Tn}{t}$ if T, n, and t are all large. He also took the distribution of N to be a normal curve about $\dfrac{Tn}{t}$ as mean with standard deviation estimated by

$$\sigma_N^2 = \frac{Tu(T+t)(t+u)}{t^3} \quad \dots \dots \dots \quad (2)$$

where the numbers are all large.

Pearson re-examined this problem in his 1928 paper because he felt La Place's urn statement did not fit the actual problem since "we are not taking a second sample from an infinite population. We have only one sample and we want to learn something about the population from which it has been sampled, which is finite in extent, although its extent is unknown. We do know, however, that it contains T white balls, i.e. births in all France".

Assuming the sample n to be a random sample of the finite population N and on the basis of inverse probabilities (Bayes' Theorem), Pearson finds that the modal value of the distribution of the possible values of N is

$$\widetilde{N} = u + T + \frac{u(T-t)}{t} = \frac{nT}{t}. \quad \dots \dots \dots \quad (3)$$

the mean value is

$$\overline{N} = u + T + \frac{(u+1)(T-t+1)}{(t-2)} \quad \dots \dots \dots \quad (4)$$

and the variance is

$$\sigma_N^2 = \frac{(u+1)(T-t+1)(n-1)(T-1)}{(t-2)^2(t-3)} \quad \dots \dots \quad (5)$$

where t, u, and T are all large, La Place's case,

$$\overline{N} = \widetilde{N} = \frac{nT}{t} \quad \dots \dots \dots \dots \quad (6)$$

and

$$\sigma_N^2 = \frac{Tu(T-t)(t+u)}{t^3} \quad \dots \dots \dots \dots \quad (7)$$

This estimate of σ_N^2 is different than that of La Place, the disagreement being attributed by Pearson to La Place's taking his sampled population as if it were a second sample independent of that already taken.

Pearson's paper seems to have been generally overlooked by zoologists dealing with similar problems.

Some applications in the literature

The formula (1) has been applied to the estimation of diverse animal populations. One of the best known of these applications is the so-called "Lincoln Index" of the duck population of North America developed by Lincoln (1930), and mentioned in the textbook of Leopold (1935) the monograph of Kendeigh (1944), the manual of Wright (1939), and elsewhere. He used the ducks banded at stations in North America as his marked members, and the kill by hunters as his sample of the population. Lincoln's solution to the problem was stated by him as follows:

"Given a fairly accurate statement showing the number of wild ducks killed in North America in any one season, then the total number of ducks present on the continent for that season may be estimated by a percentage computation, based on the relation that the total number of banded ducks killed during their first season as band carriers bears to the total number killed."

The inaccuracies of kill records and the incomplete return of bands were recognized as sources of error. No attempt was made to estimate the statistical error.

A rather naive application was made by Vorhees and Taylor (1933). These workers computed the number of jackrabbits on fenced cattle ranges of Arizona by taking the ratio of jackrabbits seen to the number of cattle seen in a strip equal in width to the apparent flushing distance of the jackrabbits, and comparing this ratio with the known number of cattle on the range. In this case the cattle would represent the "marked" members of the population of rabbits plus cattle. It seems rather doubtful that the ratio in the sample would be a fair estimate of the ratio in the population because of the obviously different visibility of cows and rabbits, even in a strip of narrow width.

Jackson (1933) developed a method of computing the population of tsetse flies in a closed area by means of marking flies with colored paint and taking a sample to determine the ratio of marked to unmarked. He said:

"In any area which is isolated from the remainder of the fly-infested bush it is evident that some estimate of the total number contained in the fly population can be obtained by marking a known number of flies and subsequently finding what proportion these form of the total population. If the delay between marking and recapture be short, the change in the constitution of the population owing to birth and death of individual flies will not have had time to affect appreciably the estimate obtained. If the delay be long the deaths of the marked flies and the emergence of new individuals will have lowered the proportion of marked to unmarked flies."

He made no attempt here to estimate the sampling errors.

In a later paper (1936) Jackson states that he discovered this method independently in 1930, but meanwhile became cognizant of Lincoln's work and hastens to credit Lincoln with the method. In this paper he also developed methods of applying the marking technique to an area, not closed, in which emigration and immigration are taking place, and also devised a correction for birth and death rates. These methods are not applicable to the present research, and will not be considered further in this paper.

Jackson mentioned, also, that a representative sample of the population as regards mark ratios would be obtained (referring now to our simple case) if *either* the marking *or* the subsequent sampling is carried out in a non-selective fashion. This is of considerable practical importance. It is not necessary that *both* be non-selective. If the marks are randomly, or evenly, distributed in the population, any sample of n members will yield a consistent estimate of the mark-ratio in the population. (The term "mark-ratio" or "tag-ratio" will be used in this thesis to mean the quotient of the number of marked members in a group divided by the total members in the group). Similarly, a representative sample of the population will yield a consistent estimate of the mark-ratio regardless of the distribution of marked members in the population.

Sato (1938) estimated the stock of red salmon in the Western North Pacific. He stated:

"The stock of red salmon may be estimated by the formula $Y:X=S:Z$, where Y is the number of tagged fishes, X the number of recaptured fishes, and Z the total catch of the fish."

His estimate of 94.7×10^6 individuals in 1936 was made from 1358 marked fish and 177 recaptures among a sample of $12,339 \times 10^3$. He made no attempt to estimate the reliability of the result. It may be seen from (7), however, that the sampling error is actually quite large.

Green and Evans (1940) employed this method for computing populations of snowshoe hares. Hares were trapped and banded during a long "precensus period" lasting all winter and up to mid-April. The banded hares at liberty from these operations were taken as the known number of marked members, and the ratio of marked to unmarked was determined during a short "census period" in April. The formula employed by these authors is essentially (1) since they take:

$$\frac{\text{"Hares banded in precensus period}}{\text{Other hares present in precensus period}}$$

$$= \frac{\text{"New-banded hares trapped in census period}}{\text{Other hares trapped in census period}} \quad \ldots \ldots \ldots \quad (8)$$

and compute the number of "other (unmarked) hares present in precensus period", and add it to the number of marked hares to get the total population. This is a slight variation of the method previously outlined.

These authors consider the effects of several possible sources of error in the application of the method. They show that migration in and out of the area of study is unimportant. The "evenness" of the sampling is also considered. They state that ". . . . it is essential that trapping throughout the area be uniform during the census retrap in the spring. . . . Uniformity need not be so rigidly maintained during the precensus period." This, of course, is a special case of the rule that either the sampling for tagging must be uniform, or the subsequent sampling for tag-ratio must be such as to yield a representative sample of the whole population.

Green and Evans also consider the "error of random sampling." Using the notation of Green and Evans, we find they take:

$p =$ proportion of hares trapped in census period that were not banded (trapped) in precensus period

$P =$ number of the hares trapped in census period that were not trapped (banded) in precensus period

$N =$ total number of hares trapped in the census period

$$p = \frac{P}{N}$$

They then take σ_p for the standard deviation of p and state that

$$\sigma_p = \sqrt{\frac{pq}{N}} \qquad \qquad \cdots \cdots \cdots \cdots \cdots \cdots \quad (9)$$

where $q = 1 - p$.

Taking $P \pm 2\sigma_p N$, and employing these values in place of the second quotient in their formula (8), they arrive at an estimate of the error of sampling. They conclude that "if we use $2\sigma_p$ as our range on either side of the figure obtained we are almost certain to include the correct figure for p, since twice the standard deviation on either side of the mean includes 95 per cent of a normal distribution curve."

While this estimate of the reliability of the population estimate is better than none and, indeed, will give an idea of limits within which the population may be expected to fall it suffers from a lack of precision. The formula (9) gives the standard deviation of p in repeated samples of size N from a population of infinite size. Since in the present case the population is finite, and N is large with respect to it, the formula for the standard deviation of p should be

$$\sigma^2_p = \frac{R-N}{R-1} \frac{pq}{N}$$

Where $R =$ the number in the population, (Cramer, 1946, page 516, Kendall, 1944, page 203). Thus Green and Evans' limits would tend to be excessively broad.

Green and Evans' estimate also has the same objection that Pearson raised to La Place's solution (see page 6 above), that this treats the problem of a further sample from a population in which the value of p is known, which is not quite the same thing as determining the error of the estimate of the population from the single sample available.

Dice (1941) refers to the paper by Green and Evans and considers a number of practical factors to be taken into account in carrying out the sampling when employing this method.

Knut Dahl (1943 pp. 139-143) has applied the method of marked members to enumeration of trout in a lake. In a small lake on the west coast of Norway, of 250,000 square meters, trout were captured by beach seine and marked. During a second fishing 8 to 14 days later he determined the number of marked and unmarked fish captured. From the number of marked fish liberated divided by the number of marked fish recaptured he computed a "Gjenfangstkvotient" by

which the total fish taken in the second fishing was multiplied to obtain the total population. This is, of course, the same as (1), where $\frac{T}{t}$ is the "Gjenfangstk-votient."

Ricker (1942) mentions the simple case here considered, although he uses a method of repeated tagging and sampling on the stationary populations of pond fishes dealt with in his paper. This method will be reviewed subsequently.

In a later paper, Ricker (1945a) employs the formula (1), which he calls "the Petersen method" after the Danish investigator who is said to have used it on plaice. Ricker's field procedure is similar to that of Green and Evans on hares in that he used the number of fish marked during a precensus period and the mark-ratio during a later period. He also writes in regard to the sampling consideration we have discussed earlier in relation to Jackson (1936) that:

> "The principle involved here is that if either the marking *or* the search for recaptured fish is made on only a part of a homogeneous population, the Petersen estimate will still apply to the whole population. If both marking and search are made in only a fraction of the population, the estimate applies to whichever fraction is larger."

Cagle (1946) employed marked lizards to estimate their population on a section of Tinian Island by the employment of the method formulated in (1). He marked 127 individuals by clipping their toes and in a sample of 52 found 12 marked yielding an estimated population of roughly 500 individuals. He did not consider the problem of sampling error.

Some further theoretical considerations

AN ALTERNATIVE DERIVATION

Formulae (3) to (7) were reached by Pearson by means of Bayes' theorem, which is objected to as invalid by some mathematical statisticians (Kendall, 1944, p. 176 et seq.). Dr. S. Lee Crump has suggested (private communication) that an estimate of N may be arrived at by other means, as follows. Drawing samples of fixed size n from a population N of which T are marked, the probability that in a sample of n, t are marked is

$$P(t) = \frac{(N-n)\ !\ n\ !\ T\ !\ (N-T)\ !}{N\ !\ t\ !\ (T-t)\ !\ (n-t)\ !\ (N-T-n+t)\ !} \quad . \quad . \quad (10)$$

whence

$$E\left\{\frac{(n+1)(T+1)}{(t+1)}\right\} = N+1 - P(0)(N-T-n) \quad . \quad . \quad (11)$$

where $E(\ )$ denotes mathematical expectation and $P(0)$ is the probability of getting no tags in the sample.

This means that $\quad \dfrac{(n+1)(T+1)}{(t+1)} - 1 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (12)$

is an estimate of N biased by an amount $P(0)(N-T-n)$. If conditions are such that a sample of n with no marked individuals is very unlikely, the bias is negligible. We may say that (12) is an effectively unbiased estimate of N.

Where the numbers are all large, (12) reduces immediately to (1) or (6).

Unfortunately, an estimate of the variance of the estimate of N given in (12) has not yet been obtained.

Chapman (1948) considered the problem of determining the value or values of N which make $P(t)$, formula (10), a maximum and concluded that the maximum likelihood estimate of N is $\frac{nT}{t}$, or if this is fractional, the integer immediately below $\frac{nT}{t}$.

CONFIDENCE LIMITS ON THE POPULATION ESTIMATE

The method of confidence intervals, due to Neyman (1934), may be employed to determine the range of values within which we may expect N to lie. This method is perhaps preferable to the employment of the method by which (7) was derived, for theoretical reasons. A discussion of the theory of confidence intervals is beyond the scope of this paper, for which reference is made to the original paper of Neyman or to the discussion of Cramer (1946, p. 507 et seq.) or that of Kendall (1946, p. 62 et seq.).

The confidence limits of the estimate of the tag-ratio in the population may be obtained as follows (Cramer, 1946, p. 515):

"Suppose we have a population consisting of a finite number N of individuals, Np of which possess a certain attribute A, while the remaining $Nq=N-Np$ do not possess A. It is now required to estimate the unknown proportion p . . . . Let us draw a random sample of n individuals *without* replacement, and observe the number v of individuals in the sample possessing the attribute A. In current text-books on probability, it is shown that we have

$$E\left(\frac{v}{n}\right)=p \qquad D^2\left(\frac{v}{n}\right) = \frac{N-n}{N-1} \cdot \frac{pq}{n}$$

Further the variable $p^* = \frac{v}{n}$ is approximately normally distributed, when n and $N-n$ are large. Taking p^* as an estimate of p, we now assume as above that the error of approximation in the normal distribution can be neglected. The probability that p^* lies between the limits $p \pm \lambda \sqrt{\frac{N-n}{N-1} \cdot \frac{pq}{n}}$ is then equal to ϵ, where λ has the same significance as in the preceding example." (Note: where λ was stated to be the $100\epsilon\%$ value of a normal deviate, and ϵ is the confidence level).

In Cramer's notation E( ) denotes mathematical expectation (or mean value) and $D^2($) denotes the variance.

N and n have the same meaning as in our earlier formulae, (1 to 12). p is equal to $\frac{T}{N}$, and v is equal to t in those formulae.

For any given value of N, n, and T we can calculate the limits within which $p* = \frac{t}{n}$ may be expected to fall for a given confidence level, ϵ, by the formula

$$p \pm \lambda \sqrt{\frac{N-n}{N-1} \cdot \frac{pq}{n}} \qquad \cdots \cdots \cdots \cdots \cdots \cdots \quad (13)$$

where $p = \frac{T}{N}$ and $q = 1 - p$.

Given values of n and T from an experiment, we can, then, by means of (13) calculate for various values of p, as ordinates, the limits within which $p*$, the tag-ratio of the sample, as abscissae, may be expected to fall for a given value of the confidence level ϵ. The curves connecting these points will form the confidence limits corresponding to various values of sample tag-ratio $p* = \frac{t}{n}$. Since to every value of p there corresponds a value of N, these curves also give the confidence limits of our estimate of the size of the population made by the formula

$$N* = \frac{T}{p*} \cdot \qquad \cdots \cdots \cdots \cdots \cdots \cdots \cdots \cdots \quad (14)$$

which is the same as (1), of course

A numerical example may make this clear. Suppose that in a given experiment we have placed 1000 tagged fish in the population and plan to draw a sample of 2000 fish for determining the tag-ratio. By means of (13) we can compute for values of population tag-ratio, p, the limits within which $p*$ will be expected to fall in, say, 95% of the cases ($\epsilon = .95$). In Figure 1, we have calculated and plotted these limits for part of the range of p for this example. The ordinates on this graph are values of p, and the abscissae are values of p*. Going horizontally across the graph for a given value of p we come to the values of $p*$ within which samples of 2000 from a population having a true tag-ratio of p would be expected to fall in 95% of the cases. By the theory developed by Neyman the loci of such points for various values of p form the 95% confidence limits for values of $p*$. For a given value of $p*$ we go along the vertical to the intersections with these loci to find the confidence limits for that value of $p*$. Thus, suppose that we draw our sample of 2000 and find that it contains 100 tagged fish. Our estimate of the tag-ratio in the population is .05, and from Figure 1 we find for this value of $p*$ the 95% confidence limits are .042 and .059. Since we know there are 1000 tagged fish in the population, our estimate of the population by (14) is 20,000 with 95% confidence limits 16,950 and 24,800. On the right hand edge of the graph we have plotted the values of N corresponding to tag-ratio values of the same ordinates on the left hand edge, in order to exhibit graphically the relationship between the two.

Such a chart as this may be computed for any particular experiment. The entire range of values of p need not be included; it is sufficient in practice to compute the values to include the region within which $p*$ is expected to fall.

For values of n which are small with respect to N, so that $\frac{N-n}{N-1}$ approaches 1, (13) approaches the form appropriate for the binomial. Clopper and Pearson (1934) have computed and charted the confidence limits of the binomial for a

large number of values of n for 95% and 99% confidence levels. Since the limits for the binomial fall in every case outside the limits given by (13), these charts may be used to obtain upper and lower limits on the sample value of p^* even where n is not small in relation to N. This involves, of course, a considerable loss of efficiency when n is not small in relation to N, so that the employment of (13) would seem to be generally preferable in such cases.
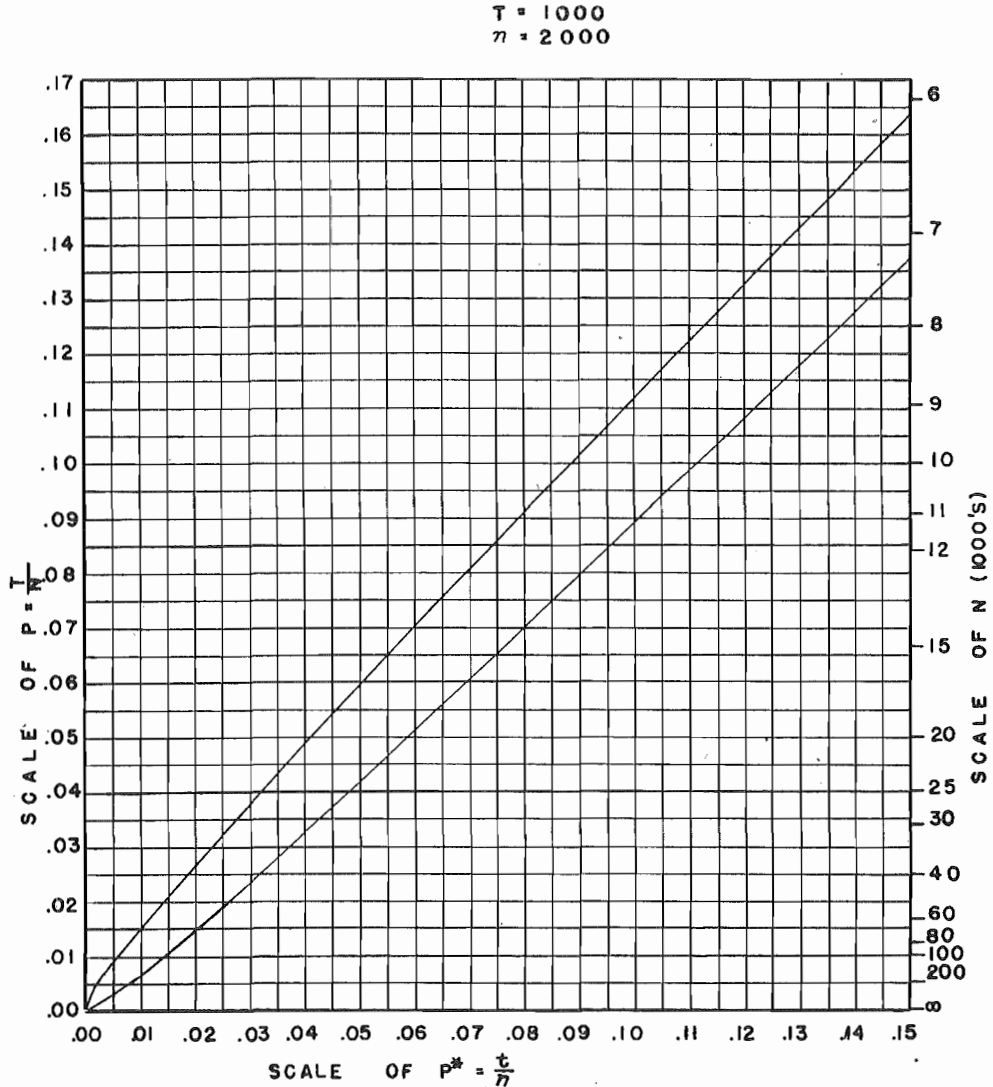
FIGURE 1. Confidence limits on sample tag-ratios and on estimated population numbers, at a confidence level of 95 per cent, for experiment involving 1000 tagged individuals and samples of 2000.

Chapman (1948) has considered the Poisson approximation to the distribution of expected numbers of tag recoveries where the tag-ratio is low, in addition to the binomial and normal approximations, as bases for confidence interval estimates of N. He has tabulated useful confidence limits for the Poisson distribution and

discussed practical criteria for judging which distribution to choose as a basis of estimation for various values of n and $\frac{t}{n}$. This paper became available to me after completion of my own limited work presented above.

As is indicated by Chapman's example on page 81 of his paper, for experiments involving numbers of tagged fish, T, and subsequent samples, n, of the magnitude with which we are dealing in most of our salmon-tagging experiments, the differences in confidence limits resulting from the several distributions which might be employed are not very great and in practice it would make little difference which we chose. He recommends which distribution to employ for various situations; for values of $n>1000$ and $t/n>0.05$ he recommends the normal-hypergeometric distribution, which has been employed by me in my example above.

Repeated sampling of a constant population

Where the population of an area remains constant over an appreciable period of time, it is possible to arrive at an estimate based on repeated sampling and marking. This method is not applicable to adult salmon populations, but, because of its wide application to other fish populations, it will be briefly reviewed for sake of completeness.

In order to census the population by this method, a sampling station or group of stations is established which will result in a random sample of all parts of the population. Samples are drawn at intervals, the fish tagged and replaced. Records are kept for each sample of the number of fish caught and the number of recaptures. According to Schnabel (1938) who solved the problem of estimating the population from the resulting data, "If it be assumed that each sample be drawn at random and that the population of the lake remain constant throughout the period under consideration, it is possible to obtain an estimate of the total number of fish in the lake from the data of the census."

We may let N be the total population, as before, T_i be the number of tagged fish in the lake when the ith sample is drawn, n_i be the total number in the ith sample, consisting of t_i tagged fish recaptured and u_i untagged. Miss Schnabel finds that where K samples are drawn the method of maximum likelihood gives as an estimate of N the positive real root of the Kth order equations

$$\sum_{i=1}^{K} \frac{u_i \, T_i}{N-T_i} = \sum_{i=1}^{K} t_i \qquad \qquad \dots \qquad (15)$$

which can be expanded in the form

$$\sum_{i=1}^{K} \frac{u_i \, T_i}{N}\left(1 + \frac{T_i}{N} + \frac{T_i^2}{N^2} + \cdots\right) = \sum_{i=1}^{K} t_i \qquad \dots \qquad (16)$$

By taking sufficient terms in (16) the root may be approximated as closely as desired. Schnabel states that 3 terms of the series are usually sufficient, and that the computations necessary for higher approximations are often prohibitive.

Schnabel also considers some special cases of (16). By writing the equation (15) in the form

$$\sum_{i=1}^{K} \frac{n_i T_i - t_i N}{N - T_i} = 0 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (17)$$

it may be seen that if T_i is negligible compared to N, the root of (15) is approximately

$$\frac{\displaystyle\sum_{i=1}^{K} n_i T_i}{\displaystyle\sum_{i=1}^{K} t_i} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (18)$$

This is the formula which has been employed by fisheries workers in practice.

Next Schnabel points out that if $T_i = T$ for all i

$$N = \frac{T \displaystyle\sum_{i}^{K} n_i}{\displaystyle\sum_{i=1}^{K} t_i} . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (19)$$

and states that "This formula is applicable to the data of experiments in which the number tagged is held constant after a certain point. This method has the disadvantage that the data taken before T becomes constant are not utilized."

It may be readily seen that if we consider the sum of the samples in this last case as a single large sample, (19) is identical with (1). Thus the simple case considered earlier may be regarded as a special case of the method of the present section.

Schnabel's formula (18) has been employed by Ricker (1942, 1945a) to estimate fish populations of lakes and ponds in Indiana. Ricker has assumed that, in situations where this formula is applicable, the fiducial limits of the Poisson distribution applied to Σt_i would give some idea of the variability ascribable to random sampling (Ricker 1945b), but also states, "an estimate of error obtained directly from the data themselves, for both the general and the special case, is to be desired."

Underhill (1941) applied this method and formula (18) to the computation of a chub sucker population of a pond in New York, and Roach (1943) has done the same in estimating the white bass population of an Ohio lake.

Schumacher and Eschmeyer (1943) have devised an estimate of N from repeated samplings which is different from that of Schnabel. They assume that the weight, or value, of each sample is proportional to the number of fish in the sample. Under this assumption, an estimate of N is arrived at by minimizing

the sum of the squares of the weighted discrepancies of the $\dfrac{T_i}{N}$ from their esti-

mates $\dfrac{t_i}{n_i}$. This leads to the formula

$$N = \frac{\sum\limits_{i=1}^{K} T_i^2 n_i}{\sum\limits_{i=1}^{K} T_i t_i} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (20)$$

which is applied by these authors to the estimation of fish populations of a pond in Tennessee.

These authors have also derived an expression for the sampling error of N. They take as the standard error of N the square root of

$$\frac{N^3 s^2}{\sum\limits_{i=1}^{K} T_i t_i} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (21)$$

where

$$s^2 = \frac{1}{K-1} \left[\sum_{i=1}^{K} \frac{t_i^2}{n_i} - \frac{1}{N} \sum_{i=1}^{K} T_i t_i \right]$$

In the last formula I have corrected a typographical error which appears in the original paper (formula 3, page 234) and which Professor Schumacher has kindly pointed out in a private communication.

Ricker (1945b) has investigated the relative efficiency of Schumacher's estimate (20) and Schnabel's formula (18). He states, "From an exchange of letters with Dr. Schumacher it appears that the efficiency of this expression is at a maximum when $\dfrac{T}{N}$ is equal to 0.5, whereas Schnabel's second, or approximate formula becomes most efficient as $(T/N) \rightarrow 0$, and the two formulae are of equal efficiency when $T/N = 0.25$. Consequently Schnabel's form will ordinarily be best, since the value of T/N rises gradually from a very small initial magnitude, and, except on quite small bodies of water, will not often exceed 0.25 even when the experiment comes to an end. Of course Schnabel's long formula, carried to several terms, can always be used if the best possible estimate is desired; but the labor of computation will rarely be warranted, considering the magnitude of the sampling and probably systematic errors in such experiments."

Krumholz (1944) has made a practical check of the accuracy of estimation of a fish population by repeated sampling, marking by clipped fins, and the application of Schnabel's formula (18). He computed the population of fish over 45 millimeters in length in the North Basin of Twin Lake, Michigan, in this

manner and then poisoned the area with rotenone and counted the fish population directly. He concluded:

> "The estimate from netting operations was very close to that obtained by poisoning in this first check on the fin-clipping method for estimating fish populations. Further studies of this type are needed to prove definitely the accuracy of the method. . . . Other checks of this method will be made when conditions permit."

Estimation of a changing population

The salmon spawning in a given stream or lake do not form a single, homogeneous, completely mixed population. As we shall see in a later section, there is a tendency for the fish which migrate to the spawning grounds earliest to complete their spawning and die earliest; there results a positive correlation between time of migration past a point below the spawning grounds and the time of appearance on, and of death at, the spawning grounds. If, now, we are tagging fish below the spawning grounds, or even on these grounds, and later sampling for tag-ratios, the "mixing" of the fish between tagging and sampling is not complete, and this may need to be taken into consideration in our estimation of the population.

Since there exists this correlation between time of tagging and time of subsequent sampling, the samples drawn during any particular part of the season do not represent all parts of the population equally; the sample is not a random sample of the whole population. The possible effects of this on our estimates by (1) are easily seen. If, as has already been pointed out, all parts of the run have the same tag-ratio, if the tags are "evenly distributed", it will make no difference whether the samples represent the various parts of the run equally or not. Likewise, if the run is "evenly" sampled on the spawning grounds, that is if the probability of a given fish being included in the sample is not a function of the time of sampling (and, therefore, not a function of the time of tagging), any uneven distribution of tags by time of migration will have no effect. If, on the other hand, the probability of a fish being tagged (the tag-ratio) varies with the time of tagging, and the probability of being sampled varies with the time of sampling, and there also exists a correlation between time of tagging and time of sampling, it is obvious that the tag-ratio in the total sample for the season will differ from that of the population to some extent, depending on the magnitudes of these factors.

It is the purpose of this section to indicate a method of estimating the population by which these errors may be reduced when the tagging is done by means of numbered tags, so that the relation between time of tagging and time of recovery may be estimated. We are indebted to Dr. S. Lee Crump of the Iowa State College Statistical Laboratory for much assistance with the mathematics involved. This analysis will apply to the situation where the fish are being tagged below the spawning grounds and are sampled as dead fish on the spawning grounds.

If our tagged fish have been marked by numbered tags, we know both the date of tagging and date of recovery for each one recovered. This makes it possible to tabulate the recoveries by time of tagging and time of recovery, using

as a time interval a convenient period of days. The notations for the elements involved in the discussion of this section, in addition to those introduced before, are as follows:

Let:

N_a = the total number of fish passing the point of tagging during the ath period of tagging. ($a = 1, 2, 3, \ldots, a$)

T_a = the number of these fish which are tagged during the ath tagging period.

n_{ai} = the number of fish out of the Na that are subsequently recovered during the ith recovery period. ($i = 1, 2, 3, \ldots, s$)

T_{ai} = the number of fish out of the Ta that die and are thus available to be recovered during the ith recovery period.

m_{ai} = the number of fish tagged during the ath period of tagging and recovered during the ith period of recovery.

m'_{ai} = the number of untagged fish passing the point of tagging during the ath tagging period and recovered during the ith recovery period.

The following summation conventions are employed:

$$\sum_i m_{ai} = m_a. \qquad\qquad \sum_a m_{ai} = m_{.i}$$

$$\sum_i m'_{ai} = m'_a. \qquad\qquad \sum_a m'_{ai} = m'_{.i}$$

$$\sum_i n_{ai} = n_a. \qquad\qquad \sum_a \sum_i m_{ai} = m_{..}$$

Obviously, $m_a. + m'_a. = n_a$,

Also let:

$$m_{.i} + m'_{.i} = c_i.$$

N_i = the number of fish dying on the spawning grounds during the ith recovery period.

$$q_a = \frac{\sum_i n_{ai}}{N_a}$$

$$p_i = \frac{\sum_a T_{ai}}{N_i}$$

The data available from a given experiment can be laid out in a table, as follows:

		PERIOD OF TAGGING (α)				Total tagged fish recovered	Total fish recovered
		1	2	3 . . . a			
PERIOD OF RECOVERY (i)	1	m_{11}	m_{21}	m_{31} . . . m_{a1}		$m_{\cdot 1}$	c_1
	2	m_{12}	m_{22}	m_{32} . . . m_{a2}		$m_{\cdot 2}$	c_2
	3	m_{13}	m_{23}	m_{33} . . . m_{a3}		$m_{\cdot 3}$	c_3
	.	.	.	. . . .		.	.
	.	.	.	. . . .		.	.
	.	.	.	. . . .		.	.
	s	m_{1s}	m_{2s}	m_{3s} . . . m_{as}		$m_{\cdot s}$	c_s
Total tagged fish recovered		$m_{1\cdot}$	$m_{2\cdot}$	$m_{3\cdot}$ . . . $m_{a\cdot}$		$m_{\cdot\cdot}$ ($= t$)	
Total fish tagged		T_1	T_2	T_3 . . . T_a			

Of course, $\sum\limits_{a} T_a = T$

and, $\sum\limits_{i} c_i = n.$

Now the number of fish passing the tagging point during α which die during period i might be estimated by

$$ n_{ai}{}^* = \frac{m_{ai}}{p_{ai}}. \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad (22) $$

(I shall denote "estimate of" by the asterisk herein) where p_{ai} is the probability of a fish being tagged during α and recovered during i. This probability is unknown, and our best available estimate of it would seem to be the joint probability $p_i q_a$, where these terms are as defined above. This amounts to taking as the probability of recovery the average probability of recovery of all the fish passing the tagging point during α, and as the probability of their being tagged the average probability of being tagged of all the fish dying during period i.

If the samples drawn for tagging and the samples later drawn for tag-ratios

are representative of the parts of the population from which they are drawn, p_i and q_a may be estimated from the data as follows:

$$q_a^* = \frac{m_{a.}}{T_a} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (23)$$

$$p_i^* = \frac{m_{.i}}{c_i}$$

The estimate of n_{ai} is, then, given by

$$n_{ai}^* = \frac{m_{ai}}{q_a^* p_i^*}$$

which is equivalent to

$$n_{ai}^* = m_{ai} \frac{T_a}{m_a} \frac{c_i}{m_{.i}} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (24)$$

The estimate of the total population is obtained by summing all these n_{ai}^*, thus

$$N^* = \sum_a \sum_i m_{ai} \frac{T_a}{m_{a.}} \frac{c_i}{m_{.i}} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (25)$$

A somewhat more rigorous derivation, based on Bayes' theorem, has been suggested by Dr. Crump.

The problem is to estimate the $n_{a.}$ and the q_a ; if we can do this, we can take as our estimate of N, $N^* = \sum_a \frac{n_a^*.}{q_a^*}$

Let $P(i/a)$ be the probability that a fish tagged during the ath period dies and is recovered during the ith recovery period. Now we have c_i fish taken during the ith recovery period to be allocated over the "a" tagging periods, and hence we want the probability that a fish taken during the ith recovery period is one of those which passed the tagging point during the ath tagging period. Denote by $P(a/i)$ the desired probability, and by $P(a)$ the true proportion of the n fish recovered which passed the tagging point during the ath tagging period. Then by Bayes' theorem

$$P(a/i) = \frac{P(i/a)P(a)}{\sum_a P(i/a)P(a)} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (26)$$

We have the problem of estimating the $P(i/a) P(a)$. Now,

$$P(a) = \frac{\sum_i n_{ai}}{n}$$

and we may estimate $P(a)$ by

$$P^*(a) = \frac{m_{a.}}{m_{..}} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (27)$$

To estimate $P(i/a)$ we may use

$$P^*(i/a) = \frac{m_{ai}}{m_a.} \qquad \dots \qquad (28)$$

Then our estimate of $P(a/i)$ becomes

$$P^*(a/i) = \frac{\dfrac{m_a.}{m..}\cdot\dfrac{m_{ai}}{m_a.}}{\sum \dfrac{m_a.}{m..}\cdot\dfrac{m_{ai}}{m_a.}} = \frac{\dfrac{m_{ai}}{m..}}{\dfrac{m.i}{m..}} = \frac{m_{ai}}{m.i} \qquad (29)$$

This gives us for an estimate of $n_a.$

$$n_a^*. = \sum_i c_i P^*(a/i) = \sum_i c_i \frac{m_{ai}}{m.i} \qquad \dots \qquad (30)$$

Taking our estimate of q_a as before (23), and as our estimate of N

$$N^* = \sum_a \frac{n_a.^*}{q_a^*} \qquad \dots \qquad (31)$$

we have, then,

$$N^* = \sum_a \sum_i c_i \frac{m_{ai}}{m.i} \frac{T_a}{m_a.} \qquad \dots \qquad (32)$$

which is the same result obtained in (25)

From (25) or (32) it may be seen that where the tagging or the sampling is uniform, this estimate reverts to the simple case first discussed. For, if the probability of being tagged is always constant for all i the expected value of

$$\frac{c_i}{m.i} = \frac{n}{m..}, \text{ a constant}$$

Then,

$$N^* = \sum_a \sum_i m_{ai} \frac{T_a}{m_a.} \frac{n}{m..} = \frac{Tn}{m..}, \qquad \dots \qquad (33)$$

which is identical with (1) since $m.. \equiv t$ in (1).

Likewise, if the probability of being recovered is constant, the expected value of $\dfrac{T_a}{m_a.} = \dfrac{T}{m..}$, a constant.

Then,

$$N^* = \sum_a \sum_i m_{ai} \frac{c_i}{m.i} \frac{T}{m..} = \frac{Tn}{m..} \qquad \dots \qquad (34)$$

AREA OF STUDY — THE HARRISON-LILLOOET RIVER SYSTEM

The Harrison-Lillooet System contains the most important sockeye spawning grounds below Hells Gate, Cultus Lake and the Pitt River being the only other localities in the Lower Fraser section supporting runs of any appreciable magnitude. This system was chosen for these investigations for a number of reasons. The accessibility of the areas of field work seemed quite good. The major spawning grounds of the system, the Birkenhead River, Weaver Creek, and Harrison Rapids, are moderately accessible. Some other parts of the system are less easily reached, however, and reaching the Skookumchuck, which became a very important tagging location, requires a long trip by boat and by horse or on foot. It is completely inaccessible to motor vehicles. One of the greatest virtues of the area is that the runs to Weaver Creek and the Birkenhead River are quite large each year and do not exhibit the very large cyclic fluctuations characteristic of the important runs to the upper Fraser. The runs of the system occur both early and late. It is possible to intercept them at various points enroute to the spawning beds for tagging purposes.

The greatest disadvantage, the importance of which was not realized until demonstrated by experience, is that the spawning streams of the system are all subject to very violent flood conditions during the periods of heavy fall rains. This makes it quite impossible to keep any sort of ordinary counting fence continuously in operation during the period of upstream migration. The failure to recognize the source of difficulty caused the plan of investigation to be greatly modified during the very first season of work, as will be narrated later.

The general location of the Harrison-Lillooet River system and the spatial relationships of its components are shown in the map presented herewith, Fig. 2.

Harrison River

The Harrison River flows from Harrison Lake southwesterly twelve miles to the Fraser River, which it enters on the north bank 60 miles above the mouth and 18 miles above the upper limit of the commercial fishery, which is at Mission. Almost the entire flow of the Harrison is derived from Harrison Lake, the Chehalis River being the only large tributary below the Lake. During the summer and fall, the waters of the Harrison River are quite opaque from glacial silt which is brought down into Harrison Lake by the Lillooet River, which is itself of glacial origin, and which has several tributaries from other glaciers. In 1941, for example, the maximum and minimum depths at which a white, six-inch Secchi disc disappeared at the Harrison trap (see map), was 51 inches and 15 inches, respectively, between August 5 and November 26, the lower value occurring in August and the higher in late September.

The Harrison River, above the mouth of Morris Creek, flows between hills which drop precipitously to the river. The banks become low below this point, broadening out into the valley of the Chehalis. The gravel brought down by the Chehalis has filled the channel of the Harrison opposite the mouth of the Chehalis and this, together with the steep gradient through this area, has given rise to the famous Harrison Rapids. A narrow channel, deep enough to accommodate

HARRISON — LILLOOET SYSTEM
AND
LOWER FRASER RIVER

SCALE - MILES

4 2 0 4 8 12 16

LILLOOET

25 Mile Cr.
Railway Cr.
BIRKENHEAD LAKE
BIRKENHEAD
Kierstadt Cr.
Salmon Slough
Ryan Cr.
Poole Cr.
RIVER
McKenzie Cr.
Owl Cr.
Miller Cr.
Pemberton Cr.
Lillooet
LILLOOET LAKE
GREEN R.
Slough

WEAVER LAKE
Weaver Cr.
East Cr.
MORRIS LAKE
Morris Cr.
HARRISON RIVER
TROUT LAKE
Hatchery Cr.

TENAS LAKE

SKOOKUMCHUCK

Douglas Cr.
LITTLE HARRISON LAKE
Big Silver Cr.
Hornet Cr.
HARRISON
Sloquet Cr.
15 Mile Cr.
20 Mile Cr.
Mysterious Cr.
LAKE

PITT LAKE
STAVE LAKE
CHEHALIS R.
PITT R.

BURRARD INLET
VANCOUVER
NEW WESTMINSTER
LULU ISLAND
GULF OF GEORGIA
FRASER RIVER
MISSION
VEDDER R.
CULTUS LAKE

Harrison Rapids
Harrison Bay
Trap Location

CANADA
U.S.A.

FIGURE 2. Map of Harrison-Lillooet River System, showing locations of lakes and streams.

tug boats and other small craft, has been dredged out through the rapids. Below the rapids, the Harrison becomes broader and deeper with a consequently lower velocity, widening out above the mouth into Harrison Bay, but becoming narrow and of increased velocity again in the last half mile above the Fraser. The level of the Harrison River and the velocity of flow is quite variable, depending on the levels of the Fraser River and of Harrison Lake. Both exhibit rather large fluctuations, not closely related, depending on the run-off conditions in their respective watersheds.

Weaver Creek, flowing into very small Morris Lake, which empties to the Harrison by Morris Creek, is the home stream of one of the large regular runs of which a detailed spawning ground study was made in the course of this work.

Along both sides of the channel in Harrison Rapids is located a rather extensive gravel area extending from the channel to shore, and a distance of about 1,000 yards along the length of the river, which is utilized by a distinctive race of sockeye, quite numerous in some years. The main spawning area seems to be to the eastward of the channel, but some sockeye also spawn in the broad area west of the channel. These fish, spawning in the main river, produce progeny which go to sea soon after hatching, omitting the year or more of lacustrine life characteristic of most sockeye.

A very few sockeye spawners have occasionally been reported from the Chehalis, but none were observed there during the period of our study.

Harrison Lake and its Tributaries

Harrison Lake, 36 miles long, is surrounded by high, rugged mountains. Short, rapid tributaries enter it at various places along the shore. Most of these streams are unsuitable for the spawning of salmon, and most become impassible to migratory fishes a short distance above the lake. Those in which no salmon occurred during our study are omitted from the map (Fig. 2).

Hatchery Creek, near the outlet of the lake, is the site of the one-time Harrison Hatchery. A power turbine, situated on the stream less than 100 yards above the mouth, takes its waters from a dam located at the outlet of Trout Lake. During most of the sockeye spawning season, it takes the entire flow, leaving only the area below the power house discharge available to the fish. A very small group of sockeye utilizes this spawning area each year.

Big Silver Creek is frequented by sockeye spawners only as far up as the vicinity of Hornet Creek. It had a moderately large run during one year of our study, 1940, and insignificant numbers in the other two years.

Fifteen Mile, Twenty Mile, and Mysterious Creeks are frequented in their lower reaches by insignificant numbers of sockeye spawners.

Douglas Creek is available to salmon in its lower mile only, being blocked above that by a high falls. It has a regular run of sockeye in the available area, but is not of major importance as a spawning stream. This stream enters Little Harrison Lake, which communicates with Harrison Lake by a channel navigable by small craft.

Lillooet River and Tributaries

The principal tributary of Harrison Lake is the Lillooet River. This river rises in the extensive ice fields to the south of Chilko Lake, and flows southeasterly 117 miles to Harrison Lake. Thirty-three miles above Harrison Lake the river widens out into two long, narrow lakes, Tenas Lake, 5 miles long, and Lillooet Lake, 16 miles long, separated by three-quarters of a mile of fast water. The section above Lillooet Lake is referred to for convenience as the Upper Lillooet, while that below Tenas Lake is known as the Lower Lillooet.

The Lillooet River is very heavily laden with glacial silt. During the period of salmon migration, the water is at all times so opaque that objects disappear a few inches below the surface. This is well illustrated by Secchi disc readings taken at Skookumchuck, 19 miles above Harrison Lake. Between August 8 and September 30, 1941, the period of upstream migration of sockeye at that point, the white Secchi disc disappeared at between five inches and six and one-half inches. Salmon, of course, are not visible under such conditions unless they come very near the surface.

The Lower Lillooet River flows rapidly down a narrow valley between high mountains. The short, torrential tributaries in this section are unsuitable for sockeye spawners, and none are known to spawn in any of them. A small colony of sockeye, discovered spawning in the main Lillooet River just below the mouth of Sloquet Creek in 1940, is the only known group of sockeye spawners in this section.

One of the most noteworthy geographical features of the Lower Lillooet in relation to the ecology of the sockeye salmon is the Skookumchuck, a term derived from the Chinook jargon meaning "strong water". At a point roughly nineteen miles above Harrison Lake, the river bed is constricted to a narrow passage between high cliffs on either side. The swift, fast-dropping water at this point offers a difficult passage to upstream salmon migrants and offers to their migration a partial blockade, the effectiveness of which is a function of the volume of flow of the river. This place has been the site of a fishery pursued by the local Indian inhabitants since the earliest times. It affords an excellent location for capturing specimens for tagging research.

Above Lillooet Lake there opens up a broad valley, to a width of approximately 1½ miles, which extends some 25 to 30 miles above the lake. This valley, which is often referred to as Pemberton Meadows, contains a total area of some 40,000 acres which is excellent farm land. The Lillooet meanders down this valley at a low gradient and is subject, therefore, to flood conditions after prolonged or heavy rains, or during periods of prolonged thawing of the glaciers at the headwaters. It is at all times heavily discolored with glacial silt.

In the area immediately above the Lillooet Lake, in addition to the main channel, there is a small subsidiary channel, which is interconnected with the main channel in several places. This subsidiary channel, known locally as Lillooet Slough, lies to the north of the main channel. Into Lillooet Slough, at a point approximately three and one-half miles above Lillooet Lake, flows the Birkenhead River, the home stream of one of the largest and most dependable sockeye runs

in the Harrison River system. The Birkenhead is a large, clear stream and its volume of flow is sufficiently great in relation to that of Lillooet Slough that the latter is at most times transparent to a depth of several feet.

The Birkenhead River is frequented by sockeye as far up as Poole Creek. During the period of our studies, however, no sockeye were seen beyond seven miles upstream, and nearly the entire spawning population confined itself to the lowest mile of the stream. The first 200 yards of Lillooet Slough below the mouth of the Birkenhead was also utilized by sockeye spawners to a limited extent in 1941, and scattering pairs spawned there in 1940. The large colony of sockeye of the Birkenhead River is the only known group of any size in the Lillooet River drainage, and our tagging experiments have shown, as will be demonstrated later, that this colony was of a size to account for at least 70% of the sockeye ascending past Skookumchuck in 1940 and 1941. The Birkenhead has an easy gradient, 1.1% from the mouth to Owl Creek, and salmon thus have easy access to the extensive spawning area. It is subject to violent floods during the period of the fall rains. These are a very great inconvenience to the experimental biologist, and may be somewhat detrimental to the salmon by virtue of their scouring action on the stream bed wherein the eggs are deposited.

Several tributaries of the Upper Lillooet, other than the Birkenhead, are known to be utilized by small groups of sockeye spawners, in some years at least. These are the Green River, Miller Creek, Pemberton Creek, McKenzie Creek, Kierstad Creek, Salmon Slough, John Sandy Creek, Railroad Creek, Ryan Creek, and Twenty-five Mile Creek. These are shown on the map of the area given herewith. The runs of sockeye to each of these streams are, as far as known, never large and in many years sockeye are entirely absent from them.

Green River is a sizeable stream of glacial origin flowing into the Lillooet on its west side. It is made impassible to salmon by Nairn Falls, five miles above the mouth. Sockeye are known to occur here because of infrequent Indian gill net catches at the mouth, but are not readily observed because of the extreme opacity of the water.

Miller Creek, a small stream five miles long, on the West side of the Lillooet River 10 or 11 miles above the lake, is also heavily laden with glacial silt, which renders observation of fishes almost impossible. Sockeye are known to utilize gravel beds in the lower half mile for spawning.

The other streams listed above are all small, clear streams in which the more or less negligible groups of sockeye spawners which visit them may be easily observed.

The Indians and Indian Fisheries of the Area

Several Indian Reservations are located in the Harrison-Lillooet watershed from the mouth of the Harrison River to Pemberton. The Indians inhabiting them have certain fishing rights permitting them to take limited quantities of salmon for their own use, and these rights are exercised to a greater or lesser degree at various places. The Indian fisheries are a source of some useful recovery data in the course of tagging experiments, and are at the same time a slight complicating factor in the analysis of some of the population data.

Indians residing at the mouth of the Harrison, and at other places along the Fraser River in the vicinity, carry on gill net fishing in the Fraser River itself.

A small group of Indians living along the banks of the Harrison River near the Rapids carries on some fishing in the Harrison in that vicinity by means of set gill nets. They seldom put out sockeye nets, however, since they find much more desirable the large spring salmon which occur in the same area.

A group of Indians of the Douglas Band, some 53 in number, live near the head of Harrison Lake. These people occasionally put out sockeye set nets in the mouth of the Lillooet River or in Little Harrison Lake. Estimates of their catches are not available, but probably never amount to over two or three hundred fish in a season. These people, like those from other reservations along the Lower Lillooet, are usually absent during the greater part of the sockeye migration. Those who are not regularly engaged in logging or other occupations, habitually go to the hop fields near Agassiz and Chilliwack during this season for employment as pickers.

The Skookumchuck, a point of difficult passage for salmon, is the historical site of a fishery carried on by means of long handled dip nets. The Indians construct platforms, overhanging the banks of the river, just below the points of difficult passage on either side and stand on these to fish for the salmon. The dip net (see Figure 3) consists of a long handle with an oval shaped frame at the end, some two feet wide by four feet long, to which is attached the bag-shaped net by rings which slide easily on the frame, except at the outermost end of the oval where the net is firmly affixed to the frame. A long, loose cord extends from the edge of the bag closest to the handle to a point near the balance of the entire apparatus, where it is firmly attached. In operation the net is pulled open by means of this cord and held open while the net is thrust deep into the water slightly upstream from the point where the fisherman stands. The net is then swept downstream with a positive pull, so that it is moving slightly faster than the water. During this motion, the net is held open by the pull of the net against the frame, the bag of the net extending upstream from the frame. At the end of the downstream sweep, the fisherman pulls the net out of the water by pulling on the handle along its axis. The net and water are now moving downstream at about the same speed, so that the net is no longer held open by the downstream pull of the fisherman. Thus, as the handle is pulled out of the water, the rings slip along the frame and the net is pursed shut. Any fish, swimming upstream, that is enveloped by the downstream-moving net is thus entrapped in the closed net and may be easily lifted from the water to the platform on which the fisherman is standing.

The Indians living in the vicinity of the Skookumchuck also fish by means of set gill nets placed in the river some distance below the Skookumchuck itself.

The catch of sockeye and other salmon at Skookumchuck was the primary source of protein food for the local Indians before the advent of civilization, but in modern times has become increasingly less important. Now the great majority of the people prefer to engage in hop-picking or other paid occupations during the salmon season instead of putting up dried fish for winter. The 120 or so people resident in the village near the fishing grounds take only relatively few salmon
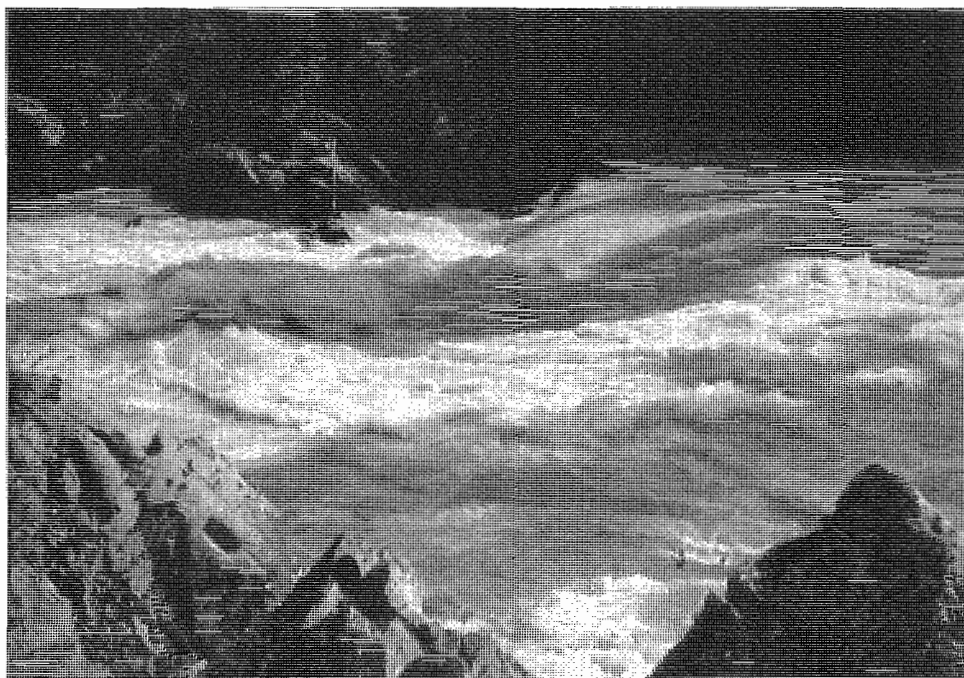
FIGURE 3. Two views of the Skookumchuck on Lillooet River. Upper photograph showing the method of dip-net fishing employed by the Indians at Skookumchuck.

each year. The sockeye catch for personal use was estimated at 150 in 1940 and 275 in 1941 from records kept by our tagging party at Skookumchuck.

A small band of Indians, about 50 in number, living near the 24 mile post on the Douglas-Tenas Lake portage, catches a few fish by dip net near there. These Indians also fish with gill nets in Tenas Lake. In 1941 the local fishery guardian reported 50 sockeye taken in these places by the Indians.

Indians living along Lillooet Lake and members of the large reservation near Pemberton fish by means of gill nets in Lillooet Lake. In 1940 and 1941 their estimated catches were 383 and 358 sockeye, respectively, (estimated by local guardian).

The largest sockeye catches by Indians are made by gaff hooks from the spawning grounds of the Birkenhead River. A fairly accurate census was made of these catches in 1939, 1940, and 1941, in which years they amounted to 2,795, 3,712, and 3,313 fish, respectively. Part of these were used fresh and part were smoked and dried. The Indians fishing in the Birkenhead are members of the large settlement, some 330 in number, living on a reservation adjacent to the mouth of the Birkenhead River. Their fishing is limited to that amount which, in the opinion of the local guardian, can be safely taken from the run, and he sets closing dates for the fishing.

SOCKEYE SALMON POPULATIONS OF THE HARRISON SYSTEM — DESCRIPTIVE SKETCH

The sockeye populations of the Harrison System are naturally separated into three groups by time of spawning. The earliest group spawns in the tributaries of the Lillooet River and in the streams tributary to the upper half of Harrison Lake. These salmon arrive on the spawning grounds near the first of September, are at maximum abundance on the spawning grounds toward the latter part of that month, and are nearly all through spawning by the middle of October, although a few stragglers continue through the first ten days of November. This group may be designated the Early Run. The sockeye which spawn in the tributaries to Morris Lake and in Hatchery Creek near the lower end of Harrison Lake arrive on the spawning grounds in early October, are present there in maximal numbers in late October and early November, and continue to spawn until the first week in December. This group of sockeye may be referred to as the Weaver Creek-Hatchery Creek group. Finally, a very characteristic population of sockeye spawns on the gravel bars adjacent to the Harrison Rapids from about November 1 to December 15, with a peak abundance about November 20. These fish are designated the Harrison Rapids population.

The various groups of sockeye in the Harrison River System form one of the classic examples of racial differentiation of salmonoid fishes. C. H. Gilbert studied the scale markings and other characteristics of sockeye from Harrison Rapids, Morris Creek, and the Birkenhead River and demonstrated marked differences among these populations. He stated in his 1919 paper:

"A very conspicuous instance of racial differentiation is furnished by the Harrison watershed. We do not know how many distinct spawning areas it may have contained. Several minor colonies, like that frequenting Silver Creek, are now practically exterminated. . . . A very limited number of late spawners still frequent the slack water of the main river above Harrison Rapids, the vanishing remnant of a once fine run visits the lake at the head of Morris Creek, and a considerable run still goes up the Birkenhead. Both the Birkenhead and the Morris Creek fish pass over the very spawning beds at Harrison Rapids, but none of them tarries there. An examination of 200 specimens, laboriously gathered in Harrison Rapids in 1918 by Mr. Robertson, failed to yield a single fish which had been spawned elsewhere than in the beds of the rapids. Not one could on even a cursory examination be confused with those constituting either the Morris Creek or the Birkenhead colony. Not one of the Harrison Rapids fish was found among over 400 specimens examined from Morris Creek, and over 200 from Skookumchuck and the Birkenhead. No Morris Creek strays were found in the Birkenhead and no Birkenhead fish were found in Morris Creek, in spite of the fact that all the Birkenhead fish passed the mouth of Morris Creek on their way. In these cases, evidently, the law of segregation is most strictly in force; yet it seems impossible to imagine a locality better suited to straying of the spawning fish with resulting mixture of populations. That it does not occur here, where fish pass over and pass by one another's spawning grounds, gives confidence that the same law rules everywhere, though the evidence of it may be less compelling."

The Harrison System sockeye runs also offer an excellent example of the disastrous results that can sometimes result from "conservation" operations based on inadequate knowledge of a species and erroneous assumptions as to its life history. The Dominion Government operated an egg taking station at Morris Creek from 1885 on. According to Gilbert (1919) this was the only egg taking station in the Province until 1901 and for many years after that date it still served as the principal source of eggs, first for the Bon Accord Hatchery near New Westminster and later for the hatchery located at Hatchery Creek on Harrison Lake. He states that:

> "None of the fry in the early days were returned to Morris Creek as it was not believed that such a procedure was necessary to maintain the spawning run. Even in 1902 Mr. Babcock wrote: 'It is generally believed that fish bred in a given watershed, such as the Fraser, return to it upon reaching maturity, and there is considerable evidence to warrant it. It has not, however, been settled, and probably never will be, that the fish bred in a given tributary of a large river seek only that tributary to spawn.' Believing, then, that any increase in the run to a large river would equally benefit all the tributaries, there seemed no reason for laboriously returning fry to Morris Lake in order that they should return there and help maintain the spawning run. Knowing, as we now do, that salmon will in general return to the district where they are liberated, the fate of the Morris Creek run seems to have been inevitable. It has steadily dwindled with the years until it can no longer be depended on for any considerable take of eggs. Natural propagation was reduced to a minimum in order to obtain eggs for the hatcheries, while the hatchery-reared fry did not at maturity return to Morris Creek. The same has been the history of Silver Creek, where the Dominion Government placed a weir in August, 1902, and took nearly two and a half million eggs, which were transferred to the hatchery near New Westminster. The run in Silver Creek is now practically extinct, and we cannot doubt that this process has been hastened by failure to replenish its run through the planting of fry."

Happily, the Morris Creek run, or as we prefer to call it the Weaver Creek run, since Weaver Creek rather than Morris Creek is at present the actual spawning grounds of all of this population, has recuperated until now it seems to be quite large in relation to the amount of the spawning grounds in the stream. The Silver Creek run has been less fortunate, but in at least one year of the cycle is no longer "practically extinct", since an estimated 10,000 sockeye spawned there in 1940.

Early Run Populations

The group of sockeye that we are pleased to group together under the term "Early Run" consists of a number of diverse local populations, having in common the habit of migrating to their spawning grounds at about the same season. The populations making up this group consist of the very large and important population spawning in the Birkenhead River; several rather insignificant populations spawning in the various tributaries of the Upper Lillooet, which amount in the aggregate to only a fraction of the Birkenhead population; the small populations spawning in Douglas and Silver Creeks, tributary to Harrison Lake (the latter having had a moderately large run, however, in 1940); and the completely negli-

gible numbers of spawners in several other tributaries to the upper half of Harrison Lake.

Birkenhead River

The population of sockeye which spawns in the Birkenhead River is the largest in the Fraser watershed below Hell's Gate, and appears in large numbers with great regularity. The estimates of abundance made annually by Mr. Babcock of the British Columbia Provincial Fisheries Department until 1933, and since then by the Dominion Fisheries Inspectors, indicate that the runs appear in roughly equal abundance each year and show little or no evidence of any single dominant cycle, although the escapements to the spawning grounds, as reported by Babcock (1902 to 1932), have fluctuated rather widely from time to time. The egg-take records at the Pemberton hatchery also show considerable non-periodic fluctuations; it is not clear, however, that these egg-take records reflect corresponding variations in the size of the escapement, bcause of the variable fraction of the run which was allowed to spawn naturally. It has been pointed out by Thompson (1945) that the years of apparent low escapement to the Birkenhead do not correspond to the periods of general Fraser River "depletion", which were largely attributable to the Hell's Gate water levels which did not affect runs to the Harrison system.

The Birkenhead sockeye supported a hatchery from 1905 to 1935, when all the British Columbia hatcheries were closed. Here eggs were taken and the fry held until absorption of the yolk sac. They were not reared beyond the yolk-sac stage.

TABLE 1

Take of Eggs at Pemberton Hatchery (Birkenhead River)

Year	Eggs Taken	Year	Eggs Taken
1905	28,000,000	1921	26,053,000
1906	21,500,000	1922	26,000,000
1907	28,000,000	1923	30,629,000
1908	20,757,000	1924	31,200,000
1909	28,000,000	1925	40,418,000
1910	7,000,000	1926	45,350,000
1911	12,500,000	1927	37,000,000
1912	25,000,000	1928	35,010,000
1913	25,000,000	1929	18,000,000
1914	15,220,000	1930	35,209,925
1915	25,250,000	1931	20,425,000
1916	25,750,000	1932	22,710,000
1917	5,270,000	1933	10,680,000
1918	11,960,000	1934	20,400,000
1919	31,655,000	1935	24,410,000
1920	26,000,000		

The record of eggs taken, as kept by the Dominion Fisheries Department, is recapitulated from Thompson (1945) in our Table 1. It is apparent that although the egg-takes fluctuated considerably they are of about the same size in the later

years as in the earlier years of operation. This record, however, is somewhat misleading as an index to the relative sizes of the populations from year to year, since a variable fraction was taken by the hatchery men. From examination of the remains of structures on the river banks, and from conversations with local inhabitants and employees of the Dominion Fisheries Department, it has been possible to ascertain that the take of eggs was maintained by the expedient of including an ever increasing share of the population in the operation. The first fence for capturing sockeye was placed some distance above Owl Creek. As the eggs became harder to get, fences were erected at successively lower points until the last fence was located at the lowest practicable place for establishing the conventional type of fence for capturing upstream migrants (see Figure 9). In the last few years of operation the captures at this fence fell so low that they were supplemented by gaffing ripe fish out of the stream below. At the time of our study the preponderate majority of sockeye were found spawning well below the former site of the lowest fence, and the number of sockeye ascending above that point could by no means supply as many eggs as were taken by the hatchery in its last years of operation.

Gilbert (1918) from his studies of the various runs of the Fraser watershed, by means of size frequencies and scales, concluded that the Birkenhead fish are a distinct group from those of Morris Creek and other streams tributary to Harrison Lake. He wrote:

> "The fish of Birkenhead Creek examined at the Pemberton Hatchery, ally themselves definitely with the up-river colonies. Although they pass through Harrison Lake on their way to the Birkenhead, they are remarkably distinct from any of the late-running sockeyes of Morris Creek and the other districts drawn upon by the Harrison Hatchery. The fish are small in comparison, and were largely four years old, both in 1916 and 1917. Our best estimate based on the samples presented is that 75 per cent of the Pemberton fish are four years old. But the greatest difference lies in the small size of the nuclear region of the scale and the low number of nuclear rings."

The following year Gilbert (1919) also said of the Birkenhead run:

> "This affluent of the Harrison has now the most reliable sockeye run, and is the only spawning district of value remaining in this watershed. Its present importance is due in part doubtless to the fact that it was not drawn on for hatchery purposes until a much later date than Morris Creek and the Harrison Lake region, and in perhaps larger part to the significant fact that the output of the hatchery is constantly planted in the Birkenhead and helps maintain the run.
>
> "The characteristics of the Birkenhead race in 1918 are in general the same as those described for the 1916 run. The growth of fingerlings in fresh water must be much less than in the case of the Morris Creek and Harrison Lake fingerlings. The nuclear area of the scale averages small with densely crowded rings. . . . ."

Gilbert also examined specimens from the Skookumchuck and found that the same age composition, size frequency, and scale sculpturing was to be observed in the populations at both localities.

The Birkenhead run maintained itself remarkably well, although there is good evidence, noted above, that the hatchery had progressively more difficulty in getting its egg-take and in the last years of hatchery operation some decrease in the escapement became obvious. In 1929 there was a notable drop in numbers and the hatchery was only able to take 18,000,000 eggs although 95% of the run was processed and almost no fish were allowed to spawn naturally, whereas in most years the natural beds were "abundantly seeded". The run of 1930 was "most satisfactory" but in 1931 the hatchery egg-take again fell off in spite of the fact that about ⅗ of the run was taken. In 1932 the run was estimated at only 75% of the brood year and in 1933 it was recorded as "quite disappointing" by the Dominion Supervisor of Fisheries who blamed the decrease on the Indian fishery. In 1934 the run was reported as "disappointing", but it was noted that the mile and a quarter below the hatchery fence was well seeded. All hatcheries were shut down after 1935.

Since the Birkenhead run perpetuated itself quite satisfactorily, no eggs or fry were shipped in to that hatchery. However, a sizable share of the egg-take was shipped to other streams, including those of the lower Harrison. Babcock (1930) recapitulated the shipments from the Birkenhead hatchery for four years. The following tabulation is a summarization of those data:

Year	Number of eggs taken Pemberton hatchery	Number of eggs and fry planted in other places	Localities of planting
1925	40,418,000	16,802,000	Skeena R., Eagle R., Morris Cr., Gates Cr., Adie L., Gates L.
1926	45,350,000	24,216,000	Skeena R., Morris Cr., Gates Cr., Eagle R., Adie L., Gates L.
1927	37,000,000	16,182,000	Francois L., Horsefly R., Skeena R., Adie L., Gates L., Anderson L.
1928	35,010,000	15,863,000	Horsefly R., Gates Cr., Skeena R., Adie, L., Anderson L., Gates L.

The general ineffectiveness of such transplantation of sockeye eggs is evidenced by (1) the failure of the plants to develop any appreciable run in localities where the runs were already small and (2) the fact that, in spite of the extensive transplantations carried out in many tributaries of the Fraser, various streams to which eggs were transplanted, such as Morris Creek (see also page 37), still have runs the racial characters of which are distinct from the others and which, indeed, correspond rather closely to the descriptions published by Gilbert some thirty years ago.

Other Upper Lillooet spawning grounds

As we have stated earlier, several of the small tributaries of the Upper Lillooet are frequented by small runs of sockeye. It has been presumed that in the aggregate these runs are a very small part of the total escapement to the Upper Lillooet, the greater part of which spawns in the Birkenhead River. Our

tagging results have confirmed this for 1940 and 1941 at least, as will appear later (p. 85). The Lillooet itself is so opaque because of glacial silt that sockeye can be detected therein only with difficulty. Some of its tributaries offer similarly low visibility, and others are very inaccessible. The knowledge regarding the approximate size of the runs to those tributaries where sockeye are known to spawn is summarized below, based on the estimates of the local fisheries guardians (data obtained from the Dominion Fisheries Department and interviews with guardians) :

Green River	— 100 - 1000. Indians occasionally take a few with gill nets. (There was no fishing done here during the three years of my investigation.)
Johnson Creek	— 10 fish reported in 1930.
Kierstad Creek	— 0 to 100.
McKenzie Creek	— 50 to 100.
Miller Creek	— 100 to 5,000 (very heavy glacial silt, fish very hard to see.)
Pemberton Creek	— 0 to 100.
Salmon Slough	— 0 to 500.
John Sandy Creek	— 0 to 100.
Railroad Creek	— 50 to 500.
Ryan Creek	— 50 to 100.
25 Mile Creek	— 100 to 1,000.

Runs to these various streams are entirely absent in some years.

The above estimates, if anywhere near accurate, indicate that there are no other streams than the Birkenhead which constitute important sockeye spawning areas in the Upper Lillooet region.

The observed time of spawning in these various streams corresponds to that in the Birkenhead River.

Tributaries of Harrison Lake

The sockeye runs to the streams tributary to the upper end of Harrison Lake spawn during September and October and presumably ascend to their spawning grounds from the sea at about the same time as the Birkenhead fish.

15 Mile Creek, Mysterious Creek and 20 Mile Creek are frequented by entirely insignificant numbers of sockeye spawners. The reports of the Dominion guardians for 1934 to 1937 show either none or a very few, up to 50 or 100, at most for these streams. The only exceptions are 20 Mile Creek in 1937 when 100 to 300 were reported, and 15 Mile Creek in 1936 when 100 to 300 were reported. None of the Commission observers have ever seen as many as 50 sockeye in any of these streams.

The sockeye of Douglas Creek are easy to see in this small, clear stream of restricted area. Since 1935, reports of 100 or less have been usual, but in 1937 the Dominion observers reported 500 to 1000 and in 1940 and 1941 the Commission

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observers estimated similarly large values (500 to 1000, and 700 to 1100, respectively). Since the Dominion guardians reported no sockeye in 1935 and 50 to 100 in 1936, a marked increase must have occurred in one cycle, whether it be four or five years for this stream, unless the above estimates are very greatly in error.

Silver Creek, also known as Big Silver Creek, is a fine, large tributary which had sockeye runs estimated by the Dominion guardians as none in 1935, 500 to 1000 in 1936 and 50 to 100 in 1937. A tremendous increase occurred in 1940 if these estimates are correct, since 2416 carcasses were actually examined and the run was estimated to be at least 10,000. The 1941 escapement which was estimated at at least 1000 is likewise a great increase over the cycle year.

The details of the history of the runs to the Harrison Lake tributaries are obscure. The hatchery people began to utilize them as a source of sockeye eggs in 1902 when Babcock (1903) recorded that nearly 2.5 million eggs were taken and transported to the hatchery near New Westminster. In 1905 a hatchery was constructed on the shores of Harrison Lake at the mouth of a tiny stream running from Trout Lake to Harrison Lake. This stream, now known as Hatchery Creek, served as a water supply for the hatchery. This hatchery obtained eggs from the streams tributary to Harrison Lake, from Weaver Creek, and in later years a few from Harrison Rapids. There was also considerable transshipment of eggs between this hatchery and one constructed several years later on Cultus Lake. The published hatchery records do not make it possible to segregate the egg-takes from the various sources.

According to Gilbert (1919), (see page 31 above), the Silver Creek run was almost exterminated by 1918 and may be only now recuperating. The other streams may never have had runs of any size, but it is certain that, except for the small group in Douglas Creek, they are at present insignificant.

Late Run Populations

The late run populations consist of three groups of sockeye: (1) The population of Weaver Creek, (2) the population of Hatchery Creek and (3) the Harrison Rapids population. As will appear below, there is reason to treat the Weaver Creek and Hatchery Creek fish as a unit, while the Harrison Rapids supports a very unique and distinct sockeye population.

Weaver Creek

Weaver Creek, also called Morris Creek in the literature, a relatively small stream averaging about 25 feet in width and two feet in depth, is accessible to sockeye only in its lower three miles, being blocked by high falls above that point. Two small tributaries are available to sockeye also; Steelhead Creek is passable to salmon for about 1100 yards before a high falls is reached and Wolfe Creek is passable for about 350 yards below a high falls. Weaver Creek empties into Morris Lake, a small body of water less than a half mile in diameter, which communicates with the Harrison River by Morris Creek.

This quite restricted spawning area supports a sockeye population which has reached 10,000 to 20,000 in recent years according to the estimates of the fisheries

guardians, and from the older literature it seems to have had a flourishing population since early days. The Dominion Fisheries Department began utilizing the stream as a source of eggs in 1885 and continued, with little difficulty, to obtain eggs there for many years, in spite of the fact that none of the fry were returned to the stream. As noted earlier (page 31) the home stream theory had not yet been established as a fact, so the eggs from Weaver Creek were taken to the Bon Accord hatchery near New Westminster and the fry were liberated in the Fraser near that point. In 1905 a hatchery was built at the mouth of Trout Creek (now known as Hatchery Creek) on Harrison Lake, and thereafter the eggs from Weaver Creek were hatched at that establishment, although extensive transshipments were made also to the hatcheries at Cultus Lake, Pitt Lake, and elsewhere. Apparently the Weaver Creek run was able to maintain itself during this period on the basis of that part of the population which was able to spawn naturally in the stream. Weaver Creek, like the other streams of the Harrison watershed, is subject to very heavy "flash" floods during the period of the fall rains. These floods which inundate any ordinary fence or trap in the lower reaches of the stream insure the run against complete capture. Babcock's reports often refer to these high water conditions on the Harrison and the old hatchery employees confirm them.

In 1909 Babcock reported that there was a very light run to the entire Harrison-Lillooet system and that it had not been possible to fill the Harrison Lake Hatchery in spite of "every possible effort to obtain eggs from the tributaries of Harrison Lake and River". Only 1,000,000 eggs were obtained from Morris Creek in this year compared with 16,000,000 in 1905, the cycle year. In his report for 1914, Babcock reported the egg-take as 2,400,000 and stated "The decline in the run to Morris Creek is one of the most interesting features in the sockeye run to the Fraser of the last two big years. The decline in the runs to Morris Creek is attributable to the fact that none of the fry hatched from eggs collected there were returned to its waters. Plants of fry were made there in 1909. If plants are continued at Morris Creek for a period of years, it will be interesting to note the results".

In spite of the fry planting program, the runs continued to fall off. In 1916 "Less eggs were recovered there this year than in any recent season" and in 1917 Babcock reported that the run to Harrison Lake and its tributaries (including Weaver Creek) was the smallest ever recorded there.

In subsequent years the run appears to have maintained itself at a rather low level, with some fluctuations, although the reports given by Babcock are incomplete and obscure. The records of eggs incubated at the Harrison Hatchery do not allow of distinction between sources. In addition to the eggs taken from Weaver Creek and Harrison Lake streams, eggs were transshiped from Cultus Lake and Pitt Lake in some years. In 1918 20,000,000 eggs were imported from Alaska.

The sockeye population of Weaver Creek, in spite of all outside interference, has maintained itself as a distinct racial unit. These salmon are distinguishable on the spawning grounds on the basis of size and coloration from both the "Early Run" sockeye and the spawners of Harrison Rapids (see below). Weaver Creek

fish are of generally duller nuptual colors than those of the populations belonging to the Early Run and are of larger average size than the Harrison Rapids spawners. Gilbert in 1917 and 1918 observed these size differences, and also differences in the scale sculpturing which may be yet observed today. Whereas the Birkenhead fish have small, densely crowded nuclei on the scales, the scales of the Weaver Creek fish have large, sharply defined nuclear regions. Quoting Gilbert's (1918) report:

> "Morris Creek would seem to have been an ideal hatching and rearing ground for the sockeye. . . . Examination of the scales of the fish now running show a striking uniformity of their development. They form an impressively homogeneous lot. All have large sharply defined nuclear regions, testifying to a vigorous growth during their first year, which is uniformly passed in the lake . . . ."

During the three years of our study (1939 to 1941) all the sockeye passing through Morris Creek spawned in Weaver Creek or its tributaries, except for a few score fish in 1941 which spawned in a tiny tributary to the east side of Morris Lake. This little stream, about two yards wide, contains about 50 linear yards of spawning gravel and was utilized by sockeye only in 1941.

Hatchery Creek

In the course of its operation from 1905 to 1925 the Harrison Lake Hatchery built up a run of fish which returned on maturity to the outflow from the hatchery ponds. In some years the numbers of these fish must have been considerable; in 1919, for example, Babcock reported that this run was greater than that of any of the natural streams tributary to Harrison Lake and that 4,000,000 eggs were taken from it.

At present, almost the entire outflow from the dam at Trout Lake goes through a power turbine, and the stream bed proper is normally dry during the fall months when the sockeye are running. The few hundred fish comprising the Hatchery Creek run spawn, therefore, in the discharge stream, a channel about 75 yards long and 8 to 10 feet wide between the power house and the lake, or in Harrison Lake adjacent to the mouth of the creek.

In physical appearance these fish are identical with Weaver Creek fish. Gilbert (1918) found that they were not distinguishable by means of their scale sculpturing. They also migrate at the same time and spawn at the same time as the Weaver Creek fish. It looks very much as if of all the various races of fish, fry from which were liberated at Harrison Hatchery, only a few Weaver Creek fish were able to permanently adapt themselves to this new environment.

Harrison Rapids

Sockeye salmon normally spawn in streams tributary to lakes in which the young fish spend one or more years before descending to the sea. Among the sockeye caught off the Fraser River, however, Gilbert discovered a small percentage of individuals the scales of which indicated they had gone to sea immediately after hatching and were therefore called by him "sea-type" specimens (Gilbert 1913, 1915). He also noted that this class of fish was not evenly

distributed through the run, but always appeared only among the late migrants. In his 1918 paper he announced the discovery of the spawning area of this group:

"Examination of spawning fish in the tributaries heretofore given has failed to discover the presence of fish of sea-type. But we present three photographs, Figs. 6, 7 and 8, to illustrate the very peculiar characteristics of the sockeyes which comprise the group spawning at Harrison Rapids. A comparison with the photographs of scales from other spawning districts shows clearly the striking way in which the scales of the Harrison are marked. The centres of the scales are wholly dissimilar from those of other spawning grounds. The nuclear region does not consist of a sharply defined area marked by the fine lines produced during growth in fresh water, and passing abruptly into the widely spaced lines indicative of sea-growth. On the contrary, the lines gradually widen from the centre outwards and pass by insensible degrees into the growth of the second year. Not only is there no evident lake-growth, there is commonly lacking a definite margin to the first year's growth, a definite winter-band of crowded rings. This is the form we have come to recognize as the sea-type, and as the individuals pass to sea as soon as they are free-swimming and before scales have developed, the scales contain no record of their brief life in fresh water. The photographs presented should be compared with those of sea-type given in our report for 1914, Figs. 1 to 5.

"It is a noteworthy fact that this group, which is not numerously represented in any sockeye run, should comprise the great majority, if not indeed all, of the individuals resorting to a single spawning area of the Fraser. We found none of this type in the Chilcotin, the Birkenhead, Cultus Lake, Pitt Lake, or Morris Creek. There were only two doubtful examples from the Harrison Hatchery. It is entirely possible that the sea-type individuals found in the Fraser River run are largely, if not wholly, the product of one spawning district. Practically all of them may result from eggs deposited in the Harrison River below the lake, and may owe their habit of passing to sea as fry to the fact that no lake is there available as a residence. If this be true it will explain the early seaward migration of the fry, while the prevalence of sea-type adults on the Harrison River spawning-grounds will furnish a clear-cut case of the parent-stream theory as applied to the tributaries of a river. After migrating from Harrison Rapids as fry, those which survive not only turn into the Harrison when they come to spawn, but they return to the very gravel-beds in which as eggs their parents deposited them.

"In his report of the year 1903, Mr. Babcock writes (page 24): 'A considerable number of the late run of salmon spawn in this river (i.e. Harrison River) at the end of the season, but the majority of the late run of sockeye which enter the Harrison pass into Morris Creek and Morris Lake. . . . ' The consistently late-running habit of sockeyes of sea-type in the Fraser is then in entire accord with the theory that they are bound largely for Harrison River."

In 1919 Gilbert wrote:

"As was observed in 1916 and during previous years, sockeyes belonging to the type which alone frequents the Harrison Rapids spawning-beds—the sea-type—make their appearance during the latter part of the run only, at the mouth of the river and in the approaches to it. In 1916 the first to appear were taken on July 17th, and after that date they occurred constantly to the close of the season".

.   .   .   .

"In 1918, as in 1916, we failed to find any individuals of sea-type spawning in any part of the Fraser River basin other than Harrison Rapids.

Upwards of a thousand specimens were examined from other spawning districts, in which it might be thought an occasional sea-type individual might be found, if only as a stray. The fact that not one individual was discovered elsewhere, when coupled with the further fact that every Harrison Rapids sockeye belonged to this group, furnishes the strongest possible evidence of the return of spawning fish to their native districts".

In a later paper (Gilbert, 1920) he points out that:

"The only spawning grounds for the sea-type sockeyes known to us within the Fraser basin are found in a slack-water stretch of the Harrison River below Harrison Lake and a short distance below the mouth of Morris Creek. No lake exists below these spawning beds, either in the Harrison or in the Fraser River."

In 1922, speaking of scale readings of fish taken at Sooke traps, he said:

"As throwing additional light on the definite schedule of events which characterizes the Fraser River run of sockeyes, we again note that the run of individuals which had proceeded to sea shortly after hatching, and as soon as they became free-swimming, did not begin in this year until after the middle of July. The first capture in 1920 was on July 19th. In 1916 the first was observed on July 17th, and in 1918 on July 14th. In 1919 one occurred very exceptionally on June 9th, but as none appeared between that date and July 15th, and they appeared daily after that date, July 15th is properly to be selected as the beginning of the run in 1919. So close a chronology as July 14th, 15th, 17th and 19th for the first appearance of the fish of this type in the runs of four different years is striking evidence of the regularity with which the run is conducted year by year. Individuals of sea-type and those of the two-years-in-lake type are the only ones that can with certainty be recognized always in a composite assemblage, such as that which comprises the Fraser River run. Could we detect locality groups as unerringly and segregate them from the general mass, we cannot doubt that they too would appear in regular sequence and on fairly regular dates."

The opacity of the Harrison River as a result of its burden of glacial silt already has been referred to (page 22). The resulting low visibility of the spawning sockeye on the spawning areas adjacent to Harrison Rapids makes an accurate count or even a good estimate of numbers completely impossible. The fisheries guardians have, therefore, often contented themselves with such general statements as "good numbers", "run above average", et cetera. In Table 2 is summarized the available records of the observations and estimates by the fishery guardians. The accuracy of these estimates is open to great doubt because of the extremely unfavorable conditions for observation. Our own experience with this area leads us to believe that any estimate based on visual observations alone can be little more than a guess.

Since the sea-type sockeye spawn, presumably, exclusively, or at least primarily, only at Harrison Rapids, their occurrence in the commercial catch yields a rough estimate of the size of the Harrison Rapids run and its variation from year to year. Dr. Gilbert kept track year by year of the numbers of sea-type sockeye occurring in samples of the commercial catch at the traps near the lower tip of Vancouver Island at Sooke. After 1925 this work was continued until 1938

by Dr. and Mrs. W. A. Clemens. From the data in these various papers there have been compiled in Table 3 the percentages of 3-year-old and 4-year-old sea-type sockeye in the samples. It is noteworthy that these fish do not, apparently, follow a 4-year cycle since the two age groups are, on the average, about equally represented in the catch.

TABLE 2

Available Record of the Extent of Sockeye Spawning at
Harrison River Rapids

1915	Nov. 15 - ?	Good run
1916		
1917		
1918		
1919		"Run above average"
1920		
1921	Oct. 15 - Nov. 10	"Good run"
1922		
1923		Present*
1924		Present*
1925		Present*
1926		
1927		
1928	Sept. - Oct. 31	Good numbers
1929	Sept. 7 -	4,000 - 5,000
1930	Oct. 6-12 -	Large numbers
1931		50 - 100
1932		"Heavy run"
1933		300±
1934		
1935	Sept. 20 - Nov. 30	50 - 100
1936	Nov. 14 - Dec. 12	5,000 - 10,000
1937	Nov. 15 - Dec. 4	100 - 300
1938	Sept. 22 - Dec. 10	5,000 - 10,000
1939	Nov.	200±
1940	Nov.	5,000 - 10,000

*Netted spawning fish for hatchery.

If it is assumed that the sample at Sooke is a representative sample of the Fraser River runs each year, and that the total commercial catch is similarly representative, weighting the percentages in the fourth column of Table 3 by the total catch will give us an estimate of the catch of sea-type fish each year. These values are computed in Table 4. Since the intensity of the fishery is not known, it is not possible to estimate the size of the escapement to the spawning grounds. The intensity may be something over 50%, however, as indicated by the Commission's tagging experiments (McKay, Howard, and Killick, 1945). From a review of tagging and other data on Pacific salmon populations Foerster (1945) has concluded "For sockeye salmon from 40 to 75 or 80% of the runs are taken by the commercial fishery . . . ." At 50% the escapement would equal the catch. If 80% were caught each year and 20% went to the spawning areas, the escape-

ment would be as indicated in the last column of Table 4. These computations give us at least some idea of the order of magnitude of the population to be expected at Harrison Rapids. It may be noted that they do not agree well with the fisheries guardian's estimates, since years of relatively large catches of sea-type fish (e.g. 1931 and 1933) correspond to low estimates by the observers and vice versa (e.g. 1936 or 1929).

From the foregoing data it seems safe to conclude that: (1) There has been a very sizable run to the Harrison Rapids in many former years, (2) Estimates made on the spawning grounds are likely to be unreliable because of the low visibility, (3) the run seems to have suffered a rather sharp decline in 1935, 1936 and 1937.

TABLE 3

Percentages of Sea-type Fish in Samples of Sockeye Catch at Sooke Traps.*

Year	3 year old	4 year old	Total	Number of fish in sample
1919	3.1	1.8	4.9	——
1920	1.9	0.9	2.8	1950
1921	0.5	2.0	2.5	1038
1922	6.3	5.6	11.9	892
1923	6.7	9.9	16.6	947
1924	0.5	2.0	2.5	1563
1925	2.2	0.0	2.2	1229
1926	2.0	2.5	4.5	1124
1927	1.9	2.2	4.1	1371
1928	2.0	0.7	2.7	1004
1929	0.1	0.2	0.3	1286
1930	0.3	0.7	1.0	1534
1931	2.0	2.0	4.0	1465
1932	0.8	0.8	1.6	1313
1933	1.4	0.6	2.0	2345
1934	0.1	1.2	1.3	1059
1935	0.4	1.3	1.7	1108
1936	0.0	0.0	0.0	826
1937	0.2	0.2	0.4	1693

1938 Discontinued study when IPSFC started its researches.

*Data from Clemens and Clemens (1927 to 1937) and Clemens (1938).

TABLE 4

Estimation of Size of Run of Sea-type Sockeye in the Fraser River

Year	Catch in* 1000's of fish	% sea-type (Table 3)	Estimated number sea-type in catch	Sea-type escapement if catch is 80%
1919	1249	4.9	61,000	15,000
1920	1210	2.8	33,000	8,000
1921	1686	2.5	42,000	10,000
1922	1094	11.9	130,000	32,000
1923	857	16.6	142,000	36,000
1924	1214	2.5	30,000	8,000
1925	1829	2.2	40,000	10,000
1926	1382	4.5	62,000	16,000
1927	1783	4.1	73,000	18,000
1928	942	2.7	25,000	6,000
1929	2059	0.3	6,000	1,000
1930	4588	1.0	45,000	11,000
1931	1434	4.0	57,000	14,000
1932	1587	1.6	25,000	6,000
1933	2450	2.0	49,000	12,000
1934	5020	1.3	65,000	16,000
1935	1050	1.7	18,000	4,000
1936	2260	0.0	0	0
1937	1170	0.4	5,000	1,000

*1918 to 1934 from Rounsefel and Kelez (1938).
1935 to 1937 estimated from pack, (pack figures from Rept. B.C.
Fisheries Dept. for 1939, page K84) using same number of fish per case
as in last previous year of the four year cycle.
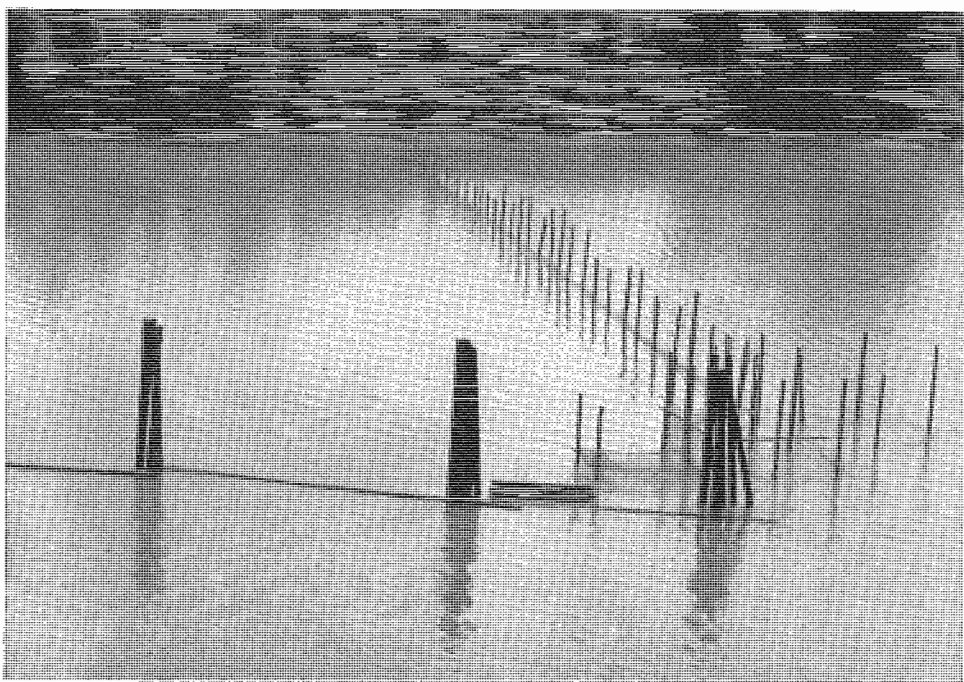
FIGURE 4. Photograph of the salmon trap in the Harrison River, 1939. The dolphins in the foreground were erected in order to prevent damage to the trap by log booms which are towed down the channel, from the right-hand side of which the photograph was taken.

FIGURE 5. Photograph taken at Harrison Trap to show the type of tag employed and the position of its attachment.

METHODS OF COLLECTION AND SOURCES OF DATA

Tagging Operations

Tagging near the mouth of the Harrison River

In 1939 a fish trap of piling and trap-wire was erected in the Harrison River just above Harrison Bay. The Harrison River is a navigable stream, so we could not obstruct the channel, but the trap was extended out into the river to the very edge of the channel. The location of the trap is shown in Figure 2 and a photograph showing its design is to be seen in Figure 4. This is the standard pound-net type of fish trap employed on the Columbia River, and was constructed under the supervision of two commercial trap fishermen from the Columbia River.

During 1939 the trap was fished from August 11 to November 3, during which time 1145 sockeye were captured. 734 of these were tagged by means of white button tags and 367 were marked by excision of the adipose fin. The latter mark was employed as a partial means of determining whether the tags themselves caused any mortality among the sockeye during their subsequent migration. It was believed that the ratio of tagged fish to fish with excised adiposes among the fish on the spawning grounds compared with the 1:2 ratio at the trap could be used for this purpose. It turned out, however, that this was not true. In the first place it proved difficult to determine with certainty whether or not the adipose fin had been excised on spawned-out fish which had been dead for some time and were, therefore, partly decomposed and covered with fungus. In the second place, the fewness of the recoveries made determination of significance of any differences most uncertain. Subsequent treatment of the 1939 Harrison tagging data will, therefore, deal with the tagged fish only.

The tags employed were pairs of white, laminated, celluloid discs 13.5 mm in diameter pierced in the center with a hole of about ½ mm. One of each pair of discs bore a number, by means of which the identity of the individual fish could later be established when it was recaptured. Tagging was carried on from a small scow, (visible just below the second dolphin downstream in Figure 4) which was brought alongside the spiller of the trap. Two men were required in the tagging operation, and three could work even more effectively. A fish was removed from the spiller of the trap by means of a dip net and placed in the tagging box, a wooden box to the inside of which is attached a canvas trough. One man, wearing wet wool gloves, grasping the salmon by the head and caudal peduncle, held the fish immobile in the canvas trough while his partner affixed the paired tags. (Figure 5). The paired tags were fastened, one on either side of the body, just below the anterior edge of the dorsal fin, by a nickel pin. The tagging operation consisted of placing the numbered disc, numbered side out, on the pin, pushing the pin through the fish, putting the blank disc on the protruding end of the pin, cutting the pin to proper length, and twisting the free end of the pin in a particular manner to hold the tags securely and snugly, but not too tightly, against the fish. A centimeter scale in the side of the trough near the bottom allowed the fork length of the fish to be read during this operation. After being tagged, the sockeye was shoved out of the box through a sliding door in the end, which allowed it to

drop directly into the river. The entire tagging operation took less than a minute for each fish.

The trap was operated again in 1940, from June 20 to October 21. The starting date was set early to determine the time of appearance of the earliest migrants, since in 1939 fish were taken from the very first day of operation. In 1940 no sockeye were captured until August 5, which is only a few days earlier than the date of the first operation in 1939. It seems likely, therefore, that the 1939 operation also covered practically the entire period of the early run. Some sockeye were still ascending the river on October 20, 1940, when the trap was put out of action by a heavy flood. It was not deemed worthwhile to repair it so late in the season however.

During the 1940 season a total of 280 sockeye were captured and tagged with white disc tags, just as described above.

The 1939 and 1940 operations showed that the trap was much more effective on the late run fish than on the early run fish and, indeed, too small a fraction of the early run was being tagged for purposes of population estimation. The total catches in 1940 were, furthermore, pitifully small. The trap was, therefore, extensively remodelled in 1941 with the object of improving its efficiency, particularly in the early part of the season. The improvement in efficiency over the earlier design was not particularly outstanding, and the early run was apparently sampled even less effectively than in 1939. It became abundantly clear as a result of the three seasons operations that this type of trap does not sample evenly the fish passing it at different times, and it seems doubtful whether a trap could be designed that would do so.

During 1941 the trap was operated from August 5 to November 26 and thus sampled all the runs, including that of Harrison Rapids, although with varying efficiency. A total of 1149 sockeye were tagged with the white disc tags beneath the anterior edge of the dorsal fin.

The early run fish at the Harrison trap are sexually so immature that it is not possible to determine the sex without committing a large percentage of errors. Therefore, the fish passing the trap are lumped as to sex, except for "jacks" which can be determined by their size. These "jack" sockeye were three year old precociously mature fish which were almost almost invariably males. Of many hundreds examined on the spawning grounds after death only 2 females were found during the course of this study. Jack sockeye were numerous in the early run in both 1940 and 1941, but were almost entirely lacking in 1939, as shown by their occurrence on the spawning beds. In 1940, however, the Harrison trap employed a mesh of net in the spiller (final compartment) which allowed these small fish to escape. A smaller mesh was employed in 1941 and 44 of these small fish were caught and tagged.

Tagging at the Skookumchuck

Reconnaissance in 1939 indicated that here was an excellent locality for sampling the run to the Birkenhead and other upper Lillooet tributaries. We have already described and pictured the Indian dip-net fishery at this place (Figure 3).

It was determined that fish could be obtained for tagging from Indian fishermen for a very small fee, so tagging was done here in 1940 and 1941.

The Indian fishermen employed for this purpose put their catches of sockeye either directly in the tagging box or into a live car located adjacent to the fishing platforms, depending on whether or not the taggers could keep up with the rate of catching. The fish, either direct from the dip net or taken from the live car, were placed in the tagging box and tagged in the same manner as described before, except that at the Skookumchuck the tags were affixed below the *posterior* edge of the dorsal fin. By varying the position of the tags for each locality of tagging it is possible later to determine the locality of tagging for the dead fish on the spawning grounds in the small fraction of cases when the tag has been lost or removed by an Indian fisherman. The lost or removed tag leaves a characteristic scar by the position of which the tagging locality may be determined in such cases. It is also possible to tell the locality of tagging of live, tagged fish on the redds by means of the location of the tag.

A total of 2146 tags were placed on sockeye at the Skookumchuck in 1940 and 2102 in 1941. The total numbers of each sex tagged each year were: 826 males, 1159 females, 161 jacks (male) in 1940, and 556 males, 715 females, 831 jacks (male) in 1941. At this stage of migration it is possible to distinguish the sexes with a negligible chance of error. The jack males are tabulated separately from the large males which are simply designated "males." Throughout this thesis this practice will be followed: "males" will mean large males only, unless otherwise specified.

Tagging at Birkenhead River

A fence was constructed in the Birkenhead River prior to the appearance of the sockeye in 1939. This fence was of similar design to the usual hatchery fence but was supported primarily by cables rather than the "horses" usually employed. This fence, a photograph of which is shown in Figure 6, was located at the site of the last fence employed by the hatcherymen during the days of operation of the hatchery (see Figure 9). Some of the materials used in the old hatchery fence can be seen on the far bank, in the upper picture, Figure 6. We used the picket sections from the old fence in our structure.

The original plan of these experiments involved counting the entire Birkenhead run through this fence and tagging a fraction, thus giving the materials for a study, similar to that being conducted simultaneously at Cultus Lake, to evaluate the tagging method of population enumeration against the fence count. Three practical factors made this impossible in practice: (1) It was discovered that only a small fraction of the run now spawns above the fence site, as has already been discussed. This is the lowest feasible site for this type of fence, elsewhere the banks are too low. (2) The fence was not entirely "fish tight"; tagging below the fence showed that a few fish were getting above the fence without being counted. (3) Finally, the Birkenhead is subject to tremendous floods following the fall rains, during which the fence was completely inundated. As a result we abandoned this phase of the study.

Since it was found impracticable to count the entire run in a stream like the Birkenhead, experiments were directed toward tagging a fraction of the run without complete enumeration in order to furnish data for estimation of the run on the spawning grounds by the tagging method, for comparison with results of tagging lower in the river system (Skookumchuck and Harrison), and for study with respect to evaluating the tagging method in practical operation on such a stream. To this end we conducted in 1939 trials of the construction of a simple type of trap, consisting of a wire fence suspended by an overhead cable, with a tunnel leading the fish into a pen. The photograph in Figure 7 will make clear its general plan of construction. This type of trap can be erected almost anywhere on a stream, so long as it is accessible for the transportation of the necessary materials. During the flood periods it can be raised clear of the water or dropped flat in the bed of the stream until the flood is passed, to avoid damage from logs and debris brought down by the flood waters. The initial experiments proving successful, this type of fence was employed in 1940 and 1941, the 1941 version being more efficient than that of 1940, however. It was erected at a point below the original hatchery fence but well above the mouth of the river (Figure 9). This was the lowest point to which materials could be transported.

Although a fair share of the run spawns below this site, migration up and down past the trap results in a good part of those fish spawning below being subject to capture. The type of trap employed in 1940 and 1941 differs from the fence in that the fence is a complete barrier, except for possible "leaks" so that fish which go up past it do not have the opportunity of going back down again. The trap, on the other hand, is not a complete barrier and retrograde migration is not precluded. Thus, since the salmon move up and down the stream to some degree, the population spawning below the fence is sampled to some extent also.

Sockeye were tagged at the Birkenhead River with the same white disc used elsewhere, but here it was placed at the nape to enable tag scars from lost Birkenhead tags to be distinguished from Harrison or Skookumchuck tag scars, and to make possible the recognition of the tagging locality of live, tagged sockeye on the redds.

The 93 fish, 47 males and 46 females, tagged in 1939 represent only a fraction of the fish captured at the fence, which totalled 473. As explained above, the original idea was to tag a fraction only and then test the calculated population by the weir count. Only after the bulk of the run had passed did it become obvious that this was impracticable. As the season progressed we discovered the inherent difficulties of the operation noted above, and in addition it was discovered that the fence had not been completed before a good share of the run had passed above it.

The tagging in 1940 of 283 males, 155 females, and 1 jack, represented almost the entire catch of the trap which was 477 fish. In 1941 the trap was made more efficient and 3473 sockeye were captured; this was somewhat more than we could conveniently handle, and more than was needed to give the approximately 1:20 tag ratio desired, so only 613 males, 892 females, and 846 jacks were tagged.

FIGURE 6. Birkenhead fence erected in 1939. Photo, shortly after completion in early September.
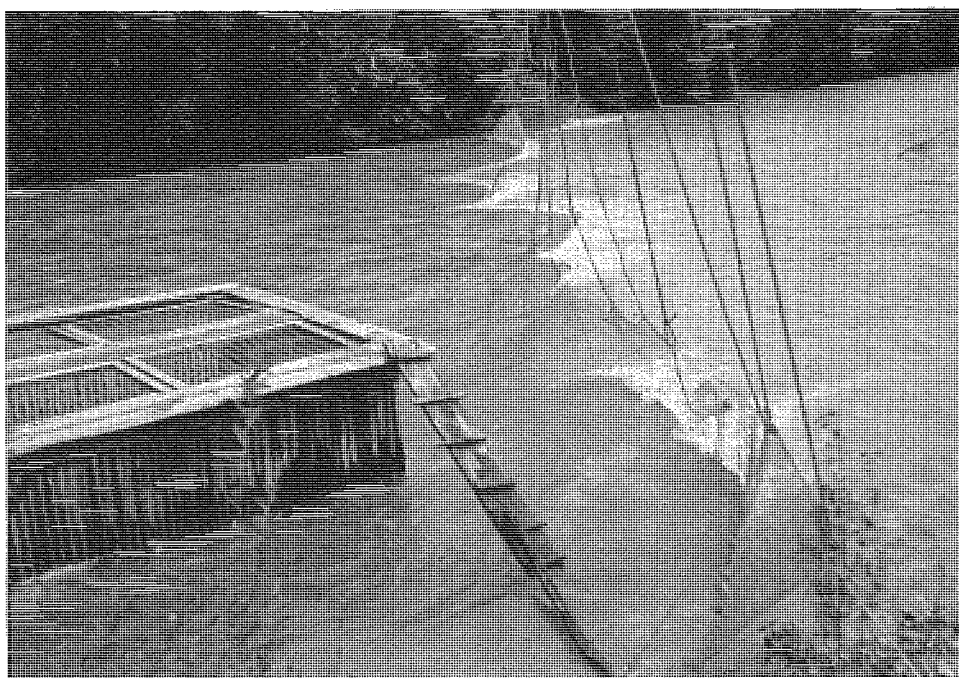
FIGURE 7. Upstream aspect of trap employed in the Birkenhead in 1940 and 1941.

In both 1940 and 1941 the trap was put in operation well in advance of the arrival of the sockeye so that fish of the entire season were subject to sampling by the trap.

In 1940 we did not expect the large run of jack salmon which occurred, since no jacks had appeared in 1939 and there was no record of any appreciable number of jacks in earlier years. As a result of the considerable numbers in 1940, the trap pen, which in that year was not constructed to retain such small fish, was rebuilt and a fair number were caught and tagged in 1941.

Marking at Weaver Creek

As we have mentioned previously, Weaver Creek was for many years prior to the final discontinuance of salmon culture in the Province a source of sockeye eggs, which were obtained from fish captured at a fence located just above Morris Lake. In 1940 and 1941 we erected a picket-type fence at this same point (Figure 10). This fence is depicted in Figure 8. Flood conditions at times put the fence out of operation. In addition to the flooding of Weaver Creek, for a time in October 1940 high water in the Harrison River so raised the levels of Morris Creek and Morris Lake that the fence at Weaver Creek and all the surrounding lowlands were flooded. During this period the whole fence was a couple of feet under water.

Because of these frequent floods, characteristic of this stream in the fall months, it was not possible to make a complete fence-count of the run. The fence was used merely as a trap by means of which could be obtained a large sample
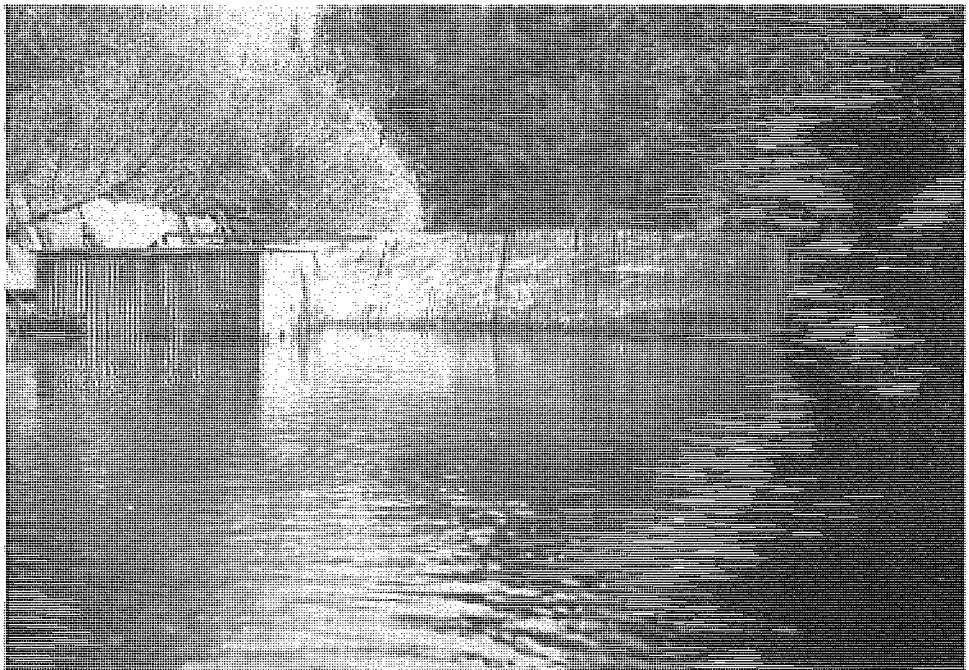
FIGURE 8. Fence in Weaver Creek at a very low water level.

of the run for examination in regard to tags placed on the fish at Harrison Trap and for tagging at the mouth of Weaver Creek. 1689 sockeye were captured by this means in 1940, and 1888 in 1941.

In 1940 the stream bed was dry until October 11 so no fish could ascend. Meanwhile a number of sockeye assembled in Morris Lake off the mouth. Very heavy rains occurred on October 11, 12, and 13 which washed a hole under the newly constructed fence and allowed this group of fish to ascend without being captured. The fence was repaired immediately, but subsequently the Harrison River rose and caused the fence to be inundated for a considerable period. As a consequence, the run was very unevenly sampled, the early part being far less well represented in the samples than the latter parts of the run. 563 fish, 58 males and 505 females, were marked by the celluloid disc tags, affixed at the nape to enable them to be immediately distinguished from the Harrison tags placed below the anterior edge of the dorsal fin. This represented about one out of 30 fish in the total run. In addition twice as many, 93 male and 1033 female, sockeye were marked by the excision of the left ventral fin by means of pruning shears.

Marking part of the run by means of tags and another similar part by fin-clipping was done in order to determine whether any differences in time of death or in distribution in the stream would result from the two methods of marking. Since the clipping is a very rapid operation involving far less handling of the fish than the tagging, it was expected that possible unfavorable effects of the greater handling necessary in the tagging operation might be revealed by comparison of the recoveries from the two methods. A ratio of 1:2 of tags to clips was maintained as closely as practicable throughout the whole season.

In the fall of 1941 there was a low flow of water in Weaver Creek all during the month of September. Our fence there was completed on September 18 and on September 19 two sockeye were captured. A few fish straggled into the stream on succeeding days, a total of 14 having entered the trap by September 28. The fish started ascending in fair numbers with the advent of heavy rains and resulting increased stream flow on September 30, and continued running through November 13, when the fence was removed. For 11 days in October the fence was completely out of operation because of flood waters, and for three days it was in only partial operation. In November it was partially inundated three days and completely so on one day. The numbers of sockeye captured were 398 male and 1490 female. The tags employed were the white celluloid tags affixed at the nape, as before. Only 743 sockeye, 168 male and 575 female, of the 1888 captured were tagged because this was sufficient to give an average tag density of about 1 in 12 fish, which was considered ample for our purposes. In the latter part of the season, after October 20 in particular, tagging all the fish trapped would have been inadvisable because during this period the fish captured represented one hundred per cent of the migrants except in the four days in November mentioned above. Our objective was to tag representatively as nearly as practicable about ten per cent of the migrants except in the four days in November mentioned above. upstream during flood periods and was not subject to tagging, the tagging was by no means equally effective on all parts of the run. This lack of representativeness

in the distribution of tags on the migrants past a given point is a phenomenon which in general can be anticipated in tagging experiments on salmon runs, and the effects of this on the subsequent analysis of the data is one of the problems on which it is hoped this thesis will shed some light.

Sampling After Marking

The technique of enumerating a fish population by means of marked members consists essentially of the following: a sample is drawn and, after the individuals are marked, returned to the population; subsequently a second sample is drawn consisting of some marked and some unmarked members. From the numbers of marked and unmarked members in the sample, and the known number of marked members placed in the population as a result of the prior sampling, the number of individuals in the entire population is estimated. In the present case, in addition to arriving at an estimate of population numbers, we are also interested in examining some of the factors which may affect the distribution of the marked members in the population, and so affect the estimate of population size.

We have already described the various samplings at Harrison Trap, Skookumchuck, Weaver Creek and Birkenhead River by means of which marked members were inserted into the populations under study. We have now to describe the drawing of subsequent samples after the marking. Samples were drawn by three methods: live fish captures by trap or dip net, counts of live tagged and untagged fish on the redds, examination of dead fish on the spawning grounds.

Capture of live fish

It has been described above how the Birkenhead run was sampled at the Skookumchuck in 1940 and 1941, and in the Birkenhead River in all three years, for the purpose of obtaining individuals to mark. We have also described the samples drawn at Weaver Creek for the same purpose. These samples, in addition, serve as samples from which tag-ratios may be estimated for tagging done lower down the river system. The fish caught at the mouth of Weaver Creek consist of unmarked fish and fish marked at the Harrison Trap. The fish caught at Skookumchuck are a sample of the Upper Lillooet runs after being subject to marking at Harrison Trap. The fish captured at the trap near the mouth of the Birkenhead are a sample of that run after being subject to marking both at Harrison Trap and at Skookumchuck.

Live fish counts on the redds

Counts of fish observable visually were made periodically throughout each season at the spawning grounds. The numbers of fish seen were recorded according to whether they were tagged or untagged and, in case a fish was tagged, it was also recorded at what locality the tag had been affixed. This was possible, because, as we have already related, the location of the tag on the fish was different for different tagging stations at which samples were taken of the same run. These data make possible only the determination of the ratio of tagged fish to total fish observed, and do not enable the time of tagging of the tagged fish to be determined as is the case in the other two sampling methods. Also, it would seem that there

BIRKENHEAD RIVER
SPAWNING GROUNDS
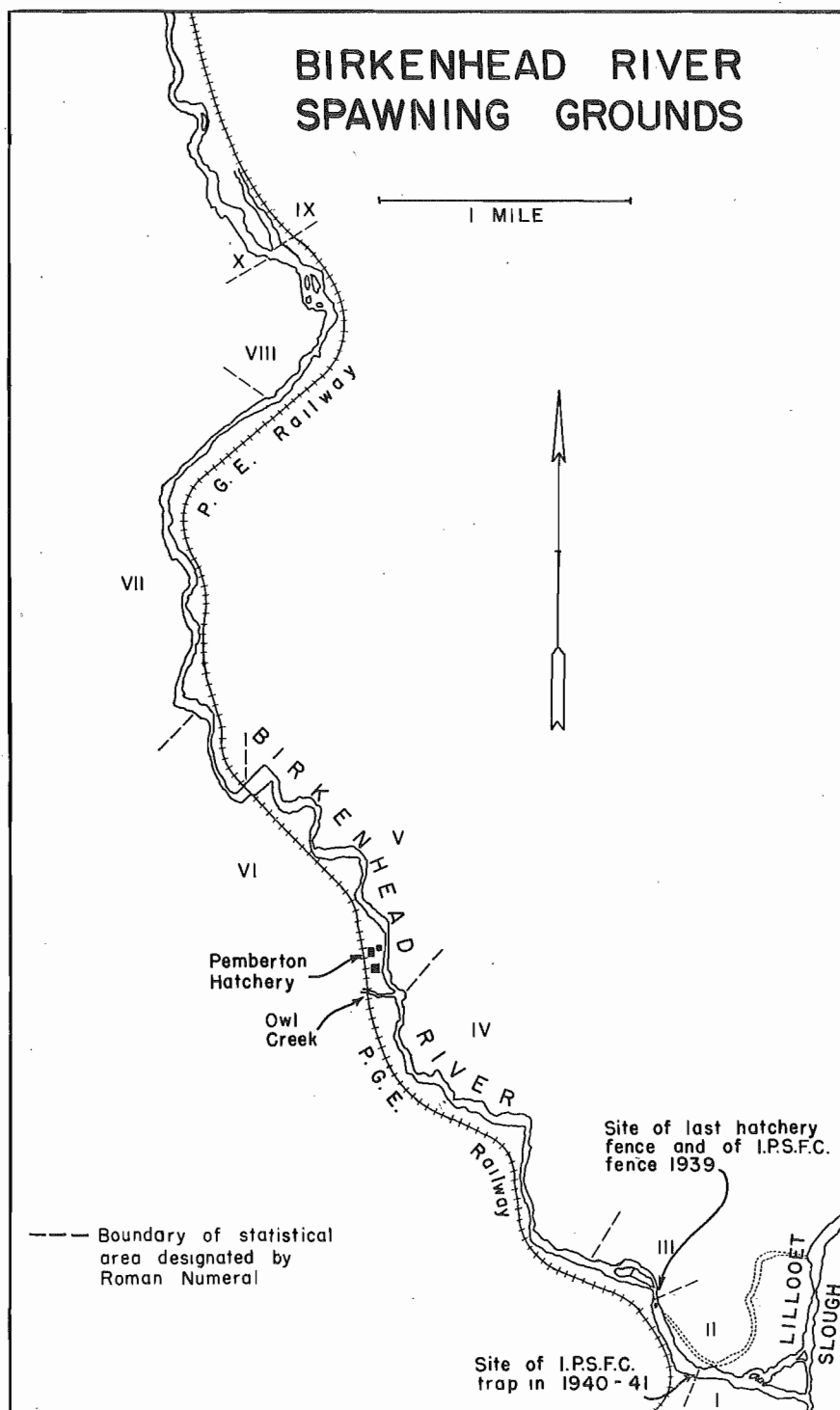
FIGURE 9. Birkenhead River spawning grounds.

is somewhat more opportunity for observer bias because of the necessity for the observer to exercise choice as to which fish are included in the sample. Particularly on the larger streams, such as the Birkenhead, some fish are seen at such a distance or under such circumstances that one cannot ascertain with certainty whether or not the fish is tagged. It is therefore necessary for the observer to choose which fish are seen so clearly that they may be fairly included in his sample.

Dead fish samples

The examination of the carcasses of dead fish on the spawning grounds offers an excellent opportunity for sampling the population with a minimum of observer bias. For purposes of this sampling the Birkenhead River was divided into convenient statistical areas (Figure 9). During each of the three seasons under consideration each of these areas was patrolled not less often than once a week after the fish started dying, and every dead fish seen was examined. For each fish examined there were recorded date, sex, statistical area, degree of completeness of spawning estimated to the nearest 25 per cent, if tagged the locality of tagging and tag number (from which date of tagging could be determined). The fish was also examined for the characteristic scar left by a tag which had been lost or removed. In addition, it was recorded whether or not the carcass was "fresh." A fresh carcass is one in which the flesh has undergone no noticeable decomposition as judged by firmness of flesh, absence of putrescent odor, and lack of fungus beyond that normal for live spawners. A "fresh" dead fish has been dead only one or two days at most, although the time will vary within this, depending on the state of the weather and the water temperature. After examination of the carcass, it was chopped in half with a large fish knife to preclude duplication of observation. This was sampling without replacement.

In addition to the dead fish obtained by patrolling the stream at intervals, a very large number of dead and dying fish were obtained from the upstream face of the fence across the stream. These were removed every day, except when floods or other circumstances prevented, and examined in the same manner as described above. Sampling of dead fish both along the stream and at the fence was continued until all live fish had disappeared from the stream and recoveries of dead fish became so few as to be negligible.

At Weaver Creek exactly this same procedure was followed in 1940 and 1941. In 1939, when only Harrison tags were present on the fish, the stream was visited at approximately weekly intervals during the season and examination was made of only part of the dead fish in the stream. The dead fish examined were not recorded by carcass condition. Furthermore, the carcasses were disposed of by throwing them out into the brush along the stream rather than by chopping in half. Statistical areas used on this stream in 1940 and 1941 are shown in Figure 10. Little East Creek, a very tiny tributary to Morris Lake across from Weaver Creek, which had a few spawners in 1941 at the same time as the Weaver Creek run, was covered routinely each week while fish were dying there.

Silver Creek and Douglas Creek were each patrolled several times during the season in 1940 and 1941 and the same procedure followed as above regarding dead fish. No division into statistical areas was made in these streams. These
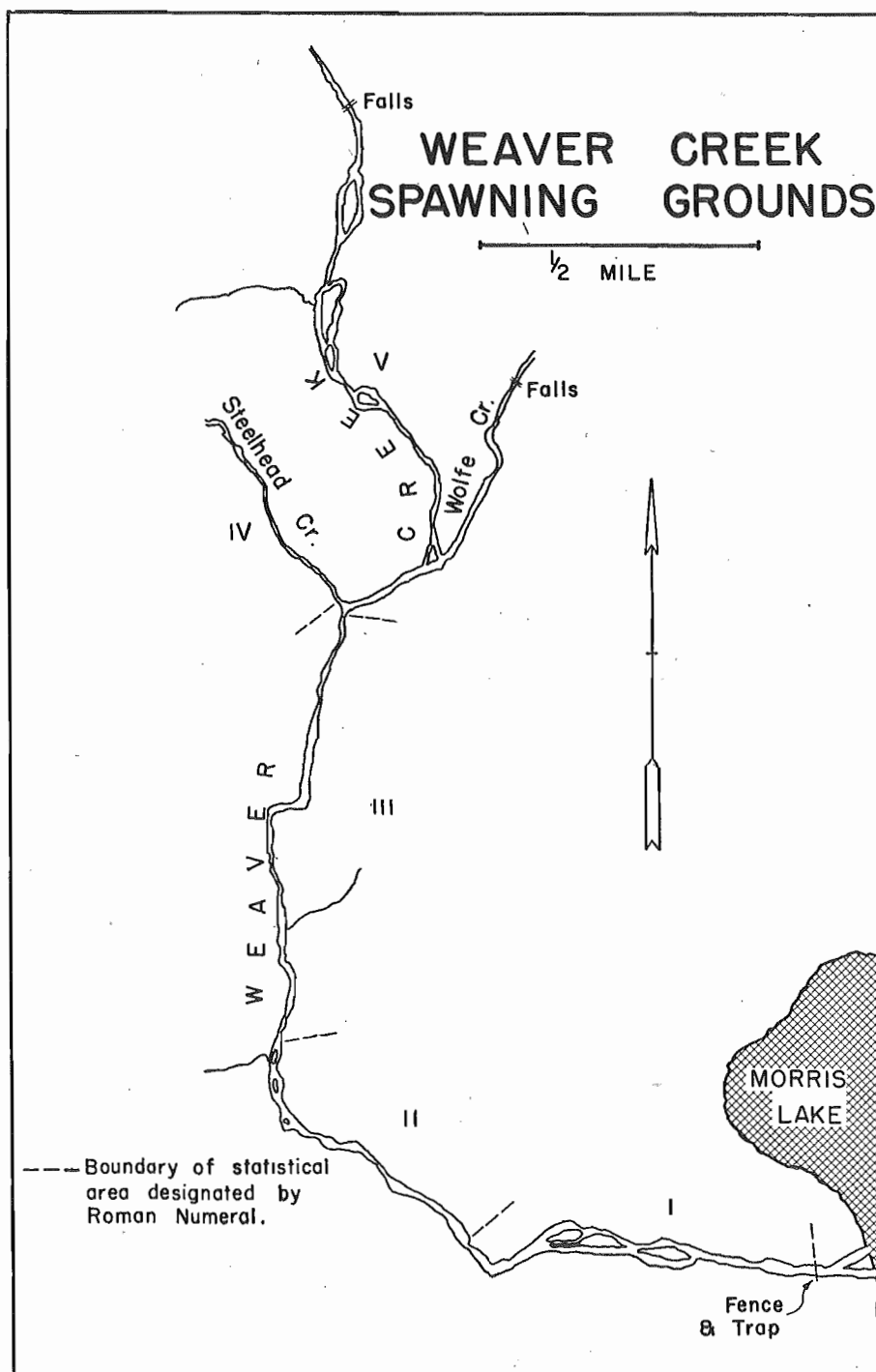
FIGURE 10. Spawning grounds of Weaver Creek

streams were each visited on only two occasions in 1939; the runs were so very small (in Douglas Creek a total of 138 fish were seen, and in Silver Creek 26 fish) that regular visits were not deemed worthwhile.

Hatchery Creek, the very small sockeye population of which spawns at the same time as Weaver Creek fish, was visited each week in 1940 and 1941 and the dead fish examined as above described.

Harrison Rapids was the object of a regular dead-fish sampling program only in 1941. In that year the banks of the Harrison River adjacent to and below these spawning grounds were carefully patrolled at least once a week and the dead sockeye examined in the standard fashion throughout the entire season.

The several tributaries of the Harrison System mentioned in the earlier part of this paper as having tiny populations of sockeye received scant attention. These groups form such an infinitesimal part of the total that effort in sampling them would not have been worthwhile. Each was observed by representatives of either the Salmon Commission or the Dominion Government, however, so that if any worthwhile population of spawners had shown up it could have been included. Such a contingency arose at Silver Creek in 1940 when an unexpectedly large sockeye run appeared in that stream, and was therefore made the subject of regular live counts and dead fish sampling.

Indian catch

The Indians of the Pemberton Band take sockeye on the spawning grounds of the Birkenhead River by means of gaff hooks. Since they can select the fish they wish to gaff, it is possible that they might remove tagged fish selectively if they desired to do so. This was discouraged by the fact that no rewards were paid for returned tags and, indeed, no attempt was made to remove tags from any tagged fish the Indians caught. After the first natural curiosity wore off early in the 1939 season and each fisherman got a souvenir tag or two, no special attention seemed to be paid to the tagged fish. As a means of studying this more exactly, however, counts were made each season of a large sample of the Indian catch either on the river bank or at the smokehouses before they were butchered, and the numbers of tagged and untagged fish recorded; recorded also were tag scars, where tags had been removed. Tags were not removed by the observer in any case, and tag numbers were taken only when it could be done without attracting the attention of the Indians.

SEPARATION OF POPULATIONS AT HARRISON TRAP

In tagging experiments with fish captured at Weaver Creek and at the Birkenhead River, we are dealing with a single population in each case. The tagging operations at Skookumchuck also were conducted essentially on a single population, because the Birkenhead race constitutes an overwhelming majority of the fish spawning in the upper Lillooet region. The tagging experiments at Harrison Trap, in contrast, involved all the races of the Harrison System. A casual inspection of the tag-ratio data was sufficient to indicate that the ratio of Harrison tagged fish to total fish was very different for the different races, therefore it is essential that we be able to determine in some manner the numbers of fish of each race tagged at the Harrison Trap before we can proceed very far with the analysis of these data. It has proven possible to estimate the number of fish tagged at Harrison Trap which were bound for each of the major spawning streams by considering the time of migration past Harrison Trap in conjunction with the characteristics of the racial peculiarities in the structure of the scales, reflecting racial differences in habitats and growth rates.

Separation of Races by Time of Migration

Recovery of tagged fish

The recovery of tagged fish on the spawning grounds, or enroute thereto in the case of fish taken in the Lillooet River and Lillooet Lakes, offers a means of determining the time of passage past Harrison Trap of representative members of the various populations involved. Tables 5, 6 and 7 show for each of the three years separately the numbers of fish tagged each week and the localities of recovery of all recoveries from each weekly group. From these tables we might infer that the fish tagged at Harrison Trap in August and up to about 20 September in 1939 and 1941 were exclusively bound for the Upper Lillooet River (we will consider all the fish of the Upper Lillooet as Birkenhead fish, except where otherwise specifically noted) except for the rather unimportant Douglas Creek group which migrates past Harrison Trap at the same time. In 1940 the Silver Creek population, which in that year was quite large, was represented by two recoveries tagged at Harrison Trap in August. The Birkenhead fish continue to be represented by small numbers of sockeye well into early October. From the time of appearance of fish on the Silver Creek spawning grounds in 1940 it seems certain that all the Silver Creek fish pass Harrison Trap well before the middle of September: the bulk of the fish arrived on the spawning grounds in late August and early September; they were dying in large numbers in mid-September; by October 1 the few live fish visible were less than 10% of the numbers visible on September 8; by mid-October no live fish and only 10 dead fish were to be found. The two tags recovered, which passed the Harrison Trap during the week ending August 24, were recovered from dead fish on September 23 and September 24, an elapsed time of a month.

The Weaver Creek fish begin passing Harrison Trap shortly after September 20 and continue throughout October. There is, thus, some overlap in times of

TABLE 5.

Number of Sockeye Tagged at the Mouth of the Harrison River, and the Recoveries of Tagged Fish from Various Localities, by Time of Tagging — 1939

Date of Tagging (Week ending)	Number Tagged Harrison Trap	RECOVERIES AT							
		Birkenhead River	Lillooet Lake	Douglas Creek	Lillooet R. above mouth	Weaver Creek	Hatchery Creek	Harrison Bay	Fraser River
Aug. 12	16	1	1*	1					
19	34	3							3
26	65	6							3
Sept. 2	51	9							
9	20	1							1
16	24								1
23	63	1			1*	1			3
30	89					3		1	4
Oct. 7	70	1			1*	6			1
14	54					5			2
21	187					12	1		2
28	51					2			3
Nov. 4	10								
Total	734	22	1	1	2	29	1	1	23

*Indian gill net catch

migration of the Birkenhead run and the Weaver Creek run. This is illustrated by the tables cited, and also by the following data:

Latest date of tagging of Birkenhead fish recovered			Earliest date of tagging of Weaver Creek fish recovered
1939	October	3	September 21
1940	August	29	September 27
1941	September	30	September 27

While the period of overlap is not great, it is yet sufficient to make a somewhat inaccurate separation of these two races on a time basis alone. There seems to be no overlap in times of migration of Silver Creek and Weaver Creek fish.

It may also be seen, from Table 7 in particular, that the fish spawning in Harrison Rapids tend to run somewhat later than Weaver Creek fish, but their times of migration are so nearly coincident that there is no hope of separating them on a time basis.

The little group of Hatchery Creek fish, which is apparently a small self-perpetuating group which arose from Weaver Creek stock transplanted by the hatchery, seems to be in all respects identical with Weaver Creek fish, certainly so regarding migration time. We will consider the Hatchery Creek fish a part of the Weaver Creek population as far as the Harrison Trap tagging is concerned.

TABLE 6

Number of Sockeye Tagged at the Mouth of the Harrison River, and the Recoveries of Tagged Fish from Various Localities, by Time of Tagging — 1940

Date of Tagging (Week ending)	Number Tagged Harrison Trap	RECOVERIES AT				
		Birkenhead River	Douglas Creek	Silver Creek	Weaver Creek	Fraser River
Aug. 10	1					
17	10					
24	18			2		2
31	11	1				
Sept. 7	13					
14	10					
21	13		1			
28	23				2	
Oct. 5	93				9	3
12	70				8	2
19	17				5	1
26	1					
Totals	280	1	1	2	24	8

TABLE 7

Number of Sockeye Tagged at the Mouth of the Harrison River, and the Recoveries of Tagged Fish from Various Localities, by Time of Tagging — 1941

Date of Tagging (Week ending)	Number Tagged Harrison Trap		RECOVERIES AT					
	All Sockeye	Jacks only	Birkenhead River*	Skookum-chuck*	Weaver Creek (incl. East Cr.)	Hatchery Creek	Harrison Rapids	Fraser River
Aug. 9	22	8	1 (1)					2
16	105	29	2 (2)	1 (1)				3
23	14	3	2	1				1
30								
Sept. 6								
13	7	1						
20	1							
27	15			..	1			1
Oct. 4	119	3	1		28		1	1
11	373				164	2	1	2
18	235				112	1	2	1
25	36				8		1	2
Nov. 1	38				1			2
8	95						1	2
15	57				1		2	
22	14							
29	18						1	
Totals	1149	44	6 (3)	2 (1)	315	3	9	17

*Jacks as shown in parentheses

Summing up, considering all the tiny groups of the Upper Lillooet as part of the Birkenhead population, and considering East Creek and Hatchery Creek fish as part of the Weaver Creek population, we have four major populations to separate, i.e., those of the Birkenhead River, of Silver Creek, of Weaver Creek, and of Harrison Rapids. The Birkenhead population slightly overlaps those of Weaver Creek and Harrison Rapids in respect to migration time past Harrison Trap. The Silver Creek population cannot be separated at all from the Birkenhead population on the basis of time of migration past Harrison Trap, nor can the Weaver Creek and Harrison Rapids groups be distinguished on this basis. The Silver Creek population, however, can be separated completely from those of Weaver Creek and Harrison Rapids solely on the basis of time of migration past Harrison Trap.

Jack salmon in the Birkenhead population

Further evidence on the time of passage of Harrison Trap by the Birkenhead run is offered by the occurrence of jacks (3-year-old fish, almost exclusively males). The Birkenhead run had a very large percentage of these fish in both 1940 and 1941, but only in 1941 was the spiller of the Harrison Trap designed to retain them. The fish are always easily recognizable as jacks by their size. A negligible number of jacks occurred elsewhere than in the Birkenhead in 1941, so that the occurrence of such fish in the Harrison Trap catches may be used as an indication of the time of migration of the Birkenhead run. As may be seen from Table 7, this evidence is completely in accord with the evidence from recovery of tagged fish.

Separation of Races by Means of Scale Patterns

Since it has proven impossible to make the required determination of numbers of Harrison tagged fish belonging to each major population solely on the basis of time of capture at the trap, it has been necessary to employ collateral data from the scale patterns. Scales were taken from approximately 20 per cent of the fish tagged at Harrison Trap in each of the three seasons. These were taken routinely for age reading purposes, and it was not foreseen that they would be necessary in connection with the population enumeration studies being considered in the present work; it is only by fortunate chance that these essential data are available.

Studies of C. H. Gilbert

Gilbert, in a series of papers beginning in 1913, studied the scale patterns of Fraser River sockeye with the objective of using them both to determine the ages of the fish and also to elucidate various other problems in the life history of the species. In the very first paper of the series (Gilbert 1913) he noted the occurrence of scales with "sea-type" nuclear areas, so called because they were very similar to those of humpback and dog salmon, both of which proceed to sea immediately on hatching. He correctly interpreted these scales as indicating that the fish possessing them had gone to sea soon after hatching, and the first year's growth was therefore made in salt water. We have already seen how he

subsequently discovered that the fish spawning on the Harrison Rapids redds are all of this type and are therefore readily distinguishable from other sockeye of the Harrison system, and probably from any other group in the Fraser River.

Gilbert also pointed out in his 1913 paper that the sea-type fish seem to have grown more rapidly during the first year than if they had remained in fresh water, and that to a certain extent they seem to maintain this preponderance in size in succeeding years. In 1914 he stated:

"One constant feature in sea-type individuals from the Fraser is clearly shown in Figs. 1 to 5 of this report. Growth during the first two years is so extensive that the mature stature is almost attained and growth is greatly checked in subsequent seasons. This throws the winter bands of the second and third years well out towards the margin of the scale. . . ."

We have already quoted on page 39 his description of the Harrison Rapids scales given in his 1918 paper.

He examined, in 1918, 200 spawners from Harrison Rapids, and in his 1919 paper he states:

"The 200 specimens examined in 1918 had all had the history above outlined. Not one of them exhibited in the centre of its scale any trace of growth of the young in fresh water. All had passed down to sea as young fry before any portion of the scales had made their appearance.

. . . .

"Figs. 1 to 5 are from the spawning race at Harrison Rapids. Each contains the extensive first year's growth which occurs wholly in salt water, together with a varying proportion of the second year's growth. The boundary between the two years in these cases is not a sharp one, leading to the conclusion that fry which descend to the sea in their first year suffer less interruption to their growth during their first fall and winter in the sea than is the case with those which pass their first year or their first two years in fresh water. Rarely, however, a slackening of growth in the Harrison Rapids fish at the close of their first year is indicated by a definite line of demarcation at its outer edge. When this exists there are thirty-two to forty rings or lines of growth belonging to the first year.

. . . .

"In 1918, as in 1916, we failed to find any individuals of sea-type spawning in any part of the Fraser River basin other than Harrison Rapids. Upwards of a thousand specimens were examined from other spawning districts, in which it might be thought an occasional sea-type individual might be found, if only as a stray. The fact that not one individual was discovered elsewhere, when coupled with the further fact that every Harrison Rapids sockeye belonged to this group, furnishes the strongest possible evidence of return of spawning fish to their native districts."

In 1916 and 1917 Gilbert examined collections of scales from Morris (Weaver) Creek, Harrison Hatchery, Silver Creek, and the Pemberton Hatchery (Birkenhead River). He reported on the examination of these scales in his 1918 paper. From Silver Creek he had but 6 specimens, of which he said "All are five-

year fish with very large nuclear regions, but our material is too scanty for characterization of the race."

He found that the Birkenhead fish "ally themselves definitely with the upriver colonies." He found that they were different from fish of Morris Creek or other districts drawn on by the Harrison Hatchery in size, but that "the greatest difference lies in the small size of the nuclear region of the scale and the low number of nuclear rings." A similar small freshwater growth was found for fish from the Chilcotin River, a tributary of the upper Fraser. The Birkenhead fish were also found to have a small growth in the first year at sea. In this respect it was stated:

> "Figs. 1 and 2, from the Birkenhead River, show not only the small nuclear region provided with slender irregular rings, but the very small first year's growth in the sea, both being characteristic of the Birkenhead fish."

In contrast to the Birkenhead fish, he says of the Weaver Creek fish:

> "Fig. 4 shows an average Morris Creek scale, with strong, large, regular nuclear region, sharply distinguished from growth in the sea. The second year's growth is large."

There is also presented a table in this paper showing the frequency distributions of numbers of nuclear rings for fish from the various spawning grounds. The Pemberton fish have clearly less rings than Weaver Creek, and Harrison Hatchery fish, but there is a considerable zone of overlap. Little or no difference is evident for fish of Weaver Creek and Harrison Hatchery, and the six Silver Creek fish are in the same range of ring-counts. Chilcotin fish and Birkenhead fish are similar.

Among his 1916 material he found the following percentages of 2-year-in-lake sockeye: Morris Creek, none; Harrison Hatchery, 1.5 per cent; Pemberton Hatchery, 10 per cent.

In 1918, in addition to the collections at Harrison Rapids, Gilbert also examined collections from the following places in the Harrison system: Harrison Hatchery, Birkenhead River, and Skookumchuck on the Lillooet River.

In regard to the Morris Creek fish, he stated:

> "Examination of the scales of the fish now running shows a striking uniformity in their development. They form an impressively homogeneous lot. All have large sharply defined nuclear regions, testifying to a vigorous growth during their first year, which is uniformly passed in the lake. . . .
>
> "No individuals from this district had lived two years in the lake before migrating, and none had proceeded to sea in their first year".

Of the Birkenhead River he said:

> "The characteristics of the Birkenhead race in 1918 are in general the same as those described for the 1916 run. The growth of the fingerlings in fresh water must be much less than in the case of the Morris Creek and Harrison Lake fingerlings. The nuclear area of the scale averages small with densely crowded rings. These were somewhat more numerous in 1918 than

in either of the two years preceding and the extremes range far more widely. . . . While the nuclear regions average small and the number of rings in the great majority of individuals is less than sixteen (the mode lying somewhere between eight and eleven), occasional specimens have nuclear rings running as high as nineteen, twenty, and twenty-one. Furthermore, the frequency curve for nuclear rings in 1918 has none of the regularity so well defined in 1916 and 1917. The irregularities in 1918 are equally marked and are similar, whether the specimens were procured at the Skookumchuck or at the Pemberton Hatchery on the Birkenhead. . . . In spite of the variation in nuclear rings, racial peculiarities are apparent. Especially marked is the small size of the first year's growth in the sea, a character that was also conspicuous in the two years preceding. Occasionally this is carried so far that the first year's growth in the sea resembles a second year in a lake, but only one undoubted two-years-in-lake individual was observed".

Gilbert in this 1919 paper gives a tabulation of frequency of numbers of nuclear rings on scales from the various localities which shows the close agreement of Skookumchuck and Birkenhead specimens and the great difference between them and the fish from Weaver Creek and Harrison Hatchery, but showing again that there is an overlap in this character between the two races.

A number of scales from the Chilcotin River were studied from the 1918 run and it was found that they were characterized by a small, crowded nucleus and a small first year's growth in the sea, similar to the Birkenhead fish.

In contrast to the 10 per cent of 2-year-in-lake fish found in the Birkenhead run in 1916, only one specimen of this type was found in 1918 among 288 examples from Skookumchuck and Pemberton.

Characteristics of scales from the different Harrison races

Since Gilbert concluded that the different races of the Harrison system were to be distinguished by their scales, it seemed that this offered a means of completing the separation of the runs at the Harrison Trap. We therefore set about to establish criteria for distinguishing the various groups. The problem was to distinguish Birkenhead from Silver Creek fish; Birkenhead from Weaver Creek fish; and Harrison Rapids fish from fish of both Weaver Creek and Birkenhead River.

For establishing criteria we examined series of scales taken from the spawning grounds of each of these races during the fall of 1940. Scales were taken from the side of the fish above the lateral line, below and slightly behind the dorsal fin. Scales of Birkenhead River fish are characterized by a small, crowded nucleus with many breaks and interruptions in the nuclear rings, and by a relatively small growth during the first year in the sea. Silver Creek scales and Weaver Creek scales may be recognized by their large, regular nuclei with more regular, unbroken nuclear rings and by a larger growth during the first year at sea than in the case of the Birkenhead scales. Silver Creek and Weaver Creek scales are scarcely different, although the size both at the end of the sojourn in the lake and at the end of the first sea year seems to average somewhat larger in the case of the Silver Creek fish. Harrison Rapids sockeye are, of course, immediately recognizable by the sea-type centers, adequately described by Gilbert, and by the

large size at the second winter. The position of the first winter check on the scales is either entirely indeterminable or questionable in most cases. In some cases, however, a first winter check is visible. In some cases the growth of the first year looks similar to a vigorous lacustrine growth. However, there is also generally a very much greater growth during the second year than occurs in Weaver Creek fish, and this serves as a further distinguishing character of Harrison Rapids fish.

While the above description serves to characterize the different races, something more quantitative is desirable as a basis for segregation of the individual fish of unknown destination; we therefore measured the radii of the nucleus and of the annuli, along an anterior-posterior axis, from the center of the scale, at a magnification of 44 diameters. A higher magnification of 135 diameters was employed to make a more careful examination to determine the position of the edge of the nucleus in some cases. The measurements were made with a millimeter scale on a projected image, and the data given are, hence, in terms of millimeters at a magnification of 44 diameters. Whereas Gilbert employed a count of the nuclear rings as a criterion of relative nuclear size, and therefore of amount of lacustrine growth, we preferred to use a measurement instead for two reasons: first, the interrupted nature of the rings on some fish, particularly of the Birkenhead group, makes this count difficult and somewhat uncertain; second, the growth beyond the nucleus cannot be satisfactorily handled in such a manner and measurement has, therefore, to be resorted to in any case. The ring-count has an advantage over scale measurement in that it is presumably quite independent of the position from which the scale was taken, whereas the measurement method requires the scales be taken from a comparable part of the body on all fish. This was fortunately anticipated, however, and the various field assistants had been instructed to take the scales from the particular site above noted.

Among scale samples from 77 Birkenhead fish, there were 21 of the two-year-in-lake type, or 27 per cent. Mr. J. A. R. Hamilton of the Commission staff examined a larger group of fish from the Skookumchuck and found 26.2 per cent of two-year-in-lake fish. No fish of this type were found in either the Weaver Creek or Silver Creek samples in 1940.

In Figure 11 are plotted the frequencies of occurrence of nuclear radii for scales from the various spawning areas for one-year-in-lake fish. It may be seen that a majority of such fish from the Birkenhead may be distinguished from Weaver Creek fish or from Silver Creek fish by this character, but that there is some overlap.

The radii to the second winter rings are plotted as frequency curves in Figure 12 for these same fish, plus the Harrison Rapids fish. Depicted here is the smaller size of Birkenhead fish at the end of the first year in the sea compared with Weaver Creek or Silver Creek fish. One of the most interesting things in this graph is, however, the extremely large size of the Harrison Rapids fish at the second winter. This character alone is sufficient to distinguish them entirely from the Birkenhead fish, and in most cases from Weaver Creek fish. The combination of the sea-type nucleus and a second-winter annulus above 80 mm. at a magnification of 44 diameters appears sufficient to identify a Harrison Rapids fish and is the criterion applied for this purpose to fish captured at Harrison Trap.
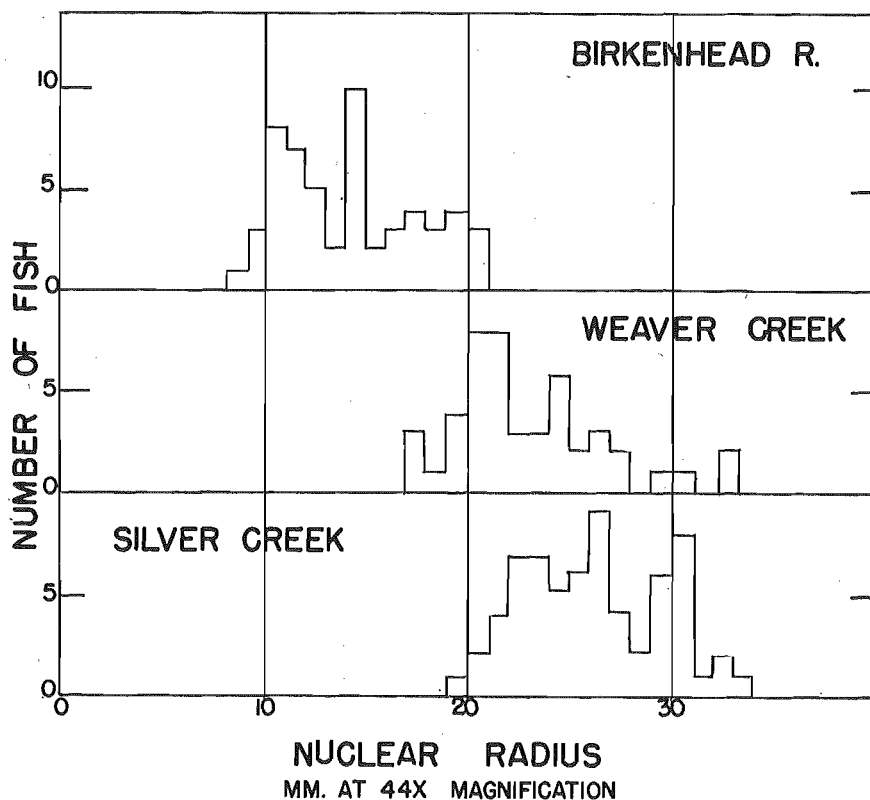
FIGURE 11. Frequency distributions of nuclear radius of scales from fish from various
Harrison system spawning grounds, 1940.

Since the radii to the nuclei and to the second annuli each shows considerable
overlap as between Birkenhead and Silver Creek, and between Birkenhead and
Weaver Creek fish, the joint distributions of these variables were studied. Figure
13 depicts the joint distribution of these characters for 65 Silver Creek and 54
Birkenhead fish. A slight overlap is evident, 4 Birkenhead fish and 3 Silver
Creek fish falling within the area of overlap of the limits of variation of fish from
the two localities. Lines on the figure indicate the limits for each race as deter-
mined from these samples. Using this joint distribution of nuclear radius and
radius to the first annulus as a means of segregating individual fish we would, on
the basis of these samples, expect to be able to definitely assign the locality of
destination in about 95 per cent of the cases and be unable to do so in about 5 per
cent of the cases. An occasional specimen from one locality might possibly, of
course, even fall clear outside of the limits here established for its group, in which
case it would be wrongly assigned. On the basis of the data presented here, how-
ever, that would be expected to occur in less than one case in 50.
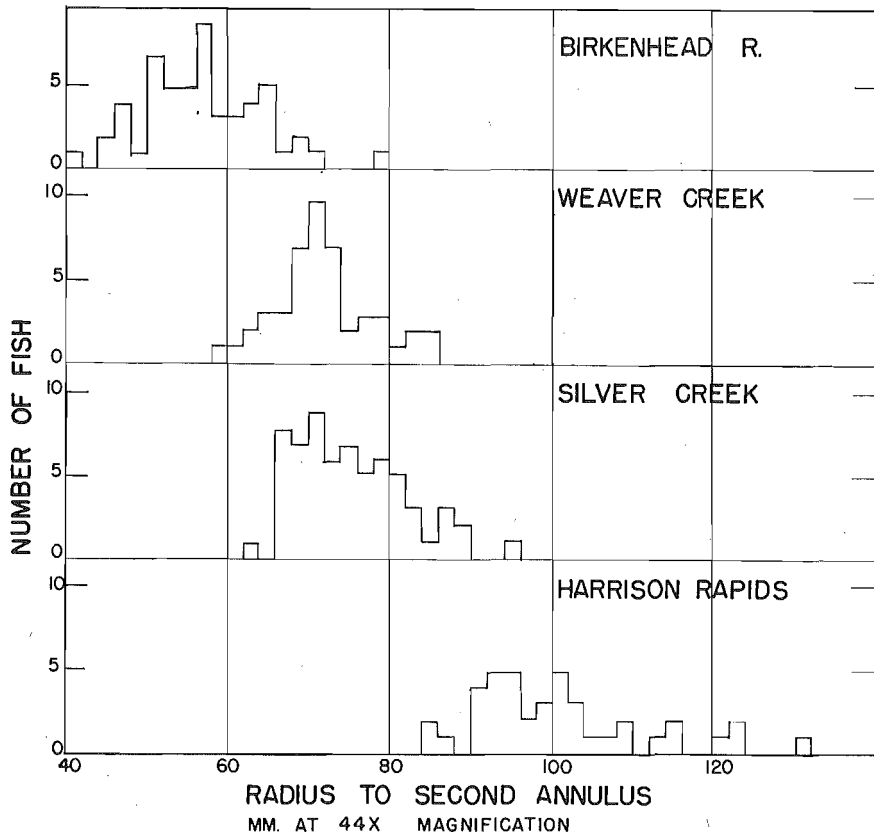
FIGURE 12. Frequency distributions of radius to second annulus of scales from fish from various Harrison system spawning grounds, 1940.

In Figure 14 are plotted the joint distributions of these same variables for the 54 Birkenhead fish and 47 Weaver Creek fish. Here the degree of overlap is much greater, 9 Birkenhead and 15 Weaver Creek fish being indistinguishable. In applying this joint distribution as a criterion for separating these two races we would expect to be able to do so successfully in about 75% of the cases and have about 25% of the cases in which a decision could not be reached. Again, completely erroneous assignments would be expected to occur in less than one case in 50.

We have seen that the small group of Douglas Creek fish migrates past Harrison Trap at the same time as Birkenhead and Silver Creek fish. A collection of 32 scales from that spawning area made in 1940 was examined, and of the 30 readable scales (2 having regenerated centers) 7 were found to be two-year-in-lake fish. The one-year-in-lake fish presented scale patterns almost identical with those in the Birkenhead River. Applying the joint criterion of size of nucleus and radius to first sea check in Figure 13, they would all be assigned to the Birkenhead group. Therefore, we will have to consider the Douglas Creek fish as part of the Birkenhead group for segregation at the Harrison Trap.
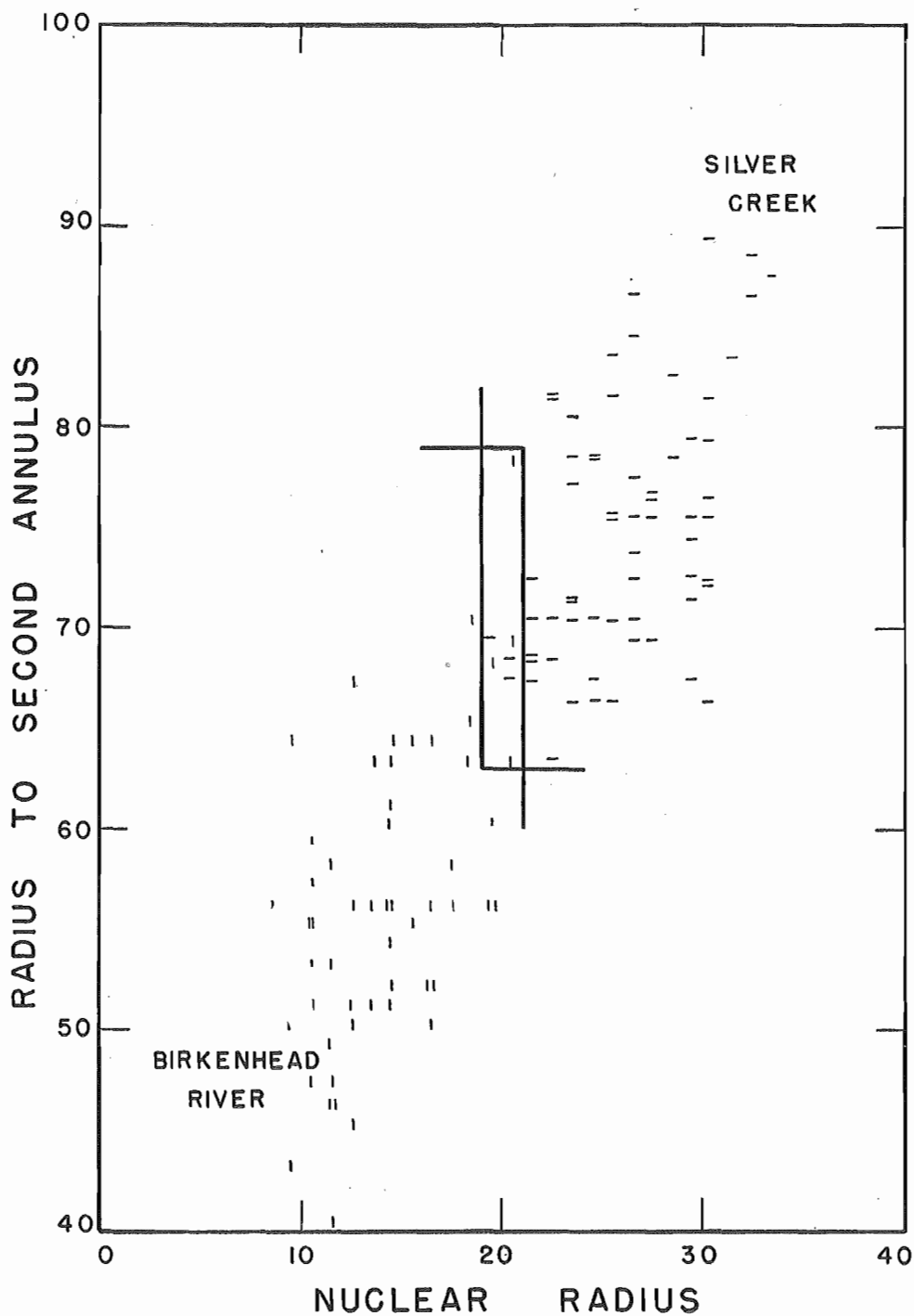
FIGURE 13. Joint distributions of radius to second annulus and nuclear radius of scales from 1940 samples taken on the spawning grounds of the Birkenhead River and Silver Creek.

Estimated Segregation of Runs at Harrison Trap

Assignment of race by scale pattern and time of migration

On the basis of the above studies the following procedure was followed in judging the locality of destination of fish from which scales were taken at Harrison Trap: The scales were projected at a magnification of 44 diameters and the radii to the edge of the nucleus and to the second winter annulus were measured. The central part of the scale was examined in greater detail at a magnification of 135 diameters.

Scales which because of regenerated centers could not be read were recorded as unreadable.

Scales having a sea-type center were assigned to Harrison Rapids. The further criterion of radius to second annulus (Figure 12) served as an additional basis of judgment in cases where it was doubtful whether or not the nucleus was of the sea-type.

Scales from one-year-in-lake fish taken from fish captured at Harrison Trap after 20 September were referred to Figure 14 for determination of race. They were recorded as questionable whether Birkenhead or Weaver Creek if their dimensions were such as to put them in the area of overlap shown in this figure.

Scales from one-year-in-lake fish taken at Harrison Trap before 20 September were assigned to Birkenhead or Silver Creek according to Figure 13, those falling in the area of overlap being recorded as questionable whether Birkenhead or Silver Creek.

Two-year-in-lake fish were assigned according to growth during the first year in the lake. During the period prior to 20 September of each year, no two-year-in-lake scales were taken which showed a growth during the first year, as judged from nuclear growths of one-year-in-lake fish of known origin, which could be assigned to other than Birkenhead fish. A few such fish during the period after 20 September showed so great a first year's lacustrine growth that they seemed obviously Weaver Creek fish and were so assigned. These were, however, very few in number; three fish in 1939, none in 1940, three in 1941. Their misassignment would make no great difference in the estimate.

Verification of method by recovered tagged fish

Seventy-five tagged fish which were assigned by this method were later recovered on the spawning grounds. Four errors of assignment were made in these seventy-five cases (see Table 8). All four of these errors were cases where fish assigned to Harrison Rapids were actually fish bound for Weaver Creek. This indicates that the difficulty in distinguishing a sea-type nucleus, plus the overlap of radius to second annulus of Weaver Creek and Harrison Rapids fish may lead to errors in a few cases. Apparently in such cases the error was in favor of Harrison Rapids.
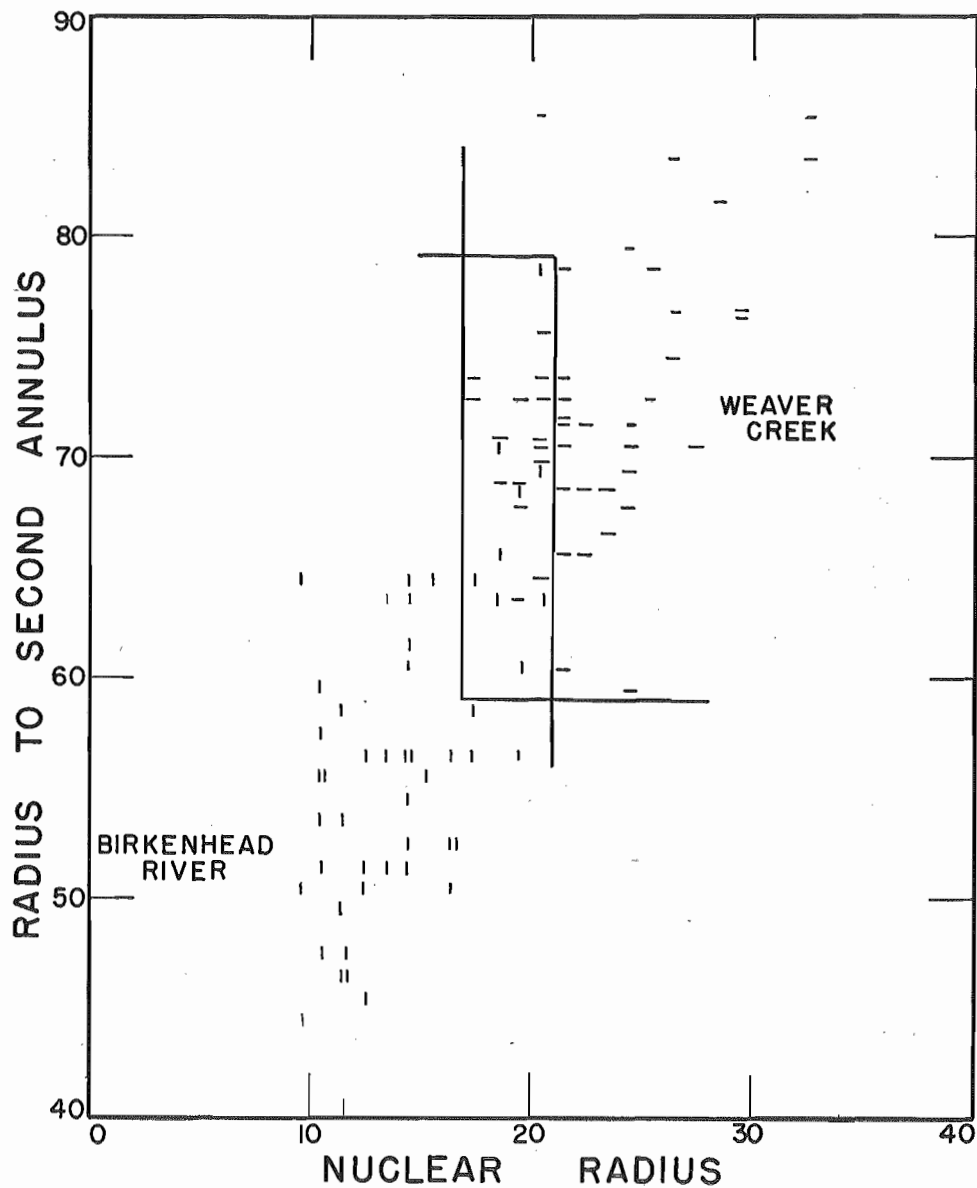
FIGURE 14. Joint distributions of radius to second annulus and nuclear radius of scales from 1940 samples taken on the spawning grounds of the Birkenhead River and Weaver Creek.

TABLE 8

Data Relating to Accuracy of Scale Readings of
Harrison Tagged Fish Which Were Subsequently
Recovered in Their Home Streams

Year	Number of Cases	Errors of Interpretation
1939	10	1
1940	7	0
1941	58	3
Totals	75	4

1939 season

The data are presented in Table 9.

The 145 scale samples from the 734 fish tagged were not distributed among the weekly groups tagged exactly in proportion to the numbers in each of those groups. This is not, therefore, the most desirable sampling design. Having no prior knowledge of the variation within groups, one would best take samples from each group in strict proportion to the number in the group (Neyman 1934). This was done in the two following years.

The table shows the number of scales examined and their assignment according to the criteria outlined above. The estimation of the numbers of fish tagged, during a given weekly period, belonging to each of the four racial groups was accomplished by applying to the total number of fish tagged in that period the proportion, in the sample from which scales were taken, of fish of the various groups. In making these estimates the following assumptions were made:

(1) An "unreadable" scale had a probability of belonging to a given group proportional to the occurrence of fish of that group in the readable part of the sample for that week.

(2) Fish which were questionable between two localities, such as B-W?, had a probability of belonging to one of these localities proportional to the frequency of occurrence of fish definitely assigned to that locality during that week.

Using the total fish tagged, the scale readings as shown, and these two assumptions, the estimated numbers of fish belonging to each run was calculated and tabulated.

Although no scale samples were taken during the week ending August 12, all 16 fish tagged were assigned to the Birkenhead group, for obvious reasons.

The single fish definitely assigned to Silver Creek in the week ending August 9 is quite likely an error, since the Silver Creek run was so small this year as to be practically negligible. However, the resulting estimates are not affected thereby to any noticeable extent, since the assignment of this fish to the Birkenhead River would add only one fish to the estimated numbers of tagged fish in that run.

TABLE 9

Estimated Segregation by Locality of Origin of Sockeye Tagged at Harrison Trap in 1939

Tagging Period	Number Tagged	Scales Examined	Scale Readings						Unreadable	Estimated Segregation			
			B	S	B-S?	W	B-W?	H		B	S	W	H
Week Ending													
Aug. 12	16	0								16			
19	34	2	1		1					34			
26	65	17	13		2				2	65			
Sept. 2	51	14	13		1					51			
9	20	15	14	1						19	1		
16	24	12	10		1				1	24			
23	63	8	3			4	1			27		36	
30	89	17	2			12	1	2		11		68	10
Oct. 7	70	18	2			9	1	5	1	9		40	21
14	54	16				11		4	1			40	14
21	187	16				8	1	5	2			120	67
28	51	7				4	1	2				36	15
Nov. 4	10	3				1		1	1			5	5
Totals	734	145	58	1	5	49	5	19	8	256	1	345	132

B = Birkenhead
S = Silver Creek
W = Weaver Creek
H = Harrison Rapids

B-S? = Questionable whether Birkenhead or Silver Creek
B-W? = Questionable whether Birkenhead or Weaver Creek

1940 season

The data are presented in Table 10.

The estimates were made in the same manner and under the same assumptions as given for 1939.

The sampling design for drawing scale samples from a fifth of the fish tagged was greatly improved in this season, in that a scale sample was taken from every fifth fish tagged, except in a few cases when the adjacent fish was used ·instead.

1941 season

The data are presented in Tables 11, 12, and 13.

The improved design for taking scale samples of 1940, whereby each weekly group of tagged fish was sampled according to the number of members in the group, was applied in 1941 also. The loss of a few samples after sampling and a few inadvertent omissions, however, result in some groups, such as those for weeks ending October 11 and October 18, to be sampled in somewhat lower proportion than the rest. Since the calculations are made for each weekly group separately this does not result in any bias in the estimates, of course, but the efficiency of the estimates are theoretically not likely to be quite as high as possible under these circumstances.

A complicating factor was introduced into the Harrison Trap experiments in 1941 by the occurrence of the very serious blockade at Hell's Gate (Thompson 1945) in that year. A number of the blockaded fish dropped back down the Fraser River and some entered the Harrison and were taken at Harrison Trap. Direct evidence to this effect was the capture in 1941 at Harrison Trap of 10 fish which had been tagged at Hell's Gate.

Other, untagged, Hell's Gate fish which had dropped down the Fraser River, ascended the Harrison, and been captured in Harrison Trap were recognizable by their badly battered appearance, with very badly bruised heads and worn-down snouts. They were to be distinguished from the Harrison fish of the late runs also by their brighter colors, red bodies and green heads, characteristic of upper Fraser sockeye and differing from the dull colors of late run Harrison fish. The field assistants at the Harrison Trap recorded the occurrence of such individuals, and in Table 12 are given the number of such fish, presumed to have been Hell's Gate fish, which were tagged at Harrison Trap each week. Of this group 7 were recovered: 5 in Weaver Creek, 1 in Hatchery Creek and 1 on the shore of Harrison Bay. The recoveries of a few of these supposed Hell's Gate fish in Weaver and Hatchery Creek does not indicate the Harrison Trap assistant was in error in his determination, however, but rather that a few of the fish blockaded at Hell's Gate made their way up the Harrison River to these streams. This is affirmed by the fact that two fish tagged at Hell's Gate were recovered in Weaver Creek, and so establishes beyond doubt that such blockaded fish did drop down the Fraser and ascend the Harrison and enter Weaver Creek.

TABLE 10

Estimated Segregation by Locality of Origin of Sockeye Tagged at Harrison Trap in 1940

Tagging Period	Number Tagged	Scales Examined	Scale Readings						Unreadable	Estimated Segregation			
			B	S	B-S?	W	B-W?	H		B	S	W	H
Week Ending													
Aug. 10	1	0								1			
17	10	1	1							10			
24	18	3	1	2						6	12		
31	11	3	1	2						4	7		
Sept. 7	13	2	2							13			
14	10	2		1	1						10		
21	13	2	2							13			
28	23	5	2			1	1		1	15		8	
Oct. 5	93	14				8	2	4				66	27
12	70	13				9	1	3				54	16
19	17	4				2		2				9	8
26	1	0										1	
Totals	280	49	9	5	1	20	4	9	1	62	29	138	51

B = Birkenhead
S = Silver Creek
W = Weaver Creek
H = Harrison Rapids

B-S? = Questionable whether Birkenhead or Silver Creek
B-W? = Questionable whether Birkenhead or Weaver Creek

TABLE 11

Assignment to Racial Groups of Sockeye Tagged at Harrison Trap in 1941 from Which Scales Were Taken

Tagging Period	Number Tagged	Scales Examined	Scale Readings						Unreadable
			B	S	B-S?	W	B-W?	H	
Week Ending									
Aug. 9	22	4	3	1					
16	105	20	14+3*		2				1
23	14	3	2+1*						
30									
Sept. 6									
13	7	1	1						
20	1								
27	15	3	3						
Oct. 4	119	20	2*			10	3*	5	
11	373	69				55	2+1*	5	6
18	235	37	2*			27		5	3
25	36	7				4	1+1*	1	
Nov. 1	38	7				1		6	
8	95	18						17	1
15	57	11				1		9	1
22	14	3						3	
29	18	2						1	1
Totals	1149	205	23+8*	1	2	98	3+5*	52	13

B = Birkenhead   B-S? = Questionable whether Birkenhead or Silver Creek
S = Silver Creek   B-W? = Questionable whether Birkenhead or Weaver Creek
W = Weaver Creek   Numbers with asterisks indicate fish which, from the appearance and
H = Harrison Rapids   condition at Harrison Trap, were believed to be Hell's Gate fish.

In Table 11 we have indicated by an asterisk those fish belonging to this supposed Hell's Gate group from which scale samples were taken. It is significant that the interpretation of the scales, which was made without reference to the notations of the field assistants at Harrison Trap, placed all of these fish in either the "Birkenhead" or the "Questionable whether Birkenhead or Weaver Creek" categories. As has been noted earlier (pages 63, 64), the upper Fraser fish have scale patterns very similar to Birkenhead fish. It would be expected, therefore, that their assignment on the basis of the criteria employed would be to these groups.

For estimating the number of fish tagged from each run in 1941, the Hell's Gate fish were first removed from consideration, both in the case of all fish tagged and those from which scale samples were taken. The remaining fish are those which presumably originated somewhere in the Harrison system. The revised data are given in Table 22. From these data the numbers of fish belonging to each run were computed from the scale readings and total fish tagged, in the same manner as in 1939 and 1940, outlined above.

TABLE 12

Numbers of Fish Tagged at Harrison Trap in 1941; Believed to Have Been Fish from Those Blockaded at Hell's Gate, and Numbers of Recoveries from this Group

	Number of Fish	Recoveries
Week Ending		
Aug. 9		
16	10	
23	4	
30		
Sept. 6		
13		
20	1	
27	3	
Oct. 4	12	2 in Weaver Creek
11	8	1 in Weaver Creek
18	9	1 in Weaver Creek 1 in Hatchery Creek 1 on shore of Harrison Bay
25	9	1 in Weaver Creek
Nov. 1	5	
8	7	
15	1	
Totals	69	7

The Silver Creek run in 1941 appears from these estimates to have been a good deal smaller in relation to the other early run groups than in 1940. This corresponds with the estimates of abundance on the spawning grounds in the two years.

It may be noted that in 1941 the number of fish in the B-W? category is very small in comparison to the number of Weaver Creek fish. From our studies of 1940 scales of known origin it would be expected that a much larger number would be questionable. The reason why the number is so small is that the Weaver Creek fish, as judged by the one-year-in-lake fish taken at Harrison Trap after October 10, so late that they could not belong to the Birkenhead group, and must therefore be Weaver Creek fish, exhibited an exceptionally large freshwater growth. The nuclear radius of these fish is so great as to distinguish practically all of them from the Birkenhead fish on this basis alone. The Birkenhead fish seemed to exhibit no difference of lacustrine growth in the different years in question.

TABLE 13

Estimated Segregation by Locality of Origin of Sockeye Tagged at Harrison Trap in 1941,
Hell's Gate Fish Being First Removed

Tagging Period	Number Tagged (1)	Scales Examined (2)	Scale Readings						Unreadable	Estimated Segregation			
			B	S	B-S?	W	B-W?	H		B	S	W	H
Week Ending													
Aug. 9	22	4	3	1						16	6		
16	95	17	14		2				1	95			
23	10	2	2							10			
30													
Sept. 6													
13	7	1	1							7			
20													
27	12	3	3							12			
Oct. 4	107	15				10		5				71	36
11	365	68				55	2	5	6			335	30
18	226	35				27		5	3			191	35
25	27	6				4	1	1				23	4
Nov. 1	33	7				1		6				5	28
8	88	18						17	1				88
15	56	11				1		9	1			6	50
22	14	3						3					14
29	18	2						1	1				18
Totals	1080	192	23	1	2	98	3	52	13	140	6	631	303

B = Birkenhead
S = Silver Creek
W = Weaver Creek
H = Harrison Rapids

B-S? = Questionable whether Birkenhead or Silver Creek
B-W? = Questionable whether Birkenhead or Weaver Creek
(1) Less numbers, given in Table 21, of Hell's Gate fish
(2) Less scales from Hell's Gate fish.
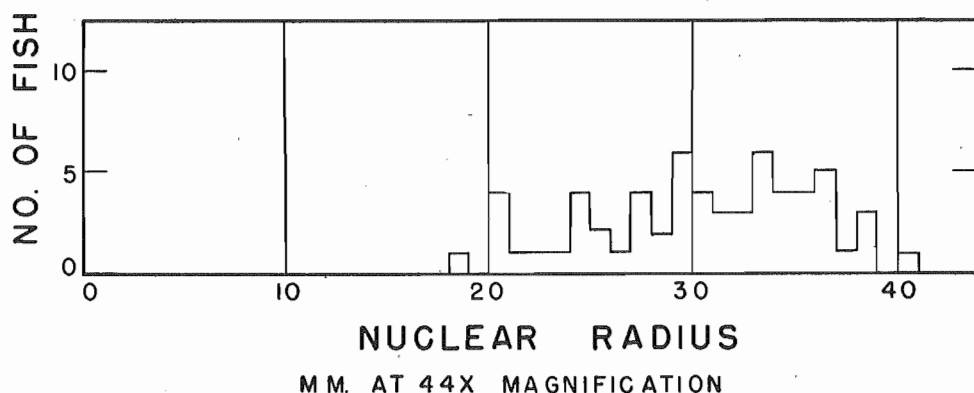
FIGURE 15. Frequency distribution of nuclear radius of scales from Weaver Creek fish taken at Harrison Trap in 1941.

It must be-emphasized that the numbers estimated for a particular week of tagging are subject to considerable sampling error. It would not be well, therefore, to place great reliance on the estimated numbers for the individual week. The total numbers for the season have a much higher degree of accuracy, however, by the nature of the addition of random errors. To determine analytically the precise degree of the error is a task the magnitude of which is not warranted by the results to be gained in this particular study.

MORTALITY DURING MIGRATION AND ON THE SPAWNING GROUNDS IN RELATION TO ENUMERATION BY MARKED MEMBERS

Importance to Enumeration by Marked Members

The estimation of a population by marked members, as has been previously stated, depends on (1) a knowledge of the number of marked members in the population and (2) an estimate of the ratio of marked members to total members in the population. If between the time of marking and the time of sampling for ratio of marked to total members there is no loss of either marked or unmarked members from the population, the number of marks put out may be taken as the number of marks in the population, and the ratio of marked to total members at the time of sampling would be also a fair estimate of this ratio at the time of marking.

If, however, there is a loss of members from the population the situation is modified. Suppose, first, that there is a certain unknown rate of loss of members from the population and that it is the same for both marked and unmarked members. In this case, the estimate, made some time after the marking, of the ratio of marked members to total members would yield the same value, except of course for random errors, as the value at the time of marking. The number of marked members in this case is, however, known only for the time of marking. The estimate of the size of the population, made from the number of marks put out and the estimated ratio of marked to total members, is correct only for the time (and place if migration occurs) of marking, and will differ from the size of the population at the time of the mark-ratio sampling. Such a situation could occur where marks are put on salmon at a considerable distance from the spawning grounds and an unknown rate of mortality, equal on both marked and unmarked fish, reduces the population enroute to the spawning grounds where the mark-ratio sampling is done. In such a case the population estimate would be correct for the locality of marking but not correct for the spawning grounds.

Again, consider the situation where between the time (and place) of marking and the time (and place) of mark-ratio sampling there is a selective removal of marked members from the population. In this case if we estimate the numbers in the population under the assumptions that the number of marked members equals the marked members liberated, and that the estimated mark-ratio is the same as at the time (or place) of sampling, the estimate will be incorrect for either the time and place of marking or the time and place of subsequent sampling, and the error will always be to overestimate the population. It is a matter, therefore, of very great importance, where salmon are tagged at a considerable distance below the spawning grounds, and the tag ratio estimate made on the spawning grounds, to determine as far as possible whether such losses occur and, if so, their magnitude.

A differential rate of mortality of marked and unmarked fish on the spawning grounds may or may not be serious. In the case of live fish counts, any such selective removal of marked fish would cause the estimated population to be too

high, just as in the case in the preceding paragraph. Where the mark-ratio esti-
mate is made from dead fish, however, the mortality rate of both marked and
unmarked fish is of necessity 100 per cent prior to sampling. So long as the
sampling is such that marked and unmarked fish have the same probability of
being recovered, a differential rate of mortality of the two groups would be of
no importance to the estimates. However, if there are associated with differential
rates of mortality differences in distribution in time or in space of marked and
unmarked members resulting in their being sampled in such a manner that the
average probability of being recovered is different for marked and unmarked
fish, the population estimates will be in error in this case also.

The investigation of the problems of mortality during migration, and of
differential mortality of marked fish both during migration and on the spawning
grounds is, thus, of fundamental importance.

Mortality En Route to the Spawning Grounds

Direct evidence

That some fish do die in the river enroute to the spawning grounds, and from
causes other than tagging, is shown by the dead fish removed from the lead of
the Harrison Trap. In each of the three years a few dead sockeye salmon were
found against the upstream side of the lead during cleaning operations, from the
very beginning of the season. In the early part of the season, in August and early
September, these fish were, of course, fish bound for the Upper Lillooet region
or to the tributaries of the upper end of Harrison Lake. During the latter part of
September they may include some Weaver Creek fish. The fish taken in August
and September were almost entirely unripe fish which had died without any dis-
charge of the sexual products. An occasional female was found from which part
or all of the eggs had been lost, but this was probably from causes other than
spawning.

No record was kept of these fish against the trap lead in 1939, but in 1940
and 1941 records were kept showing the date, sex, condition of spoilage of the
carcass (as an index of recency of death), loss of eggs, and pertinent remarks.
Seven sockeye were taken from the trap lead in 1940 prior to October 1. Dead
fish taken after October 1 are not considered because shortly after that date fish
bound for Harrison Rapids begin arriving and, since their spawning area is only
a mile or so above the trap, dead fish from that area drift down against the trap
lead after spawning.

The occurrence of only seven dead fish up to October 1 during the 1940
season may seem to be a negligible number. However, these fish represent
the mortality over only a very small part of the migration route, and only a part
of that. When it is considered that these are only a part of the fish dying in
perhaps a mile or two of a total distance of over 100 miles, it is seen that they
may possibly be indicative of a rather considerable mortality enroute to the spawn-
ing grounds.

Since during the 1941 season there were a rather large number of sockeye
which had been blocked at Hell's Gate and which dropped down the Fraser and

ascended the Harrison, it is probable that the larger number (28) of dead fish on the trap lead in 1941 compared with 1940 may be attributed to the presence of a good number of such "Hell's Gate" fish. Indeed, one of these fish had been tagged at Hell's Gate.

Two of these fish recovered dead on the trap lead in 1941 had been tagged only one day and three days earlier. Both of these fish were ones which had been badly injured by a previous escape from gill nets. This suggests a possible cause of some of the deaths, which will be investigated further below.

Another cause of some mortality in the Harrison River and in Harrison Lake is predation by seals. These animals are rather numerous in Harrison River and Lake, and even a few miles up the Lillooet River, during the season of salmon migration, and have been seen by me to catch sockeye salmon. Two of the fish recovered had been "seal bitten." The extent of mortality from such predation is unknown; it may or may not be of much importance.

Mortality among fish escaping gill nets

As noted above, a suggested cause of some losses during the migration between the commercial fishing areas and the spawning grounds is the injury which some fish sustain in passing through gill nets even though they escape them. Such fish when taken at the Harrison Trap could be recognized by the characteristic marks made by the twine of the gill nets on the anterior part of the body of the fish. These marks vary from slight abrasions of the skin to deep wounds. Gill net marks occurring on the fish tagged at Harrison Trap were recorded during each season of tagging. By examining the relative numbers of fish recovered from the gill-net-marked and non-gill-net-marked fish we may see whether the capture and escape from gill nets caused any detectable loss of fish from the population.

In Tables 14, 15 and 16 are tabulated for 1939, 1940 and 1941, respectively, the numbers of fish recovered and the number not recovered from each month's tagging from the group of fish bearing gill net marks and the group having no gill net marks. During 1941 notations were also made of those gill net injuries which were so bad that in the opinion of the tagger the fish might not live. These are indicated in Table 16 as " 'Bad' G. N. Marks".

Analysis of the seasonal totals of recoveries and non-recoveries from gill-net-marked and not-gill-net-marked fish, by computation of chi-square under the hypothesis that no difference exists between recovery rates from the two groups in a given year, yields ambiguous results. For 1941 a chi-square of 21.06 is obtained which would occur by chance less than one time in a thousand. For 1939, however, the chi-square value obtained is 1.532 a value as large as which would be expected to occur in about 21 per cent of cases by chance. In 1940 the expected values for the two groups, gill-net and non-gill-net fish, are almost exactly what would be expected under the hypothesis.

It may be observed, from the last column in each of the tables, that the percentage of gill-net-marked fish among the fish tagged markedly decreased each year as the season progressed. It is also to be seen that the rate of recovery was greater during the latter part of each season than during the early part. This relationship of decreasing fraction of net-marked fish with increasing recovery

TABLE 14

Recoveries on and Near the Spawning Grounds
of Fish Tagged at Harrison Trap, 1939,
According to Injury by Gill Nets

Month of Tagging	G. N. Marked		Not G. N. Marked		All Fish Tagged		
	Recovered	Not Recovered	Recovered	Not Recovered	Recovered	Not Recovered	% G. N. Marked
August	3	24	18	114	21	138	17.0
September	1	32	7	173	8	205	15.5
October*	1	37	26	308	27	345	10.3
Totals	5	93	51	595	56	688	

* Includes first four days of November.

TABLE 15

Recoveries on and Near the Spawning Grounds
of Fish Tagged at Harrison Trap, 1940,
According to Injury by Gill Nets

Month of Tagging	G. N. Marked		Not G. N. Marked		All Fish Tagged		
	Recovered	Not Recovered	Recovered	Not Recovered	Recovered	Not Recovered	% G. N. Marked
August	0	8	3	29	3	37	20.0
September	1	12	3	71	4	83	15.0
October	2	6	19	126	21	132	5.2
Totals	3	26	25	226	28	252	

rate may be expected to result in an apparent low rate of recovery of net-marked fish in the seasonal totals. In order to eliminate this effect, we have considered separately the data for each month of each season. The recoveries and non-recoveries from the two groups, net-marked and not-net-marked, form a 2 x 2 table for each month. The numbers in some cells are so very small the chi-square test cannot be employed in most cases. The chi-square distribution was utilized to compute the probability of obtaining at least as few recoveries as observed among the gill-net-marked fish under the hypothesis of independence between gill net injury and recovery rate for October 1941 only, when the numbers involved are all large enough to make this application valid. In all other cases the required probability under this hypothesis was computed by the exact treatment of Yates, which is described by Kendall (1944) page 303 et seq. and by Buchanan-Wollaston (1945). The probability values are tabulated in Table 17. From these values it may be seen that the recoveries from the two groups in each month do not deviate appreciably from expectations.

The lowest value in Table 28, occurring in August 1941, corresponds to a period when of 49 gill-net-marked fish, 26 were in the "bad" category. The probability value, under a hypothesis of no effect of gill net injury on recovery rate, for "bad" gill-net-marked alone, compared with uninjured is .216. For the gill-net-marked other than "bad," compared with uninjured, a probability of .253 is obtained.

There is nothing in these data to indicate that injury by gill nets reduces the chances of recovery of the tagged fish. It must be pointed out that this, like other negative results of statistical tests of significance, is a "scotch verdict." The possibility of injury by gill nets is not disproven, but if such exists the data at hand are insufficient to demonstrate it.

Evidence from tagging experiments

The data from successive tagging of the same run along its migration path can be employed to estimate the magnitude of loss of tagged fish during migration. Where fish have been tagged on or very near to the spawning grounds, the percentage recovered of this group of tagged fish among the dead fish samples may be taken as an estimate of the percentage recovery of fish dying on the spawning grounds. If we may assume that this same percentage has been recovered among the same samples from those tagged fish which reached the spawning grounds after tagging lower down the river system, we have a means of estimating the number of tagged fish from the latter experiments which probably reached the spawning grounds and, thus, by subtraction, of those which died or were otherwise lost enroute.

BIRKENHEAD EXPERIMENTS

The data for the 1940 and 1941 experiments relating to the Birkenhead run are presented in Table 18. As is shown therein, some twenty per cent of the fish tagged at our trap in the Birkenhead were recovered among the dead, spawned-out fish taken as samples on the spawning grounds. Among the same samples were found numbers of tagged fish from Skookumchuck tagging, as indicated. Assum-

TABLE 16

Recoveries on and Near the Spawning Grounds
of Fish Tagged at Harrison Trap, 1941,
According to Injury by Gill Nets

Month of Tagging	All G. N. Marks		"Bad" G. N. Marks		Uninjured		All Fish Tagged		% G. N. Marked
	Recovered	Not Recovered	Recovered	Not Recovered	Recovered	Not Recovered	Recovered	Not Recovered	
August	0	49	0	26*	6	86	6	135	34.8
September	1	8	—	—	6	28	7	36	20.9
October	27	48	0	2	289	412	316	460	9.7
November	0	14	—	—	5	170	5	184	7.4
Totals	28	119	0	28	306	696	334	815	

* Includes two fish recovered against the lead of the trap, one day and three days after tagging, green and unspawned.

ing that the same percentage of the Skookumchuck tagged fish actually present in the Birkenhead River was recovered among these dead fish samples as was recovered of the Birkenhead tagged fish, we have computed the number of Skookumchuck tagged fish estimated to be present in the Birkenhead River in each year. These come to roughly 75% of the tagged fish liberated at the Skookumchuck in each year, leaving about 25% to be accounted for otherwise than by spawners in the Birkenhead.

This discrepancy between the estimated number of Skookumchuck tagged fish in the Birkenhead and the number actually tagged at Skookumchuck may be attributed to three possible causes: (1) Loss of fish by natural mortality or capture enroute (2) Spawning in other streams than the Birkenhead, and (3) Mortality of tagged fish due to tagging.

As we have shown above, there is indeed some loss by natural mortality among adult sockeye salmon migrants, although we have no means of estimating its magnitude in this case. A small part of the "missing" tagged fish are also represented by captures enroute by Indian fishermen. From the reported size of the Indian catch and the tag-ratio estimated from Birkenhead samples, it may be estimated that 20 to 25 tags might have been taken thus, and perhaps more if the gill nets employed by the Indians fish selectively for tagged fish. In 1940, 18 such tags were actually returned to us by their captors, although no reward or other incentive was offered.

Spawners in other tributaries also may account for a good part of the fish passing Skookumchuck but not spawning in the Birkenhead. As we have described in detail earlier, there are a number of tributaries to the Lillooet above the Skookumchuck which are frequented by runs of sockeye salmon. It is not generally believed that these runs amount in total to 25% of those passing Skookumchuck, but they probably do amount to at least half of that, and perhaps more. Thus, the discrepancy between the number of tags put out at the Skookumchuck and those accounted for in the Birkenhead is explainable in large part by spawning in the other streams.

TABLE 17

Probability for Each Month of Obtaining the Observed Number or Less of Recoveries from the Gill Net Marked Fish by Chance if There Were No Effect of Gill Net Markings on Recovery Rate

	1939	1940	1941
August	.272	.502	.073**
September	.642	.897	.543
October	.201*	.920	.371
November	—	—	.678

* Includes first four days in November.
** With "Bad" G. N. subtracted, P = .253.
For "Bad" G. N. alone, P = .216.

TABLE 18

Comparison of Returns from Tagging at Different Points
Along the Migration Path, Birkenhead Run

	1940	1941
Number tagged at Birkenhead River	439	2351
Recovered in dead fish samples at Birkenhead	92	528
Per cent recovered	20.96%	22.46%
Number tagged at Skookumchuck	2146	2102
Recovered in dead fish samples at Birkenhead	331	357
Calculated number of Skookumchuck tagged fish in Birkenhead on the assumption that the same percentage of Skookumchuck tagged was was recovered as of Birkenhead tagged	1579	1590
Per cent of fish tagged at Skookumchuck thus accounted for on the Birkenhead spawning grounds	73.6%	75.6%
Number tagged at Harrison Trap assigned to "Birkenhead" group (Tables 10 and 13)	62	140
Recovered in dead fish samples at Birkenhead	3	6
Calculated number of Harrison tagged fish in Birkenhead on assumption that the same percentage of Harrison tagged fish was recovered as of Birkenhead tagged	14.3	26.7
Per cent of fish tagged at Harrison Trap thus accounted for on the Birkenhead spawning grounds	23.1%	19.1%

Since causes (1) and (2) may account for a good share of the 25% discrepancy between the number of tagged fish liberated at Skookumchuck and the number of such fish accounted for in the Birkenhead, it appears that mortality of tagged fish due to tagging cannot be large in this case. It will lie somewhere between 0% and 20%, depending on the sizes of the runs to the various streams other than the Birkenhead. It is our opinion that it will lie closer to the former figure than the latter.

It should be pointed out that these calculations are rough, since the assumption on which they are made is not exactly satisfied because there were some differences in distribution of Birkenhead and Skookumchuck tags and in the evenness of sampling among different strata of the population. A more careful analysis of the 1940 data taking into account as far as practicable these differentials led to a value of 89.4% of the Skookumchuck population accounted for by spawners in the Birkenhead in that year. This is not an appropriate place to go into the bases of this calculation; these will appear subsequently when a detailed analysis of the estimated populations will be presented. The assumption made in the computations of Table 18 is sufficient for the present purpose, which is to investigate the data to determine the degree of discrepancy between tags liberated at the Skookumchuck and accounted for in the Birkenhead. Since this discrepancy has an upper limit of about 25%, and a good part of it can be accounted for by

spawners in other streams, it seems that the mortality of tagged fish between Skookumchuck and Birkenhead is not great, but some may exist.

The same is not true of fish tagged at Harrison. Of the fish tagged at the Harrison Trap assigned to the "Birkenhead" group, only about 20% are accounted for in the Birkenhead River. The only known spawning area of any members of this group below the Skookumchuck is Douglas Creek, the population of which was of necessity included in the "Birkenhead" group at Harrison Trap (p. 67). This Douglas Creek population is very small, and the tagged fish recovered in this stream are few in number (Tables 5 to 7). We are faced with a discrepancy of about 80% between the "Birkenhead" fish passing Harrison Trap and those accounted for in the Birkenhead River. If the Birkenhead spawners amount to 75% of all the fish passing the Skookumchuck, this would mean that of the Harrison tagged fish about .20/.75, or 33%, probably reached the Skookumchuck. This leaves 67% to be accounted for below that point.

In 1939, 23 sockeye of the estimated 256 which had been tagged at the Harrison Trap were recovered among the dead fish samples on the Birkenhead spawning grounds. In this year we had no adequate experiments whereby to estimate the per cent recovery of dead fish, but if we were to presume it to be about 22 per cent as in 1940 and 1941, the 23 recoveries would represent about 104 Harrison tagged sockeye present among the Birkenhead fish. This is 40.7 per cent of the 256 liberated, or about twice the value for 1940 or 1941. It is evident that either (1) a larger share of the Birkenhead fish tagged at Harrison reached the Birkenhead in 1939 or (2) the 22 per cent estimate of dead fish recovered in 1939 is far too low. We recovered 4106 carcasses in 1939. From our inadequate experiments of that year we arrived at a population estimate of 15,300 for the whole population in the Birkenhead River. This would correspond to an average recovery as dead fish of 27 per cent. On this basis, the 23 Harrison-tagged recoveries would correspond to 85 fish on the spawning grounds, or 33 per cent of the 256 liberated. Although these estimates are not very reliable, there seems some reason to believe that perhaps the per cent of Harrison-tagged fish accounted for was actually higher in 1939 than in the other two years. Even the higher value of 40.7% accounted for, however, leaves a very large part of the tagged fish unaccounted for in that year also.

A small part of the missing tags is accounted for by retrograde migrants from Harrison Trap captured by fishermen in the Fraser River (Tables 5 to 7). Since an intensive campaign for the return of recovered tags was conducted there in connection with other tagging experiments at the mouth of the Fraser, it is quite likely that the recoveries listed under "Fraser River" in the tables include most of the Harrison tags recaptured in the Fraser River. It is evident that these constitute only a small fraction of the tags unaccounted for.

There seem to be only three possible alternatives: (1) There is a large body of sockeye spawning in some unknown place or places in the Harrison system, below the Skookumchuck, about twice as large as the known Upper Lillooet populations (2) There is a very heavy mortality of migrants, both tagged and untagged, between the mouth of the Harrison River and the Skookumchuck or (3) There is a heavy differential mortality of tagged fish between these two points.

The first of these hypotheses seems definitely untenable. Fisheries officers and residents have been over this watershed for many years and it is unlikely that so large a body of spawners would pass unnoticed. Field observers of the I.P.S.F.C. have patrolled most of the area rather carefully and have seen no signs of such a population. It is very unlikely that such an undiscovered population exists. The second hypothesis may be partly true. We have indicated above that there is definitely known to be some mortality of untagged fish in the Harrison and its magnitude may be larger than is commonly supposed. The third hypothesis is also undoubtedly partly true. As has been mentioned earlier, it has been shown at Cultus Lake (Howard 1948) that some, although slight, adverse effects of handling and tagging the fish were evident even where no very difficult migration was in prospect.

It must be concluded that the serious loss of tagged fish between the Harrison Trap and the Birkenhead River is probably the combined result of natural mortality during migration and of a differential mortality of tagged fish, the relative importance of the two not being susceptible of determination from the existing data. This loss is so great, whichever the cause, that the measurement of the size of the Upper Lillooet spawning populations by means of tagging at the mouth of the Harrison is hopeless. It is barely possible, of course, that the greater part of the loss is due to natural causes, in which case this offers us a means of estimating it, and of thus estimating the Upper Lillooet population, plus that of Douglas Creek, passing the mouth of the Harrison River as about three to four times the number of fish that reach the spawning grounds. This seems to me to be a rather remote possibility, however.

WEAVER CREEK EXPERIMENTS

In Table 19 are tabulated the data pertaining to the tagging experiments conducted on the Weaver Creek run in 1940 and 1941. The recovery among dead fish samples of fish tagged at the fence at the mouth of the stream was 44.6% and 54.8% in 1940 and 1941 respectively. Assuming that these same percentages were recovered, among the same samples of dead fish, of the fish tagged at Harrison Trap reaching the Weaver Creek spawning areas, we have calculated the number of Harrison-tagged fish probably present on the Weaver Creek spawning grounds. It will be observed that the fraction of the tags liberated at Harrison Trap assigned to the "Weaver Creek" group which are thus accounted for on the Weaver Creek spawning grounds is quite different in the two years, and that in 1940 in particular a large fraction of the tags remains unaccounted for.

In 1940 the Harrison Trap apparently operated effectively on the first part of the run only, and not very effectively at that, since so few fish were captured. This is illustrated by the ratio of Harrison-tagged to total fish among the dead fish samples in successive weeks of recovery at Weaver Creek, Table 20. The heavy concentration of tags near the beginning of the season on the spawning grounds is the more remarkable because there is, as we will show subsequently, a good deal of mixing of fish between passage of Harrison Trap and death on the spawning grounds at Weaver Creek. It seems possible, therefore, that the low average recovery rate of Harrison tags might be the result of a concentration

of the few Harrison tags in the early part of the run almost exclusively, coupled with a low recovery rate of fish on the spawning grounds during the early part of the season compared with the later part. The evidence available does not, however, lend any support to this idea. As will be shown later (Table 67) the recovery rate of dead fish on the Weaver Creek spawning grounds, as measured by fish tagged at the mouth of Weaver Creek, was not, apparently, lower during the early part of the run.

A further possibility is that the early part of the run failed to reach the spawning grounds. In 1940, Weaver Creek was dry at its mouth until October 11, when heavy rains furnished enough water to allow fish to ascend, and meanwhile numbers of fish assembled in Morris Lake. Some of these may have perished, and if this early part of the run bore a very large fraction of all the tags put on at Harrison Trap, this could account for many or all of those not accounted for in Weaver Creek.

A third possibility, of course, is that a good share of the tagged fish perished between the Harrison Trap and Weaver Creek as the result of the tagging operation. If so, and this is something we cannot determine of course, this was peculiar to that year alone, since the 1941 data show a very large part of the fish tagged at Harrison Trap to be accounted for. In the light of the results of recoveries from taggings at Skookumchuck during two different years being so similar to each other, such wide variations between years is not to be expected under ordinary circumstances where the accessibility of the stream and other physical factors are essentially the same from year to year.

TABLE 19

Comparison of Returns from Tagging at Different Points
Along the Migration Path, Weaver Creek Run

	1940	1941
Number marked fish liberated at Weaver Creek	1689	743
Recovered in dead fish samples at Weaver Creek	754	407
Per cent recovered	44.6%	54.8%
Number tagged at Harrison Trap assigned to "Weaver Creek" group (Tables 10 and 13)	138	631
Recovered in dead fish samples at Weaver Creek	24	264
Calculated number of Harrison-tagged fish in Weaver Creek on the assumption that the same percentage of Harrison tagged fish was recovered as of Weaver Creek tagged	53.8	482
Per cent of Harrison tagged fish thus accounted for on the Weaver Creek spawning grounds	39.0%	76.4%

TABLE 20

Harrison Tag Ratios Among Weaver Creek Dead Fish
Samples, by Week of Recovery, 1940

Recovery Period		Total Fish in Sample	Harrison Tagged	Tag Ratio	Fish Per Tag
Week Ending					
October	19	120	3	.0250	40.0
	26	1126	8	.0071	140.8
November	2	2230	7	.0031	318.6
	9	3376	5	.0015	675.2
	16	482	1		
	23	226	0	.0011	938.0
	30	216	0		
December	7	40	0		

In the above consideration of the 1940 data, we have neglected the possibility that the missing tagged fish might have gone to Hatchery Creek, because that seems impossible from direct observation of the fish in that stream. As noted before, the "Weaver Creek" group at Harrison Trap includes fish bound for Hatchery Creek, since the scale markings and season of migration of the two are indistinguishable. However, this small stream was visited regularly, and if any large number of tagged fish were present, they would have been observed. Actually, 204 dead fish were recovered there including only one tagged; the total run might have been as high as 1000 fish at the outside, which would account for perhaps 5 of the missing tags.

Apparently, we are unable to answer satisfactorily the question as to whether the missing tags are the result of mortality enroute to the spawning grounds of an early part of the run, or are a statistical aberration due to faulty sampling techniques. Whatever the cause, however, we can certainly conclude that where only a small part of the run is tagged and the tags are very unevenly distributed over the entire run, there is a good chance that the experiment will come up with a very wrong answer as to the size of the run. In the present case, an estimate of Weaver Creek spawners based on the Harrison tagging and Weaver Creek recoveries would have been almost three times too high in 1940.

That such a large share of missing tags is not to be expected if the run is more adequately and evenly sampled when tagging, is shown by the Weaver Creek data of 1941. As may be seen from Table 21, a larger share of the Weaver Creek fish were captured at Harrison than in 1940, and the tags were much more nearly evenly distributed over the run. This is a more "normal" experiment. In this case, performing the calculations as before, we find that 76.4% of the tags liberated at Harrison Trap are accounted for in Weaver Creek. Another 8 tags or so may be accounted for in Little East Creek across Morris Lake (4 were recovered

among 45 dead fish and recovery was perhaps about 50%, as in Weaver Creek), 10 among a few fish in the stretch between Weaver Creek fence and the lake (we recovered 5 among 113 fish) and 8 in Hatchery Creek (where 4 were recovered among 83 fish). These estimates for other streams are probably minimal since the recovery rate in Little East Creek and Hatchery Creek was probably not as high as in Weaver Creek, because these streams had no fence to prevent dead fish from drifting away into the lake below. If, however, we use these numbers we find that about 508, or 80.5%, is our best estimate of the 631 tags assigned in Table 13 to the Weaver Creek group which are accounted for on the spawning grounds. This, of course, differs significantly from 100%, indicating that there are yet fish unaccounted for which can reasonably be concluded to be mortalities between Harrison Trap and the spawning grounds. These, however, are few enough so that we still would have a reasonably close estimate of the run from the data provided by the tagging at Harrison Trap and recovery on the Weaver Creek spawning grounds. In this particular situation, this is of limited practical usefulness, since the Weaver Creek run can more easily be evaluated by tagging at the mouth of the stream itself. In a similar situation where more than one stream is involved, as for instance if the Hatchery Creek run were of large size also, this sort of tagging might be applied to evaluate both runs simultaneously.

TABLE 21

Harrison Tag Ratios Among Weaver Creek Dead Fish
Samples, by Week of Recovery, 1941

Recovery Period		Total Fish in Sample	Harrison Tagged	Fish per Tag
Week Ending				
October	18			
(and before)		29	0	—
	25	1488	84	17.7
November	1	2268	149	15.3
	8	657	22	29.8
	15	412	6	68.6
	22	116	3	38.6

Mortality on the Spawning Grounds

As has been mentioned before, Howard's (1948) analysis of the tagging experiments conducted at Cultus Lake in 1938 and 1939, employing a high tag ratio of known value on populations of known size, revealed a small differential mortality of the tagged fish. It was found that in the area immediately above the fence, where the tagging was done, the tags were more frequent than one would expect, while in the lake proper they were slightly less frequent than expected, from which it may be inferred that the handling and tagging caused some fish to die soon after being released. Except for the recoveries immediately above the fence, however, the effect, while statistically significant, was not suf-

ficiently great to affect the estimate of the size of the population from a practical standpoint, and could only be detected by refined statistical procedures.

Comparison of tag-ratios from live counts with the estimated population tag ratios

Our data are not of a nature to permit detection of differential mortality of tagged and untagged fish on the spawning grounds unless such differential mortality be quite large. The only data bearing directly on the problem are the counts of the tag ratios of live fish on the spawning grounds as compared with the tag ratios among the fish after death.

If the tagged fish among the population of fish on the redds were dying at a faster rate than the untagged, the average tag ratio among the live fish would be reduced thereby, and would be lower than the true tag ratio for the population. The tag ratio among the dead fish, however, is a fair estimate of the true tag ratio regardless of such differential mortality (presuming of course that the sampling is such that all dead fish have an equal chance of inclusion in the samples, or any differential sampling of different groups of dead fish is suitably taken into account).

It will be shown in a later chapter (Tables 52, 53, 66, and 71) that the tag ratios among the live fish counted on the redds during the 1940 season, both in the Birkenhead River and in Weaver Creek, both for taggings in the respective streams and for taggings at more remote places, were such that they agreed with the values expected from analysis of the recoveries of dead fish. This indicates that, within the errors of estimate corresponding to the tag ratio values and recovery rates in these experiments, any differential mortality of tagged and untagged fish on the spawning grounds was negligible. It will also be shown in the last chapter that in most cases the live counts yield population estimates very similar to those arrived at from dead fish samples for both 1940 and 1941, thus indicating little or no premature mortality of tagged fish on the spawning grounds.

Fin clipping versus tagging

As noted previously when describing methods of study, in 1940 we marked part of the run at Weaver Creek by tagging and another part by clipping a ventral fin, the two kinds of marks being maintained in a 1:2 ratio throughout the season. Since the clipping is a very rapid operation it was believed that any unfavorable effect of handling or keeping the fish out of water incident to tagging might be discovered by comparing the recoveries from the two groups.

Now if the recoveries of the two types of marks return in the same ratio (1:2) as the liberations, from all subdivisions of the Weaver Creek population, both with respect to time period of recovery and area of the stream from which recovery is made, we should be justified in concluding there is no difference between them as far as influence on mortality or migration within the stream is concerned.

In Table 22 these recoveries, subdivided by time of recovery, have been tabulated and compared with the recoveries which would be expected on the hypothesis of an even 1:2 ratio. It is evident that the data agree with the hypo-

TABLE 22

Comparison of Recoveries of Tagged and Fin-clipped Sockeye, Segregated
by Periods of Recovery, With the Expected Numbers Under
a 1:2 Hypothesis. Weaver Creek, 1940.

Date of Recovery	Tags	Clips	Total	Expected Tags	Expected Clips	Chi-Square
(Week ending)						
October 19	2	1	3	1.00	2.00	1.5000
26	13	22	35	11.67	23.33	.2273
November 2	26	53	79	26.33	52.67	.0061
9	140	245	385	128.33	256.67	1.5917
16	20	65	85	28.33	56.67	3.6737
23	26	57	83	27.67	55.33	.1511
30	33	39	72	24.00	48.00	5.0625
December 7	5	7	12	4.00	8.00	.3750
Total						12.5874
Pooled	265	489	754	251.33	502.67	1.1152

	d.f.	Chi-square	P
Total	8	12.5874	.13
Pooled	1	1.1152	.29
Interaction	7	11.4722	.12

TABLE 23

Comparison of Recoveries of Tagged and Fin-clipped Sockeye, Segregated
by Areas of Recovery, With the Expected Numbers Under
a 1:2 Hypothesis, Weaver Creek, 1940.

Area	Tags	Clips	Total	Expected Tags	Expected Clips	Chi-Square
Fence	117	208	325	108.33	216.67	1.0407
Area I	76	143	219	73.00	146.00	.1848
Area II	29	62	91	30.33	60.67	.0874
Area III	17	38	55	18.33	36.67	.1447
Area IV & V	26	38	64	21.33	42.67	1.5335
Total						2.9911
Pooled	265	489	754	251.33	502.67	1.1152

	d.f.	Chi-square	P
Total	5	2.9911	.70
Pooled	1	1.1152	.29
Interaction	4	1.8759	.76

thesis. Similar agreement with the hypothesis is shown in Table 23, where the recoveries are subdivided by the area of the stream in which the fish were recovered as dead.

These data indicate that the tagged fish and fin-clipped fish remained distributed throughout the stream and throughout the various recovery periods in the same ratio in which liberated, and that there is no evidence that the two groups suffered differential mortality, or behaved differently with regard to migration within the stream. The greater handling involved in tagging the fish than in fin clipping them resulted in no additional unfavorable effects so far as we can detect.

NATURE OF THE SPAWNING MIGRATION. ANALYSIS OF DATA FROM RECOVERY OF TAGGED FISH

The application of the tagging method for enumerating salmon populations is to a considerable degree dependent upon the nature of the spawning migration, in particular upon the degree of mixing of the fish in the population between the tagging and the sampling for tag-ratios. In the sense in which it is used here "migration" includes all the changes of location in space and time of the fish between passage of the tagging point and arrival at the place where samples are drawn for tag-ratios. Thus, in this special sense, what happens to the carcasses of dead, spawned-out salmon before sampling is "migration". It is perhaps a poor term, but is employed for lack of a better.

As has been previously shown, if the population mixes up completely between tagging and subsequent samplings, like the balls in an urn experiment, it is unimportant how the individual fish are drawn for tagging or how they are drawn in the later sampling, since any sample will, in such a case, be representative as regards tag-ratio. In such a case the formulae of the "simple case" (p. 5 et seq.) may be applied directly to the pooled data of all samples with no further consideration. Moreover, in such a case we would expect to find no correlation between date of tagging and date of recovery of the recovered tagged fish. Conversely, if there were no mixing up of the fish in the population, so that the fish appeared in the samples in the same order that they were tagged, we would expect to find a very high correlation between date of tagging and date of recovery. By examining the correlations between date of tagging and date of recovery of the recovered tagged fish we may, then, form an idea of the degree of mixing which takes place during the spawning migration.

The basic data in this section are presented in a series of figures wherein are plotted, with dates of tagging as abscissae and dates of recovery as ordinates, the frequency of occurrence of recoveries characterized by a given date of tagging and a given date of recovery (See Figure 18 as an example). An oblique line across the figure is the locus of points of which the abscissae are equal to the ordinates. Distance vertically above this line represents time elapsed between tagging and recovery. On each of these charts has also been entered certain constants computed for the distribution: n, the number of recoveries represented; d, the average days between date of tagging and date of recovery of all recoveries, measuring average speed of migration; r, the product moment correlation coefficient, measuring the amount of mixing between tagging and recovery; b, the coefficient of mean square linear regression of date of recovery on date of tagging, which may be taken as an indication of the change in speed of migration (This will be discussed further below).

Birkenhead Population

Harrison tagging

As may be seen from Table 24, wherein are recapitulated data from the various experiments, the number of fish recovered from the Harrison taggings were too few to employ in a study of mixing during migration, with perhaps the

TABLE 24

Recapitulation of Average Duration of Migration of Tagged Fish, and of Correlation and Regression Coefficients of Date of Recovery on Date of Tagging

	POINT OF TAGGING										
Point of recovery and year	*Harrison Trap*			*Skookumchuck*				*Birkenhead Trap*			
	d	*r*	*n*	*d*	*r*	*b*	*n*	*d*	*r*	*b*	*n*
Skookumchuck											
1941	22.5		2								
Birkenhead Trap (live fish)											
1939	18		1								
1940				18.3	.80	1.14	29				
1941	37		1	16.7	.72	.70	113				
Birkenhead (dead fish) Fresh dead only											
1940	47		1	30.9	.62	.66	206	12.0	.71	.61	55
1941	47.0		3	30.0	.48	.58	254	12.2	.65	.66	383 (1)
								13.2	.66	.65	289 (2)
Birkenhead (dead fish) All recoveries								9.0	.68	.59	94 (3)
1939	41.6	.40	14					16.3			31
1940	47		1	32.1	.47	.53	299	13.7	.68	.85	83
1941	46.7		6	31.9	.52	.86	343	15.1	.55	.80	520

d = average days from tagging to recovery.
r = product moment correlation of date of tagging with date of recovery.
b = regression coefficient of mean square linear regression of date of recovery on date of tagging.
n = number of recoveries.

(1) = all recoveries.
(2) = large fish only.
(3) = jacks only.

single exception of 1939 when 14 recoveries were made from dead fish on the spawning grounds of the Birkenhead, yielding a correlation coefficient of 0.40 which is not significant at the 5% level. The individual recoveries are plotted in Figure 16. In this same year, in addition, 10 fish tagged at Harrison were recovered from live fish on the spawning grounds, not at any particularly defined point in the migration, however. These, too, are plotted in Figure 16, and show a correlation of 0.75 which is significant at the 5% level but not at the 1% level.

These meagre data are inconclusive as to whether the fish mix completely between the Harrison Trap and the Birkenhead spawning grounds but suggest that considerable mixing does occur. Further study of this point is not profitable in view of the earlier conclusions regarding the uselessness of the Harrison taggings for enumerating the Birkenhead populations (p. 88).

Skookumchuck tagging

RECAPTURES AT BIRKENHEAD TRAP

Tagging at the Skookumchuck and recovery at the trap in the Birkenhead tends to measure what takes place between passage of the Skookumchuck and arrival on the spawning grounds, before the effect of mixing on the spawning grounds due to differential time of death and differential delay in recovery of carcasses is effective. The recoveries of this sort in 1940 and 1941 are plotted in Figures 17 and 18, respectively.

As may be seen from these figures and from the recapitulations in Table 24, the correlation between date of tagging and date of capture in the trap was rather high and nearly the same in both years, indicating that the mixing of the fish between these two points was not very great.

As remarked above, the regression coefficients, "b", have been computed for these distributions to indicate the degree to which the time between tagging and recovery tends to decrease as the season progresses. Such a tendency among sockeye salmon was exhibited by Thompson (1945) in his study of the 1942 Adams River run. He found that the median number of days between tagging at Hell's Gate and recovery at Adams River decreased as the season progressed, as also did the first and ninth deciles and the fastest recoveries. His data were for all sorts of recoveries lumped together, from live fish newly arrived at the river, from freshly dead fish, and from old carcasses. He could not distinguish between delays in recovery and rates of movement, hence he placed special emphasis on the quick recoveries presumably as being indicative of the rate of movement. It was found that "the time required, including delays in movement and in recovery, lessened in about the same proportion for quick and slow recoveries as the season progressed".

The regression coefficient should measure a tendency of migration speed to change with time, and is simpler to compute. If there is no average change, the regression coefficient will be 1.00. A decrease in migration speed during the season will result in a larger coefficient, while an increase in speed with time will result in a smaller coefficient. The 29 recoveries of 1940 show no tendency for migration speed to decrease with time; a "b" of 1.14 actually would indicate
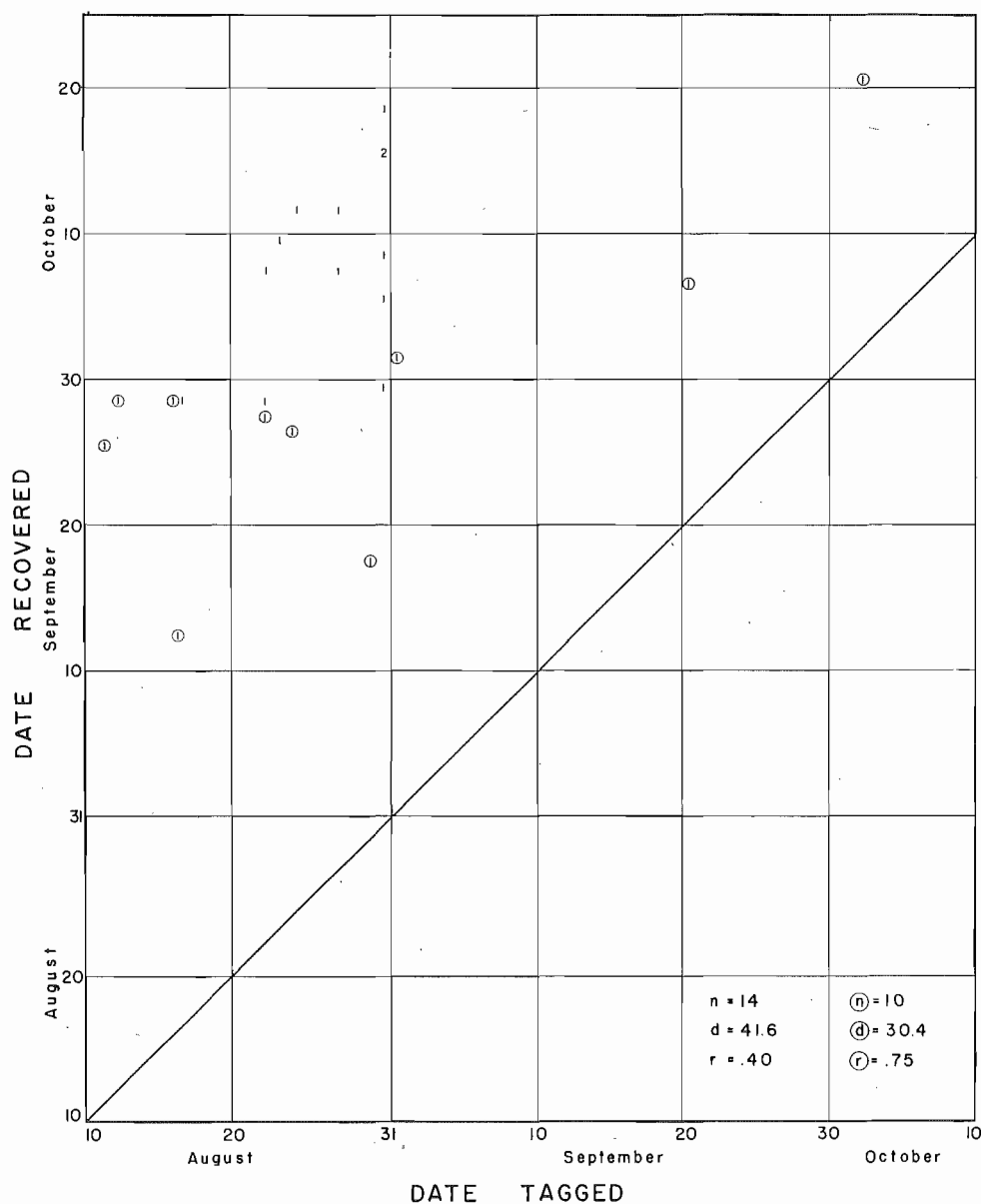
FIGURE 16. Recoveries by dates of tagging and recovery of fish tagged at Harrison Trap and recovered on the Birkenhead spawning grounds as dead fish (plain numerals) and as live fish caught in the trap, in seining operations, or by Indian fishermen (circled numerals), 1939.

an increase except that the data are too few for the difference between this value and 1.00 to be significant. In 1941 when 113 recoveries were involved the coefficient is definitely less than one, while at the same time the value of "r" is about the same as in the previous season. The average speed of migration did increase as the season progressed. In this case delay in recovery can be involved only to a very limited degree since these data are for live fish captured in the Birkenhead trap.

In Table 24, it may be noted that all values of "b", with the single exception noted above, are less than one, indicating that there is in all cases a general tendency for the time between tagging and recovery to decrease as the season progresses. This is to some degree a consequence and accompanying phenomenon of mixing of the fish between tagging and recovery. The fish as tagged occur in an ordered sequence. Mixing, i.e. change in this sequence when the fish are recovered, will usually involve fish being recovered at the same time with or before fish earlier in the tagging sequence, resulting in a decreased lapsed time between tagging and recovery of fish tagged later as compared with fish tagged earlier. In particular, if mixing were absolutely complete so that there were no correlation between date of tagging and date of recovery, the expected value of "b" would be zero.

TABLE 25

Average Days Between Tagging and Recovery of Fish Tagged at Skookumchuck and Recaptured Alive at Birkenhead Trap, 1940

	n	d
Males	23	19.0
Females	6	15.5
Total	29	18.3

$n =$ number of recoveries
$d =$ average days from tagging to recovery

TABLE 26

Average Days Between Tagging and Recovery of Fish Tagged at Skookumchuck and Recaptured Alive at Birkenhead Trap, 1941

	n	d
Males	19	17.6
Females	53	16.6
Total large fish	72	16.9
Jacks	41*	16.3
Total	113	16.7

* includes 6 gilled in fence
$n =$ number of recoveries
$d =$ average days between tagging and recovery

FIGURE 17. Recoveries by dates of tagging and recovery of fish tagged at Skookumchuck and recovered as live fish captured in the Birkenhead trap, 1940.

The data in Figure 17 include both males and females, but no jacks, while those in Figure 18 include both sexes of large fish and a number of jacks in addition. In order to learn whether any marked differences in rate of migration between sex groups is evident, the average elapsed times were computed for each sex and size category and listed in Tables 25 and 26. Where the number of cases involved is enough to give a reliable average, there is no evidence of any appreciable differences in speed of migration, although the females and jacks had a slightly higher apparent speed of migration than the large males.

RECOVERIES AMONG DEAD FISH

In addition to the mixing during the journey to the spawning area, mixing may occur among the fish on the spawning grounds as a result of differential times of death and, in addition, some mixing may occur due to differential delay in recovering the tags after the fish have died. The degree of mixing which occurs, on the average, as a result of all these factors under the recovery conditions obtaining in the Birkenhead may be judged from the recoveries from all the dead fish considered together, both fresh dead and older carcasses. The factor of delay in recovery after death is doubtless subject to greater variations from year to year, as a result of vagaries in weather and stream flow, than is that due to time of death of the fish. If recoveries from fresh dead fish alone are considered, the delay factor is eliminated to a large degree and we deal only with time elapsed between tagging and death. For this reason we have treated separately the data for "fresh dead only" and "all recoveries" in the following analyses.

In Figure 21 are recorded all recoveries on the spawning grounds for the 1940 experiment and similar data for 1941 are tabulated in Figure 22. The corresponding data for recoveries from fresh dead fish only are given in Figures 19 and 20. The statistics computed from these distributions are recapitulated in the appropriate columns of Table 24.

Correlations of .62 and .48 for the fresh dead fish indicate that although there is some mixing between tagging and death, it is by no means complete.

The average speed of migration is similar in the two years when all fresh dead recoveries are considered. In Tables 27 and 28 these data are broken down by sex and size categories from which it may be seen that the average time between tagging and recovery is practically the same for both sexes of large fish and in both years. The jacks seem to have a bit shorter elapsed time between tagging and recovery than the large fish.

When the recoveries from the dead other than fresh are added to the recoveries from fresh dead fish, the results are appreciably the same as before. The average time between tagging and recovery increases but remains about the same for each of the two years. The values of "r" for the two years are much the same and, while somewhat lower on the average, are at about the same level as for fresh dead fish only, indicating that the adding of the delayed recoveries to the recoveries soon after death only slightly increases the total mixing effect.

From Table 27 it may be seen that the average addition to the elapsed time due to delay in recovery of delayed recoveries, as judged by the difference between apparent migration speeds of fresh dead and dead other than fresh, was about
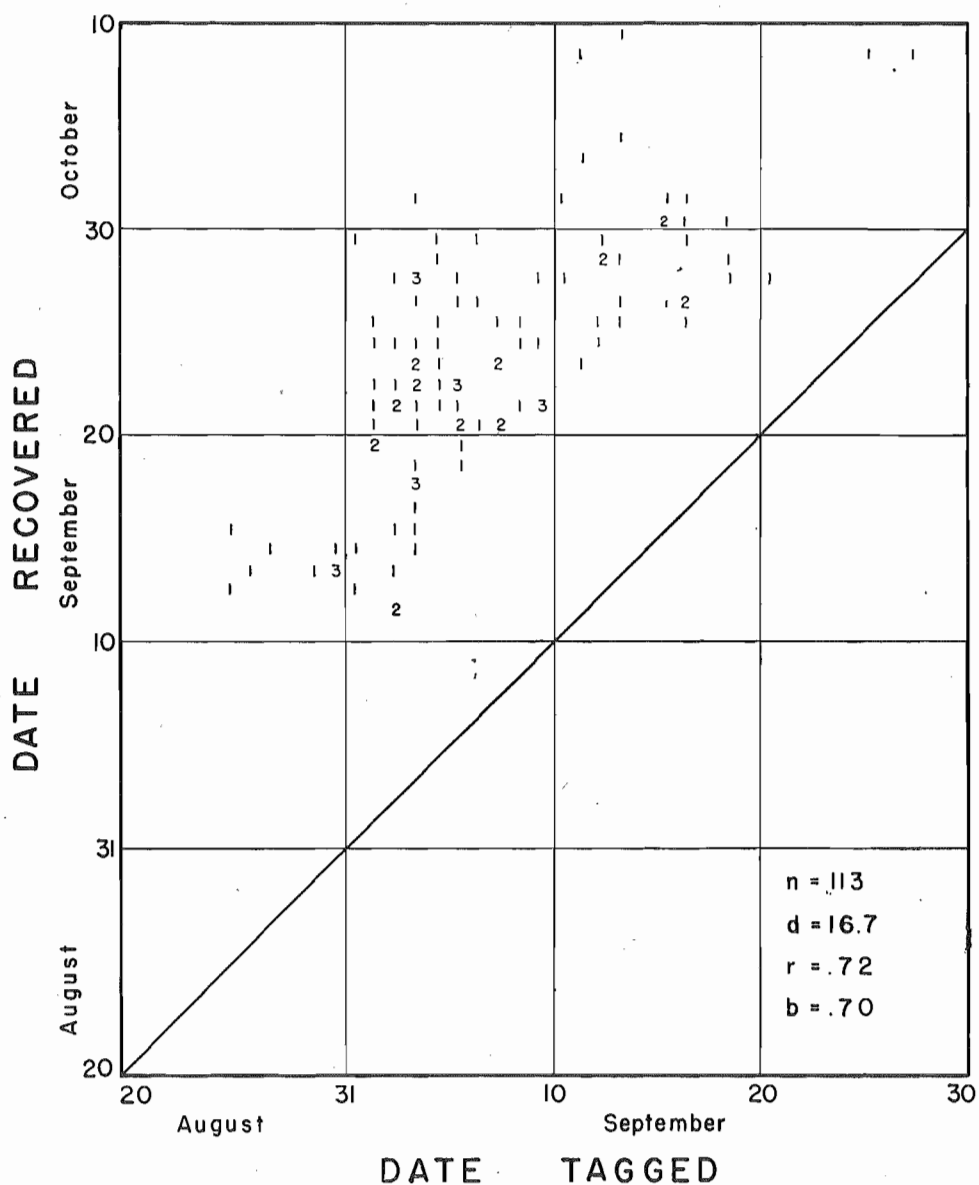
FIGURE 18. Recoveries by dates of tagging and recovery of fish tagged at the Skookumchuck and recovered when recaptured alive at the Birkenhead trap, 1941.

three and a half days in 1940, and was nearly equal for large males and large females (the jacks are too few to be considered). In 1941, however (Table 28), the values are quite different for males and females, being 10.4 and 3.7 days, respectively, while for the jacks it is 9.7 days. These data exhibit no systematic
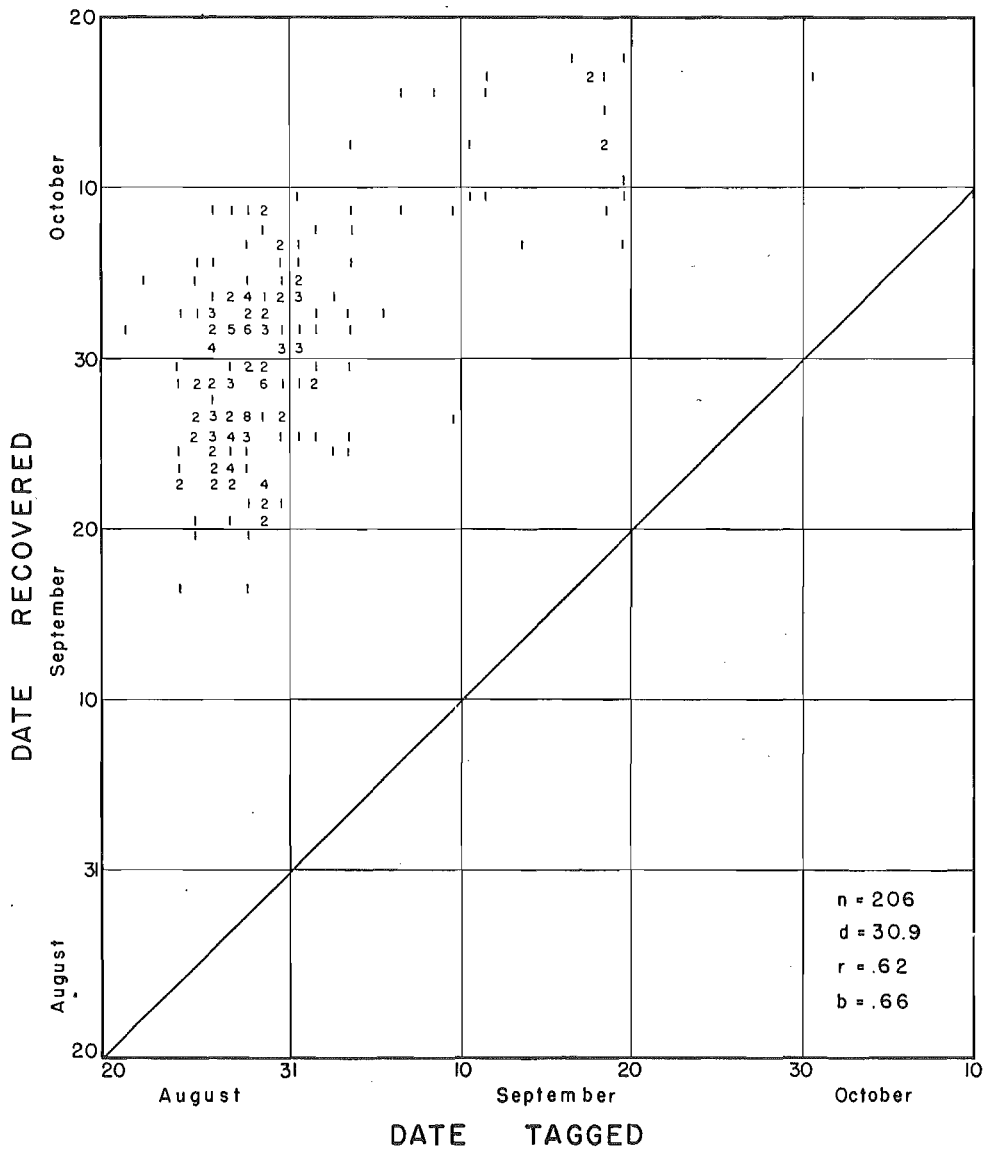
FIGURE 19. Recoveries by dates of tagging and recovery of fish tagged at Skookumchuck and
   recovered on the Birkenhead spawning grounds as dead fish (fresh large dead only), 1940.

effects connected with sex or size but indicate the possibility of seasonal differ-
ences in duration of delay of delayed recoveries. We will examine this further
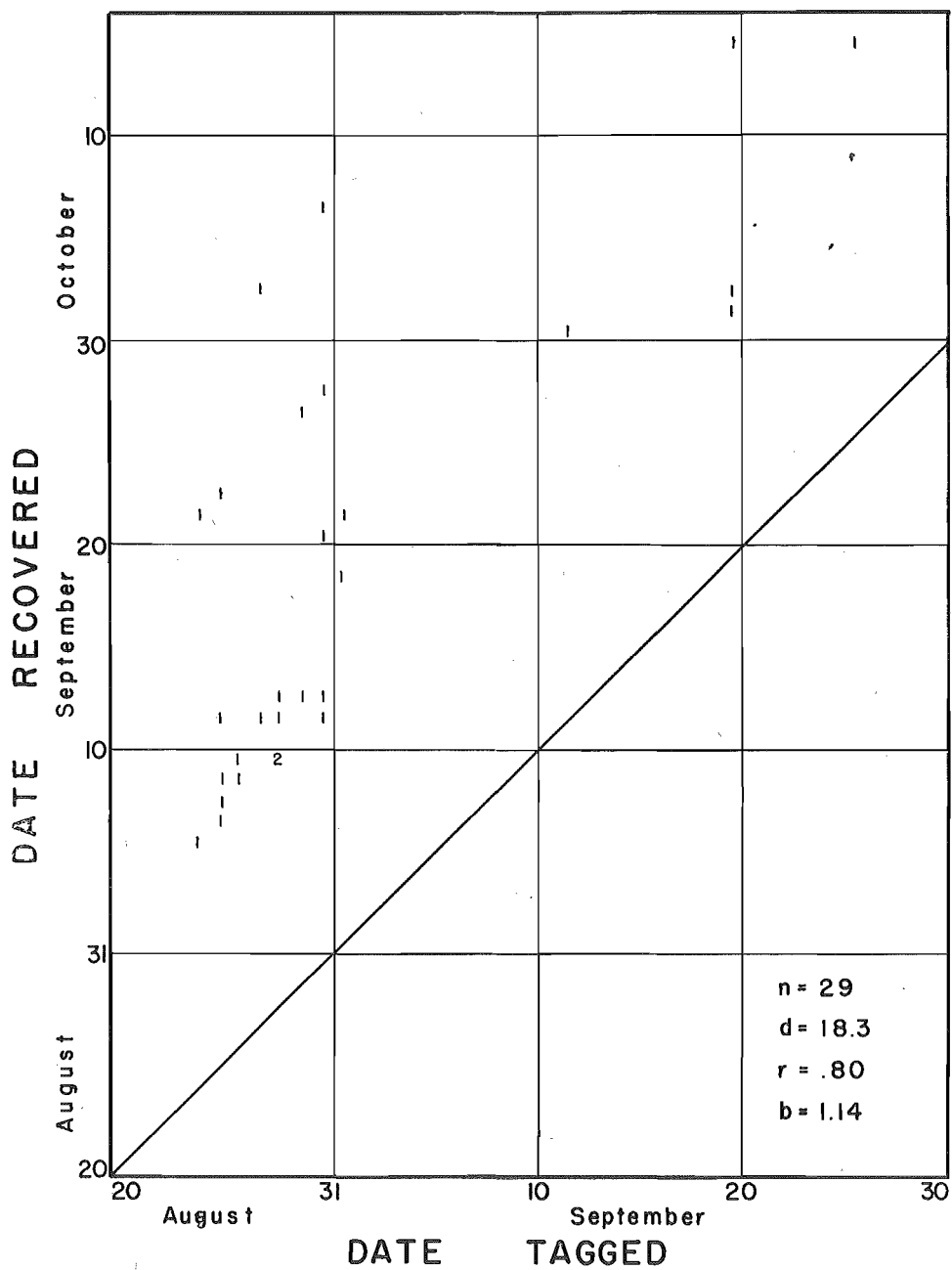below on the basis of the Birkenhead tag liberations.
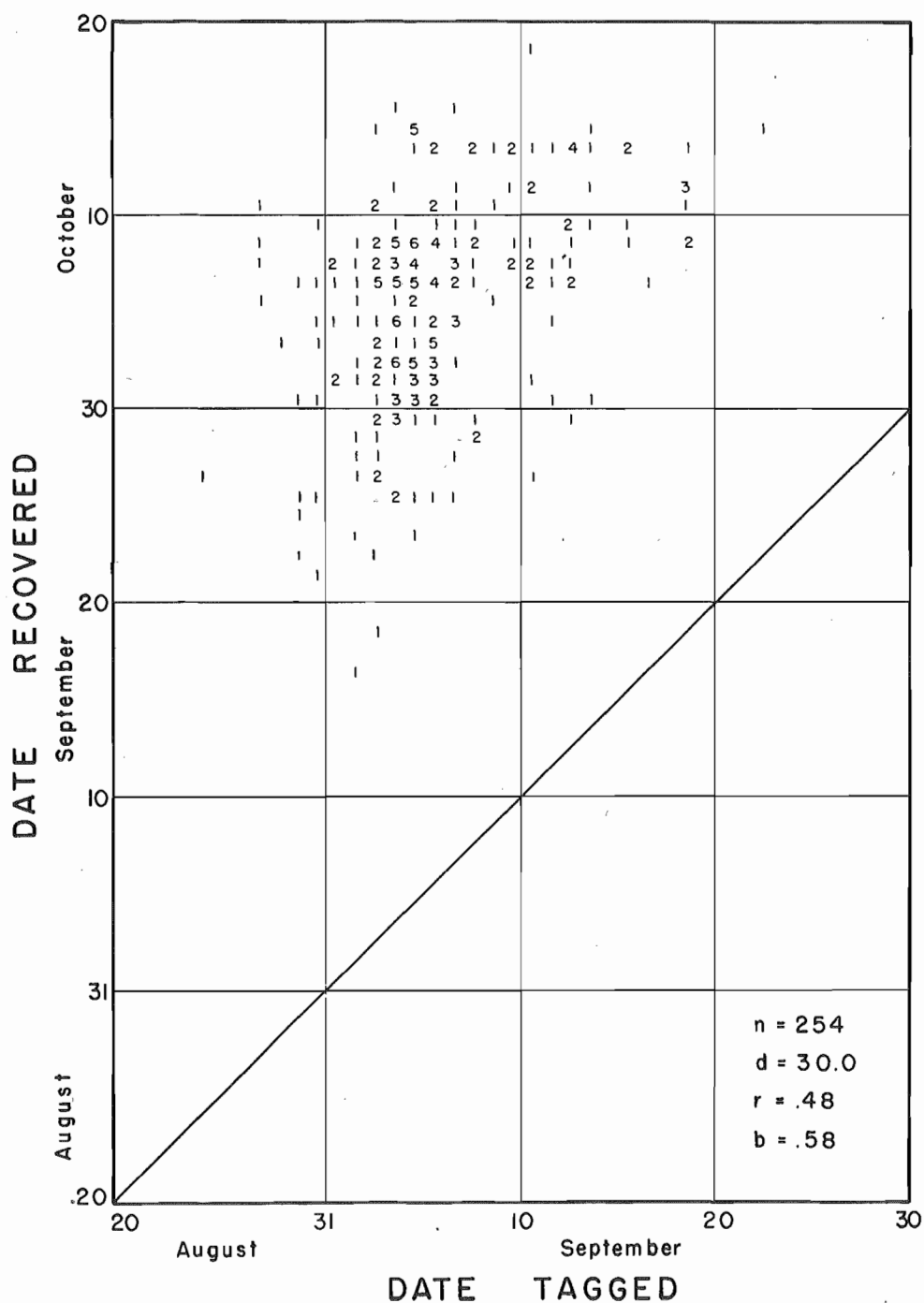
FIGURE 20. Recoveries by dates of tagging and recovery of fish tagged at Skookumchuck and recovered on the Birkenhead spawning grounds as dead fish (fresh dead only), 1941.

TABLE 27

Average Days Between Tagging and Recovery of Fish Tagged at Skookumchuck
and Recovered Dead on the Birkenhead Spawning Grounds, 1940

	Recoveries of Fresh Dead		Recoveries of Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	87	31.3	28	35.1	115	32.2
Females	119	30.8	65	34.3	184	32.0
Total large fish	206	30.9	93	34.5	299	32.1
Jacks	8	25.5	3	33.0	11	27.5
Total	214	30.8	96	34.5	310	31.9

d = average days between tagging and recovery
n = number of recoveries

TABLE 28

Average Time Between Tagging and Recovery of Fish Tagged at Skookumchuck
and Recovered Dead on the Birkenhead Spawning Grounds, 1941

	Fresh Dead		Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	51	29.5	24	39.9	75	32.8
Females	115	31.1	40	34.8	155	32.0
Total large fish	166	30.6	64	36.7	230	32.3
Jacks	88	29.0	25	38.7	113	31.2
Total	254	30.0	89	37.3	343	31.9

d = average days between tagging and recovery
n = number of recoveries

Birkenhead tagging[1]

From the fact that the values of the correlation and regression coefficients
resulting from Skookumchuck tag recoveries among dead spawned-out fish were
found to be markedly lower than the corresponding coefficients for recaptures at
the Birkenhead trap (fish newly arriving in the river) it may be inferred that a
good deal of mixing of the population takes place on the spawning ground. Since
the low coefficients were characteristic of data from fresh dead alone as well as
for all recoveries, it may be inferred that much of this mixing is the result of

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[1]Data for 1939 are insufficiently extensive or representative to be included in this section.
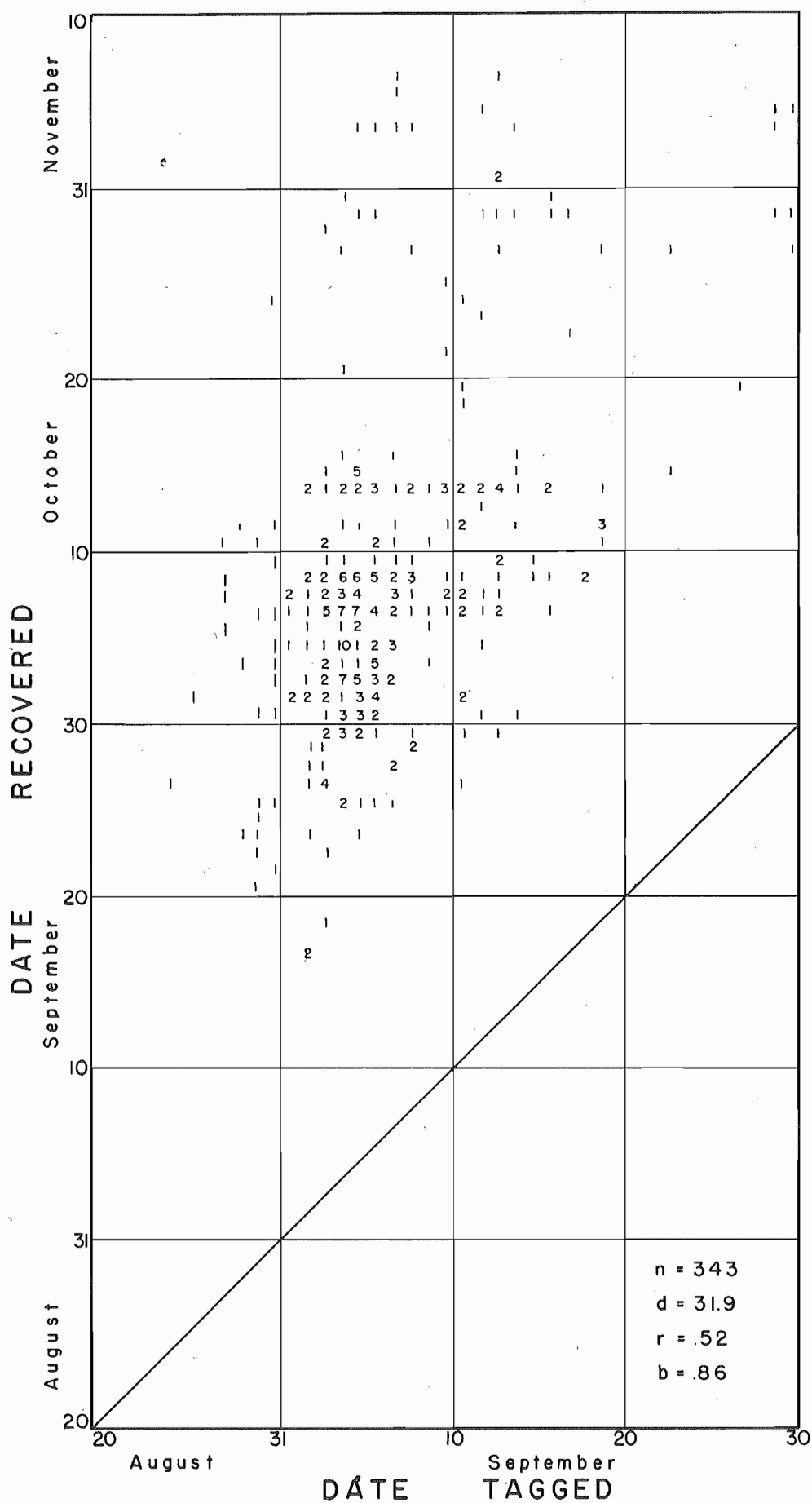
FIGURE 21. Recoveries by dates of tagging and recovery of fish tagged at Skookumchuck and

FIGURE 22. Recoveries by dates of tagging and recovery of fish tagged at Skookumchuck and recovered as dead fish on the spawning grounds of the Birkenhead (all dead large fish recoveries), 1940.

differential time of death of fish tagged at the same time and is independent of delay in recovery of carcasses.

These conclusions are capable of independent verification by means of data from recovery of tags liberated at the Birkenhead trap. The data are plotted in Figures 23 and 24, in the usual manner, for fresh dead only and all dead for the
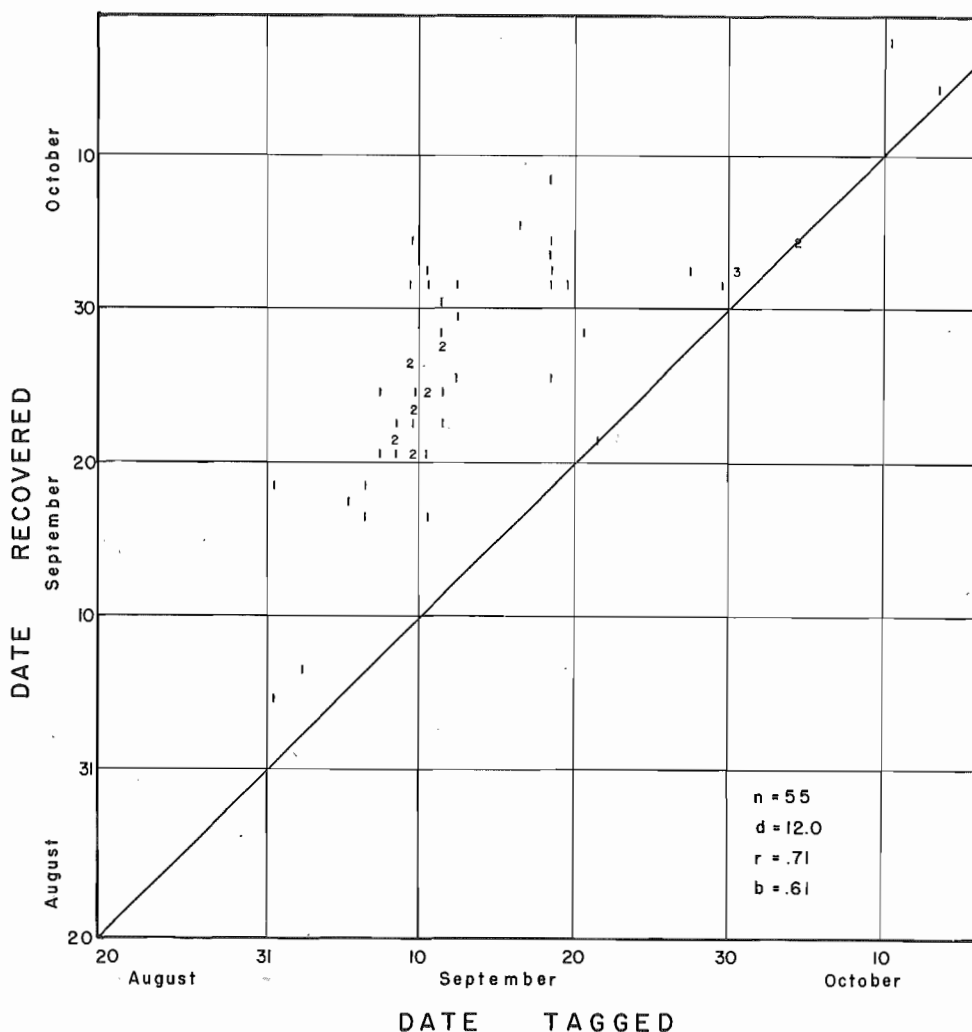
FIGURE 23. Recoveries by dates of tagging and recovery of fish tagged at the Birkenhead trap and recovered on the spawning grounds as fresh dead, 1940.

1940 season. The more numerous data of the 1941 experiment are similarly presented in Figures 25 and 26. Since the 1941 data include a number of tagged jacks while the 1940 data do not, extra figures, Figures 27 and 28, have been prepared for the 1941 fresh dead, one for large fish alone and one for jacks alone, in order to study the effect of inclusion or exclusion of jacks in the regressions. The constants for all these distributions are recapitulated in the last columns of Table 24.

In the first place it may be seen from Table 24, as well as from the separate figures, that mixing is not at all complete. Indeed, as may be seen from the graphical representations, there must of necessity be a positive correlation between date of tagging and date of recovery, because some fish tagged early in the season are
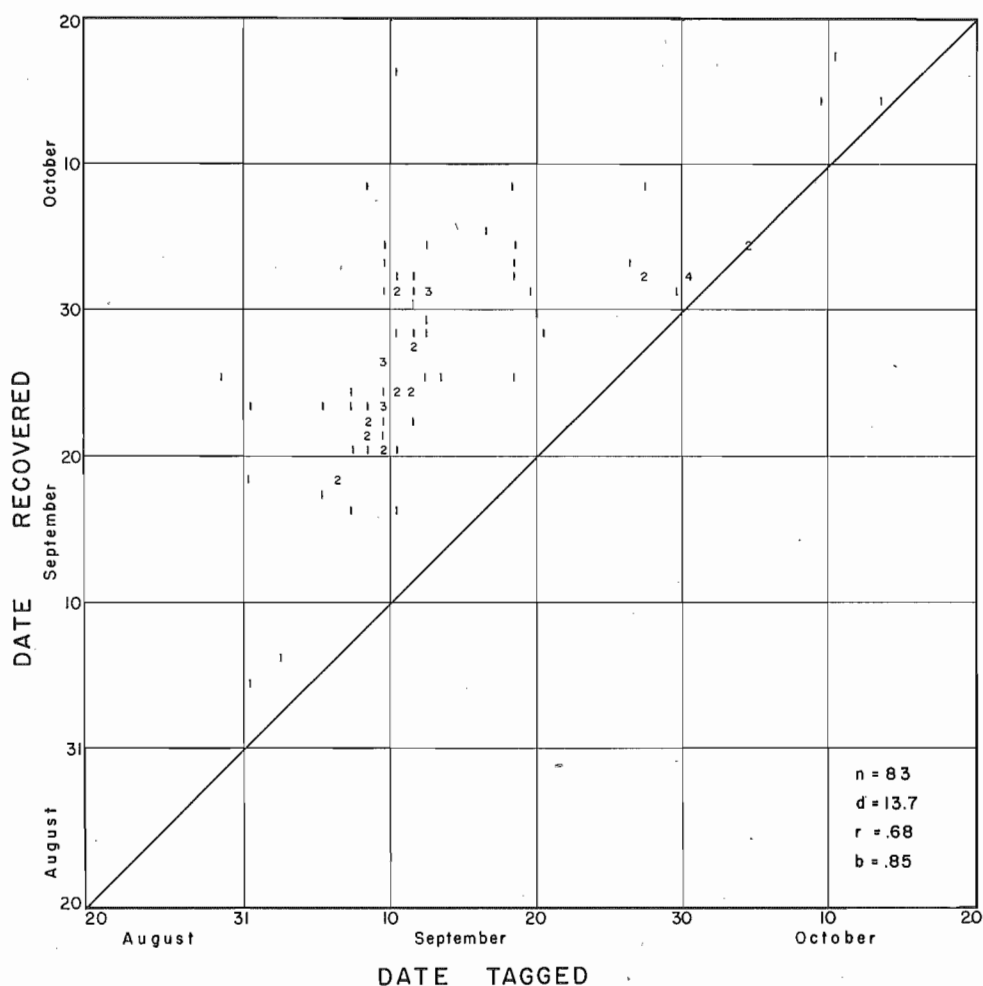
FIGURE 24. Recoveries by dates of tagging and recovery of fish tagged at the Birkenhead trap and recovered on the spawning grounds (all recoveries), 1940.

dead and recovered before the tagging of some others tagged later in the season. This same was true, but to a lesser degree, of recoveries from the Skookumchuck taggings. The relationship of the duration of the run and the time between tagging and recovery is such that an absolutely thorough mixing up of the population is physically impossible. This may be the principal factor involved, although there seems also to be a definite tendency for fish to maintain their order of migration aside from this limitation, particularly between Skookumchuck and Birkenhead trap (Figures 21 and 22).

The comparison of correlation coefficients for the same years and the same categories of data (fresh dead or all dead) shows that in every case the coefficients are lower for the Skookumchuck tags recovered among the samples than for the Birkenhead tags recovered among the same samples. The differences are, however,
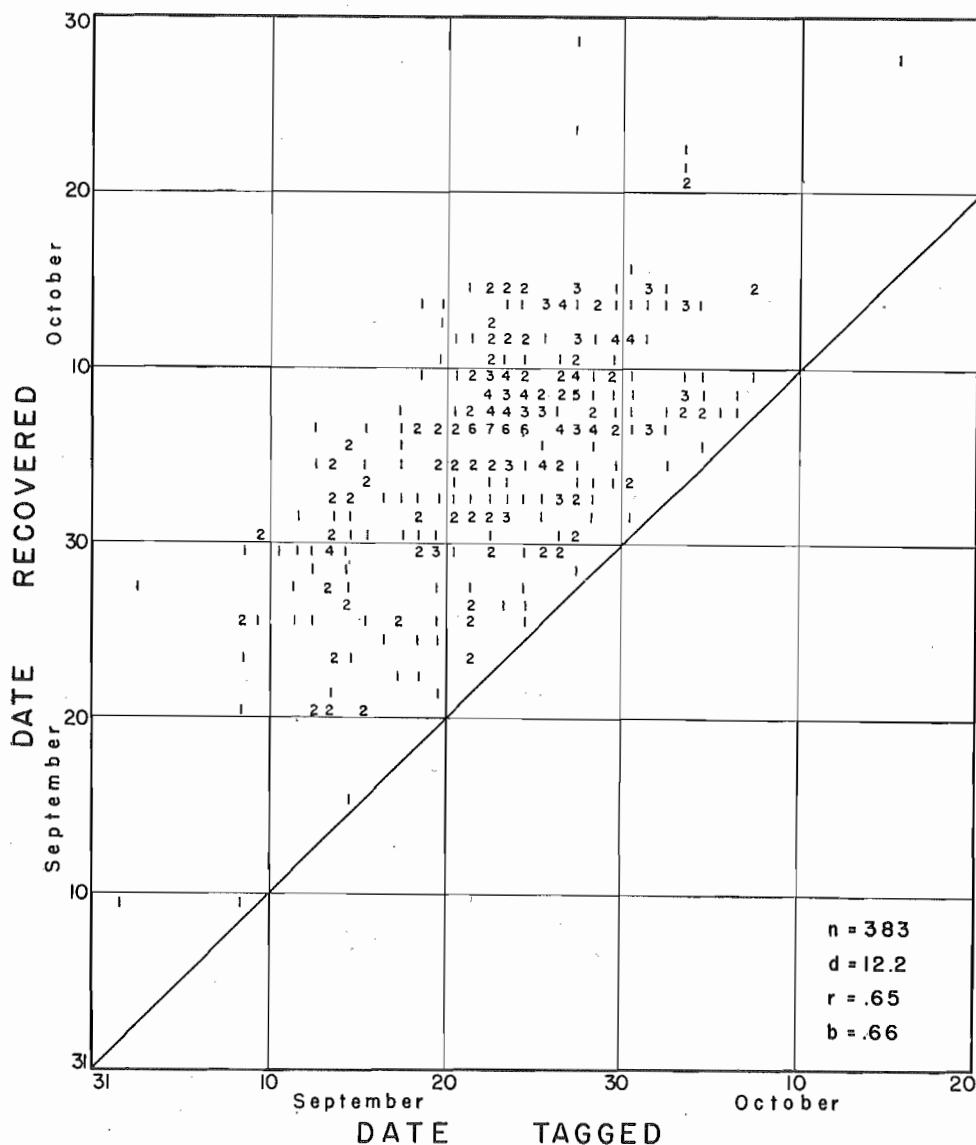
FIGURE 25. Recoveries by dates of tagging and recovery of fish tagged at the Birkenhead trap and recovered as dead fish on the spawning grounds (fresh dead only), 1941.

not large. This supports the conclusion arrived at from the Skookumchuck tags recovered at the Birkenhead trap, that while some mixing takes place during the passage between the Skookumchuck and the spawning grounds it is quite incomplete. A good deal of the mixing is again seen to have occurred between time of capture at the Birkenhead trap and time of death.

The correlation coefficients for all recoveries is only slightly less than that for fresh dead only in 1940, .68 as compared with .71. In 1941 the disparity is
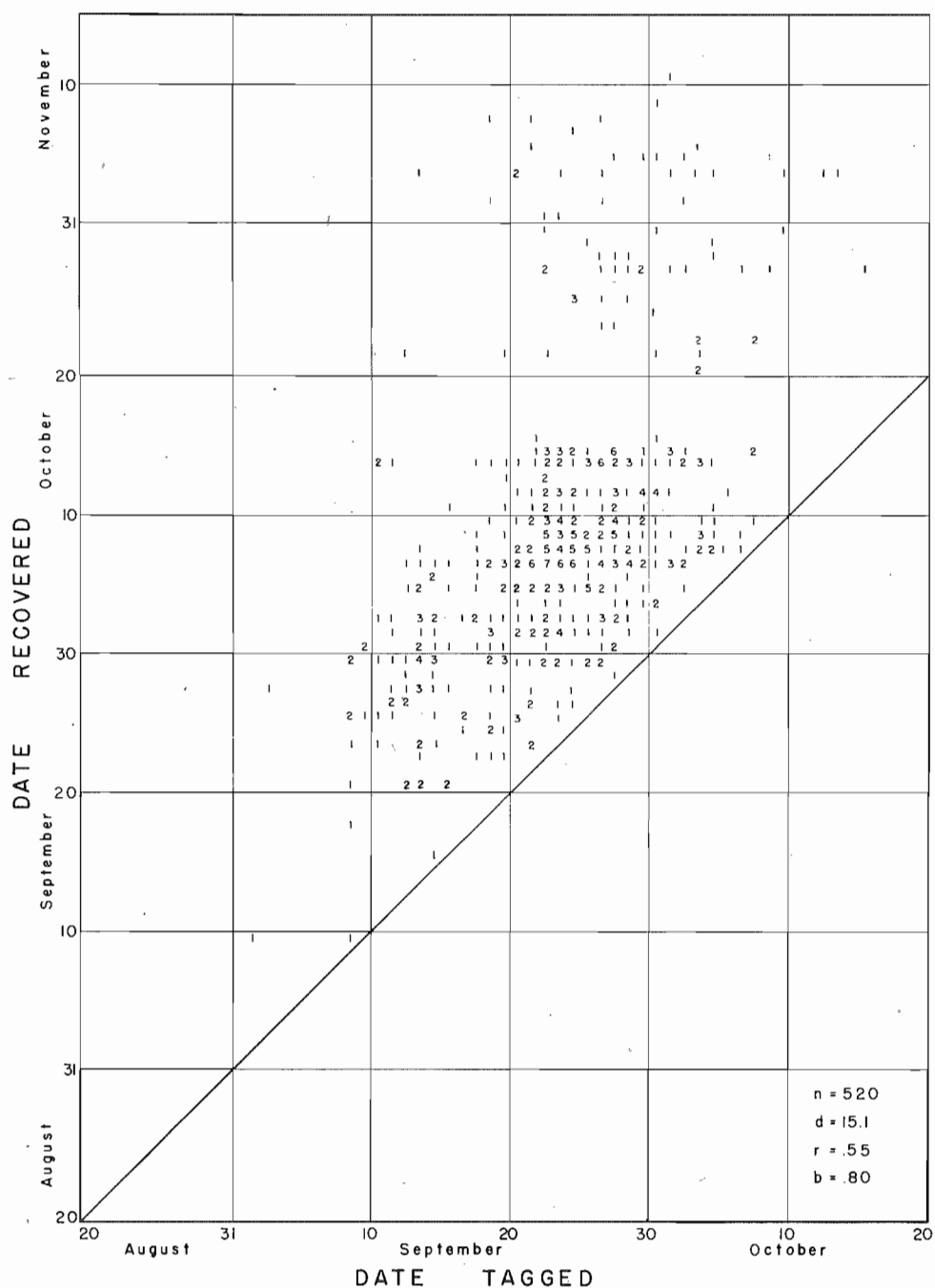
FIGURE 26. Recoveries by dates of tagging and recovery of fish tagged at the Birkenhead trap and recovered as dead fish on the spawning grounds (all recoveries), 1941.
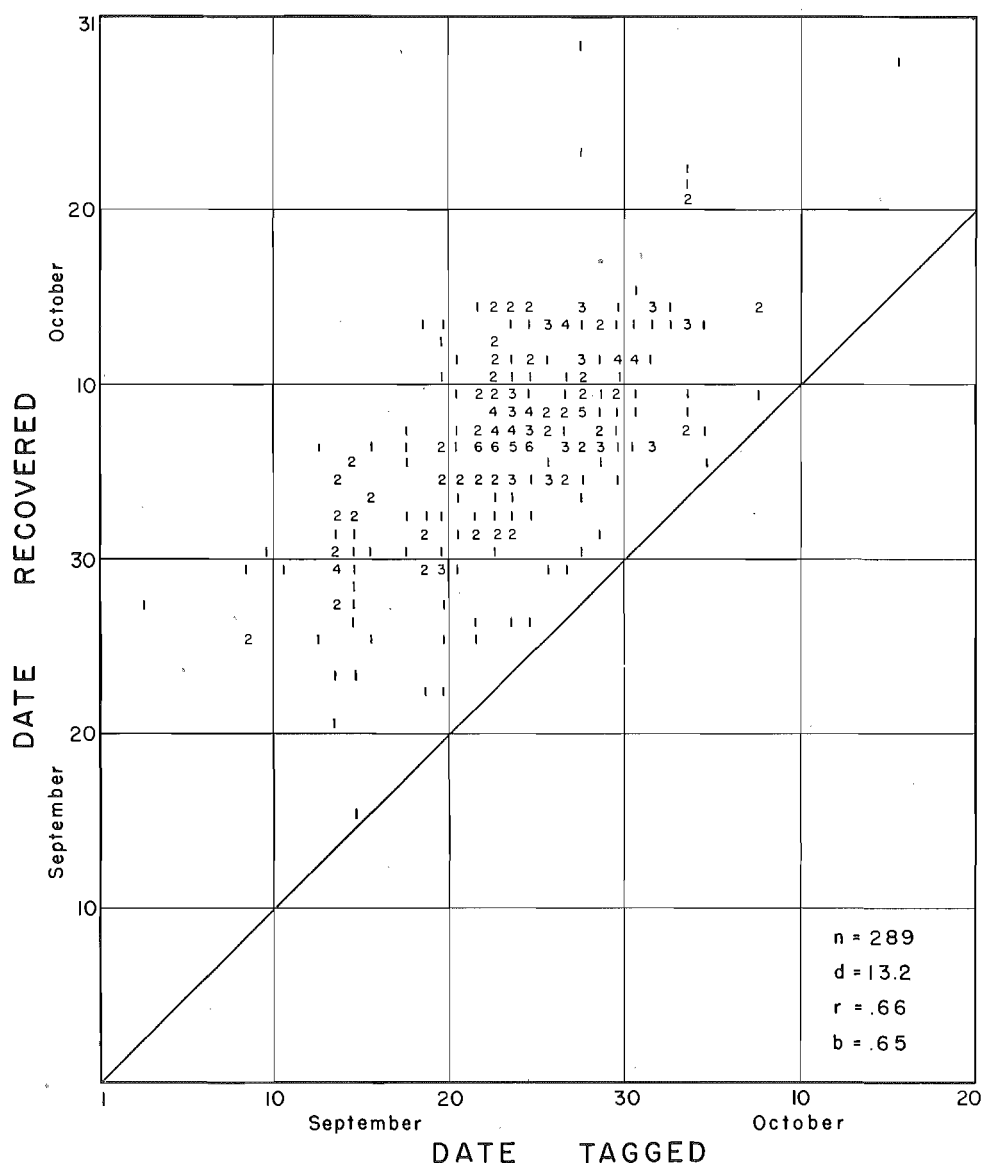
FIGURE 27. Recoveries by dates of tagging and recovery of fish tagged at the Birkenhead trap and recovered as dead fish on the spawning grounds (fresh dead large fish only), 1941.

greater between coefficients .55 and .65, but is yet not very great. This again indicates that much of the total mixing on the spawning grounds may be attributed to differential time of death of individuals.

As noted above, the coefficients for fresh dead fish for 1941, the only year when jacks were captured in the Birkenhead trap, were computed for the large fish and the jacks separately. The values are recapitulated in the appropriate place in Table 24 as well as being entered on Figures 27 and 28. From Table 24 it may
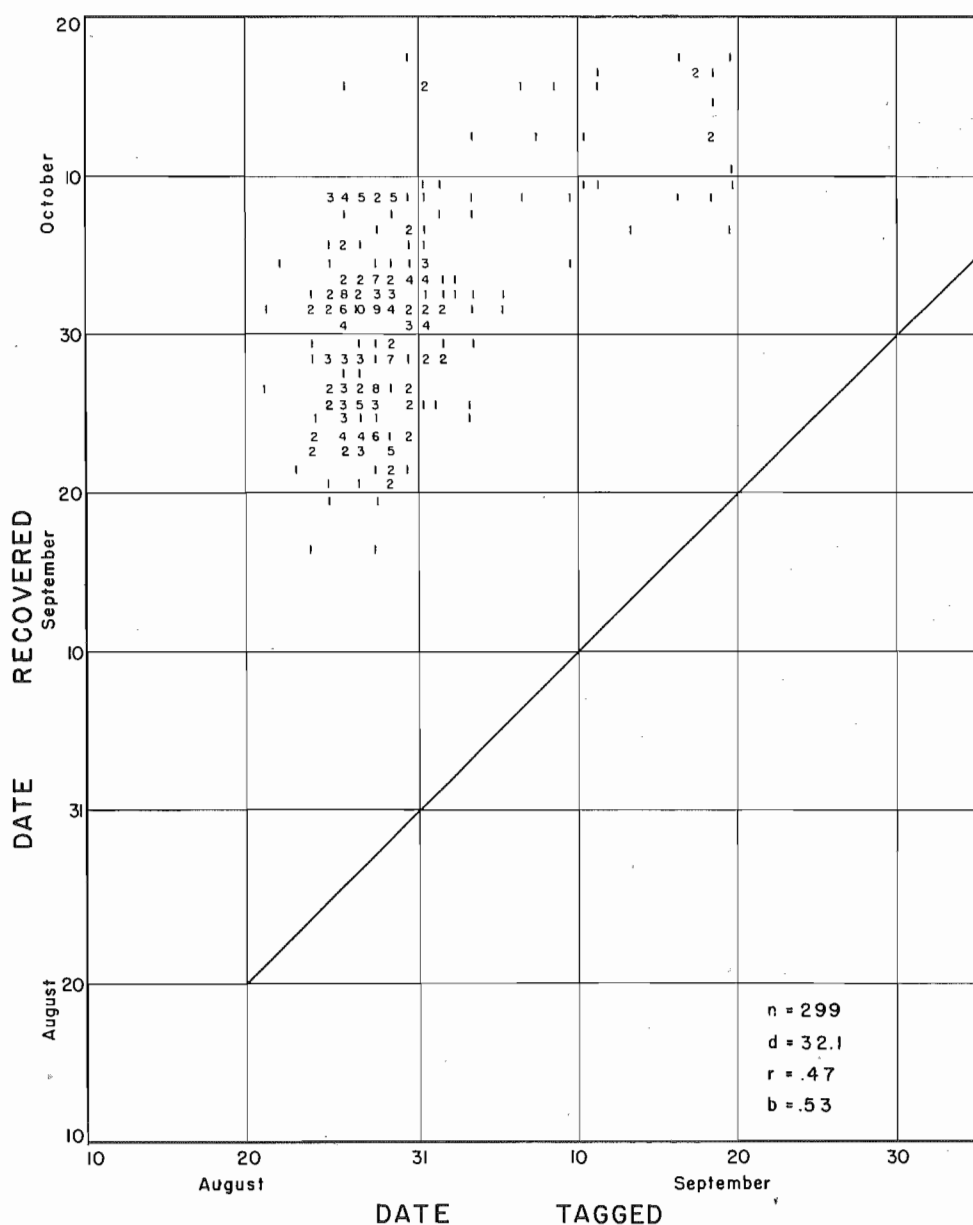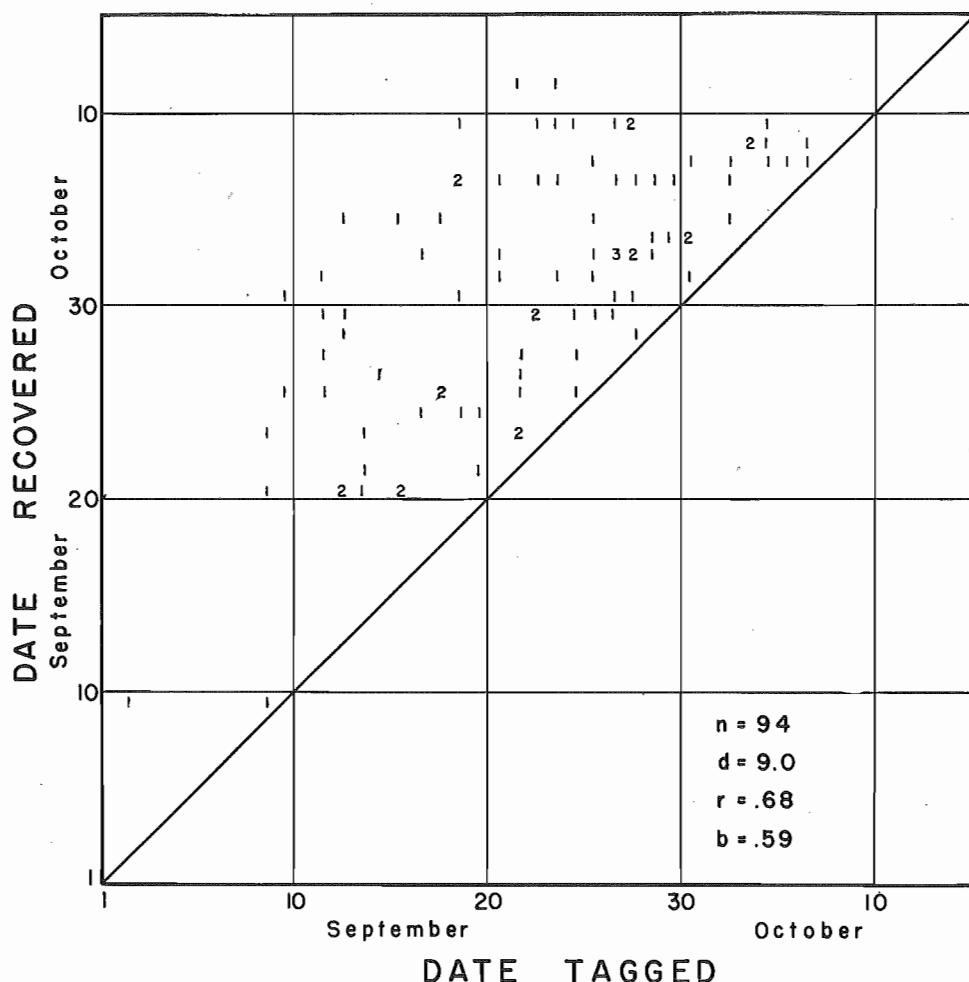
FIGURE 28. Recoveries by dates of tagging and recovery of fish tagged at the Birkenhead trap and recovered as dead fish on the spawning grounds (fresh dead jacks only), 1941.

be seen that the value of "r" for jacks alone is slightly higher than for the large fish alone. The value for the combined data is slightly lower than either. This is to be attributed to the difference between categories in average time between tagging and recapture, the jacks having a shorter time between tagging and recovery than the large fish.

The average time between tagging and recovery is broken down by sex, size and carcass condition categories for 1940 and 1941 in Tables 29 and 30. Among the fresh dead, where presumably little or no delay in recovery after death was effective, the males had a shorter period between tagging and death than the females in 1940 but about the same, in fact a bit longer, than the females in 1941. Among the old carcasses the average time period was longest for females in both years. Considering these data and those treated earlier from the Skookum-

chuck tagging it seems unwarranted to assert that there are regular sex-connected differences in times between tagging and recovery of large fish.

In the case of the jacks, however, the 1941 data definitely show a considerably shorter average time between tagging and recovery of these fish than obtained for large sockeye. This difference is much larger than in the case of Skookumchuck tagged jacks in either year.

TABLE 29

Average Days Between Tagging and Recovery of Fish Tagged at the Birkenhead Trap and Recovered Dead on the spawning Grounds, 1940

	Fresh Dead		Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	33	11.0	15	16.0	48	12.6
Females	22	13.5	13	17.6	35	15.0
Total	55	12.0	28	16.8	83	13.7

d = average days between tagging and recovery
n = number of recoveries

TABLE 30

Average Time Between Tagging and Recovery of Fish Tagged at the Birkenhead Trap and Recovered Dead on the Spawning Grounds, 1941

	Fresh Dead		Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	83	13.6	25	22.9	108	15.7
Females	206	13.1	69	25.6	275	16.2
Total large fish	289	13.2	94	24.9	383	16.1
Jacks	94	9.0	43	19.2	137	12.2
Total	383	12.2	137	23.1	520	15.1

n = number of recoveries
d = average days between tagging and recovery

The value of "d" for the large fresh dead is much the same in both 1940 and 1941, just as we found in the case of the Skookumchuck tags. Again, as we found before from the Skookumchuck data, the values of "d" for dead other than fresh are considerably greater in 1941 than in 1940. It seems that the time required for migration, spawning and death may be more or less uniform from

year to year, but that the sampling conditions are such that we may expect a considerable variation in the average delay between death and recovery of the delayed recoveries.

Weaver Creek Population

Harrison tagging

RECAPTURES AT WEAVER CREEK FENCE

Fish were tagged at Harrison Trap in all three years, but only in 1940 and 1941 was a trap in operation at the mouth of Weaver Creek.

Data on fish tagged at Harrison Trap and recaptured alive at the mouth of Weaver Creek may be expected to give direct evidence on the speed of migration and mixing during migration between those two points. In 1940, only four such fish were recovered, all on the 19th of October, after being gone from the Harrison Trap for six, ten, eleven, and eighteen days (average 11.2). These data are too meager to shed much light on mixing, of course.

The 1941 data were more abundant. In that year, ninety-nine recoveries were made at the Weaver Creek trap throughout the course of the run. These are shown in the usual fashion in Figure 29 and the computed values recapitulated in Table 31. The mixing effect, while not complete, is considerable as evinced by an "r" of .50. In spite of the much shorter distance and migration time between Harrison and Weaver Creek than between Skookumchuck and the Birkenhead, a lower value of "r" was obtained for the former. This is associated with the concentration of the recoveries into a shorter range of time, a lower apparent "dispersion" of the run, at Weaver Creek than at the Birkenhead. This is, however, to some extent at least, a spurious effect resulting from the flooding out of the Weaver Creek fence in mid-October during which period a good number of fish undoubtedly went upstream without being subject to sampling. Since the sampling was conducted largely on only the latter part of the run, the mixing within that part is naturally greater than would be expected within the whole population. It is also to be noted that these fish exhibit a net upstream movement, in miles per day, much less than that of the fish moving from Skookumchuck to the Birkenhead, which gives a greater opportunity for mixing enroute. This is, in my opinion, probably due to the greater proximity of the tagging point to the spawning grounds, although some other reason is not excluded.

Males and females recaptured at the fence had sensibly the same rate of migration between the Harrison Trap and Weaver Creek fence (Table 32) in 1941, the average elapsed time being 7.8 and 8.8 days, respectively.

RECOVERIES AMONG DEAD FISH

During 1939, recoveries were made in Weaver Creek on visits at intervals of about a week, and the fish examined were not recorded by condition of freshness of carcass. These data are obviously unsuitable for determination of mixing during migration. The average days between tagging and recovery of the twenty-one recoveries was 24.5 (Table 31), higher than the averages for 1940 and 1941. Since recoveries were made only at weekly intervals, the mean delay in recovery would be expected to be about three days higher than where recovering was done more nearly continuously.

TABLE 31

Recapitulation of Average Duration of Migration of Tagged Fish, and of Correlation and Regression
Coefficients of Date of Recovery on Date of Tagging

| Point of recovery and year | POINT OF TAGGING | | | | | | | |
| | Harrison Trap | | | | Weaver Creek Fence | | | |
	d	r	b	n	d	r	b	n
Weaver Creek fence (live fish)								
1940	11.1			4				
1941	8.6	.50	.55	99				
Weaver Creek (dead fish) Fresh dead only								
1940	17.5	.39	.52	12	8.8	.87	1.02	161
1941	16.1	.38	.30	204	9.3	.76	.66	287
Weaver Creek (dead fish) All recoveries								
1939	24.5			21				
1940	21.6	.33	.43	23	12.7	.63	.89	270
1941	17.3	.25	.29	262	11.4	.56	.57	401

d = average days from tagging to recovery.
r = product moment correlation of date of tagging with date of recovery.
b = regression coefficient of mean square linear regression.
n = number of recoveries.
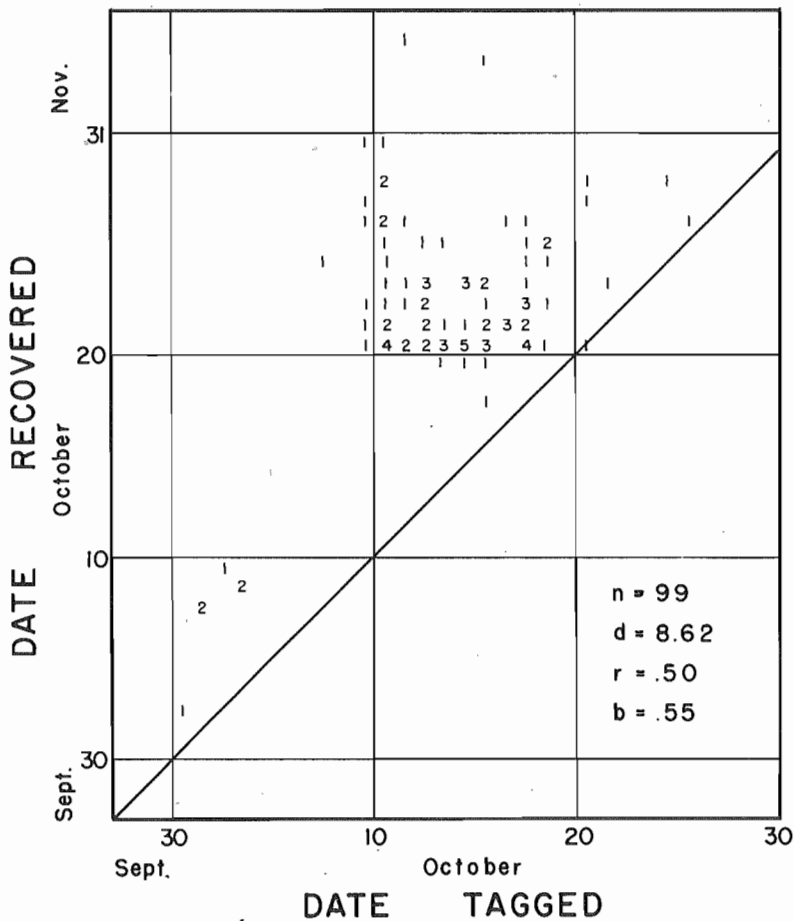
FIGURE 29. Recoveries by dates of tagging and recovery of fish tagged at Harrison Trap and recaptured alive in the trap at the mouth of Weaver Creek, 1941.

In Figures 31 and 33 are recorded the data for 1940 and 1941 on recoveries among fresh dead fish of tags placed on fish at Harrison Trap, and in Figures 30 and 32 are the corresponding data for recoveries among all the dead fish examined in those two years. The statistics for these distributions are recapitulated in Table 31.

Coefficients of correlation of .39 and .38 for fresh dead recoveries in 1940 and 1941, respectively, again support the conclusion that there is a good deal of mixing between Harrison Trap and Weaver Creek. In 1940, this is based on only twenty-four fish, of course, (and also as will be shown later, in 1940 the tagged fish were proportionally more numerous in the early part of the run) so that we may discount to some extent the low value of "r". In 1941, however, when 204 recoveries were made among fresh dead carcasses, the coefficient is still low so that there is little doubt but that rather considerable mixing takes place

FIGURE 30. Recoveries by dates of tagging and recovery of fish tagged at Harrison
Trap and recovered as dead fish on the Weaver spawning grounds
(all recoveries), 1940.
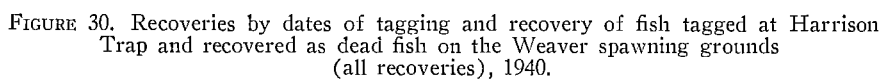
between Harrison Trap and Weaver Creek. In fact, the degree of mixing between Harrison Trap and Weaver Creek, although a much shorter distance, is more than that between Skookumchuck and Birkenhead. That more chance of mixing enroute can occur in the former case is perhaps not surprising if we consider that to negotiate the few miles between the Harrison Trap and Weaver Creek, the average tagged fish took about nine days, while to negotiate the many times longer distance between Skookumchuck and the Birkenhead, a tagged fish took only about seventeen days. Since the rate of upstream movement is much less between Harrison Trap and Weaver Creek, the opportunity for mixing is much greater. In any event, the mixing of the tagged fish between the Harrison Trap and Weaver Creek, while not complete even among the dead fish, is considerable. Correspondingly, as we would expect, the coefficients "b" are also low.

The average speed of migration among fresh dead recoveries is much the same in the two years and Table 33 indicates no important differences between sexes.

TABLE 32

Average Time Between Tagging and Recapture of Fish Tagged at the
Harrison Trap and Recaptured Alive at the Fence at the
Mouth of Weaver Creek, 1941

	n	d
Males	15	7.8
Females	83	8.8
Jacks	1	8
Total	99	8.6

n = number of recoveries
d = average days between tagging and recovery

TABLE 33

Average Time Between Tagging and Recovery of Fish Tagged at the
Harrison Trap and Recovered Dead on the Spawning
Grounds of Weaver Creek, 1941

	Fresh Dead		Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	55	17.4	10	21.5	65	18.0
Females	147	15.5	48	21.5	195	17.0
Total	204*	16.1	58	21.5	262*	17.3

n = number of recoveries
d = average days between tagging and recovery
* = includes 2 jacks not included otherwise
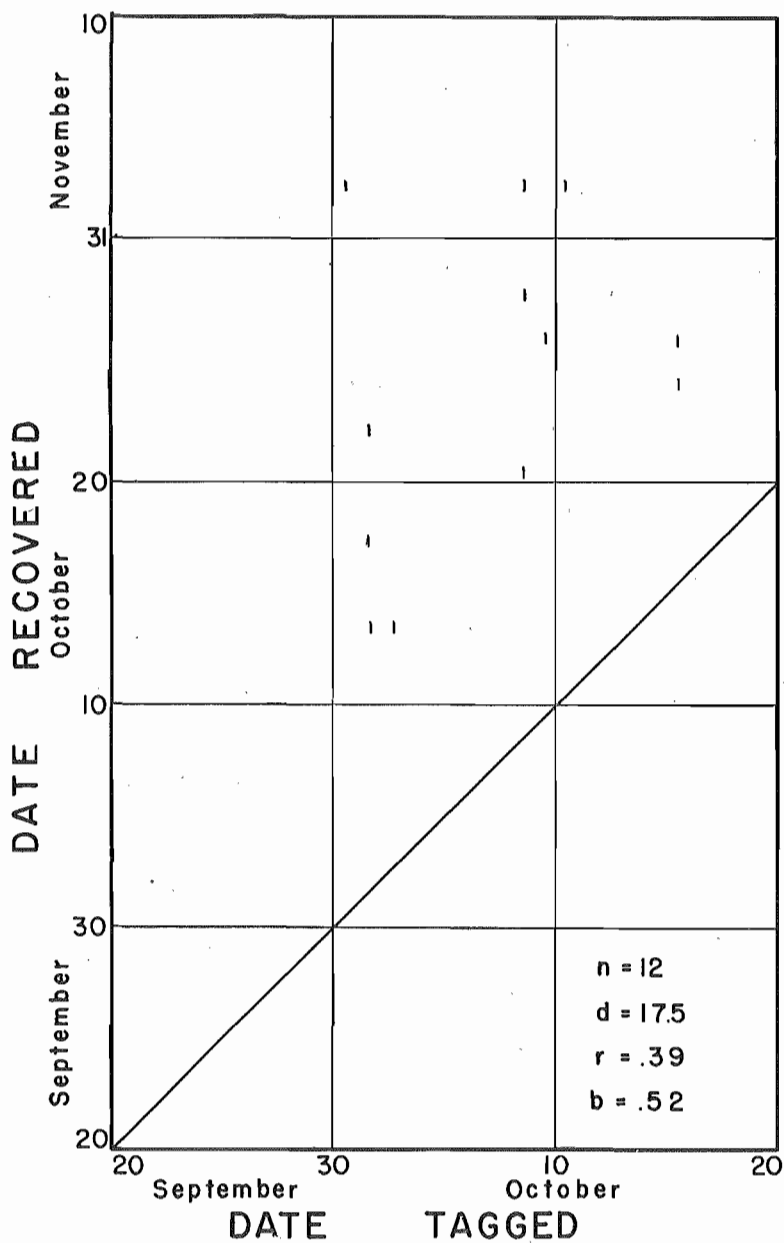
FIGURE 31. Recoveries by dates of tagging and recovery of fish tagged at Harrison Trap and recovered on the Weaver spawning grounds as dead fish (fresh dead only), 1940.

For recoveries among other than fresh dead, the rate of migration of the two sexes turns out to be identical in 1941 (the only year in which the data are sufficient for such comparison). When the recoveries from carcasses other than fresh are added to the recoveries from fresh dead carcasses, the average time of
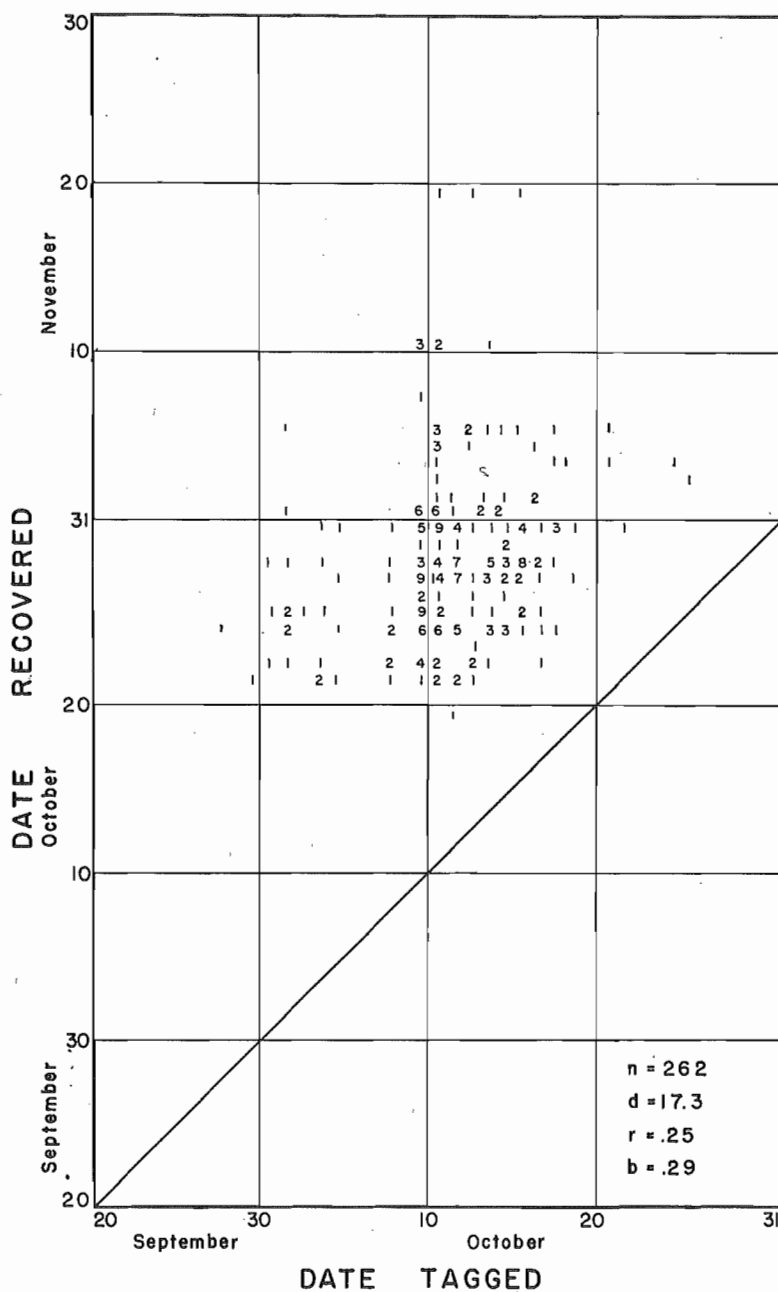
FIGURE 32. Recoveries by dates of tagging and recovery of fish tagged at Harrison Trap and recovered as dead fish on the Weaver Creek spawning grounds (all recoveries), 1941.

migration in 1941 appears to be low in comparison to 1940. This, of course, is due to a greatly increased proportion of recoveries from fresh dead carcasses in 1941 as compared with the previous year.
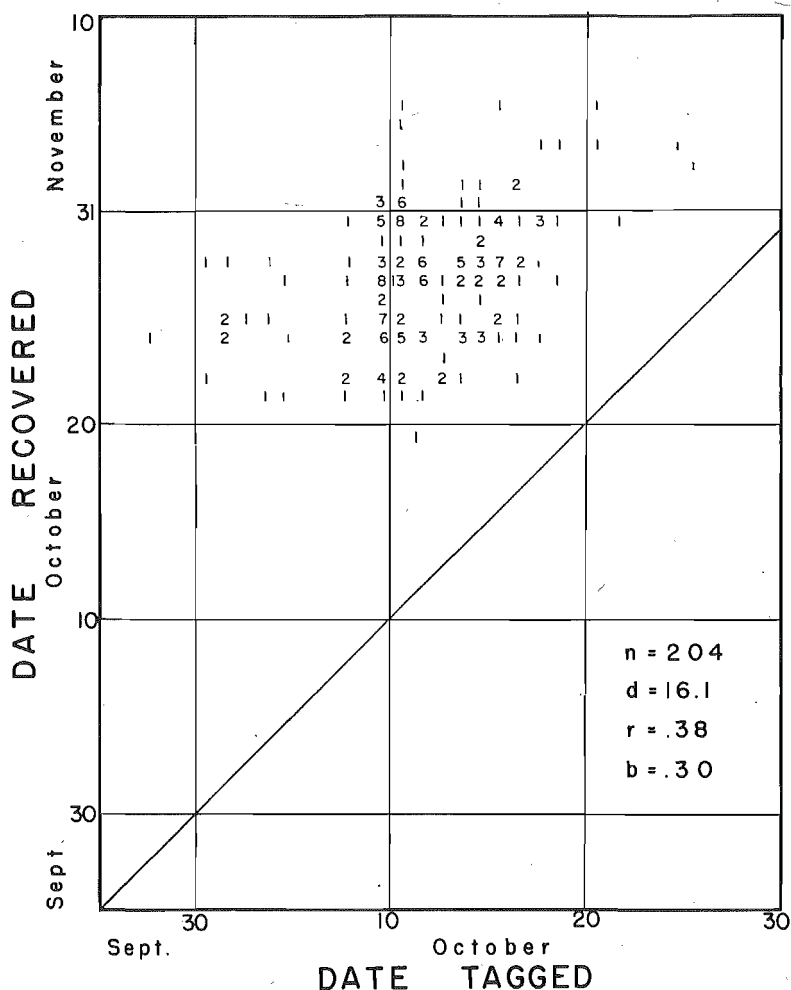
FIGURE 33. Recoveries by dates of tagging and recovery of fish tagged at Harrison Trap and recovered dead on the Weaver Creek spawning grounds (fresh dead only), 1941.

Weaver Creek tagging

From the evidence of recoveries of tagged fish on the Weaver Creek spawning grounds among dead fish tagged previously at the Harrison Trap, it was seen that the mixing of the run is rather large between these two points. We attributed this primarily to mixing during migration between the Harrison Trap and Weaver Creek rather than mixing on the spawning grounds. That this is correct is shown by the data on recoveries of fish tagged at the mouth of Weaver Creek, plotted in Figures 34 to 37 and recapitulated in appropriate columns of Table 31. The values of "r" from these several distributions are about the same level (indeed for fresh fish only are higher) than the corresponding values for fish on the Birkenhead spawning grounds. This seems to demonstrate that the mixing on the
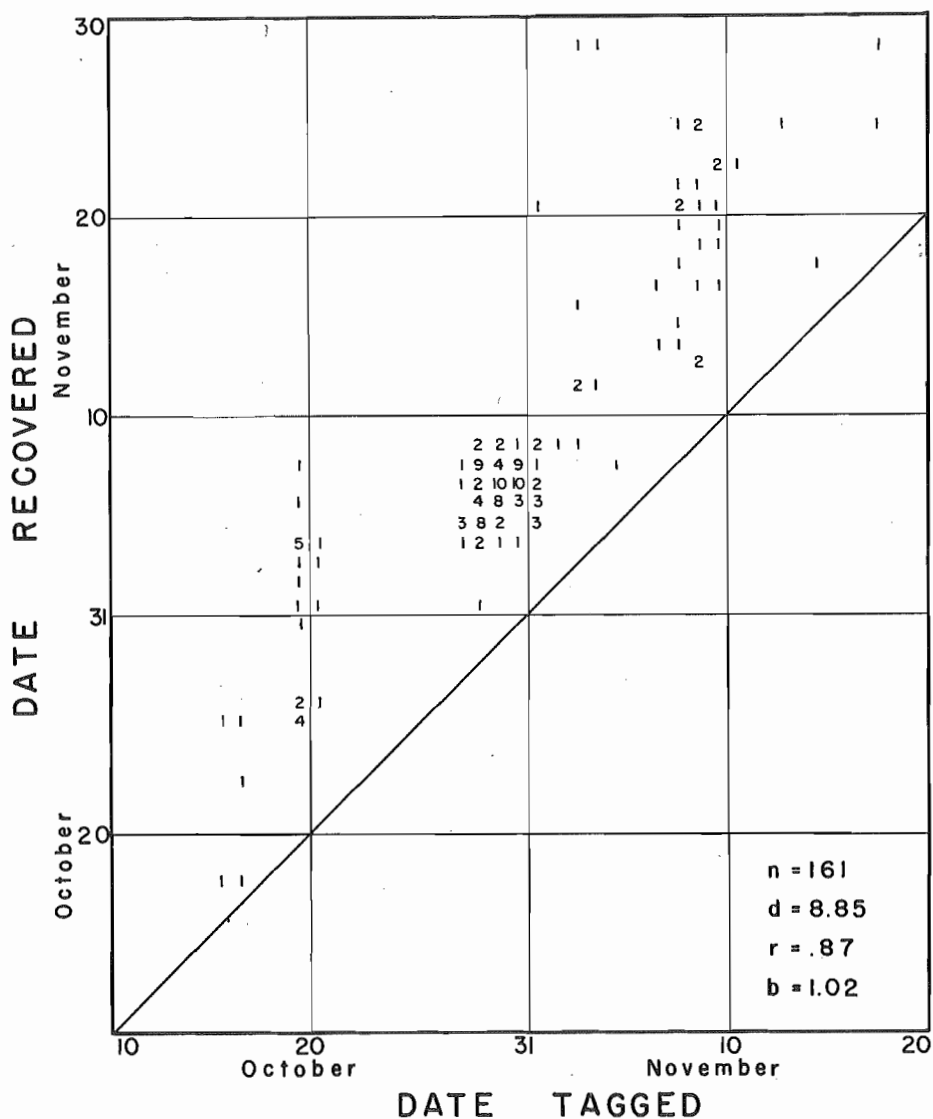
FIGURE 34. Recoveries by dates of tagging and recovery of fish tagged at the mouth of Weaver Creek and recovered dead on the spawning grounds (fresh dead only), 1940.

spawning grounds is not the responsible factor for the low values of "r" for recoveries of fish recovered from the Harrison taggings, confirming again the low value of "r" obtained first for recoveries of live fish at the fence in 1941.

The mixing of fish between time of tagging at the mouth of Weaver Creek and the time of death after spawning is not at all complete, as may be seen from Figures 34 and 36 for recoveries from fresh dead fish. Again the mechanics of the run are such that it could not be, since the time between tagging and recovery is only about nine days on the average and recoveries are spread over a thirty to
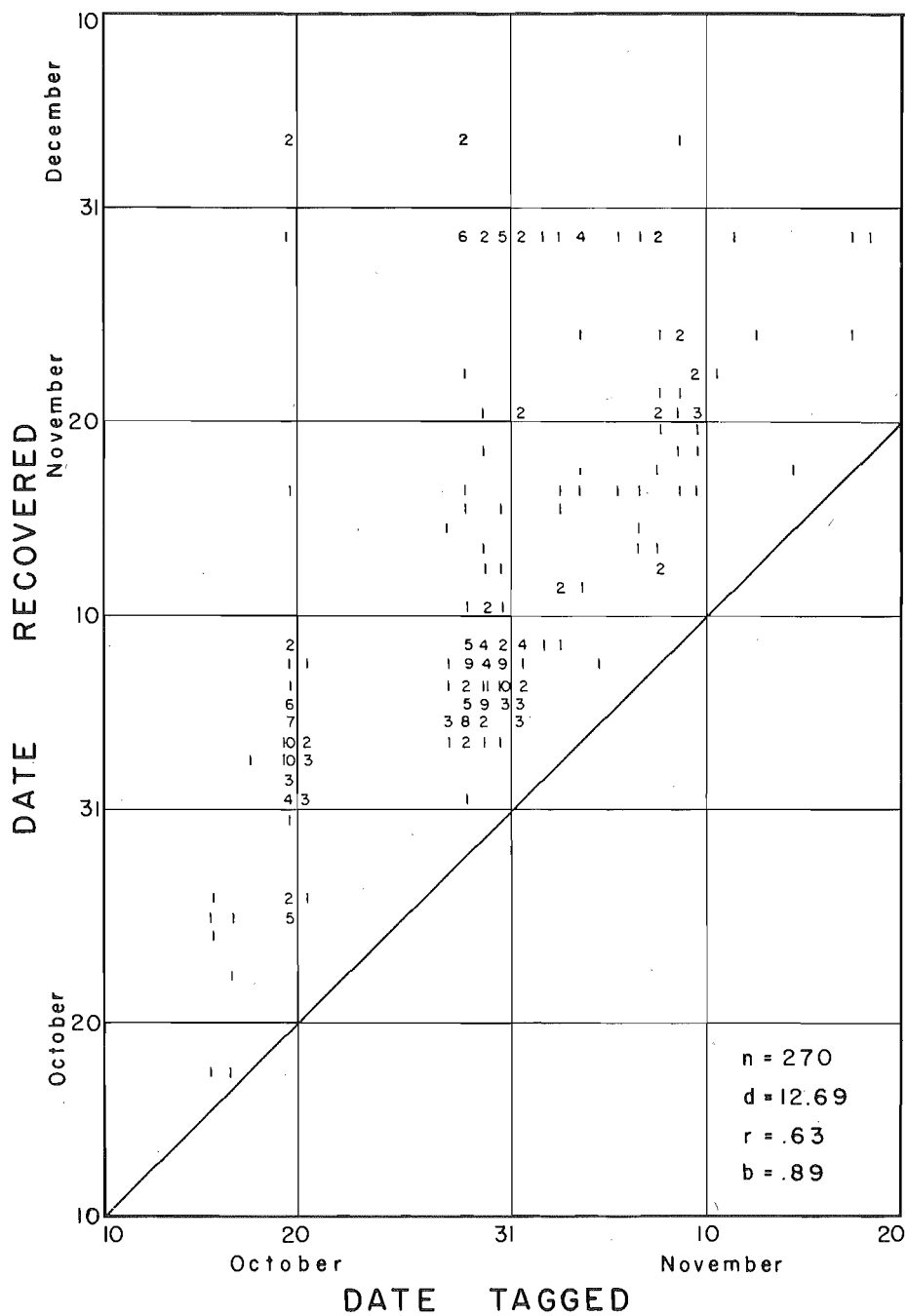
FIGURE 35. Recoveries by dates of tagging and recovery of fish tagged at the mouth of Weaver Creek and recovered dead on the spawning grounds (all recoveries), 1940.
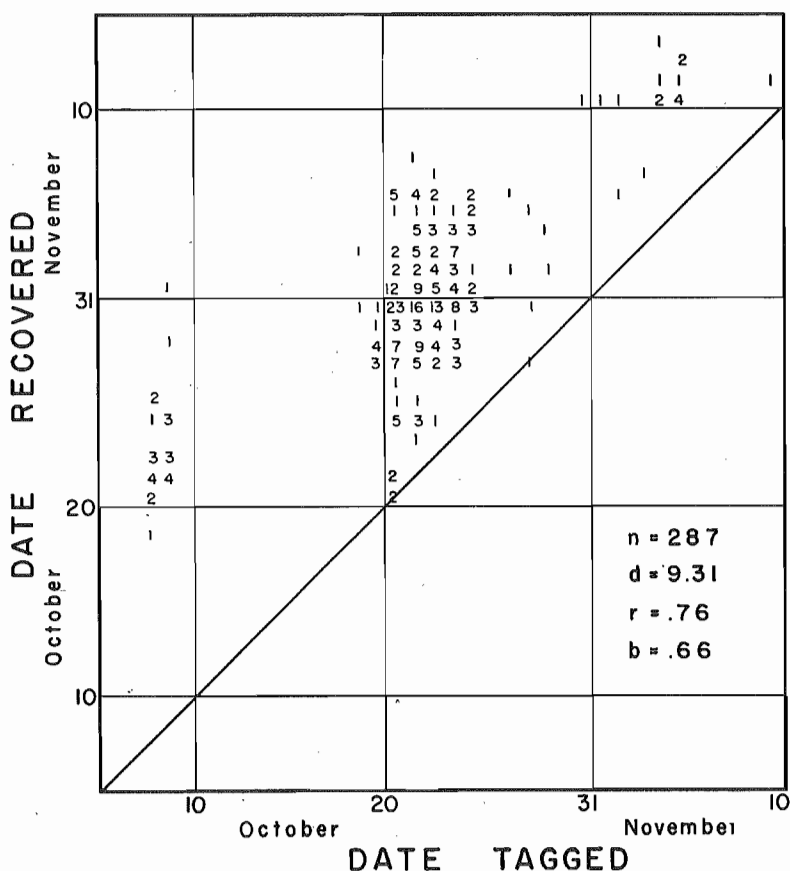
FIGURE 36. Recoveries by dates of tagging and recovery of fish tagged at the mouth of Weaver Creek and recovered as dead fish on the spawning grounds (fresh dead only), 1941.

forty day period. Again the value of "r" is probably decreased to some extent in 1941 (and that for "b" also) by the absence of any data during a long period in mid-October when the fence was flooded out. These data are sufficient to indicate, however, that mixing on the Weaver Creek spawning grounds cannot be expected to be complete.

When the data for dead other than fresh are added to the data from fresh dead only (Figures 35 and 37), the total mixing effect is increased somewhat as might be expected, indeed the decrease in value of "r" is notably greater than the corresponding decrease in the case of the Birkenhead run.

To what this difference in effect on mixing of inclusion of recoveries from dead other than fresh, as between the Birkenhead and Weaver Creek runs may be attributed is not clear. From comparison of Tables 29 and 34 for 1940, it might seem that it is due to an average difference in delay in recovery after death of recoveries other than fresh, since in that year the Birkenhead recoveries other
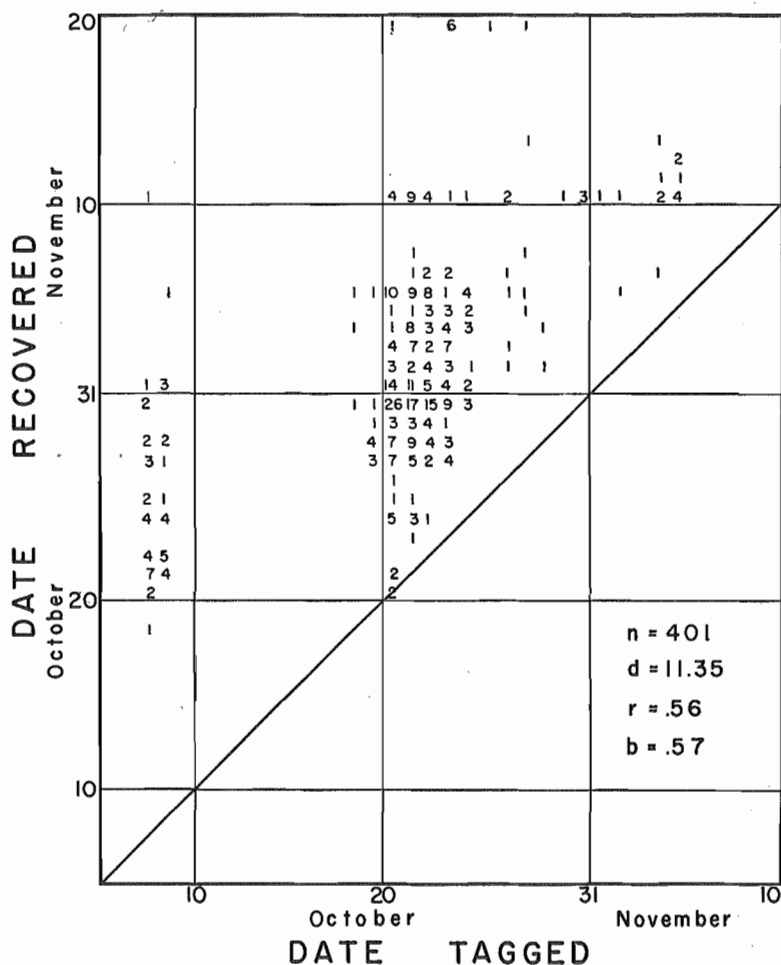
FIGURE 37. Recoveries by dates of tagging and recovery of fish tagged at the mouth of Weaver Creek and recovered as dead fish on the spawning grounds (all recoveries), 1941.

than fresh were delayed about five days beyond fresh recoveries while in Weaver Creek the delay averaged about ten days. However, in 1941, this extra delay averaged about twelve days at the Birkenhead and only seven at Weaver Creek. It does not seem profitable to investigate this point further at this time, however.

From Tables 34 and 35 it may be seen that there are revealed by our data no consistent differences between sexes in regard to rate of migration, confirming the conclusions from other experiments.

TABLE 34

Average Time Between Tagging and Recovery of Fish Tagged at the
Fence at the Mouth of Weaver Creek and Recovered
Dead on the Spawning Grounds, 1940

	Fresh Dead		Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	14	8.7	16	14.9	30	12.0
Females	147	8.9	93	19.0	240	12.8
Total	161	8.8	109	18.4	270	12.7

n = number of recoveries
d = average days between tagging and recovery

TABLE 35

Average Time Between Tagging and Recovery of Fish Tagged at the
Fence at the Mouth of Weaver Creek and Recovered
Dead on the Spawning Grounds, 1941

	Fresh Dead		Dead Other Than Fresh		All Recoveries	
	n	d	n	d	n	d
Males	66	10.6	29	18.4	95	13.0
Females	221	8.9	85	15.8	306	10.8
Total	287	9.3	114	16.5	401	11.4

n = number of recoveries
d = average days between tagging and recovery

Harrison Rapids Population

Only in 1941 did we systematically patrol the beaches below and adjacent to Harrison Rapids for recovering dead, spawned-out fish from the spawning grounds of the rapids. In that year 1380 carcasses were recovered, among which were 11 which had been tagged at Harrison Trap. Of these, two were tag-scarred fish, the tags having been lost. The remaining nine tags are too few to employ in a study of mixing during migration.

Of the nine tag recoveries, three were from fish recovered fresh. These three, two females and one male, had elapsed times of 2, 6, and 41 days between tagging and recovery. The fish recovered within 2 days was spawned-out when tagged, the one recovered within 6 days was a female ripe when tagged, while the fish out 41 days was a female tagged when she had green eggs.

Of the six fish recovered some time after death, three were tagged when green; these showed 29, 20, and 42 days between tagging and recovery. The remaining three consisted of two ripening and one ripe female when tagged; the elapsed times were 6, 9, and 12 days.

It appears that some, at least, of the Harrison Rapids spawners reach the region of the spawning grounds as much as a month or six weeks before spawning. The trap continued to catch fish of all stages of maturity from this run, which is to be expected since it was very close to the spawning grounds, and fish moving up and down the river adjacent to the spawning areas would be expected to be intercepted.

The situation on Harrison Rapids in 1941 was somewhat confused since, as we have noted earlier, a number of fish blockaded at Hell's Gate dropped down the Fraser and ascended the Harrison and died near the Harrison Rapids spawning grounds. Inasmuch, however, as the number of fish tagged at Harrison Trap from the Harrison Rapids run turned out to be insufficient to give a high enough tag-ratio that, with the percentage of recoveries made, we can make a reliable estimate of the run, this is not of practical importance, except that some of the short period recoveries noted above may have been Hell's Gate fish rather than Harrison Rapids spawners.

EFFECT OF TAGS ON SPEED OF MIGRATION

In an earlier chapter we have examined the available data for evidence of mortality during migration caused by the tags or by the tagging operation. Another effect that might result from tagging a salmon is to delay its journey to the spawning grounds, i.e., to decrease the speed of migration between the tagging point and the recovery point.

We may examine into this problem by comparing the average speed of migration between the tagging point and the recovery point with the average speed of migration of untagged fish. For the latter we do not have any precise measurement, of course, but in some cases, at least, we may identify a "mode" or a "peak" of migration as it proceeds up the river system to the spawning grounds and shows up again among the dead fish. If there is any very great discrepancy between the rate of migration of the tagged and the untagged fish, such a comparison, although not precise, should show it up. It should, however, be borne in mind that our own data are not very adequate for this kind of study, because both at the trap at the mouth of the Harrison River and at the fences in the Birkenhead River and Weaver Creek, the sampling was very uneven during the course of the run, so that the frequencies of occurrence of fish in the catches are not proportional to the number of migrants. Under these circumstances, the determination of the positions of modes is uncertain. Only rather large discrepancies between rates of migration of tagged and untagged fish would, therefore, be expected to be shown up by these data.

Birkenhead Run

For the Birkenhead run we have data on the numbers of fish captured daily at Harrison Trap, at the Skookumchuck, at the mouth of the Birkenhead and, for the dead fish, the numbers of dead fish drifting down against the upstream face of the fence each day. These data are plotted in Figures 38 to 40 as frequency histograms.

In 1939, no data exist for the Skookumchuck and the "dead against fence" were cut off perhaps at their peak in October by a flood which took out the fence. The mode at Harrison Trap on about August 23 may be doubtfully identified with the mode of captures at the Birkenhead fence, falling near September 20, and even more doubtfully with a mode of dead at the fence at October 16.

Similarly, in 1940, Figure 39, a doubtful mode may be indicated at Harrison Trap near August 20, and peaks at Skookumchuck August 27, Birkenhead Trap September 10, and for dead at the fence September 30.

For 1941, Figure 40, we may estimate the modes to be at Harrison August 15, Skookumchuck September 4, Birkenhead Trap September 23, and for dead at the fence about October 10.

From these values was prepared Table 36 which summarizes the indicated time elapsed between the different points. These values may be compared with the corresponding values from Table 24 for the recoveries of tagged fish. In general, this comparison is favorable to the hypothesis that the tagged fish were not delayed in their migration.
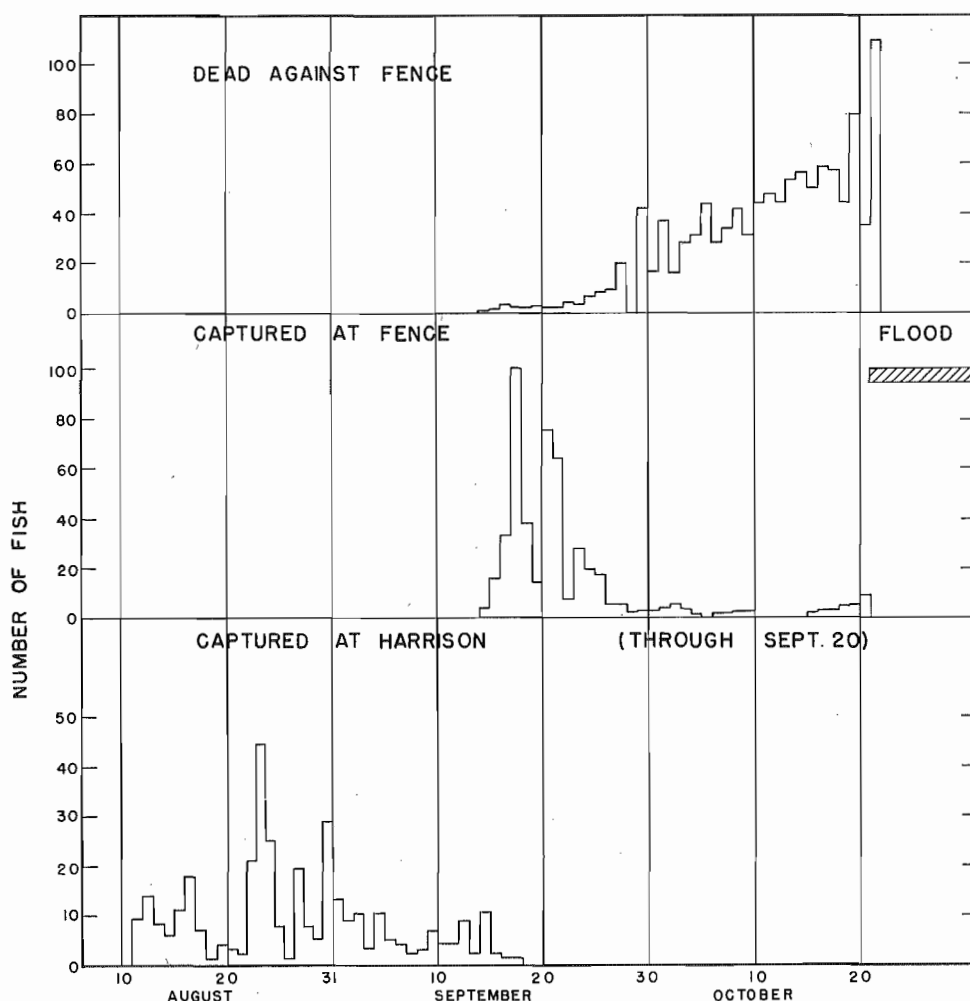
FIGURE 38. Frequency of occurrence of sockeye of the early (Birkenhead) run at various
points along the migration path, 1939.

For migration time between Harrison Trap and the various points above, no
major discrepancies are noted between the two tables, except for the migration
to Skookumchuck in 1940, which is deduced to be only eight days for the untagged
fish. Upon closer examination, it will be seen that 1940 is lower than the other
two years in respect to the deduced migration time of untagged fish from the
Harrison Trap to the Birkenhead Trap, and for the time elapsed between the
Harrison Trap and dead against the Birkenhead fence also. Probably the uncertain
value of August 20 for the mode at the Harrison Trap is erroneous, and should
be earlier. The elapsed time to "dead at Birkenhead fence" is in general longer
for the untagged fish than for the tagged.

As between Skookumchuck and the Birkenhead the data from the two tables
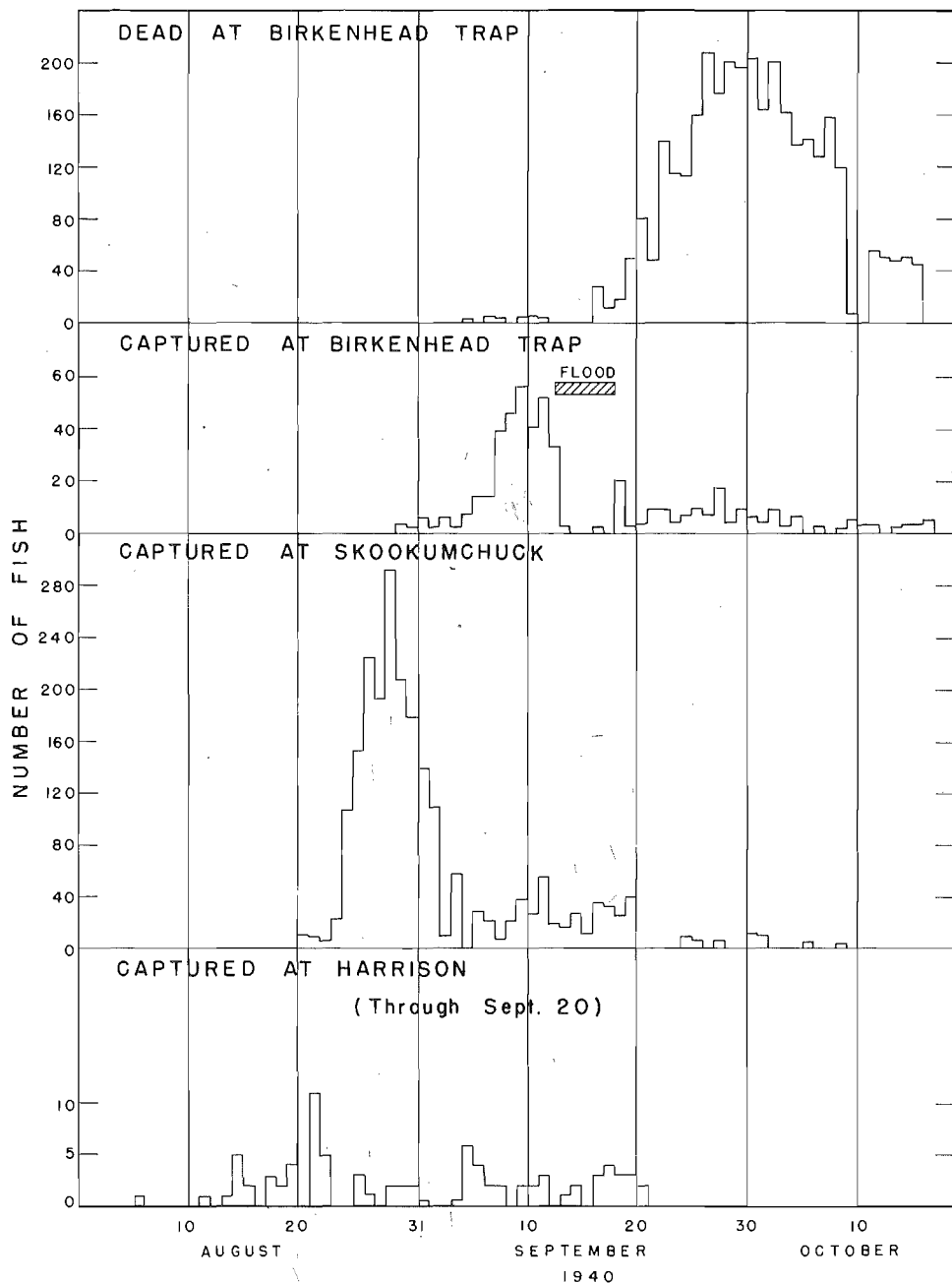
FIGURE 39. Frequency of occurrence of sockeye of the early (Birkenhead) run at various points along the migration path, 1940.
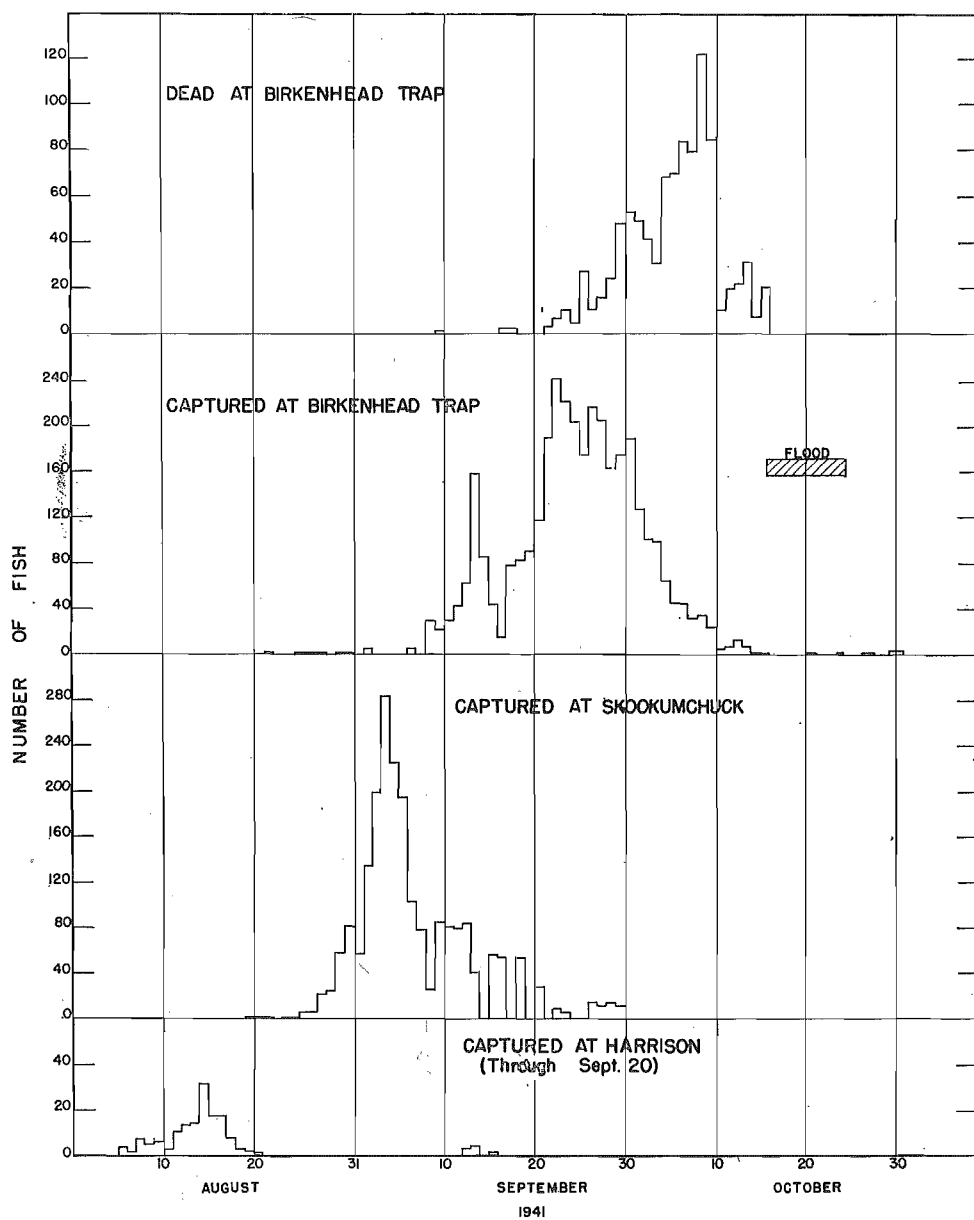
FIGURE 40. Frequency of occurrence of sockeye of the early (Birkenhead) run at various points along the migration path, 1941.

seem to agree quite well, although in the case of the dead fish, the untagged fish seem to have a somewhat longer time of migration.

In the case of the elapsed time between capture at the Birkenhead Trap and occurrence as dead fish there seems to be a longer time involved for the untagged than the tagged fish. This, as well as the similar phenomenon noted in the next

two paragraphs above, is perhaps to be attributed to the fact that the fish sampled as dead against the fence are not representative of the total run as regards time distribution of death after spawning.

In any event, there is no evidence here that the tagged fish which completed their journey took an appreciably longer time to do so than the rest of the run, and therefore such evidence as we have seems to show that the bearing of a tag does not slow the fish down. The data are not adequate for a final conclusion in this respect, however.

TABLE 36

Speed of Migration Estimated from Approximate Positions of
Modes of Frequency Distributions at Various Points
Along the Migration Path, Birkenhead Run

To	From		
	Harrison Trap	*Skookumchuck*	*Birkenhead Trap*
Skookumchuck			
1939	—		
1940	8		
1941	20		
Birkenhead Trap			
1939	28	—	
1940	22	14	
1941	39	19	
Dead at Birkenhead Fence			
1939	54	—	26
1940	42	34	20
1941	56	36	17

Weaver Creek Run

Similar data for the Weaver Creek run may be deduced from the frequency distributions of Figures 41 and 42, for the 1940 and 1941 seasons, respectively. The peak of the migration of the run at Harrison Trap in 1940 appears to have been about October 1. The peak at Weaver Creek fence is most doubtful because of the inundations of the fence right at the height of the run, but it may have been about October 19. The peak of occurrence of dead fish drifting down against the fence was, apparently, about November 4.

In 1941, we again were troubled by floods at Weaver Creek, making the determination of the peak of migration at the fence most doubtful. Modes may be identified from Figure 42 as October 9 at Harrison Trap, October 20 at Weaver Trap (doubtful, of course), and November 4 for dead fish against the fence.
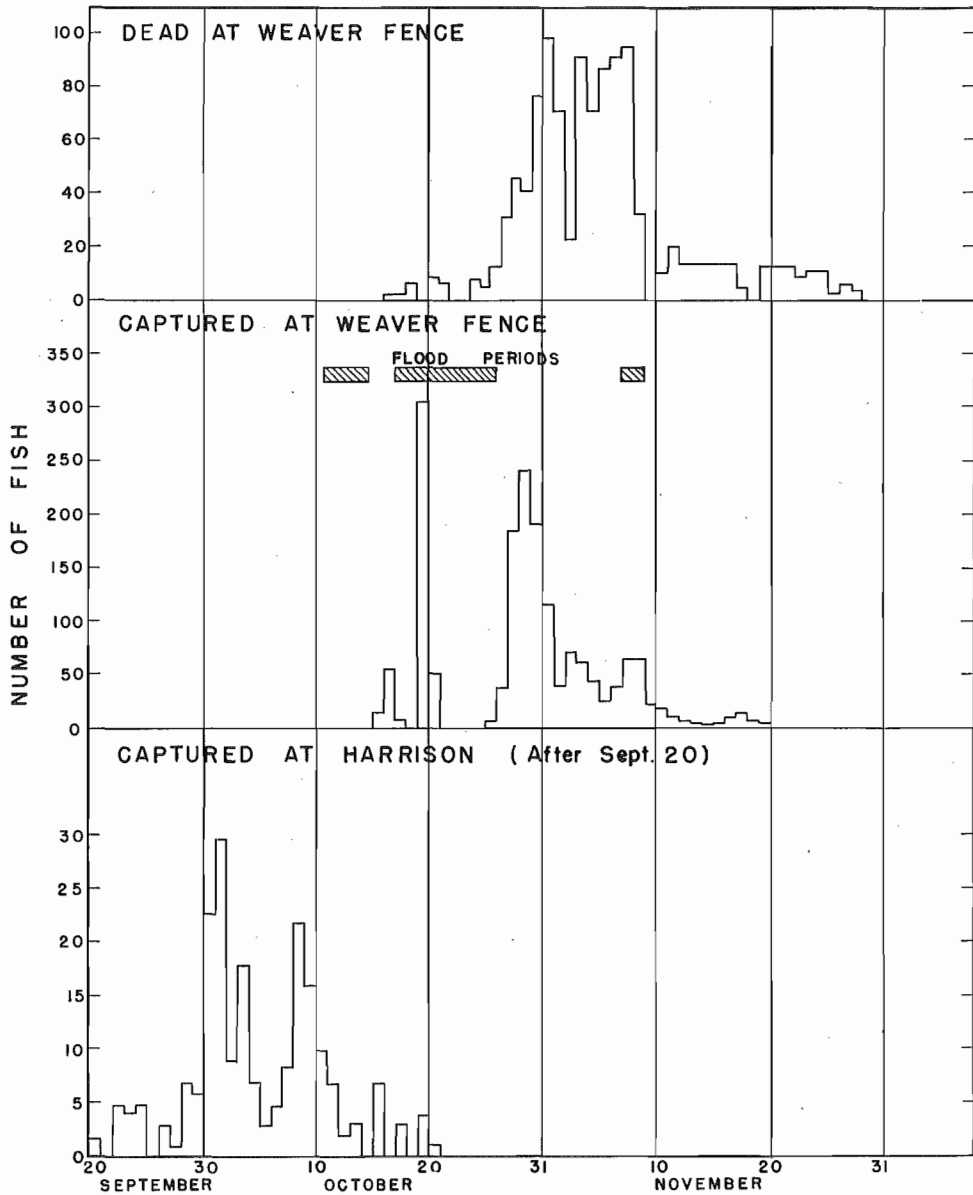
FIGURE 41. Frequency of occurrence of sockeye of the late (Weaver Creek) run at various points along the migration path, 1940.

The resulting values for time of migration between the different points are tabulated in Table 37 and may be compared with the corresponding values determined from recovery of tagged fish given in Table 31.

For the elapsed time between tagging at Weaver Creek fence and recovery after death after spawning, these values in Table 37 are similar, but in each year two or three days higher than the corresponding values of Table 31 for tagged fish.
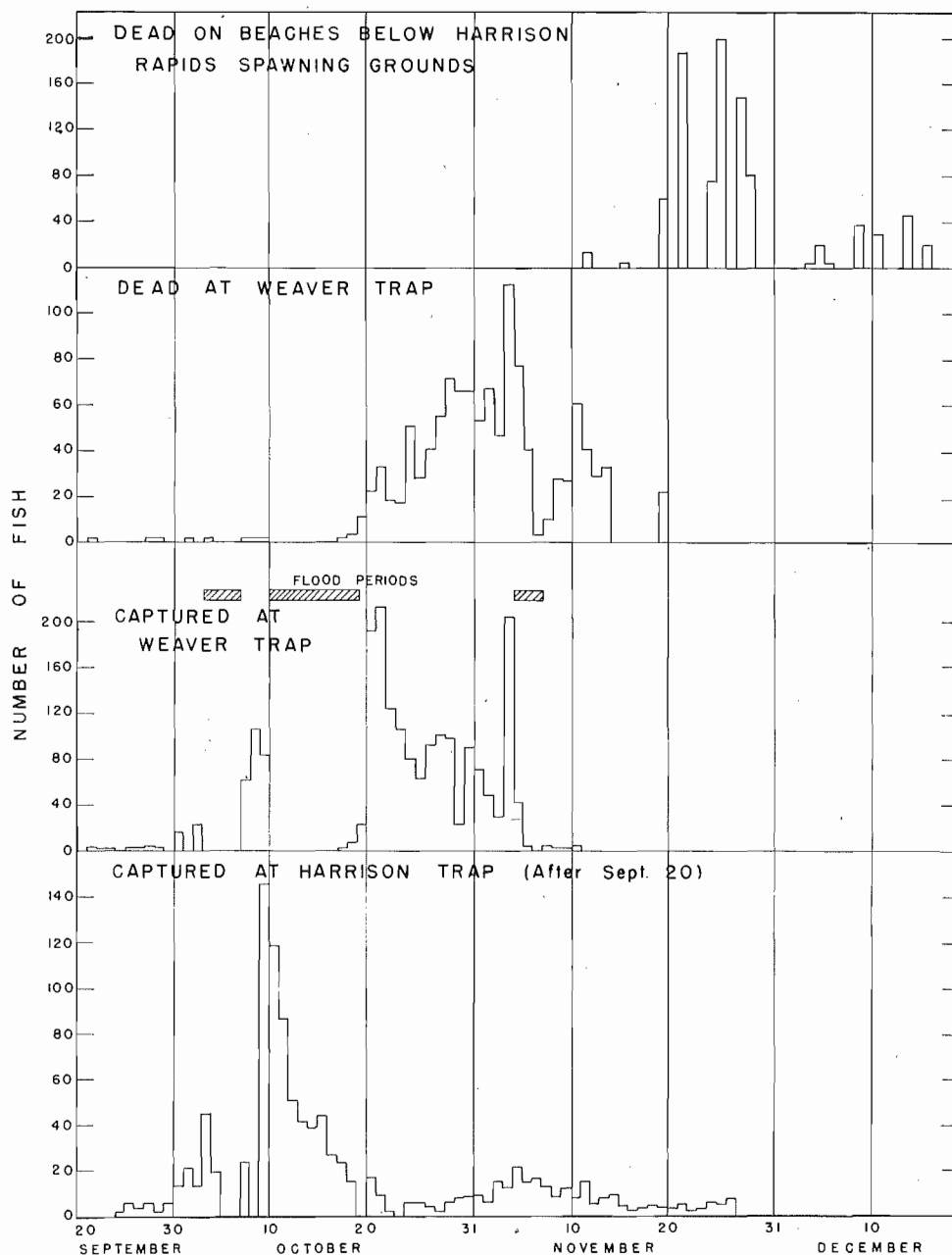
FIGURE 42. Frequency of occurrence of sockeye of the late runs (Weaver Creek and Harrison Rapids) at various points along their migration path, 1941.

In the case of elapsed time between Harrison Trap and occurrence either as live fish or dead fish at the Weaver Creek fence, the apparent elapsed time of migration, as inferred from the positions of the modes of frequency of occurrence at the places in question, is notably higher, especially so in 1940, than the values obtained from recovery of tagged fish, given in Table 31. The reason for this is most likely attributable to the fact that, as we have shown in Tables 20 and 21, the Harrison Trap fished with very much higher efficiency on the early part of the Weaver Creek run in 1940 than on the later part, and a similar but less marked difference was evident also in 1941. Such a differential efficiency of the trap would cause the modes of frequency of capture to occur earlier than the peak of actual migration past the trap. The modes in the bottom panels of Figures 41 and 42 are doubtless too early as a result of this.

In any event, we must again conclude that there is no good evidence here that the tagged fish which reached the spawning stream were delayed in their migration by tagging, although admittedly the data available for examining this point are far from adequate.

TABLE 37

Speed of Migration Estimated from Approximate Positions of Modes of
Frequency Distributions at Various Points Along the
Migration Path, Weaver Creek Run

	From	
To	Harrison Trap	Weaver Creek Trap
Weaver Creek Trap		
1940	18	
1941	11	
Dead at Weaver Creek Fence		
1940	33	15
1941	25	14

ANALYSIS OF THE DISTRIBUTION OF TAGS THROUGHOUT THE POPULATION AND OF THE EVENNESS OF SAMPLING FOR TAG-RATIOS

Importance to Our Problem

We have seen in a previous chapter that while some mixing takes place between tagging and subsequent sampling, in all cases this mixing is incomplete, with the possible exception of the fish tagged at Harrison Trap and recovered at the Birkenhead River, which can be disregarded, because in that case the loss of tagged fish enroute is so great that a population calculation based on such an experiment is without value. Since in all the other situations investigated the mixing is incomplete, we cannot assume that our marked members are distributed throughout the population in a completely random manner.

In such a situation as this, where the population does not mix completely between the initial tagging and subsequent sampling for tag ratios, the discussion of the theory of the "changing population" (page 17) will apply. It will be recalled that it was found that if the tags are uniformly distributed throughout the population, regardless of how the subsequent sampling is done, the tag-ratios in the samples will equal the tag-ratio in the population as a whole, except for random error, and the theory of the simple case, where the population is completely mixed, may be applied in making a population estimate. Likewise, it was shown that if the sampling of the population for tag-ratios is uniform over all parts of the population, so that each member has the same chance of being included in the sampling, the tag-ratio of the sum of all the samples will approximate, within the error of random sampling, the tag-ratio in the whole population, and, therefore, in this case also the problem of estimation reverts to the simple case. It thus becomes of importance to see whether in practice sufficient "evenness" of tagging or subsequent sampling is obtained so that the theory of the simple case may be employed in making the population estimate, or whether the stratification of the population may also need to be taken into account.

We have several kinds of samples available for estimating tag-ratios, as discussed earlier in the section on "methods of collection and sources of data". It will be of value to compare results from these different kinds of samples, each of which has certain advantages and disadvantages.

Because of the very large amount of computation necessary to effect a fairly complete analysis, and because the data from a single year bring out the important features of the problem, the analysis of this chapter has been confined to the single season of 1940, except in the case of the Harrison tagging experiments on the Weaver Creek run, the 1940 results of which were sufficiently anomalous that study of the 1941 data seemed desirable. It will be seen in the next chapter, also, that by comparing the population values arrived at by computations based on alternative hypotheses the major conclusions from analyses of the 1940 data are also confirmed by the 1941 experiments.

Birkenhead Population — Skookumchuck Experiments

The tagging data for these experiments and the methods of subsequent sampling for tag-ratios of the fish in the Birkenhead River have also already been described. Three kinds of samples are available for estimating Skookumchuck tag-ratios among Birkenhead spawners: live fish taken at the Birkenhead trap, counts of live fish on the spawning grounds, and dead fish samples. We will deal first with the dead fish.

Dead fish samples

The dead fish samples were obtained in two ways, first the dead fish against the upstream side of the fence, and second dead fish on the banks and bottom of the river. The former were removed and tabulated each day when the fence was cleaned, while the latter were recovered on patrols of the stream, as earlier discussed.

In Table 38 is given a recapitulation by statistical areas of all the Skookumchuck tag-ratio data from Birkenhead dead fish. It will be observed that an appreciable number of the recoveries of tagged fish consisted of specimens from which the tag was gone, only the characteristic scar being present. These tag losses are mostly the result of Indian gaff-hook fishing. As noted earlier, the Indian fishermen gaff many more fish than they use, throwing back those not wanted, although keeping as souvenirs some of the tags from unwanted fish. This, it was found, does not significantly affect the tag-ratio if both tags and tag scars are counted as tagged fish. In Table 39 is made a comparison of the tag-ratios among Indian-caught (and retained) fish and among the dead fish samples. The "tagged" include both tags and tag scars in each case. Jack sockeye have been excluded because the Indians take only large fish and there is also, as we will show later, a difference in the tag-ratios among large fish and jacks. The tag-ratio among the Indian-caught fish in this table is higher than that of the dead fish samples, but a Chi-square test indicates that this difference is of doubtful significance. Comparing the tag-ratios of the Indian catch with the tag-ratios among fresh carcasses only (a restricted category of the dead fish samples) we find the Indian catch again to have a higher tag-ratio, but not significantly so, as shown in Table 40. Effect of the Indian fishing on the tag-ratio seems to be either absent or sufficiently slight as to be within the range of random error of these experiments, if we include both tagged and tag-scarred fish among the "tagged".

HOMOGENEITY OF TAG-RATIO DATA

In Table 41 are tabulated the number of fish tagged of each sex category at the Skookumchuck and the recoveries made from dead fish samples in the Birkenhead, and from the basic data have been computed and tabulated the rates of recovery and the tag-ratios in each case. (In this table we have tabulated both the tag-ratio and its reciprocal, the "fish per tag". In subsequent tables the "fish per tag" is usually the value tabulated, because it avoids small decimal values and is perhaps easier to visualize than the tag-ratio itself). It appears that the recovery rates and tag-ratios for the two sexes of large fish were similar, but that the tag-

TABLE 38

Summary by Sexes and Areas of Skookumchuck Tag-Ratio Data Obtained
From Birkenhead River Dead Fish
1940

	MALE		FEMALE		JACKS		TOTAL	
Area	*Total*	*Tagged**	*Total*	*Tagged*	*Total*	*Tagged*	*Total*	*Tagged*
I	250	14+0	328	18+0	39	1+0	617	33+0
Fence . . .	1281	77+9	1701	108+7	397	9+0	3379	194+16
II	560	21+0	868	51+5	68	1+0	1496	73+5
III	31	1+0	56	4+0	8	0+0	95	5+0
IV to X	37	2+0	69	3+0	5	0+0	111	5+0
Total	2159	115+9	3022	184+12	517	11+0	5698	310+21

*The two numbers given are tags and tag scars. Thus, 77+9 means 77 tags plus 9 tag scars.

TABLE 39

Comparison of Skookumchuck Tag-ratios Among Indian-caught Fish
and Among Samples of Dead Large Fish
1940

	Untagged	*Tagged*	*Total*	*Expected Untagged*	*Expected Tagged*	*Chi-Square*
Dead in River	4861	320	5181	4850.14	330.86	.3808
Indian Catch	402	39	441	412.84	28.16	4.4575
Totals	5263	359	5622	5262.98	359.02	4.8383

Chi-square $=$ 4.8383
p $=$ .028

TABLE 40

Comparison of Skookumchuck Tag-ratios Among Indian-caught Fish
and Among Fresh Dead Samples
1940

	Untagged	*Tagged*	*Total*	*Expected Untagged*	*Expected Tagged*	*Chi-Square*
Fresh Dead in River	3216	219	3435	3206.36	228.64	0.4354
Indian Catch	402	39	441	411.65	29.35	3.3990
Totals	3618	258	3876			3.8344

Chi-square $=$ 3.8344
$df =$ 1
$p =$ .052

ratio and rate of recovery were lower for the jacks than for the larger fish. In order to test this objectively, and in order to examine the data for internal homo-geneity in other respects than with regard to sex and size, several different tests of homogeneity have been made.

In Table 42 the data are tabulated and tested for homogeneity with respect to sex category and statistical area of recovery. The probability value of .012 obtained indicates that the various sub-samples could scarcely have been drawn from a single homogeneous population and, since the greater share of the total Chi-square is contributed by the samples of jacks, we suspect this to be due to the tag-ratio difference between these and the larger fish. Pooling the data from the several statistical areas for each sex category it is found that there is less than one chance in a thousand that all three samples could have been drawn from a single homogeneous population. That this is due to the significantly lower tag-ratio of the jacks is shown by Table 43 wherein the data for the two sex categories of large fish alone are tested, and from which it may be seen that both the pooled data for each of the two sexes and the samples from separate statistical areas are such that they could have been drawn from a single homogeneous population.

It appears that there were no detectable differences in tag-ratios in different parts of the stream, and that large males and large females had the same tag-ratios, within limits of random error, but that the jacks had a significantly lower tag-ratio than the larger fish.

In order to determine whether the tag-ratio data are also homogeneous with respect to time of recovery, Tables 44, 45 and 46 have been constructed. In these tables the data for large fish have been partitioned according to date of recovery, first for all data (Table 44) and then, since that showed marked heterogeneity, for each sex separately. In both cases we are led to the conclusion that the samples for different weeks cannot be regarded as having been drawn from a homogeneous population as regards tag-ratios.

TABLE 41

Rates of Recovery of Skookumchuck Tags from Dead Fish in the Birkenhead and Average Tag-ratio, 1940

	Jacks	Males	Females	All Fish
Total tagged at Skookumchuck	161	826	1159	2146
Tagged fish in samples	11	124	196	331
Total fish in samples	517	2159	3022	5698
Per cent recovery	6.9	15.0	16.9	15.3
Tag-ratio	.0213	.0574	.0648	.0598
Fish per tag	47.0	17.4	15.4	16.7

TABLE 42

Test of Homogeneity of Skookumchuck Tag-ratio Samples,
Birkenhead Dead Fish, Segregated by Sex and Area
1940

	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
LARGE MALES						
Area I	236	14	250	235.48	14.52	.0197
Fence	1195	86	1281	1206.59	74.41	1.9165
Area II	539	21	560	527.47	32.53	4.3387
Areas III to X . . .	65	3	68	64.05	3.95	.2483
Total						7.2432
Pooled	2035	124	2159	2033.56	125.44	.0175
LARGE FEMALES						
Area I	310	18	328	308.95	19.05	.0516
Fence	1586	115	1701	1602.19	98.81	2.8163
Area II	812	56	868	817.52	50.42	1.3216
Areas III to X . . .	118	7	125	117.74	7.26	.0098
Total						4.2093
Pooled	2826	196	3022	2846.42	175.58	2.5212
JACK MALES						
Area I	38	1	39	36.73	2.27	.7544
Fence	388	9	397	373.94	23.06	9.1013
Area II	67	1	68	64.05	3.95	2.3391
Areas III to X . . .	13	0	13	12.24	.76	.8072
Total						13.0020
Pooled	506	11	517	486.96	30.04	12.8123
Grand Total	5367	331	5698			24.4545

	d.f.	Chi-square	P
All sexes and areas.............................	11	24.4545	.012
Between sexes	2	15.3510	<.001

From the last column of Table 44 it may be seen that the tag-ratio decreased rather continuously throughout the season for both sexes of large fish. This may be inferred to be the result of uneven tagging at Skookumchuck. Since there has been shown (Table 24) to be a good correlation between date of tagging and date of recovery, it is reasonable to presume that the trend of tag-ratios exhibited by the Birkenhead dead fish is correlated with a similar trend in the tagging at Skookumchuck.

It has been demonstrated, then, that, probably as a result of non-uniform tagging at Skookumchuck, the tag-ratios in the Birkenhead changed throughout the season; that the tag-ratios for jacks is different from that for large fish; that the difference between tag-ratios for large males and large females is not signifi-

cant; and that the sockeye were distributed within the Birkenhead in such a manner that no differences could be detected between tag-ratios from different parts of the river.

UNIFORMITY OF RECOVERY RATE

Again referring to Table 41, the rate of recovery of jacks may be seen to have been much lower than that of large fish. Since both as regards tag-ratio and rate of recovery the jacks differ from the large fish, they will have to be considered separately in any population calculation based on these data.

In order to determine whether the different parts of the population of large sockeye, as it passes the Skookumchuck, are later equally represented in the Birkenhead fish samples, the percentage recoveries from different groups of tag dates have been compared. In Table 47, the Skookumchuck tag liberations and recoveries have been segregated by four-day tagging periods and tested for homogeneity. Obviously they form a heterogenous series.

TABLE 43

Test of Homogeneity of Skookumchuck Tag-ratio Samples,
Birkenhead Dead Fish, Segregated by Sex and Area
Large Sockeye Only
1940

	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
MALES						
Area I	236	14	250	234.56	15.44	.143
Fence	1195	86	1281	1201.88	79.12	.633
Area II	539	21	560	525.41	34.59	5.969
Areas III to X . . .	65	3	68	63.80	4.20	.366
Total						7.111
Pooled	2035	124	2159	2025.65	133.35	.699
FEMALES						
Area I	310	18	328	307.74	20.26	.269
Fence	1586	115	1701	1595.94	105.06	1.000
Area II	812	56	868	814.39	53.61	.113
Areas III to X . . .	118	7	125	117.28	7.22	.071
Total						1.453
Pooled	2826	196	3022	2835.35	186.65	.499
Grand Total	4861	320	5181			8.564

	d.f.	Chi-square	P.
All sexes and areas............	7	8.564	.29
Between sexes	1	1.198	.28

TABLE 44

Test of Homogeneity of Skookumchuck Tag-ratio Samples,
Birkenhead Dead Fish, Segregated by Sex and
Time of Recovery, Large Fish Only
1940

Week Ending	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square	Fish Per Tag
LARGE MALES							
Sept. 21, 1940	112	11	123	115.34	7.66	1.5530	11.2
28	552	48	600	562.65	37.35	3.2383	12.5
Oct. 5, 1940	897	47	944	885.24	58.76	2.5098	20.0
12	373	15	388	363.85	24.15	3.6969	25.8
19	88	3	91	85.34	5.66	1.3330	30.3
LARGE FEMALES							
Sept. 21, 1940	89	6	95	89.09	5.91	.0015	15.8
28	535	60	595	557.96	37.04	15.1770	9.9
Oct. 5, 1940	1175	83	1258	1179.70	78.30	.3008	15.2
12	743	35	778	729.57	48.43	3.9714	22.2
19	257	12	269	252.26	16.74	1.4313	22.4
Totals	4821	320	5141			33.213	

$d.f. = 9$
Chi-square $= 33.213$
$P < .001$

TABLE 45

Test of Homogeneity of Skookumchuck Tag-ratio Samples,
Birkenhead Dead Fish, Segregated by Time of Recovery
Large Females Only
1940

Week Ending	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Sept. 21, 1940	89	6	95	88.78	6.22	.0083
28	535	60	595	556.06	38.94	12.1875
Oct. 5, 1940	1175	83	1258	1175.67	82.33	.0059
12	743	35	778	727.09	50.91	5.3202
19	257	12	269	251.40	17.60	1.9065
Totals	2799	196	2995			19.4284

Chi-square $= 19.4284$
$d.f. = 4$
$P < .001$

TABLE 46

Test of Homogeneity of Skookumchuck Tag-ratio Samples,
Birkenhead Dead Fish, Segregated by Time of Recovery
Large Males Only
1940

Week Ending	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Sept. 21, 1940	112	11	123	115.88	7.12	2.5905
28	552	48	600	565.33	34.67	5.4394
Oct. 5, 1940	897	47	944	889.45	54.55	1.1091
12	373	15	388	365.58	22.42	2.6063
19	88	3	91	85.74	5.26	1.0306
Totals	2022	124	2146			12.7759

Chi-square = 12.7759
d.f. = 4
P = .012

TABLE 47

Test of Homogeneity of Skookumchuck Percentage Tag Recoveries
Among Birkenhead Dead Fish Samples, Segregated by
Time of Tagging, Large Fish Only
1940

Tagging Date	Tags Recovered	Tags Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square
Aug. 20 - 23	5	39	44	6.63	37.37	.4717
24 - 27	117	543	660	99.42	560.58	3.6598
28 - 31	128	644	772	116.29	655.71	1.3882
Sept. 1 - 4	21	144	165	24.85	140.15	.7021
5 - 8	6	49	55	8.28	46.72	.7390
9 - 12	7	94	101	15.21	85.79	5.2171
13 - 16	2	68	70	10.54	59.46	8.1460
17 - 20	12	69	81	12.20	68.80	.0037
21 - Oct. 7 . .	1	36	37	5.57	31.43	4.4139
Totals	299	1686	1985			24.7415

d.f. = 8
Chi-square = 24.7415
P =   .0017

TABLE 48

Test of Homogeneity of Skookumchuck Percentage Tag Recoveries
Birkenhead Dead Fish, Segregated by Time of
Tagging, Large Fresh Dead Only
1940

Tagging Date	Tags Recovered	Tags Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square
Aug. 20 - 23	4	40	44	4.57	39.43	.0793
24 - 27	72	588	660	68.49	591.51	.2007
28 - 31	88	684	772	80.12	691.88	.8647
Sept. 1 - 4	17	148	165	17.12	147.88	.0009
5 - 8	4	51	55	5.71	49.29	.5714
9 - 12	7	94	101	10.48	90.52	1.2884
13 - 16	2	68	70	7.26	62.74	4.2520
17 - 20	11	70	81	8.41	72.59	.8900
21 - Oct. 7 . .	1	36	37	3.84	33.16	2.3436
Totals	206	1779	1985			10.4910

$$d.f. = 8$$
$$Chi\text{-}square = 10.4910$$
$$P = .23$$

The differential rate of recovery of different groups of Skookumchuck tags might, conceivably, be the result of either of two factors: first, that the fish from certain tag groups migrated in greater proportion to other streams, and second, that the fish migrated in equal proportion to the Birkenhead, but that the sampling in the Birkenhead was uneven throughout the season. The data for fresh dead fish alone validate the latter condition. When we compare the rates of recovery from fresh carcasses only of the tags for four-day tagging periods (Table 48) we find that they form a very homogeneous series of samples. If there were a differential migration to other streams than the Birkenhead, we would not expect the recoveries in the Birkenhead to be homogeneous for fresh fish. Therefore, it seems valid to conclude that when *all* dead fish are considered, the differential rate of recovery shown is the result of uneven sampling in the Birkenhead.

As to why the fresh fish samples are homogeneous while the sample for all fish is not, a closer examination of the data shed some light. In Table 49 are tabulated the per cent recovery in the Birkenhead of tags liberated at Skookum-chuck, both for all dead and fresh dead samples, together with the difference in rates for each period. It is to be seen that for early tag groups the per cent recovery from all dead is greater than from fresh dead alone, and that the difference decreases as the season progresses. The explanation for this is connected with the mechanics of sampling. There exists, as we have shown, a correlation between date of sampling and date of recovery. In recovering dead fish, the spawning area was patrolled periodically. In the case of fresh dead, other factors being equal, the probability of recovery is the same for any group, because they have

the opportunity of being recovered as fresh on only one patrol. Fish, however, which are not recovered as fresh may be recovered on subsequent patrols as tainted carcasses, rank carcasses, or skeletons. Fish which die earliest are exposed to sampling more times than fish which die later, and the probability of recovery of early fish is thereby increased over that of later fish.

TABLE 49

Per cent Recovery of Skookumchuck Tags from Large Dead Sockeye in the Birkenhead River, by Four Day Tagging Periods
1940

Tag Date		All Dead %	Fresh Dead %	Difference
August	20 - 23	11.4	9.1	2.3
	24 - 27	17.7	10.9	6.8
	28 - 31	16.6	11.4	5.2
Sept.	1 - 4	12.7	10.3	2.4
	5 - 8	10.9	7.3	3.6
	9 - 12	6.9	6.9	0
	13 - 16	2.9	2.9	0
	17 - 20	14.8	13.6	1.2
	21 - October 7	2.7	2.7	0
Total		15.16	10.38	

Live fish counts

A rapid means of determining the tag-ratio of fish on the spawning grounds is the counting of tagged and untagged fish among the live spawners. This method involves less work than dead fish sampling and is relatively rapid, but has some drawbacks. In the first place, the data cannot be segregated by sexes reliably. Also, since the numbers of the tags are not ascertained, it is not possible to partition the data by time of tagging. There is also some question as to whether the tag-ratios are not biased by virtue of the semi-subjective nature of the observations. The estimates are ordinarily made in the following manner: The observer walks slowly along the stream and counts the number of tagged fish he sees and the number of untagged fish seen, which are observed clearly enough so that a tag could have been seen if it were present. Some of the fish in the stream, while visible, are seen at such a distance, or to such poor advantage otherwise, that a tag could not be seen if it were present. In this case the fish is not included in the tag-ratio count. Since the retention or rejection of such a fish from the count involves the judgment of the observer, there is some opportunity for bias.

In order to throw some light on the adequacy of live fish counts for estimating tag-ratios, the Birkenhead observers made counts over the entire spawning area at approximately weekly intervals. These counts may be compared with the dead fish samples in order to determine whether population estimates based on such counts would give a reliable estimate of the population.

The live fish counts, as regards Skookumchuck tag-ratios, are summarized in Table 50. In Table 51 we have compared the counts made during the several periods to determine whether they can be regarded as random samples from a homogeneous population; it is shown that they may be so regarded.

In Tables 52 and 53, we have compared the tag-ratio estimates from the total of live fish counts with the tag-ratio estimates from the counts of all dead fish and large dead fish, respectively. It is seen that the differences are not significant in either case.

TABLE 50

Counts of Skookumchuck Tag-ratios
on Birkenhead Live Fish
1940

Date of Count		Untagged	Tagged	Total	Fish per Tag
September	5 - 6	15	0	15	——
	16 - 20	482	40	522	13.05
	23 - 25	1109	69	1178	17.07
October	1 - 5	1040	50	1090	21.80
	8 - 12	765	45	810	18.00
	15 - 17	257	12	269	22.42
Totals		3668	216	3884	17.98

TABLE 51

Test of Homogeneity of Counts of Skookumchuck
Tag-ratios on Birkenhead Live Fish
1940

Date		Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Sept.	5 - 6	15	0	15	14.17	.83	.8786
	11 - 20	482	40	522	492.97	29.03	4.3895
	23 - 25	1109	69	1178	1112.49	65.51	.1969
Oct.	1 - 5	1040	50	1090	1029.39	60.61	1.9667
	8 - 12	765	45	810	764.96	45.04	.0000
	15 - 17	257	12	269	254.04	14.96	.6202
Totals		3668	216	3884			8.0519

$$d.f. = 5$$
$$\text{Chi-square} = 8.0519$$
$$P = .15$$

These analyses demonstrate that the live fish counts will give us as good an estimate of the Skookumchuck population as would be obtained from the combined dead fish data. It has been shown previously that the dead fish data exhibit some non-homogeneity both with regard to tagging and sampling, and due regard to this may improve the population estimate. However, if the tagging had been even, the live counts would give as adequate an estimate of the population as would the dead fish counts. Under the actual conditions, the live counts would give a fairly good estimate of the population, albeit somewhat high (as will be shown in the next chapter).

TABLE 52

Comparison of Skookumchuck Tag-ratios from Birkenhead
Live Counts and from all Birkenhead Dead Fish
1940

	Tagged	Untagged	Total	Expected Tagged	Expected Untagged	Chi-Square
Total dead (all fish)	331	5367	5698	325.28	5372.72	.1067
Total live counts	216	3668	3884	221.72	3662.28	.1565
Totals	547	9035	9582			.2632

Chi-square = .2632
$d.f. = 1$
$P = .64$

TABLE 53

Comparison of Skookumchuck Tag-ratios from Birkenhead
Live Counts and Birkenhead Samples of
Dead Large Sockeye
1940

	Tagged	Untagged	Total	Expected Tagged	Expected Untagged	Chi-Square
Total dead large fish	320	4861	5181	306.35	4874.65	.6464
Total live counts	216	3668	3884	229.66	3654.34	.8636
Totals	536	8529	9065			1.5100

Chi-square = 1.5100
$d.f. = 1$
$P = .22$

The live counts are, therefore, quite probably of some value in estimating the tag-ratio of a population where it is not feasible to utilize the dead fish sampling method.

Birkenhead trap catches

The catches of sockeye salmon in the Birkenhead Trap may also be regarded as samples of the tag-ratio for the Skookumchuck population. These samples offer theoretical advantages over the dead fish samples, in that there is no possibility of bias in the sampling as regards tagged and untagged individuals, tagged and untagged are easier to distinguish than on "old" carcasses, possible selection of the Indian gaff-hook fishery is less, the trap *might* sample more evenly (in point of fact it did not) throughout the season. The disadvantages of the trap catches during 1940 were the small number of fish thus examined, the selective nature of the trap regarding sexes, and the uneven sampling in regard to time. These factors are discussed later under "Birkenhead population—Birkenhead experiments".

The trap was not designed to retain jack sockeye, and therefore estimates can be made for large fish only. Although the trap was selective as regards males and females, this does not influence the tag-ratio estimate since, as shown in Table 54, there is no significant difference between the tag-ratios for males and females as estimated from the trap catches.

In comparing the tag-ratio sample furnished by the trap with the tag-ratio sample furnished by all the dead fish recovered on the spawning ground (Table 55) we find that the two samples show no difference. Therefore, the calculated Skookumchuck population from the Skookumchuck tag-ratios of the Birkenhead Trap catches would not be expected to be significantly different from that calculated from the tag-ratio data of the dead-fish samples, although the standard error of the most probable value calculated from the trap catches would be larger than that from the dead fish samples because of the smaller size of the sample in the former case.

TABLE 54

Test of Homogeneity of Skookumchuck Tag-ratio Data,
Birkenhead Trap Catches, Segregated by Sexes
1940

	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Male	290	23	313	293.97	19.03	.8818
Female	158	6	164	154.03	9.97	1.6831
Total	448	29	477			2.5649

Chi-square = 2.5649
$d.f. = 1$
$P = .11$

TABLE 55

Comparison of Skookumchuck Tag-ratio Data from the Birkenhead
Trap Catches and the Birkenhead Dead Fish Samples
1940

	Untagged	Tagged	Total	Expected Tagged	Expected Untagged	Chi-Square
Live in trap................	448	29	477	29.42	447.58	.0062
Dead samples	4861	320	5181	319.58	4861.32	.0005
Totals	5309	349	5658			.0067

Chi-square $=$ .0067
$d.f. = 1$
$P > .80$

The agreement of the tag-ratios from the trap catches and the dead fish
samples supports the hypothesis that sampling of the dead fish as carried out on
dead fish was not biased in regard to presence or absence of tags, since there is
no possibility of such bias in the trap catches.

Summary

In the foregoing we have studied the distribution of tags within the popu-
lation passing the Skookumchuck and the evenness of sampling of this population,
on the basis of tags put out at Skookumchuck and samples of the population in
the Birkenhead River.

It has been shown that the large males and large females had the same tag-
ratio, but that the jacks, of which a large number were present in the Upper
Lillooet during 1940, were not as frequently tagged as the larger fish. A good
agreement was found between average tag-ratios from different parts of the
Birkenhead River. However, it was found that the tag-ratios changed significantly
as the season progressed, probably as a result of uneven tagging at the Skookum-
chuck.

The rate of recovery of jacks was lower than that of larger fish. The rate of
recovery among large fish changed significantly in different parts of the season,
as a result of the mechanics of sampling, when all recoveries are considered, but
was homogeneous for fresh carcasses alone.

Average tag-ratios from Birkenhead dead fish agreed well with tag-ratios
from live counts and trap catches.

It appears that the Birkenhead run constitutes a uniform sample of the popu-
lation passing the Skookumchuck. However, due to uneven tagging at the Skook-
umchuck and uneven sampling in the Birkenhead, together with stratification of
the population shown earlier, samples from the Birkenhead cannot be assumed to
be random samples of the run, but account should be taken of the stratification
and unevenness in sampling in estimating the population.

Birkenhead Population — Birkenhead Experiments

It has been noted that only one jack sockeye was taken during the 1940 season, because the jacks could easily escape between the pickets of the trap. It may also be shown that the trap fished selectively with respect to the sex of the larger fish. In Table 56 the sex distribution of the large sockeye captured by the trap is compared with the sex distribution of the dead sockeye recovered from the spawning beds, and it is at once apparent that these sex distributions are very different from each other. At the same time, in Table 57, we have been able to demonstrate that the percentage recovery of large males and large females, as judged by the percentage recovery of tagged fish of each variety, are not statistically different. Therefore, it is to be concluded that the trap was quite selective, capturing a higher share of the males than of the females.

TABLE 56

Comparison of Sex Ratios of Birkenhead Trap Catches
with Sex Ratios of Dead Sockeye from the
Birkenhead Spawning Beds
1940

	Large Females	Large Males	Total	Expected Female	Expected Male	Chi-Square
Dead fish	3022	2159	5181	2917	2264	8.650
Trap	164	313	477	269	208	93.989
Totals	3186	2472	5658			102.639

Chi-square $=$ 102.639
d.f. $=$ 1
$P <$ .001

TABLE 57

Comparison of Rates of Recovery of Birkenhead
Tagged Fish, Segregated by Sexes
1940

	Recovered	Not Recovered	Total	% Recovered	Expected Recovered	Expected Not Recovered	Chi-Square
Large males	55	228	283	19.4	59.44	223.56	.4197
Large Females	37	118	155	23.9	32.56	122.44	.7664
Totals	92	346	438	21.0			1.1861

Chi-square $=$ 1.1861
d.f. $=$ 1
$P =$ .28

As has been pointed out previously, the total population can be calculated from the average tag-ratio and the total number of tagged fish liberated, providing that either the tags are uniformly distributed throughout the population or the sampling is uniform on all parts of the population. Both of these conditions may be tested statistically from the recovery data of the Birkenhead tag-ratio samples. The method of sampling both the dead fish and the live fish has been described before. We have two kinds of samples: dead fish from the spawning grounds and live fish counts.

Dead fish samples

The samples of dead fish from which the Birkenhead tag-ratio data are obtained are the same samples from which we have obtained the Skookumchuck tag-ratio data. In the original sampling, Skookumchuck tags and Birkenhead tags were tabulated separately, so that by proper recombination the ratios for either group can be obtained. As noted before, the data were kept so that they may be partitioned by time or by area within the river. The data, tabulated by sex and area, are shown in Table 58.

Since the tagging was carried out on large fish alone, and since we have already shown that the jacks are recovered at a different rate than the large sockeye, the following calculations and analyses are confined to large fish only, except where otherwise specified.

HOMOGENEITY OF TAG-RATIO SAMPLES

The first question we are interested in is whether the average tag-ratio of the samples is the same as the tag-ratio for the whole population; that is, whether the tags were evenly distributed over all parts of the population.

We have already shown that the trap fished selectively as between males and females. Therefore, we would not expect the tag-ratio for males and females to be the same. This is confirmed by Table 59, where it is shown that the tag-ratio for males is different from the tag-ratio for females. We will, therefore, treat the sexes separately.

TABLE 58

Birkenhead Dead Fish Recovery,
by Sex and Area
1940

Area	Male (large)			Female (large)			Jacks			Total		
	Total	Tag	Scar	Total	Tag	Scar	Total	Tag	Scar	Total	Tag	Scar
I	250	8	0	328	2	0	39	0	0	617	10	0
Fence	1281	34	5	1701	21	1	397	0	0	3379	55	6
II	560	5	2	868	10	1	68	0	0	1496	15	3
III	31	1	0	56	1	0	8	0	0	95	2	0
IV to X	37	0	0	69	1	0	5	0	0	111	1	0
Totals	2159	48	7	3022	35	2	517	0	0	5698	83	9

TABLE 59

Comparison of Birkenhead Tag-ratios
by Sexes (Large Sockeye)
1940

	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Large male	2104	55	2159	2120.66	38.34	7.370
Large female	2985	37	3022	2968.34	53.66	5.266
Totals	5089	92	5181			12.636

$$\text{Chi-square} = 12.636$$
$$d.f. = 1$$
$$P < .001$$

In regard to distribution within the stream, we would expect that the data might be homogeneous above the fence, but we would scarcely expect the tag-ratios for dead fish below the fence to be the same as those above the fence. The fence is the dividing line between Areas I and II, so that Area I includes all the fish below the fence, while all other fish are above the fence. In Tables 60 and 61 we have tested the homogeneity of the samples in regard to area of recovery. It is shown that the samples *including* Area I are homogeneous for each sex. There is no suggestion that the Area I tag-ratios are different from those for dead fish above the fence, and we must regard them as having been drawn from a population with the same tag-ratio as the population above the fence. This was not expected, but may be reasonably explained. First, a certain number of tagged fish went below the fence while alive, since it was not fish-tight at the bottom and since during part of each 24-hour period water went over the top when the fence was plugged with dead fish and debris; this was shown by observation of tagged live fish on the spawning grounds below the fence. Probably equally important, however, is the fact that a large share of the dead fish in Area I were composed of fish which spawned above the fence and drifted down to Area I as dead fish. It is believed that most of the spawners in Area I drifted out of the Birkenhead and into the Lillooet River where they were not recovered.

It has been shown that the Birkenhead tags were evenly distributed over the dead fish samples in regard to area of the river. The distribution in regard to different parts of the season does not show the same homogeneity. In Tables 62 and 63 the data have been partitioned by the date of recovery for each sex separately. The data for the males is markedly heterogeneous and that for the females is questionable as shown by these tables. The proportion of fish tagged decreased irregularly as the season progressed.

Samples of fresh dead, consisting of 1999 females with 24 tagged and 1436 males with 37 tagged, are insufficiently large to partition and test for homogeneity by area or time periods. However, it is of value to note that on the basis of the tag-ratios of all dead fish we would expect, if the fresh fish were a random sample of all dead, to find 36.6 tagged males and 24.5 tagged females among the fresh fish

samples. These numbers are so close to the actual values that it is not worthwhile to calculate values of chi-square. The fresh fish samples agree, then, with all samples in confirming that there was a difference in the tag-ratios of the two sexes attributable, of course, to the selectivity of the trap.

TABLE 60

Comparison of Birkenhead Tag-ratios from Large Male Dead Fish,
Segregated by Area of Recovery
1940

	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Area I	242	8	250	243.63	6.37	.428
Fence	1242	39	1281	1248.37	32.63	1.277
Area II	553	7	560	545.73	14.27	4.672
Area III to X	67	1	68	66.27	1.73	.316
Totals	2104	55	2159			6.693

$$d.f. = 3$$
$$\text{Chi-Square} = 6.693$$
$$P = .082$$

TABLE 61

Comparison of Birkenhead Tag-ratios from Large Female Dead Fish,
Segregated by Area of Recovery
1940

	Untagged	Tagged	Total	Expected Untagged	Expected Tagged	Chi-Square
Area I	326	2	328	323.98	4.02	1.0276
Fence	1679	22	1701	1680.17	20.83	.0665
Area II	857	11	868	857.37	10.63	.0131
Area III to X	123	2	125	123.47	1.53	.1462
Totals	2985	37	3022			1.2534

$$\text{Chi-square} = 1.2534$$
$$d.f. = 3$$
$$P = .72$$

TABLE 62

Comparison of Birkenhead Tag-ratio Samples of Dead Large Males,
Segregated by Date of Recovery
1940

Date of Recovery	Untagged	Tagged	Total	Fish Per Tag	Expected Untagged	Expected Tagged	Chi- Square
Week Ending							
September 7 and 14	11	2	13	6.5	12.67	.33	8.6713
September 21	108	15	123	8.2	119.87	3.13	46.1904
September 28	582	18	600	33.3	584.72	15.28	0.4968
October 5	929	15	944	62.9	919.95	24.05	3.4945
October 12	385	3	388	129.3	378.12	9.88	4.9161
October 19	89	2	91	45.5	88.68	2.32	0.0453
Total	2104	55	2159	39.2			63.8144

Chi-square $= 63.8144$
$d.f. = 5$
$P < .001$

TABLE 63

Comparison of Birkenhead Tag-ratios from Samples of Dead Large Females,
Segregated by Date of Recovery
1940

Date of Recovery	Untagged	Tagged	Total	Fish Per Tag	Expected Untagged	Expected Tagged	Chi- Square
Week Ending							
September 21	93	2	95	47.5	93.83	1.17	.5961
September 28	581	14	595	42.5	587.65	7.35	6.0920
October 5	1242	16	1258	78.6	1242.46	15.54	.0138
October 12	775	3	778	259.3	768.39	9.61	4.6034
October 19	267	2	269	134.5	265.68	3.32	.5314
Totals	2958	37	2995	80.9			11.8367

Chi-square $= 11.8367$
$d.f. = 4$
$P = .018$

UNIFORMITY OF RECOVERY RATE

In regard to the rate of recovery of different tag groups, the data are tested
in Tables 64 and 65 for each sex separately. For the males the rate of recovery
of different tag groups is the same for all groups, within the limits of chance
variation. For the females, however, it is doubtful whether the recovery rate
can be regarded as uniform.

Very likely if more tags had been put out we would find the same seasonal

recovery differentials here as in the case of the Skookumchuck experiment. Since the number of tags is smaller in this case and, therefore, possible chance variation is larger, differences observed are within or near to those which might occur by chance, but a larger group of tags might show differences greater than attributable to chance, as in the case of the Skookumchuck experiment.

TABLE 64

Comparison of Recovery Rates of Birkenhead Tags, Segregated by Date of Tagging (Large Males Only)
1940

Date of Tagging	Recovered	Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square
Week Ending						
August 31 and September 7	11	55	66	11.2	54.8	.004311
September 14	23	121	144	24.4	119.6	.09808
September 21	7	15	22	3.73	18.27	3.4522
September 28 and after	7	44	51	8.64	42.36	.37471
Totals	48	235	283			3.929301

Chi-square = 3.929301
d.f. = 3
P = .27

TABLE 65

Comparison of Recovery Rates of Birkenhead Tags, Segregated by Date of Tagging (Large Females Only)
1940

Date of Tagging	Recovered	Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square
Week Ending						
September 7	2	18	20	4.53	15.47	1.8268
September 14	24	44	68	15.35	52.65	6.294
September 21	2	8	10	2.26	7.74	.038635
September 28	3	29	32	7.22	24.78	3.2761
October 5 and 12	4	21	25	5.65	19.35	.6246
Totals	35	120	155			12.06013

Chi-square = 12.06013
d.f. = 4
P = .017

TABLE 66

Counts of Birkenhead Tag-ratios on Birkenhead Live Fish, with a Comparison of the Weighted Mean Tag-ratio and the Tag-ratio from Dead Fish Recoveries
1940

Date	Untagged	Tagged	Total	Fish Per Tag	Expected Untagged	Expected Tagged	Chi-Square
Sept. 5 - 6	15	3	18	6.00			
Sept. 16 - 20	482	13	495	38.08			
Sept. 23 - 25	1109	13	1122	86.31			
Oct. 1 - 5	1040	7	1047	149.57			
Oct. 8 - 12	765	3	768	256.00			
Oct. 15 - 17	257	5	262	52.40			
Total	3668	44	3712	84.36	3658.35	53.65	1.7612
Dead fish samples	5606	92	5698	61.93	5615.65	82.35	1.1474
Grand Totals	9274	136	9410				2.8636

Chi-square $= 2.8636$
$d.f. = 1$
$P = .09$

Live counts

In Table 66 we have tabulated the live counts made during the season and compared the weighted mean value of the tag-ratio with the value obtainable from the total of all the dead fish samples. The two agree within the limits to be expected by chance variation.

Thus, a population value calculated from the tag-ratios obtained from live counts would give the same result, within limits of random error, as the use of a tag-ratio obtained from all dead fish samples combined. Both such results would tend to be in error to a degree, of course, because the lower tag-ratio and lower visibility of jacks would tend to make the mean tag-ratio from either of these kinds of samples depart from the true value.

Summary

The tagged fish liberated at the Birkenhead trap were not a random sample of the population because the trap was not designed to catch the jacks, and because, among the large fish, the males were captured in greater numbers than females in proportion to their numbers in the total run, as judged from dead fish samples.

Tag-ratios from dead fish recovered from different statistical areas were homogeneous, even including the area below the fence, so that we may regard the tags as being evenly distributed over the portions of the population available as dead fish from different sections of the stream. The tag-ratios as between different parts of the season are heterogenous, however, indicating that the tags were not evenly distributed over the run with respect to time, and the mixing between tagging and sampling was insufficient to make up for this unevenness.

Recovery rates of groups of tagged fish liberated during different parts of the season indicate some possible heterogeneity among female fish, although males showed uniform recovery rates within limits of random error. Numbers of tags involved, being less than in the case of the Skookumchuck experiments, were probably insufficient to give a good determination of existing seasonal sampling differentials.

Live counts, as in the case of the Skookumchuck tagging, agree in average tag-ratio with the corresponding value from all dead fish samples. Thus the live-count tag-ratio would give as good a determination of population, within limits of random error, as would the tag-ratio from the total dead fish samples.

Weaver Creek Population — Weaver Creek Experiments

The tagging and marking data for these experiments were given previously and the methods of tagging, marking, and subsequent sampling have already been described and need not be repeated here. It will be recalled that considerable difficulty was had with flood waters at Weaver Creek in 1940, early in the season. As in the previously described experiments on the Birkenhead, we obtained tag-ratio data both from live counts and from recovery of dead, spawned-out fish. The data from the latter source will be dealt with first.

Dead fish samples

These samples were obtained from the upstream face of the fence and from the spawning grounds. Sockeye which died and drifted against the fence were removed and recorded each day. Recoveries were made from the spawning grounds above the fence on periodic patrols at intervals of not over one week. For the purpose of locating the recaptures by sections of the stream, Weaver Creek was divided into five arbitrary areas, numbered from the fence upstream (see Figure 10).

JACKS IN THE POPULATION

In marked contrast to the high percentage of jacks in the Upper Lillooet run, we recovered only 8 jacks from Weaver Creek among a total of 7816 dead sockeye. Since the percentage of jacks is so extremely small, they will be disregarded.

COMPARISON OF DISTRIBUTIONS OF TAGS AND FIN-MARKS

It has already been shown by means of Tables 22 and 23, discussed on page 92, that the tagged fish and fin-clipped fish were distributed throughout the stream and throughout the season in the same ratio as they were liberated at the fence. There is no evidence that the two groups suffered differential mortality or behaved differently. In subsequent analyses, where date of marking of recovered fish is not required, which information is not available for any but tagged fish, we will, therefore, combine the two kinds of marks, except where otherwise specified.

UNIFORMITY OF RECOVERY RATE

In order to determine whether the sampling was such that different segments of the population were subject to the same probability of recovery among the dead

fish samples, the rate of recovery of tags put out at different times of season, and on each of the two sexes, are compared in Table 67. It may be seen, first, that the average rate of recovery of males and females, when the data are pooled for the whole season, is uniform as between sexes. Also, within each sex, the data are such that they might very well have resulted from a uniform sampling system with the single exception of tne period November 1 to 5. During this period the rate of recovery was significantly lower than during the rest of the season, as evinced by the chi-square of 15.0330 for recoveries of females during this period, which would occur by chance less than once in a thousand times. (Tagged males liberated during this period are too few to expect the results to be significantly affected.) The lower recovery rate during this single period is sufficient to make the total chi-square greater than could reasonably be expected from purely random sampling. We are at a loss to explain this low rate of recovery during this particular period, but its reality cannot be doubted. Except for this one period the recovery rate of dead fish seems to have been rather uniform and of a magnitude of about 50%.

TABLE 67

Comparison of Rates of Recovery of Weaver Creek Tags,
Segregated by Date of Tagging
1940

Period of Tagging	Recovered	Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square	Per Cent Recovered
MALES[1]							
Oct. 15 - 20	19	14	33	15.83	17.17	1.2200	57.6
Oct. 27 - 31	7	8	15	7.19	7.81	.0096	46.7
Nov. 1 - 5	2	4	6	2.88	3.12	.5170	33.3
Nov. 6 - 19	2	2	4	1.92	2.08	.0063	50.0
Total						1.7529	
Pooled	30	28	58	27.81	30.19	.3312	51.7
FEMALES							
Oct. 15 - 20	55	59	114	54.67	59.33	.0037	48.2
Oct. 27 - 31	133	109	242	116.06	125.94	4.7510	55.0
Nov. 1 - 5	17	52	69	33.09	35.91	15.0330*	24.6
Nov. 6 - 10	31	34	65	31.17	33.83	.0017	47.7
Nov. 11 - 19	4	11	15	7.19	7.81	2.7182	26.7
Total						22.5076	
Pooled	240	265	505	242.18	262.82	.0376	47.5
Grand total	270	293	563				48.0

	d.f.	Chi-square	P
Sexes and period	8	24.2605	.002
Between sexes	1	.3688	.61

HOMOGENEITY OF MARK-RATIO DATA

Due to the loss of fish past the fence during the floods in the early part of the season, a much lower fraction of the earlier-migrating parts of the population was marked than of the later-migrating parts. From the last column of Table 69 it will be seen that for each sex the mark-ratio increased rather steadily throughout the season. As shown by the chi-square tests of this table the mark-ratios from different recovery periods were, for each sex, such that they cannot possibly be considered homogeneous, although those from males would be so if it were not for the very rapid increase in mark-ratio after November 16. The average mark-ratio for the two sexes was quite different, as shown in Table 68. This, again, is the result of the floods during the early part of the season coupled with the fact that males tend, on the average, to ascend the stream somewhat earlier than females.

In Weaver Creek the fish which enter the stream earliest tend to go furthest up. There may be a similar tendency in the Birkenhead, but the heavy concentration of spawners in the areas immediately above the fence makes this difficult to measure. In Weaver Creek, a large share of the population goes as far up the stream as possible, however, so it is quite easy to see even from cursory observa-tion that there is a concentration of spawners in the upper reaches early in the season, and that late in the season the fish are concentrated lower down the stream. As a result of this, and of the progressive increase in mark-ratio with date of recovery (which is, of course, correlated with date of tagging) there was a pro-gressive decrease of mark-ratio from area to area proceeding upstream, as shown by Table 70. The samples of each sex are heterogeneous as between areas of the stream.

The tags were, then, distributed throughout the population in a most uneven fashion in Weaver Creek in 1940, as one would predict from the fact that a large part of the population proceeded upstream during a period when our fence was inoperative. The mixing of fish between tagging and recovery was insufficient to smooth out this heterogeneity.

TABLE 68

Comparison of Mark-ratios of Male and Female Dead Sockeye from Weaver Creek
1940

	Marked	Unmarked	Total	Expected Marked	Expected Unmarked	Chi-Square	Fish Per Mark
Males	73	2097	2170	209.54	1960.46	98.4813	29.73
Females	681	4957	5638	544.41	5093.59	37.9048	8.28
Total	754	7054	7808			136.3861	

Chi-square $= 136.3861$
$d.f. = 1$
$P < .001$

TABLE 69

Tests of Homogeneity of Weaver Creek Mark-ratio Data, for Each Sex,
Segregated by Time of Recovery
1940

Recovery Date	Marked	Unmarked	Total	Expected Marked	Expected Unmarked	Chi-Square	Fish Per Mark
Week Ending							
MALES							
Oct. 19.......	1	59	60	2.02	57.98	.5329	60.00
Oct. 26.......	10	388	398	13.39	384.61	.8880	39.80
Nov. 2.........	17	698	715	24.05	690.95	2.1385	42.06
Nov. 9.........	28	804	832	27.99	804.01	.0000	29.71
Nov. 16......	5	103	108	3.63	104.37	.5349	21.60
Nov. 23......	3	20	23	.77	22.23	6.6820	7.67
Nov. 30...... and							
Dec. 7.........	9	25	34	1.14	32.86	56.0726	3.78
Total.......	73	2097	2170			66.8489	

Chi-square = 66.8489
$d.f. = 6$
$P < .001$

FEMALES							
*Oct. 19.......	2	54	56	6.76	49.24	3.8118	28.00
Oct. 26.......	25	701	726	87.69	638.31	50.9742	29.04
Nov. 2.........	62	1451	1513	182.75	1330.25	90.7448	24.40
Nov. 9.........	357	2187	2544	307.28	2236.72	9.1502	7.13
Nov. 16......	80	294	374	45.17	328.83	30.5461	4.68
Nov. 23......	80	123	203	24.52	178.48	142.7772	2.54
Nov. 30 and Dec. 7	75	147	222	26.81	195.19	98.5172	2.96
Total.......	681	4957	5638			426.5215	

Chi-square = 426.5215
$d.f. = 6$
$P < .001$

Live counts

Counts of tagged and untagged live fish on the spawning grounds were made at intervals of approximately one week throughout the season. These are presented in Table 71. Surprisingly enough, in spite of the uneven tagging, which is again reflected in these data, and the stratification of the population within the stream, the seasonal totals of these live counts seem to furnish a good estimate of the true average tag-ratio of the whole population. The "true" tag-ratio, from which the expected numbers in Table 71 were computed, was calculated from the total tags liberated and the total population calculated by correcting for sampling differentials between strata by means of the theory of the changing population, formula (25). This amounts to the average tag-ratio of all dead fish weighted for any differences in sampling of different strata. As will be shown in the sequel, however, (Table 90) we might equally well have employed the unweighted tag-ratio data, since it

TABLE 70

Tests of Homogeneity of Weaver Creek Mark-ratio Data, for Each Sex,
Segregated by Areas of Recovery
1940

Area	Unmarked	Marked	Total	Expected Unmarked	Expected Marked	Chi-Square	Fish Per Mark
MALES							
Fence..........	246	25	271	261.88	9.12	28.6136	10.84
Area I........	432	26	458	442.59	15.41	7.5309	17.62
Area II.......	356	8	364	351.76	12.24	1.5198	45.50
Area III.....	373	7	380	367.22	12.78	2.7050	54.29
Areas IV and V.....	690	7	697	673.55	23.45	11.9412	99.57
Totals.....	2097	73	2170			52.3105	29.73

Chi-square = 52.3105
$d.f. = 4$
$P < .001$

Area	Unmarked	Marked	Total	Expected Unmarked	Expected Marked	Chi-Square	Fish Per Mark
FEMALES							
Fence..........	507	300	807	709.52	97.48	478.5520	2.69
Area I.........	1241	193	1434	1260.79	173.21	2.5716	7.43
Area II......	890	83	973	855.47	117.53	11.5385	11.72
Area III.....	917	48	965	848.44	116.56	45.8667	20.10
Areas IV and V.....	1402	57	1459	1282.77	176.23	91.7482	25.60
Totals.....	4957	681	5638			630.2770	8.28

Chi-square = 630.2770
$d.f. = 4$
$P < .001$

TABLE 71

Counts of Weaver Creek Tag-ratios on Weaver Creek Live Sockeye, With a
Comparison of the Weighted Mean Tag-ratio and the True Average Tag-ratio
1940

Date	Untagged	Tagged	Total	Fish Per Tag
October 13	1545	0	1545	
October 24 and 25	4053	41	4094	99.9
November 2	1379	151	1530	10.1
November 10	199	41	240	5.9
November 17	111	16	127	7.9
Totals	7287	249	7536	30.3
Expected	7267	269	7536	27.98

Chi-square = 1.5419
$d.f. = 1$
$P = .21$

will be shown that the non-uniformity of recovery rates is not sufficient to cause a significant error in the population calculation when the theory of the "simple case" is employed.

Summary

The Weaver Creek population was tagged in such a manner that the tags were quite non-uniformly distributed throughout, which was reflected in heterogeneity of mark ratios both with respect to time and area of the stream.

Sampling of the population by means of dead fish recoveries, which amounted to about half the population, was moderately uniform over different groups of migrants with the exception of those ascending early in November, the low recovery rate of which we are at a loss to explain.

Live counts again furnish as good an estimate of average tag-ratio as pooled dead fish recoveries and closely approximate our best estimate of the "true" average tag-ratio in the population.

Weaver Creek Population — Harrison Experiments

In the foregoing analyses of this chapter we have used the data from a single year only, 1940, because in each case the experiments of that year were more or less "normal", that is, presented no very unusual features. The results of earlier comparisons of data from 1940 and 1941 for the Birkenhead population, and the population calculations of the next chapter indicate that the 1940 data illustrate the essential features of the nature of the distribution of tags within the runs, and of the evenness (or lack thereof) of sampling under the usual experimental conditions to be encountered.

In the case of the Weaver Creek run of 1940, however, particularly with respect to the tagging conducted at Harrison Trap, there appeared to be some rather "abnormal" features. Table 19 indicates a very much lower percentage recovery of Harrison tags among the Weaver Creek dead fish samples in 1940 than in 1941, although the percentage recovery of Weaver Creek tags among the same samples was roughly equal in the two years. This, as pointed out on page 88, and illustrated by Table 20, was associated with a heavy concentration of tagged fish in the early part of the run, and there is some reason to believe that this early part of the run may have perished in part before reaching the spawning grounds, as a result of a complete blockade caused by Weaver Creek being completely dry at the mouth until October 11. In any event, it has been deemed desirable to study both the 1940 and 1941 data resulting from Harrison tagging on the Weaver Creek run to arrive at a fair picture of the distribution of tags and the evenness of sampling to be expected in this situation. The further fact that the Harrison tagging was on the average about 17 times more successful in 1941 than in 1940, as judged by mean tag-ratios among dead fish recoveries, making the data of the later year more extensive and therefore probably more reliable, is an added reason for extending our analysis to the 1941 data in this particular instance.

1940 data

The estimated numbers of tags placed on Weaver Creek fish at Harrison Trap during each week of the 1940 season are tabulated in Table 10. These "Weaver Creek" fish include fish bound for Hatchery Creek also. However, the latter are so few in number that they can be ignored in the analysis of distribution of tags throughout the run. The relative sizes of the spawning populations of Weaver Creek and Hatchery Creek are indicated by the recovery of 7808 dead fish on regular patrols of Weaver Creek and of 204 on similar patrols of Hatchery Creek. The only tag recovery at Hatchery Creek in 1940 was a single case of a dead sockeye with the pin only from a Harrison tag still in place.

The sampling of dead, spawned-out sockeye salmon at Weaver Creek has been previously described. As noted before, regular patrols were made of the spawning areas and, in addition, carcasses were recovered from the upstream face of the fence at the mouth of the stream. The same sample of 7808 fish which were employed in the foregoing analyses of marks put on at the Weaver Creek fence constitute the sample for study of distribution of Harrison tags.

UNIFORMITY OF RECOVERY RATES AMONG DEAD FISH

The numbers of Harrison tags recovered among Weaver Creek dead fish samples are tabulated by date of tagging in Table 72, together with the numbers of fish of the Weaver Creek run estimated to have been tagged during each week (Table 10). The mean percentage recovery was 16.6. A test of homogeneity of recovery rates of the various weeks of tagging yields a probability of .024, of borderline significance. In view of the possible error in column 4 of Table 72 (see page 78), and the fewness of the tags involved, it is unwise to place too much faith in these results as indicative of recovery rates of different parts of the run passing Harrison Trap, but there does not seem to be any good evidence of a trend in recovery rates throughout the season as shown in the last column of the table.

TABLE 72

Recovery Rates of Harrison Tags Among Weaver Creek Dead Fish Samples
and Test of Homogeneity
1940

Tagging Date	Recovered	Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square	% Recovered
Week Ending							
Sept. 28............	2	6	8	1.33	6.67	.4048	25.0
Oct. 5...............	8	58	66	11.00	55.00	.9817	12.1
Oct. 12.............	8	46	54	9.00	45.00	.1333	14.8
Oct. 19 and 26...........	5	5	10	1.67	8.33	7.9712	50.0
Totals............	23	115	138			9.4910	16.6

$$d.f. = 3$$
$$\text{Chi-square} = 9.4910$$
$$P = .024$$

HOMOGENEITY OF TAG-RATIOS

Among the 7808 dead fish recovered there were 24 which had been tagged at the Harrison Trap. These 24 tagged fish were not evenly distributed throughout the population, however, as may be seen from Table 73, wherein are shown the tag densities for each week of recovery and the chi-square test for homogeneity of same. The tag-ratios are highly heterogeneous, the ratio of tagged to total fish decreasing steadily and rapidly as the season progresses. Considering the fairly high degree of mixing of fish of this run shown between Harrison Trap and Weaver Creek (Figures 29, 32, 33 and Table 31) this indicates a very high concentration of tags on early migrants and a very low concentration on later migrants past Harrison Trap.

TABLE 73

Test of Homogeneity of Harrison Tag-ratio Samples of Weaver Creek Dead Fish, Segregated by Time of Recovery

1940

Recovery Date	Tagged	Untagged	Total	Expected Tagged	Expected Untagged	Chi-Square	Fish Per Tag
Week Ending							
Oct. 19 and 26.	11	1229	1240	3.81	1236.19	13.6103	112.7
Nov. 2...............	7	2221	2228	6.85	2221.15	.0032	318.3
Nov. 9...............	5	3371	3376	10.38	3365.62	2.7970	675.2
Nov. 16 and after......	1	963	964	2.96	961.04	1.3017	964
Totals............	24	7784	7808			17.7122	325.3

$$d.f. = 3$$
$$\text{Chi-square} = 17.7122$$
$$P < .001$$

1941 data

It has been estimated that 631 fish of the "Weaver Creek" run were tagged at Harrison Trap during 1941; the estimated number tagged each week is shown in Table 13. Again, the numbers of fish of this group spawning in Hatchery Creek and in Little East Creek were so small as to be negligible, and may be ignored in the present analyses. While 4970 dead fish were recovered by patrols for dead fish in Weaver Creek, only 84 were similarly recovered in Hatchery Creek and 45 in Little East Creek. Among the 84 Hatchery Creek fish recovered dead were 3 bearing Harrison tags, or one in 28, while among the Little East Creek dead fish samples there were 4 tagged among 45 fish, or 1 in 11.25. These ratios compare sufficiently well with the mean value of 18.7 among Weaver Creek samples (see below). The fact that the mean tag-ratios are substantially the same in all three cases, and the fish appear on the spawning grounds at about the same time makes it appear that, statistically, these two little spawning populations may be fairly treated as part of the Weaver Creek population without any great error. Their small size compared with the population of Weaver Creek proper makes the error, if any, negligible in any case.

UNIFORMITY OF RECOVERY RATES AMONG DEAD FISH

The number of Harrison tagged fish recovered among dead fish samples in Weaver Creek is tabulated by period of tagging in Table 74, together with the estimated numbers of tags placed on Weaver Creek fish at Harrison Trap during the periods in question. The rate of recovery, averaging 40.7 per cent, is much higher than in 1940. While the rates of recovery were obviously not the same throughout the season, as indicated by the probability value of .0013, the heterogeneity is attributable to low rates of recovery of tags from the last two tagging periods in Table 74. For the tagging periods before October 18, during which the bulk of the tags were put out, there is little or no evidence of heterogeneity. It appears that the bulk of these tagged fish were probably evenly sampled at Weaver Creek, only the very last part of the run suffering a low recovery rate.

Values of number of Weaver Creek fish tagged at Harrison Trap during each week in Table 74 are estimated from scale samples and are subject to considerable sampling error (page 78). Therefore, the results of these calculations do not have the same reliability as similar tests of homogeneity of recovery rates where the number of tags liberated is known with complete certainty.

TABLE 74

Recovery Rates of Harrison Tags Among Weaver Creek Dead Fish Samples, and Test of Homogeneity

1941

Period of Tagging	Recovered	Not Recovered	Total	Expected Recovered	Expected Not Recovered	Chi-Square	% Recovered
Week Ending							
Oct. 4..............	22	49	71	28.92	42.08	2.7937	31.0
Oct. 11............	146	189	335	136.44	198.56	1.1300	43.6
Oct. 18............	85	106	191	77.79	113.21	1.1273	44.5
Oct. 25............	4	19	23	9.37	13.63	5.1931	17.4
Nov. 1, 8, and 15.....	0	11	11	4.48	6.52	7.5582	0.0
Totals.........	257	374	631			17.8023	40.7

$$d.f. = 4$$
$$\text{Chi-square} = 17.8023$$
$$P = .0013$$

HOMOGENEITY OF TAG-RATIOS AMONG DEAD FISH

The operation of the Harrison Trap was apparently far more successful in 1941 than in 1940 on the Weaver Creek run, as evinced by the mean tag density of one tag per 325 fish in 1940 compared to one tag per 18.7 fish in 1941. In 1941, as in 1940, however, the Harrison tags were not evenly distributed throughout the run, in spite of the high degree of mixing between the Harrison Trap and the Weaver Creek spawning grounds (Table 31), as is revealed by Table 75

which compares the numbers of tagged and untagged fish recovered during successive recovery periods after October 18. Prior to October 18 (from September 13 to October 18) there were recovered but 29 fish, none tagged).

Table 75 indicates that the early part of the Weaver Creek run was more heavily sampled at Harrison Trap than the later part, since there is an upward trend to the fish-per-tag as the season progresses. This is much less marked than in 1940, however, indicating a more nearly even sampling at the Harrison Trap during 1941.

<div align="center">TABLE 75</div>

Test of Homogeneity of Harrison Tag-ratio Samples of Weaver Creek Dead Fish, Segregated by Time of Recovery
1941

Recovery Date	Tagged	Untagged	Total	Expected Tagged	Expected Untagged	Chi-Square	Fish Per Tag
Week Ending							
Oct. 25............	84	1404	1488	79.50	1408.50	.2690	17.7
Nov. 1............	149	2119	2268	121.18	2146.82	6.7472	15.2
Nov. 8............	22	635	657	35.10	621.90	5.1650	29.9
Nov. 15..........	6	406	412	22.01	389.99	12.3028	68.7
Nov. 22..........	3	113	116	6.20	109.80	1.7448	38.7
Totals.........	264	4677	4941			26.2288	18.72

<div align="center">

$d.f. = 4$
Chi-square $= 26.2288$
$P < .001$

</div>

TAG-RATIOS AMONG CATCHES AT WEAVER TRAP

Since there is a good deal of mixing on the spawning grounds after entry of Weaver Creek, it may be expected that the samples of the run constituted by the catches of the trap at the mouth of the stream would reveal any variations in tag-ratios more clearly than the dead fish samples. In 1940, among the 1698 live fish handled at the Weaver Creek fence, only 4 were tagged, and these were all recovered on October 19; the data are insufficient for any study of distribution of tags throughout the run. In 1941, however, the tag-ratio was much higher, and the distribution of 100 Harrison tagged fish among 1888 captured at the Weaver Trap affords a basis of studying the evenness of distribution of tags throughout the run. From the tabulation of these data in Table 76, it may be seen that the tag-ratio was relatively low during the first part of the run, rose rapidly during the week ending October 25, then fell off during the ensuing weeks. The same pattern is evident in Table 75, but dampened, as might be expected as a result of mixing between time of entry at the mouth of the stream and time of recovery as dead on the spawning grounds. The mean tag-ratio among fish captured at the mouth of the stream is almost identical with the mean value among the dead fish samples.

Summary

It may be concluded that in neither year was the tagging uniform on the Weaver Creek run at Harrison Trap, but that it was much more nearly so in 1941 than in 1940. In 1940 the few tags placed on Weaver Creek fish were concentrated on the early part of the run. This, plus the low-water conditions at the mouth of the stream early in the season, may account for the apparently abnormally low recovery rate of these tags and the anomolous results earlier obtained in Table 19. During 1941, while the tagging was not completely uniform, a fairly high tag density was obtained on all parts of the run.

Recovery of various groups of tagged fish was probably non-uniform in 1941, but appears to have been very nearly even over the major part of the run, the recovery rate falling off only at the very end of the season. The 1940 data are too meagre for reliable conclusions in regard to variation in recovery rates.

The average tag-ratio among sockeye salmon captured alive at the mouth of Weaver Creek is the same as that among samples of dead on the spawning grounds, and the intra-seasonal distribution of tag-ratios among these live fish agrees with the results obtained from samples of dead fish.

TABLE 76

Harrison Tag-ratios of Weaver Creek Trap-caught Fish
1941

Recovery Period	Tagged	Untagged	Total	Fish Per Tag
Week Ending				
September 20, 27, and				
October 4	1	49	50	50.00
October 11 and 18	6	241	247	41.17
October 25	76	707	783	10.30
November 1	15	505	520	34.67
November 8 and 15	2	286	288	144.00
Totals	100	1788	1888	18.88

ESTIMATION OF POPULATIONS, AND THE EFFECTS THEREON OF POPULATION STRATIFICATION AND NON-UNIFORMITY OF SAMPLING

In the foregoing chapters it has been demonstrated that, in general, populations of sockeye salmon do not mix completely between the time and place of tagging and the time and place of subsequent sampling for tag-ratios; indeed, in most cases the runs extend over a sufficient time that it is impossible that mixing can be complete. It has also been shown that in the general case neither the distribution of tags nor the subsequent sampling for tag-ratios is uniform over the entire population. These factors would tend to render erroneous population estimates made by the simple formulae (1) or (12).

On the other hand, although the runs extend over a considerable space of time, there tends in every case to be a heavy concentration within a relatively short space of time of the bulk of the population passing a given point on the migration path, or dying on the spawning grounds. For these short periods of tagging and subsequent sampling, which contain the major part of the population, the tagging and sampling will be generally much more nearly uniform than the data of the entire run. This phenomenon would tend to minimize the possible errors resulting from stratification and non-uniformity of sampling, since the bulk of the population is contained in only one or a few strata (periods of sampling or tagging).

Under these circumstances, the question arises as to whether the theory of the simple case is sufficient to give a reliable estimate of population numbers when applied to all data combined, whether it is desirable to compute the populations of each sex category separately by the theory of the simple case, or whether it is necessary to apply the theory of the changing population (formula 25) to arrive at a reliable estimate of population numbers. We will approach this question by computing the populations on the basis of our several tagging experiments in the years 1940 and 1941 by each of these methods and comparing results, by determining just how much effect the non-uniformities of sampling previously demonstrated have in actual practice on the estimates of total population.

Sockeye Population Passing the Skookumchuck

The sockeye population passing the Skookumchuck may be estimated from the tags liberated at that point and the subsequent tag-ratio samples in the Birkenhead River. We have adduced evidence earlier that the Birkenhead River samples include all parts of the population passing the Skookumchuck. The question to be studied here is whether the various components of the population passing the Skookumchuck were sufficiently evenly sampled either at the Skookumchuck or in the Birkenhead to permit a reliable estimate of the total numbers to be made by the theory of the simple case, and if not what modifications should be applied to arrive at a reliable estimate. From the results of our previous analysis of the 1940 sampling we have a fair idea of what results to expect. In addition to discovering to what extent the results of the computations of populations by alternative methods agree with these expectations, it will be of interest to determine whether the 1941 data yield results similar to those of 1940.

TABLE 77

Estimates of the Sockeye Population Passing the Skookumchuck, 1940

		N_1 (Formula 1)	σ_N	N_2 (Formula 12)	T	t	n	Fish Per Tag	% Recovered
	Estimates from *all* dead fish samples, Birkenhead:								
A	Jacks only	7,570	2,180	6,990	161	11	517	47.00	6.83
B	Males only	14,380	1,160	14,290	826	124	2159	17.41	15.01
C	Females only	17,870	1,130	17,800	1159	196	3022	15.42	16.91
D	All large fish	32,140	1,590	32,060	1985	320	5181	16.19	16.12
E	All fish	36,940	1,810	36,850	2146	331	5698	17.21	15.42
B+C		32,250	1,610	32,090					
A+B+C		39,820	2,710	39,080					
A+D		39,710	2,700	39,050					
	Estimates from *fresh* dead fish samples, Birkenhead:								
A′	Jacks only	8,290	2,830	7,430	161	8	412	51.50	4.97
B′	Males only	12,750	1,200	12,640	826	93	1436	15.44	11.26
C′	Females only	18,390	1,500	18,270	1159	126	1999	15.87	10.87
D′	All large fish	31,130	1,920	31,020	1985	219	3435	15.68	11.03
E′	All fish	36,370	2,210	36,230	2146	227	3847	16.95	10.58
B′+C′		31,140	1,920	30,910					
A′+B′+C′		39,430	3,420	38,340					
A′+D′		39,420	3,420	38,450					
	Estimate of all fish from tag-ratio counts on live fish in the Birkenhead:								
		38,590	2,420	38,440	2146	216	3884	17.98	

Estimate of all large fish by formula 25 (see Tables 78, 79 and 80) from Birkenhead dead fish samples:
$$N = 33,230$$

1940 experiments

In Table 77 population computations have been made by both formulae (1) and (12) from the data for all dead fish for jacks, males and females separately, for all large fish, and for all samples. The standard errors have been estimated in each case by formula (7). This same formula is also employed subsequently in all cases unless otherwise stated.

It was shown earlier that during the 1940 season large males and large females had, on the average, the same tag-ratio and that this was a higher tag-ratio than that of the jacks. Further, the rate of recovery of jacks was lower than that of large fish. As a result, the computation of the total population from all data pooled yields a lower value (36,940) than that reached by computing each category separately (39,820) or by computing jacks separately from the pooled estimate for large fish (39,710). That the latter two values are nearly identical was expected from the fact that the tag-ratios of the two sexes of large fish were, on the average, not significantly different. It is important to note that the estimate derived from all data pooled together differs by only 2,880 from that derived from the data for each category taken separately. Since this is but 1.6 standard errors of estimate and amounts to only 7.8% of the estimate from the pooled data, the improvement of estimate by taking account of the sampling differences between size and sex categories cannot be regarded as being of great importance.

Results obtained from similar computations based on data from fresh dead fish alone are essentially the same. It may be remembered that the tag-ratios on large fish changed during the season, and that the sampling was uneven with respect to different parts of the season when all dead fish samples were considered, but was uniform when samples of fresh dead fish only were considered. The almost complete identity of estimates of populations of large fish, whether fresh fish samples alone or all samples are considered, and whether or not the computations are made from the data for separate sexes or from the pooled data, demonstrates that the overall effect of the indicated bias in sampling has a negligible effect on the estimates.

We have also computed the population of large sockeye passing the Skookumchuck from the pooled data for both sexes combined from all dead fish samples, taking full account of sampling differentials both in tagging and sampling among different parts of the season, by means of formula (25). The details of the computations are presented in Tables 78, 79 and 80, and the result is recapitulated at the bottom of Table 77. The value of 33,230 is slightly higher, but insignificantly so, than the estimates made by the theory of the simple case.

The estimate from the total of all live counts is, as we expected from the earlier comparison of tag-ratios on live and dead fish, not significantly different from the estimates from dead fish samples.

For the 1940 run passing the Skookumchuck, then, it appears that a satisfactory estimate can be made from the pooled data from all dead fish, and that improvements in the estimate, by virtue of taking into account differentials in intensity of tagging and sampling, are practically negligible.

TABLE 78

Recoveries of Skookumchuck Tags in the Birkenhead River Among Dead Fish Samples
By Time of Tagging and Time of Recovery (Jacks Omitted), 1940

Recovery Date Birkenhead	TAGGING DATES — SKOOKUMCHUCK									Total Tags Recovered	Total Dead Recovered	Scars Recovered
	8–20 8–23	8–24 8–27	8–28 8–31	9–1 9–4	9–5 9–8	9–9 9–12	9–13 9–16	9–17 9–20	9–21 10–7			
Week Ending												
Sept. 7											5	
Sept. 14											11	
Sept. 21	1	4	8							13	218	4
Sept. 28	2	51	42	5						100	1195	8
Oct. 5	2	48	59	11	2	1				123	2202	7
Oct. 12		13	16	5	2	4	1	7		48	1166	2
Oct. 19		1	3		2	2	1	5	1	15	360	
Oct. 26											0	
Nov. 2											24	
Totals	5	117	128	21	6	7	2	12	1	299		
Total tagged	44	660	772	165	55	101	70	81	37			

TABLE 79

Recoveries of Table 78 With Tag Scars Proportionally Distributed

Recovery Date Birkenhead	TAGGING DATES — SKOOKUMCHUCK									Total	Total Dead Recovered	Fish Per Mark
	8–20 8–23	8–24 8–27	8–28 8–31	9–1 9–4	9–5 9–8	9–9 9–12	9–13 9–16	9–17 9–20	9–21 10–7			
Week Ending												
Sept. 7											5	
Sept. 14											11	
Sept. 21	1.31	5.23	10.46							17.00	218	12.824
Sept. 28	2.16	55.08	45.36	5.40						108.00	1195	11.065
Oct. 5	2.11	50.73	62.36	11.62	2.11	1.06				129.99	2202	16.940
Oct. 12		13.54	16.67	5.21	2.08	4.17	1.04	7.29		50.00	1166	23.320
Oct. 19		1.00	3.00		2.00	2.00	1.00	5.00	1.00	15.00	360	24.000
Oct. 26											0	
Nov. 2											24	
Totals	5.58	125.58	137.85	22.23	6.19	7.23	2.04	12.29	1.00	319.99		
Tagged	44	660	772	165	55	101	70	81	37			
% Recovered	12.682	19.027	17.856	13.473	11.255	7.158	2.914	15.173	2.703			

TABLE 80

Computation of Skookumchuck 1940 Population of Large Sockeye From Data of Table 79

Recovery Date Birkenhead	TAGGING DATES — SKOOKUMCHUCK									Totals
	8–20 8–23	8–24 8–27	8–28 8–31	9–1 9–4	9–5 9–8	9–9 9–12	9–13 9–16	9–17 9–20	9–21 10–7	
Week Ending										
Sept. 21	132	352	751							1235
Sept. 28	188	3203	2810	443						6644
Oct. 5	282	4516	5916	1461	318	251				12744
Oct. 12		1659	2177	902	431	1358	832	1120		8479
Oct. 19		126	403		426	670	824	791	888	4128
Totals	602	9856	12057	2806	1175	2279	1656	1911	888	33230

1941 experiments

In Table 81 we exhibit the results of estimating the population of sockeye passing the Skookumchuck in 1941 from the samples of all dead fish and from live counts in the Birkenhead River. Again it will be observed that the several estimates of population from the dead fish samples do not differ significantly, whether all the data are lumped together, whether large fish and jacks are estimated separately, or whether all three sex-size categories are separately estimated.

During 1941, live counts of large fish and of jacks were kept separate, which was not done during 1940. This enables us to estimate the respective populations separately from the live-count data. For large fish the results are essentially identical with the value obtained from dead fish samples. For jacks, however, the live-count yields a considerably higher value than do the dead fish samples, and the value for total population from the pooled live counts is also higher than the values derived from dead fish samples. This may be the result of lower average visibility of jacks coupled with their proportionally greater representation during 1941 than during 1940. In any case, we are led to conclude that live counts may be less reliable than dead samples, at least for jacks, and may tend to yield higher values because of the difficulty of seeing part of the tags on live fish, leading to an estimate of tag-ratio lower than that obtained from the more careful examination possible in the case of dead fish samples. On the other hand, the overall estimate of population from live counts (67,770) differs but 14% from the lowest of our estimates, from dead fish samples (59,260) which for many purposes may be sufficiently accurate.

In Tables 82, 83 and 84 we show the detailed procedure in estimating the population of all fish from the data of dead fish samples, correcting for intra-season sampling and tagging differentials, by means of formula (25). The resulting estimate is also recapitulated at the bottom of Table 81 for comparison with estimates made from the same data by the theory of the simple case. Again the result is slightly higher than the first estimates, but the difference is neither appreciable nor statistically significant. Again, such sampling differentials as may exist have not been of any practical importance in affecting the estimates.

The reason is not far to seek why the differences in intensity of tagging and subsequent sampling for tag-ratios, which we have shown earlier to exist in the 1940 data, and almost certainly could be demonstrated for 1941 also (see the marginal values in Table 83), have no practical influence on the population estimate made by formulae (1) or (12). As may be observed from study of Table 80 and Table 84, the run, although it extends over a considerable total time period, has a rather sharp "peak" both with respect to time of tagging and time of sampling on the spawning grounds. The bulk of the run is concentrated into a relatively short period of time, as a consequence of which tagging and sampling is uniform or nearly uniform over the bulk of the population. The sampling differentials, while they exist, are effective on such a small part of the population that they do not very greatly affect the outcome. Of course, if the differentials were very great the result might be significantly effective on the population estimates. Under the conditions existing in these particular experiments, however, the sampling differentials were sufficiently small, and the bulk of the run was sufficiently concentrated

TABLE 81

Estimates of the Sockeye Population Passing the Skookumchuck, 1941

	N_1 (Formula 1)	σ_N	N_2 (Formula 12)	T	t	n	n/t Fish Per Tag	t/T % Recovered
Estimates from samples of dead in Birkenhead River:								
A Jacks only	21,380	1,800	21,230	831	117	3010	25.73	14.08
B Males only	12,860	1,310	12,730	556	79	1827	23.13	14.21
C Females only	25,020	1,710	24,910	715	161	5635	35.00	22.52
D All large fish	39,520	2,260	39,390	1271	240	7462	31.09	18.88
E All fish	61,660	2,920	61,520	2102	357	10472	29.33	16.98
B+C	37,880	2,160	37,640					
A+B+C	59,260	2,810	58,870					
A+D	60,900	2,890	60,620					
Estimates from live counts in the Birkenhead River:								
Jacks only	27,100	2,450	26,880	831	104	3391	32.60	
Large fish only	40,800	2,160	40,690	1271	271	8700	32.10	
All fish	67,770	3,120	67,630	2102	375	12091	32.24	

Estimate of all fish by formula 25 (see Tables 82, 83 and 84) from Birkenhead dead fish samples:

$$N = 62,670$$

into a short time period, that the theory of the simple case gives as good an estimate for all practical purposes as the more elaborate procedure under the theory of the changing population.

Comparison of computations by formula (12) and formula (1) in Tables 77 and 81, demonstrates clearly that for the values of T, t, and n employed in any of these experiments, formula (1) is a sufficiently good approximation. We present the two values in these and in some subsequent tables to demonstrate the difference in the results from the two formulae as T, t, and n vary. In no case is the employment of the more exact formula (12) worthwhile.

Sockeye Population Spawning in the Birkenhead River

Enumeration of the Birkenhead spawning population is based on tagged fish liberated at the trap some distance above the mouth of the river, as described earlier, and subsequent sampling on the spawning grounds, both above and below the trap, to determine the tag-ratio in the population. We have shown previously that between the time of tagging and time of subsequent sampling for tag-ratios, the populaion, as judged from the marked members, does not mix completely. We have also discovered (page 157) by an analysis of the tag-ratio and recovery-rate data for 1940 that the tags were not evenly distributed over the whole population, and that the uniformity of recovery rates of tags liberated among different parts of the population is somewhat doubtful, although the data were rather too few for a firm conclusion in this respect. In the light of these apparent sampling differentials, it is of interest to compare the results of estimating the population by several alternative methods to determine whether a worthwhile improvement can be made in the estimates by taking account of various sampling differentials by estimating size of sex categories separately by the simple theory, or by employing the theory of formula (25).

1940 experiments

In Table 85 are set forth the sampling data for each sex of large fish separately, and for both combined, as well as the pooled data for all sockeye salmon, together with the computed populations for these groups. (Since the Birkenhead trap was so constructed that practically all jacks escaped in 1940, we cannot separately estimate the population of that category from the tagging data.)

From the columns of "fish per tag" and "% recovered" it may be seen that, as we have shown in detail in the earlier analyses of dead fish samples (page 157), the average tag-ratios of males and females were quite unequal, but the rates of recovery were nearly even as between these categories. In consequence, there is no significant difference in our estimates of large fish whether each sex is estimated separately or the data are pooled. Estimates based on fresh dead fish alone are not different from those based on all dead fish samples. The figure arrived at from estimating each sex separately (23,770 for all dead samples by formula 1) is lower than that from the pooled data (24,670) in consequence of the sampling differentials, but the difference is not sufficient to be significant at the tag-densities and recovery rates of this experiment.

TABLE 82

Recoveries of Skookumchuck Tags in the Birkenhead River Among Dead Fish Samples, 1941

Recovery Date Birkenhead	TAGGING DATES — SKOOKUMCHUCK								Total Tags Recovered	Total Dead Recovered	Scars Recovered
	8–18 8–26	8–27 8–30	8–31 9–3	9–4 9–7	9–8 9–11	9–12 9–15	9–17 9–19	9–20 9–29			
Week Ending											
Sept. 16			2						2	17	
Sept. 23		5	3	1					9	132	
Sept. 30	1	5	20	16	3	2			47	800	5
Oct. 7	1	8	57	53	15	3	1		138	2848	2
Oct. 14		6	21	37	15	15	8	1	103	3476	7
Oct. 21			2	1	2	1		1	7	644	
Oct. 28		1	2	1	3	1	2	2	12	1247	
Nov. 4			1	6	2	7	1	5	22	930	
Nov. 11				2		1			3	376	
Totals	2	25	108	117	40	30	12	9	343		
Total tagged	21	184	650	590	273	177	107	100			

TABLE 83

Recoveries of Table 82, With Tag Scars Proportionally Distributed

Recovery Date Birkenhead	TAGGING DATES — SKOOKUMCHUCK								Total	Total Dead Recovered	Fish Per Mark
	8–18 8–26	8–27 8–30	8–31 9–3	9–4 9–7	9–8 9–11	9–12 9–15	9–17 9–19	9–20 9–29			
Week Ending											
Sept. 16			2.00						2	17	8.50
Sept. 23		5.00	3.00	1.00					9	132	14.67
Sept. 30	1.11	5.53	22.13	17.70	3.32	2.21			52	800	15.38
Oct. 7	1.01	8.12	57.83	53.77	15.22	3.04	1.01		140	2848	20.34
Oct. 14		6.41	22.43	39.51	16.02	16.02	8.54	1.07	110	3476	31.60
Oct. 21			2.00	1.00	2.00	1.00		1.00	7	644	92.00
Oct. 28		1.00	2.00	1.00	3.00	1.00	2.00	2.00	12	1247	103.92
Nov. 4			1.00	6.00	2.00	7.00	1.00	5.00	22	930	42.27
Nov. 11				2.00		1.00			3	376	125.33
Totals	2.12	26.06	112.39	121.98	41.56	31.27	12.55	9.07	357		
Total tagged	21	184	650	590	273	177	107	100			
% Recovered	10.10	14.16	17.29	20.67	15.22	17.67	11.73	9.07			

TABLE 84

Computation of Skookumchuck 1941 Total Population From Data of Table 83

Recovery Date Birkenhead	TAGGING DATES — SKOOKUMCHUCK								
	8–18 8–26	8–27 8–30	8–31 9–3	9–4 9–7	9–8 9–11	9–12 9–15	9–17 9–19	9–20 9–29	Totals
Week Ending									
Sept. 16.............			98						98
Sept. 23.............		518	256	71					845
Sept. 30.............	169	601	1969	1317	335	192			4583
Oct. 7.................	203	1166	6803	5291	2034	350	175		16022
Oct. 14...............		1430	4099	6040	3326	2865	2301	373	20434
Oct. 21...............			1064	445	1209	521			3239
Oct. 28...............		734	1202	503	2048	588	1772	2292	9139
Nov. 4.................			244	1227	555	1675	360	2330	6391
Nov. 11...............				1213		709			1922
Totals.............	372	4449	15735	16107	9507	6900	4608	4995	62673

TABLE 85

Estimates of Sockeye Spawners in the Birkenhead River, 1940

	N_1 (Formula 1)	σ_N	N_2 (Formula 12)	T	t	n	Fish Per Tag	% Recovered
Estimates from *all* dead fish samples:								
A Males only	11,110	1,590	10,950	283	55	2159	39.25	19.43
B Females only	12,660	1,800	12,410	155	37	3022	81.68	23.87
C All large fish	24,670	2,270	24,460	438	92	5181	56.31	21.00
D All fish	27,190	2,500	26,960	439	92	5698	61.93	20.96
A+B	23,770	2,400	23,360					
Estimates from *fresh* dead fish samples:								
A′ Males only	10,980	1,660	10,740	283	37	1436	38.81	13.07
B′ Females only	12,910	2,410	12,480	155	24	1999	83.29	15.48
C′ All large fish	24,660	2,900	24,330	438	61	3435	56.31	13.93
D′ All fish	27,685	3,260	27,307	439	61	3847	63.07	13.90
A′+B′	23,890	2,930	23,220					
Estimates of all fish from tag-ratio counts on live fish:								
Count above fence only	31,710	4,810	31,000	439	39	2817	72.23	
Count in all areas	37,040	5,270	36,300	439	44	3712	84.36	

Estimate of large fish only by formula (25):

$$N = 25,770$$

The estimate of all large fish arrived at from the combined data of all dead fish recoveries, correcting for time-connected sampling differentials by formula (25), is 25,770. Again, although slightly higher than the estimates by formulae (1) or (12), this does not differ significantly from the estimates arrived at by these simple formulae. (Since the method of estimation by formula (25) has been made clear previously by the detailed numerical examples for Skookumchuck experiments, we do not give here the details of the computations for the Birkenhead experiments.)

In this case it seems that no worthwhile improvement in the population estimate results from considering the sampling differentials.

The total population, including jacks, has been estimated from the pooled data both for all dead fish recoveries and for fresh dead only. This is equivalent to assuming the recovery rate of jacks to be equal to the average recovery rate of large fish, which, in view of the data from Skookumchuck experiments, is unlikely. The estimate of 27,000-odd fish including jacks is, therefore, undoubtedly too low. If, as seems likely from other considerations, the percentage of jacks in the Birkenhead is the same as at the Skookumchuck, the number of jacks, corresponding to 24,670 large fish, would be 5,810, yielding a total population of 30,480.

We have indicated earlier (page 153) that among dead fish samples the tag-ratios were homogeneous as between fish recovered above and below the fence. This, we believe, is due to many of the fish spawning above the fence dying and drifting down to Area I, while all or most of the spawners in Area I died and drifted into Lillooet Slough where they were mostly not recovered. That the live fish on the spawning grounds of Area I had a lower tag-ratio than those on the spawning grounds above the trap, is shown by the live counts: among 2817 fish counted above the fence during the season, 39 bore tags, or 1 in 72, while counts on the same days by the same observers below the fence indicated 5 tags among 895 fish, or only 1 in 179. The estimated population from dead fish samples in Table 84 is, therefore, to be regarded as an estimate only of the part of the population which ascended past the trap and either remained above it to spawn or returned to Area I to spawn, few or none of the fish which never ascended above the trap being included.

We may arrive at a rough estimate of the number of fish of the latter sort if we assume (1) that the live counts below the fence include the same fraction of the population present, and the same fraction of the tagged fish present, as do the live counts above the fence, and (2) that tagged and untagged fish of all sex and size categories were equally likely to drop back from above the fence to below to spawn. (Note that *no* assumption is made that the tag-ratio of the live count be the same as that of the population). We may then reason as follows:

Let a = calculated population from dead fish samples

x = spawners below the fence not included in the estimate from dead fish samples (fish which never ascended above the fence)

y = spawners below the fence included in the above estimate (fish which dropped back below the fence to spawn)

then, $x+y$ = total spawners below the fence

$a-y$ = total spawners above the fence

now, if n_a and n_b represent the total live counts above and below the fence, respectively, while t_a and t_b represent the corresponding counts of tagged fish among the live counts, under the hypotheses set forth

$$\left. \begin{aligned} \frac{y}{a-y} &= \frac{t_b}{t_a} \\[1ex] \text{and} \quad & \\[1ex] \frac{x+y}{a-y} &= \frac{n_a}{n_b} \end{aligned} \right\} \quad \cdots \cdots \cdots \cdots \cdots \cdots \quad (35)$$

These equations may be solved simultaneously for x and y. If we take 27,190 as our estimate of "a" in the present case, we have

$$a = 27,190$$
$$n_a = 2817$$
$$n_b = 895$$
$$t_a = 39$$
$$t_b = 5$$

Whence,

$$\frac{y}{27,190 - y} = \frac{5}{39}$$

and,

$$\frac{x+y}{27,190 - y} = \frac{895}{2817}$$

So that,
$$x = 4,568$$
$$y = 3,089$$

From this it would be estimated that, of the 27,200 fish estimated by dead fish samples, about 3,100 spawned in Area I, but that there were probably an additional 4,600 spawners spawning in Area I not included in this estimate. This would lead to an estimate of some 31,800 fish for the total Birkenhead population. Since this underestimates the jacks as indicated above, this is a minimal value. Using the estimate of "a" arrived at by assuming jacks to be present in the same ratio as in the Skookumchuck experiments, and the Birkenhead tagging and dead fish recovery

data for large fish only, namely 30,480 (see above) we arrive at the most likely estimate for the total Birkenhead spawning population as follows:

$$a = 30,480$$
$$n_a = 2817$$
$$n_b = 895$$
$$t_a = 39$$
$$t_b = 5$$

$$\frac{y}{30,480 - y} = \frac{5}{39}$$

$$\frac{x + y}{30,480 - y} = \frac{895}{2817}$$

leading to

$$x = 5119$$

$$y = 3464$$

This gives us an estimated total of $30,480 + 5120 = 35,600$ spawners in the Birkenhead River in 1940.

In an earlier chapter (page 86) we stated that by taking into account tagging and sampling differentials as far as practicable, we estimated that 89.4% of the Skookumchuck population was accounted for by Birkenhead spawners in 1940. This is arrived at by dividing the estimate of 35,600 for Birkenhead spawners by the Skookumchuck populations estimate of 39,820 made by formula (1) from dead fish samples, each sex category being estimated separately. Any of the other estimates of total Skookumchuck population from Table 77 might have been used with very similar results.

It may be objected that in the above computations we assumed the same percentage of jacks in the Birkenhead as at the Skookumchuck, and then cannot fairly use the results to compare Birkenhead and Skookumchuck populations. This was necessary because our live counts include jacks, although the jacks were not included in the tagging experiments. We might, however, compute the population of large fish only with the aid of formulae (35) if we assume, in addition to the other assumptions made, that the same fraction of jacks was included in live counts above and below the fence. Then, applying the formulae (35) to large fish only ($a = 24,670$) we have

$$\frac{y}{24,670 - y} = \frac{5}{39}$$

and,

$$\frac{x + y}{24,670 - y} = \frac{895k}{2817k}$$

where $k =$ the fraction of large fish in the live counts

Thus,

$$x = 4,144$$
$$y = 2,803$$

This yields an estimate of a total of 28,810 *large* spawners in the Birkenhead. This, in turn, is 28,810/32,140 = 89.6% of the estimated Skookumchuck population of large fish only. This value is almost identical with the one arrived at before, but this makes no assumptions about relative percentages of any category at the Skookumchuck and in the Birkenhead.

Returning now to Table 85, we have included also estimates of populations from live counts alone. Unfortunately in 1940 we did not tabulate counts of large fish and jacks separately, so we must estimate for all sex categories combined. The counts above the fence only yield an estimated population of 31,710 which compares very closely with the estimate of 30,480 (page 182) from dead fish samples assuming the jacks to be present in the same ratio as at the Skookumchuck. It does not, furthermore, differ significantly from the estimate of 27,190 arrived at from the plain, unweighted data from all dead fish recoveries. The live counts from all areas combined, yielding an estimate for *all* spawners and not just of those which had passed the fence, lead to an estimate of 37,040 which again is very similar to the value of 35,600 from dead fish samples with a correction for spawners below the fence not included in the estimates from dead samples. Of course, since we employed the live counts in arriving at the last figure, the correspondence may be closer than would be otherwise expected. It does, however, look as if, again, the live counts yield a very useful estimate of the Birkenhead population in 1940. The very large variances of all the estimates, resulting from the low tag-ratio among Birkenhead fish in 1940, should be considered, however, in evaluating these results.

1941 experiments

Tagging in the Birkenhead in 1941 was in some respects more successful than in the preceding year. The trap was reconstructed to permit the capture and tagging of jacks in numbers roughly proportional to the relative numbers of large fish tagged, and the percentage of fish of all categories tagged was about double that of 1940. The basic data for fish tagged and dead fish recoveries from each category, and the population estimates computed therefrom are tabulated in Table 86.

It may be seen from the next to last column of Table 86 that the tag-ratios among jacks and large females were nearly equal, but that proportionally more large males were tagged than either of these categories. The recovery rates, on the other hand, were similar as between jacks and large males, while the females were recovered only about half as frequently as either of these. The consequences of these sampling differentials were, in the final result, negligible however. As may be seen from the computed population values tabulated, no significant differences are obtained whether we lump all the data, lump the large fish and compute jacks separately, or compute the population of each category separately. Neither does a correction for time-connected sampling differentials by the theory of formula (25) make any difference to the estimate. By all methods we obtain estimates in the neighborhood of 47,000 with no significant differences between them. No worthwhile improvement is obtained by considering the sampling differentials among population strata.

TABLE 86

Estimates of Sockeye Spawners in the Birkenhead River, 1941

	N_1	σ_N	N_2	T	t	n	Fish Per Tag	% Recovered
Estimates from dead fish samples:								
A Jacks only	18,320	1,390	18,220	846	139	3010	21.65	16.43
B Males only	10,090	840	10,020	613	111	1827	16.46	18.11
C Females only	18,080	880	18,040	892	278	5635	20.27	31.16
D All large fish	28,870	1,230	28,820	1505	389	7462	19.18	25.85
E All fish	46,630	1,740	46,560	2351	528	10472	19.83	22.46
B+C	28,170	1,210	28,060					
A+B+C	46,490	1,840	46,270					
A+D	47,190	1,850	47,030					
Estimates from live counts:								
Counts above fence only:								
Jacks	17,010	1,490		846	108	2172	20.11	
Large fish	18,180	710		1505	426	5145	12.08	
All fish	32,210	1,180		2351	534	7317	13.70	
Counts from all areas:								
Jacks	20,490	1,550		846	140	3391	24.22	
Large fish	26,190	930		1505	500	8700	17.40	
All fish	44,420	1,460		2351	640	12091	18.90	

Estimate of all fish by formula 25:

$$N = 47,292$$

Estimates from live fish counts yield results which are at first apparently confusing. The estimates from live counts above the fence only are a good deal lower than the estimates from all dead fish samples, indicating that either the live counts failed to fairly estimate the tag-ratios of the above-fence spawning population or, contrary to the 1940 results, the tag-ratios among dead fish samples were different above and below the fence. This latter point can be examined directly, as has been done in Table 87. It may be seen that that area below the fence had, indeed, a substantially lower tag density among dead fish samples than areas above the fence, contrary to the results in 1940 (Tables 60 and 61). Comparing the tag-ratios from live counts above the fence only with dead fish samples from the same areas, it may be seen that they are nearly identical for large fish, but that the tag-ratio is lower for the live counts among jacks, a result similar to that obtained for Skookumchuck tags in the Birkenhead population (Table 81).

The population estimates corresponding to the tag-ratio data of Table 87 for samples from above the fence only are tabulated in Table 88. Here, again, it may be seen that there is no significant difference in the estimated total population of about 34,000 fish whether we estimate by means of all data pooled or by estimating the various sex-size categories separately.

The estimates thus arrived at for fish passing the fence agree well with the live-count estimates for large fish, but in the case of the jacks the live counts show a lower tag-ratio, and correspondingly a higher population estimate, than the dead fish samples. It may be remembered that a similar result was obtained for Skook-umchuck data (Table 81); it thus appears that the live counts may be somewhat erroneous in the case of the jacks due, perhaps, to the lower visibility of these small fish, particularly when untagged.

The estimates from dead fish samples in Table 86 include, apparently, the fish passing the fence and some, or all, of the fish which did not pass the fence. From the fact that the tag-ratios of live counts from all areas combined, which presumably cover the entire population, are little different from the tag-ratios among the dead fish samples from all areas it would seem that the dead samples included practically the entire population in 1941. In this year a particular effort was made to sample below the fence, including Lillooet Slough, so such may indeed be true. We may, however, look into this a bit more critically by means of apply-ing the theory of formulae (35) to the live-count tag-ratios above and below the fence and the estimates of fish passing the fence from Table 88. Fortunately, we counted the jacks and large fish separately in 1941, so we can estimate jacks and large fish separately as well as all fish pooled.

The counts of tagged and untagged fish for both jacks and large fish below and above the fence are tabulated in columns 1, 2, 4 and 5 of Table 89, and in column 3 we have also shown the fish-per-tag for live counts below the fence. Assuming the values in Table 88 to be our best estimates of the population which once ascended above the fence and was thus subject to tagging (including both fish that stayed above and those that subsequently dropped back below to spawn), "a" in Table 89, and under the hypotheses set forth on page 182, we have calcu-lated from formulae (35) the number of additional spawners, "x", below the fence not included in "a", and thence the total population "$a + x$" for each sex-size

TABLE 87

Tag-ratio Data From Dead Fish Samples Above and Below Birkenhead Fence, 1941

	ABOVE FENCE			BELOW FENCE			TOTAL		
	Tagged	Total Fish	Fish Per Tag	Tagged	Total Fish	Fish Per Tag	Tagged	Total Fish	Fish Per Tag
Jacks only	65	1153	17.74	74	1857	25.09	139	3010	21.65
Males only	46	562	12.21	65	1265	19.46	111	1827	16.46
Females only	137	1750	12.78	141	3885	27.55	278	5635	20.27
All large fish	183	2312	12.63	206	5150	25.00	389	7462	19.18
All fish	248	3465	13.97	280	7007	25.02	528	10472	19.83

TABLE 88

Estimates of Spawners From Dead Fish Samples from Above Fence Only, Birkenhead, 1941

		N (Formula 1)	σ_N	T	t	n	Fish Per Tag	% Recovered
A	Jacks only	15,000	1740	846	65	1153	17.74	7.68
B	Males only	7,490	1020	613	46	562	12.22	7.50
C	Females only	11,390	860	892	137	1750	12.77	15.36
D	All large fish	19,010	1260	1505	183	2312	12.63	12.16
E	All fish	32,850	1900	2351	248	3465	13.97	10.55
B+C		18,880	1330					
A+B+C		33,880	2190					
A+D		34,010	2150					

category separately and for the pooled data. It is evident, first, that the results are practically identical whether we estimate the jacks and large fish separately or pool the data. The resulting estimate of total population of about 27,000 large fish and 18,000 jacks agrees both with the estimates from all dead fish samples and from live counts from all areas combined to the degree expected from random sampling errors, which in 1941 were rather small due to the relatively high tag-ratio employed.

From the foregoing it may be concluded that in 1941 there were about 46,000 spawners in the Birkenhead, including about 18,000 jacks, and that the total dead fish samples and total live counts were each adequate to give reliable estimates of the population without considering sampling differentials among strata. Contrary to 1940, the dead fish samples included the entire population, probably as a result of special efforts to sample in Lillooet Slough, giving coverage of the share of the dead fish population not thus sampled in 1940.

Sockeye Population Spawning in Weaver Creek

The population of sockeye salmon spawning in Weaver Creek may be estimated from the marked members liberated at the fence and subsequent estimates of mark-ratios. The fence was placed very near the mouth of the stream (Figure 10) and only a very few fish spawned below it, so that sensibly the entire population was subject to tagging. Thus the difficulties encountered in estimating the Birkenhead population, with which we have just dealt, are avoided here.

In 1940, fish were marked by both tagging and fin clipping, while in 1941 only tagging was employed. Very high tag densities and intensities of recovery sampling were employed in the experiments of both years, higher indeed than would be warranted in most routine enumeration work. Roughly, one fish in ten was marked each year (although the marks were by no means evenly distributed) and approximately half of all fish were recovered during subsequent sampling.

1940 experiments

We have shown earlier that the fish of Weaver Creek do not mix very completely between tagging and subsequent sampling of dead fish, and that in 1940 the marked members were very unevenly distributed throughout the population, as a result of which there was marked heterogeneity in mark-ratios both with respect to time of tagging and area of recovery. At the same time, we have shown that the recovery rates of different groups of tags were quite uniform except for a period in early November.

Under these circumstances we may expect, since the recovery rates were nearly uniform, that the pooled data would yield a fairly reliable population estimate. It is of interest to see just how much difference is made by estimation of separate strata as opposed to a pooled estimate.

In Table 90 are shown, first, the tagging and recovery data for all marked fish, including both tags and fin-clips, for each sex separately and for both sexes pooled. It is shown again that the average tag-ratio among females was about 3 times that of males, but that the recovery rates are nearly equal, as a consequence

TABLE 89

Estimates of Spawners Below Birkenhead Fence, and of Resulting Total Populations,
by Means of Live Count Data, According to Formula (35), 1941

	n_b	t_b	Fish Per Tag Below Fence	n_a	t_a	a	x	y	$a+x$
Jacks only...............	1219	32	38.1	2172	108	15,000	3,066	3,428	18,070
Large fish only........	3555	74	48.0	5145	426	19,010	8,378	2,813	27,390
All............................	4774	106	45.0	7317	534	32,850	12,443	5,440	45,290

of which the pooled estimate is almost identical to the sum of the estimates for separate sexes. Next, we have computed the analogous estimates from the data from tags only, neglecting the fin-clips. The resulting values are slightly lower in each case than the estimates from all marks, but the differences are not significant. This result was, of course, anticipated from the results of Tables 22 and 23 wherein it was shown that there were no detectable differences in any respect between recovery rates of tags and fin-clips.

To determine whether a correction for time-connected sampling differences makes any significant difference in the estimates we have also computed the population from the data on tagged fish (fin-clips cannot, of course, be used here because the time of marking of individual recovered fish is not known) by means of formula (25). The resulting estimate is slightly lower than that obtained from the same data without taking into account the sampling differences in question, but the difference is obviously not significant.

The counts of tagged and untagged live fish totaled over the season yield an estimate of the tag-ratio (as we have demonstrated earlier) not significantly different from that estimated from dead fish samples. In consequence the respective resulting population estimates are not significantly different.

1941 experiments

Tags were somewhat irregularly distributed again in 1941, but not so much so as in 1940. As shown by Table 91, the average tag-ratios of males and females were less unequal than in 1940, and recovery rates were very nearly equal. The pooled data, thus, yield a population estimate almost identical with the sums of the estimates for the two sexes considered separately.

Correcting for time-connected sampling differentials by means of the procedure of formula (25) yields an estimate within one standard error of the uncorrected estimate, even though the standard error is only 290 fish, or 3% on the population of 9060 fish.

In this experiment, again, the pooled live counts taken at weekly intervals over the season yield a result not far different from the dead fish samples. The population estimate of 8420 from the live-count data differs, however, from the estimate of 9070 from dead fish samples by 550 fish, and is significantly different. Although the difference is greater than can reasonably be expected to occur by chance, our detection of this fact is possible only because of the small standard errors on our estimates in consequence of the intensive tagging and subsequent sampling in these experiments. Under slightly less intensive sampling, the small difference would not be significant. For most practical purposes the difference is sufficiently slight to be of no importance, and the estimate of population from the live counts would probably be quite adequate.

"Weaver Creek" Population Passing Harrison Trap

Estimation of the population of sockeye salmon spawning in Weaver Creek, plus the populations of Hatchery Creek and Little East Creek, which we blanket together in the "Weaver Creek" population (the populations of Hatchery Creek

TABLE 90

Estimates of Sockeye Spawners in Weaver Creek, 1940

	N (Formula 1)	σ_N	T	t	n	Fish Per Mark	% Recovered
Estimates from dead fish samples:							
All marks							
A Males only	4,490	370	151	73	2170	29.73	48.34
B Females only	12,730	340	1538	681	5638	8.28	44.28
C Both sexes	17,490	450	1689	754	7808	10.36	44.64
A+B	17,220	500					
Tags alone							
A' Males only	4,200	530	58	30	2170	72.33	51.72
B' Females only	12,120	560	505	235	5638	23.99	46.53
C' Both sexes	16,590	730	563	265	7808	29.46	47.07
A'+B'	16,320	770					
Estimates from live counts:							
	17,039	790	563	249	7536	30.26	

Estimates of all fish, correcting for time-connected sampling differentials by formula (25):

$$N = 15,770$$

and Little East Creek being negligible in comparison with those of Weaver Creek proper as shown on pages 164 and 165), may be made by means of tagged fish liberated at Harrison Trap and subsequent sampling on the spawning grounds. It should, however, be re-emphasized that the number of Weaver Creek fish tagged at Harrison Trap has been estimated from scale examinations and therefore, "T" in formula (1) is not surely known, but is only estimated and the actual reliability of the population estimates is, therefore, something less than the values indicated in the following tabulations.

Since we are not in a position to estimate the numbers of fish of each sex tagged at Harrison Trap, the estimates must be made for all fish pooled.

1940 experiments

It has been shown earlier (page 165) that the Harrison tagging of the Weaver Creek run in 1940 was unusually uneven, the tags being concentrated in the early part of the run. We have reason to believe that this early part of the run suffered a heavy mortality before arriving on the spawning grounds, in consequence of which only 24 out of 138 Harrison tags were recovered in Weaver Creek in 1940 compared with 264 out of 631 in 1941, although the rates of recovery of Weaver Creek were rather similar in the two years (Table 19).

The consequence of this low relative rate of recovery of tagged fish in 1940 is an apparently high value for the Weaver Creek population calculated from tags liberated at Harrison Trap and tag-ratio sampling in Weaver Creek. The basic data and corresponding population estimates for all dead fish samples and for pooled live counts in Weaver Creek are shown in Table 92. The population estimates from the two estimated tag-ratios are similar, although the standard errors are large because of the small values of "T" and "t" involved. These population estimates, in the neighborhood of 40,000 fish, are obviously unreasonably high, since (Table 90) only some 16,000 fish spawned in Weaver Creek, a few hundred perhaps in Hatchery Creek and none in Little East Creek in 1940. If we had relied on this Harrison tagging experiment to estimate the spawning population we would have been far from the true value. In a case such as this where the tags are concentrated on a small part of the run, and that part is subject to unusual mortality, the method may utterly fail even though later sampling for tag-ratios may be rather uniform.

The tag recoveries are too few to apply the theory of formula (25) to the data of this season.

1941 experiments

In 1941 the Harrison tagging of the Weaver Creek fish was a good deal more successful than in the previous year. We have shown earlier (Tables 75 and 76) that on the average one fish in 18.7 was tagged, and that while the tagging was quite uneven, being heaviest on the early part of the run, a fairly high tag-ratio was obtained on all parts of the run. The mean recovery rate among Weaver Creek dead fish of the tagged fish liberated at Harrison Trap was about 41%, comparing not unfavorably with the recovery rate of Weaver Creek tags of 55%. The sampling was not uniform throughout the season, however, as we have shown

TABLE 91

Estimates of Sockeye Spawners in Weaver Creek, 1941

	N (Formula 1)	σ_N	T	t	n	Fish Per Tag	% Recovered
Estimates from dead fish samples:							
A Males only	2,610	170	168	94	1461	15.54	55.95
B Females only	6,450	240	575	313	3509	11.21	54.43
C All fish	9,070	290	743	407	4970	12.21	54.78
A+B	9,060	290					
Estimates from live counts:							
	8,420	190	743	525	5953	11.33	

Estimate of all fish, correcting for time-connected sampling differentials by formula (25):

$$N = 9,230$$

TABLE 92

Estimates of "Weaver Creek" Population Passing Harrison Trap, 1940

	N (Formula 1)	σ_N	T	t	n	Fish Per Tag
Weaver Creek dead fish samples	44,900	8,320	138	24	7808	325.3
Weaver Creek live counts	38,520	6,640	138	27	7536	279.1

earlier, hence it is of interest to see whether correction for the seasonal variations in sampling differentials makes an appreciable difference in population estimates.

Several sources of estimates of tag-ratios are available for these tagging experiments, and corresponding population estimates can be made from these several estimates of tag-ratios.

Catches of live fish at the Weaver Creek trap furnish one means of estimating Harrison tag-ratios in this population. Among 1888 fish captured at this trap, 100 bore Harrison tags, leading to an estimate of 11,910 fish in the population (Table 93, line 3). As has been shown in Table 76, the tag-ratios among different parts of the run were by no means equal, and at the same time the sampling of the run by the trap was very uneven because of high-water during part of the season. Correcting for the sampling differentials by the theory of formula (25) we arrive at an estimate of 14,320, the difference between this and the uncorrected estimate being of borderline significance.

Dead fish samples at Weaver Creek, which included about half the population, give Harrison tag-ratio data leading to a population estimate of 11,880. The addition of the 128 fish, including 12 tagged, collected in samples at Little East Creek and Hatchery Creek, makes almost no change in this estimate. Correcting the Weaver Creek dead fish data for time-connected sampling differentials leads to an estimate insignificantly higher than the uncorrected value.

Live fish counts made in Weaver Creek for Harrison tag-ratios, summed over the season, yield an estimate of 14,620 fish, which is higher, but barely significantly so, than the estimate from dead fish samples.

The several methods of estimating in this case lead to a spread of some 25% in the population estimates, the dead fish samples yielding the lowest estimate and the live counts the highest. The trap catches "corrected" for sampling differentials yield a higher estimate than the uncorrected values, but since this does not agree with the corresponding estimate from dead fish samples it may be looked upon with some suspicion; during this season there were long periods when the trap was inoperative and in order to apply formula (25) it was necessary to include many days on which no samples were actually drawn in some of the recovery periods employed. For such periods the observed tag-ratio may be a very erroneous estimate of the true tag-ratio for that stratum, and the method should not, logically, be applied.

The best estimate of the population for these experiments appears to be about 12,500 fish. Since only 9,200 fish were estimated to have spawned in Weaver Creek in 1941, and the populations of Hatchery Creek and Little East Creek could not have amounted to more than a few hundred fish, it seems that either a considerable loss of tagged or untagged fish or both occurred between Harrison Trap and the spawning grounds, or our estimates by means of the scale patterns of numbers of Weaver Creek fish tagged was erroneous. In either case, we cannot rely on tagging at Harrison Trap to estimate Weaver Creek populations unless we are content with an error of about 30%.

TABLE 93

Estimates of "Weaver Creek" Population Passing Harrison Trap, 1941

	N (Formula 1)	σ_N	T	t	n	Fish Per Tag
Dead fish samples Weaver Creek only	11,880	540	631	264	4970	18.83
Dead fish samples (Weaver, Hatchery and Little East Creeks)	11,830	530	631	272	5098	18.74
Weaver Trap catches	11,910	1060	631	100	1888	18.88
Weaver live counts	14,620	690	631	257	5953	23.16

Weaver Creek dead fish samples, corrected by formula (25) :
$$N = 12,460$$

Weaver Creek Trap catches, corrected by formula (25) :
$$N = 14,320$$

Harrison Rapids Population

Only in 1941 was systematic sampling conducted along the beaches below and adjacent to Harrison Rapids, and the rate of recovery of spawned-out fish turned out to be too low for any very reliable estimate of the spawning population. Among 1375 fish there recovered, 11 bore Harrison tags or tag-scars. If we employ the estimate of Table 13 of 303 fish of this population tagged at Harrison Trap, and assume that the 1375 dead fish include no Hell's Gate fish, we arrive by formula (1) at a population estimate of 37,870 with standard error 11,200. This estimate has such a large sampling error that it is of little value except, perhaps, to indicate that the estimates of the run of sea-type sockeye in Table 4 are of the right order of magnitude.

SUMMARY OF RESULTS

The theory of estimation of animal populations by means of marked members has been reviewed, including the problem of estimating a population, known to contain a given number of marked members, from a single sample, and also the problem of estimating the population from the data obtained by repeated sampling of a stationary population, the members drawn in the samples being marked and replaced. Both of these methods have been applied to fishes, and the first has been applied to many other kinds of animals as well. The problem of the single sample from a population containing a known number of marked members is particularly applicable to the present task of estimating salmon populations. For this case we have reviewed methods of measuring sampling errors by means of the standard error of estimate, and also by means of the theory of confidence intervals. The former is employed in this thesis in the sequel.

A formulation has also been developed of a method of estimating an animal population which is constantly changing due to additions and subtractions, where marking and subsequent sampling are carried out continuously or periodically so as to include some representatives from each stratum in both samplings. This offers a method of correcting for seasonal differences in intensity of tagging and subsequent tag-ratio sampling of different strata of a population, such as a salmon run, which changes its composition in time due to additions and subtractions resulting from migration and death.

The Harrison-Lillooet River system, which was chosen for these experiments, supports sockeye salmon runs spawning in different streams at different seasons. Although a fairly large number of streams support some sockeye salmon, the important populations are few in number. The only important "early run" population spawns in the Birkenhead River, tributary to the Upper Lillooet. The other tributaries to the Lillooet above Harrison Lake support populations which are, in the aggregate, small compared to the Birkenhead population. In some years a sizeable number of fish, which spawn at about the same season as Birkenhead fish, frequent Silver Creek, a tributary to Harrison Lake. Other populations spawning at the same time in other tributaries to upper Harrison Lake are of negligible size. A sizeable "late run" population spawns in Weaver Creek not far above the confluence of the Harrison River with the Fraser River. Except for comparatively tiny populations in one or two other small streams in the vicinity, this is the only "late run" Harrison River population of sockeye which spends the usual year or two in a lake before going to sea. There is in addition, however, a very unusual population spawning in the main Harrison River, characterized by the fact that its members migrate to sea immediately after hatching. This population is difficult to estimate by ordinary visual methods because of the opacity of the water over the spawning grounds, but consideration of the relative abundance of its members in the commercial catch leads to the conclusion that it is of considerable size in most years, although rather large fluctuations are indicated.

Tagging of adult upstream migrants was conducted at the mouth of the Harrison River to include all runs in 1939, 1940, and 1941. Tagging was also conducted at the Sookumchuck in 1940 and 1941 to tag members of the Birkenhead

run. Tagging was conducted at the mouth of Weaver Creek in 1940 and 1941, and at a short distance above the mouth of the Birkenhead in 1939, 1940 and 1941.

Sampling of dead fish on the spawning grounds was conducted in a systematic fashion in the Birkenhead River and in Weaver Creek each year, and on Harrison Rapids in 1941 only. In addition, periodic patrols were made of the small tributaries of Harrison Lake. These were systematic only in 1940 and 1941. The populations which are studied in detail in this thesis are those of the Birkenhead River and Weaver Creek, and, to a lesser extent, that of Harrison Rapids.

The 1939 data were, in general, of value primarily for furnishing preliminary information and experience on the basis of which we were able to conduct experiments in 1940 and 1941 of real value to the study of the nature of the migrations of the adult sockeye and the problems involved in estimating population numbers by means of marked members. Experience with the sudden flash floods in the watershed led us to modify the original plan of approach after the first season, as well as to greatly modify the trapping equipment in the Birkenhead River.

The sockeye populations passing Harrison Trap cannot be segregated completely on the basis of time of migration alone. However, sockeye spawning in different tributaries have scale patterns which differ rather markedly from each other. By a consideration both of time of migration and scale pattern, individual migrants trapped near the mouth of the Harrison River can be assigned to the parent stream with a remarkably small degree of error. The accuracy of the method may be verified by the recovery of marked members, the parent streams of which are estimated independently from scale patterns and time of migration; only four errors were made among 75 tagged individuals later recovered on their parent spawning grounds. Scales were taken from a sample of one fish in five at Harrison Trap, on the basis of the study of which, taken together with migration times, the number of fish tagged from each major run during each week was estimated.

A complicating factor during 1941 was the presence in the Harrison Trap catches of a fair number of sockeye which had been blocked at Hell's Gate and had dropped back down the Fraser and ascended the Harrison to our trap. These fish, which were mixed in with the "late run", could be fairly readily distinguished by their battered appearance and by their bright coloration, differing markedly from "late run" Harrison fish, and those from which scales were taken could mostly be also distinguished from Weaver Creek or Harrison Rapids fish by the scale pattern alone; hence it was not difficult to eliminate such Hell's Gate fish from further consideration. It is of interest to note, in passing, that this is a very direct confirmation of Thompson's (1945) conclusion that there was a long serious blockade at Hell's Gate in 1941, which has been doubted by some other authors.

Of the Birkenhead fish tagged at Harrison Trap such a small percentage were later recovered, compared to the rates of recovery of tags placed on members of this run on the spawning grounds, that we must conclude that there is a heavy loss between the Harrison Trap and the Birkenhead River. The unrecovered fish cannot be accounted for by spawners in other streams than the Birkenhead, and it seems very doubtful that more than a part of the loss can be accounted for by normal mortality during migration, leading to the conclusion that there probably

is a serious differential mortality among tagged fish and untagged fish during this long migration. In any event, tagging at the mouth of the Harrison cannot be employed in conjunction with subsequent sampling on the spawning grounds to arrive at any useful estimate of the size of the Birkenhead spawning population.

A suggested source of mortality of upstream migrants, injury by gill nets in the commercial fishery, was investigated and it was concluded that the evidence from our Harrison marking experiments (on all populations) contains nothing to indicate that injury by gill nets reduces the chances of subsequent recovery of tagged fish.

Analysis of rates of recovery of sockeye salmon tagged at the Skookumchuck, in comparison with recovery rates of fish tagged at the Birkenhead, indicates a discrepancy of up to about 20% between the recoveries of Skookumchuck tags and the numbers which might be expected if there were no losses by mortality or to other spawning streams than the Birkenhead. While mortality probably accounts for part of this discrepancy, spawners in other streams also account for a good part. The results of 1940 and 1941 were very nearly identical with respect to comparative recovery rates. It thus appears that tagging at the Skookumchuck and subsequent sampling on the Birkenhead may be a reliable means of estimating the Upper Lillooet spawning populations, of which the Birkenhead forms by far the major part, with a fair degree of accuracy, particularly on a comparative basis.

Similar analyses of recovery rates of Weaver Creek sockeye tagged at the Harrison Trap with recovery rates of members of the same population tagged at the mouth of Weaver Creek indicated a discrepancy of about 24% in 1941, but a discrepancy of about 61% in 1940. These discrepancies must be attributed to mortality during migration. The very large mortality of tagged fish thus indicated for 1940 is believed to be explained by the circumstance that these tagged fish were concentrated among the very early migrants in that year, and the early part of the run perished in large part because of a blockade at the mouth of Weaver Creek due to no water. In 1941, however, no such abnormality was apparent, and the discrepancy of roughly 24% can be explained only by probably uniform mortality throughout the season, either of tagged fish or of both tagged and untagged. In either event, an estimate of the Weaver Creek population based on Harrison tagging in 1941 would be rather higher than an estimate based on tagging at the mouth of the spawning stream.

Analysis of data on tag-ratios and resulting population estimates from dead fish samples and from live-count samples leads to the conclusion that any differential mortality of tagged and untagged fish on the spawning grounds which may occur is insufficient to be of importance as a source of error in estimating populations of sockeye salmon in the Harrison system by means of marked members.

A special experiment in Weaver Creek in 1940 indicated that clipping one ventral fin was as satisfactory a method of marking as tagging where total dead fish samples are to be employed as a means of estimating mark-ratios.

Studies of the mixing of sockeye salmon populations of the Birkenhead River and of Weaver Creek during the upstream migration and on the spawning grounds, by means of tagged members, indicates that mixing, while considerable in all

instances, is not complete even over such a long distance and elapsed time between marking and recovery as is involved between tagging at the Skookumchuck and recovery among spawned-out dead fish in the Birkenhead. In general, as one would expect, the shorter the average distance and time between marking and recovery, the less the degree of mixing. A good deal of mixing between tagging and recovery as dead fish does, however, occur even where fish are tagged on the spawning grounds.

There is considerable variability between seasons and areas in rates of migration and amount of mixing of tagged fish. Although large variations are observed between sexes in particular experiments there seem to be no consistent differences between sexes.

There is a very definite time-connected differential in migration rates. In all our experiments we have found a very general tendency for the time between tagging and recovery to decrease as the season progresses. This is, of course, a necessary consequence of any appreciable mixing between tagging and recovery.

Comparing times of occurrence of modes in the catch-frequency curves at successive points on the migration paths of the populations under consideration with the average rates of migration of tagged members of these populations, there seems to be fair agreement. This indicates that tags do not serve to decrease to an observable extent (in our experiments) the rates of upstream migration of the tagged individuals which were recovered. Our data are, however, not adequate for critically examining this question.

In consequence of the lack of completeness of mixing of populations between sampling for tagging and subsequent sampling for tag-ratios, coupled with uneven sampling for tagging, the different strata (by time or area) of the sockeye salmon populations studied often exhibit significant, and indeed sometimes very marked, differences in tag-ratios. Similarly, as judged by rates of recovery of tagged members of groups of fish sampled for tagging at successive time periods, there are often observed significant non-uniformities of recovery rates. In general, neither sampling for tagging nor subsequent sampling for tag-ratios is even over the whole population, and the lack of completeness of mixing between the two samplings leads, thus, to significant differences in tag-ratios and recovery rates of different population strata.

Tag-ratios from live counts were found to agree (when averaged over the season) with average tag-ratios for dead fish samples in both the Birkenhead River and Weaver Creek.

In spite of the above-mentioned sampling differentials between different strata of the population, no significant differences resulted in estimating the population of sockeye passing the Skookumchuck from Birkenhead samples of dead, spawned-out, Skookumchuck-tagged fish in either 1940 or 1941, regardless of whether all the data were pooled, the data for different sexes were employed to estimate each separately, or the "theory of the changing population" was applied to correct for time-connected sampling differentials. The only exception to this was that in 1940 the tag-ratio and recovery rate of jacks were much lower than those of large fish so that the pooled estimates including both jacks and large fish

showed a significant decrease over the estimate derived from the sums of estimates of separate strata. Samples of fresh dead fish alone yielded identical results to the total samples of dead fish.

Results agreeing in all respects with the above were obtained from estimates of the Birkenhead population based on tagging at the Birkenhead trap in 1940 and 1941 and subsequent sampling of dead fish. In these experiments, because the trap was located above the spawning grounds of some of the fish, it was necessary to develop a method of estimation utilizing both dead fish samples and live-counts for tag-ratios above and below the fence to arrive at an accurate estimate of the total population.

Tagging experiments in Weaver Creek yielded similar results. In each year tagging at the mouth of Weaver Creek and subsequent sampling of dead fish on the spawning grounds indicated that pooled samples yielded total estimates not significantly different from estimates of each sex-category made separately, or estimates correcting for time-connected sampling differentials by the theory earlier developed. Tagging at the Harrison Trap and subsequent sampling of dead fish in Weaver Creek yielded similar results, although peculiar circumstances surrounding some of the experiments render them in some degree aberrant for our study.

There is, in general, little or no improvement in the estimates corrected for sampling differentials over the population estimates arrived at by the theory of the simple case. Such non-uniformities of sampling as did occur between different parts of a run, although statistically quite significant, made no appreciable difference in the population estimate. This results from the fact that, although a salmon run extends over a long time period, the major part of the population is concentrated in a small fraction of this total period; the runs have, in general, a sharp "peak". In consequence, although the various time-strata of the population are unevenly sampled, most of such strata are of relatively minor magnitude, so that the sampling of the main part of the population is uniform or very nearly so with respect to tagging, or subsequent recovery, or both, making the theory of the simple case quite adequate for estimating the populations with which we have dealt.

Estimates based on counts of tagged and untagged live spawners summed over the season usually lead to population estimates identical, within limits of random variation, to those arrived at by dead fish samples. In some instances, however, the estimates from such live counts did differ significantly from the probably more accurate estimates based on dead fish samples. Such discrepancies are probably the result of observer bias, since there is a large subjective factor involved in judging which untagged fish are seen clearly enough that a tag would be seen if the fish in question had been tagged and so should be included in the live fish count.

Sampling of dead fish in the vicinity of Harrison Rapids included such a small part of the population that the resulting population estimates of Harrison Rapids spawners were attended by very large errors of estimate. The results indicate that this population is probably larger than has been commonly supposed, and that estimates, based on relative occurrence in the commercial catch of fish with scale nuclei of the type peculiar to this run, are of the proper order of magnitude.

CONCLUSIONS

With respect to the several objectives of this thesis as set forth in the introduction, we may conclude:

The spawning migrations of the several populations of sockeye salmon in the Harrison River system are such that they may be subjected to tagging at various places along the migration path. In the course of the migration a given population tends to mix to a degree, but mixing is not complete, at least between tagging and subsequent sampling of the sort that may be employed in practice with useful results in estimating populations. No important differences were observed between large males and large females, but in some instances jack sockeye seemed to exhibit somewhat different migratory behavior from large fish and should best be treated separately.

Although mixing is not complete, it is yet quite considerable even between time of arrival at and time of sampling after death on the spawning grounds. Further, the various strata of the population, with respect to time of migration (or time of death on the spawning grounds) are of very unequal size, so that a part of the population occupying a short migration period constitutes a very large share of the whole, in consequence of which failure to sample various strata corresponding to equal time-periods with absolute evenness is of little importance in practice.

If one tags as evenly as practicable at a point below or adjacent to the spawning grounds, and subsequently samples the dead, spawned-out fish for tag-ratios as uniformly as possible, even though considerable variations do occur in intensity of sampling, the resulting population estimates by the simple theory of formula (1) may be generally expected to yield results not significantly different from estimates arrived at correcting for differential intensity of sampling of different strata. It is recommended, however, that whenever practicable numbered tags be employed, and data be tabulated by sex-categories and time-periods, so that if the circumstances lead one to believe that the sampling differentials are of sufficient magnitude to lead to an erroneous estimate by the simple formula, the point may be investigated and, if necessary, the "theory of the changing population" applied to correct for differentials in sampling of different strata.

It is desirable, if possible, that the tags be distributed throughout the entire population, and that subsequent sampling for tag-ratios be similarly conducted in such a fashion as to include the whole population, even though the sampling of the various parts be quite uneven in both samplings. Only in such fashion does one obtain the basic data for judging whether the sampling has, in fact, been sufficiently nearly even to yield a fair estimate of the population and, if not, to correct for sampling differentials. Judging from our results, no correction will be necessary as a rule, but it would seem prudent to secure the means of judging each body of data on its own merits whenever possible.

Our experiments on the Harrison system indicate that an estimate of high precision of a given spawning population can be obtained only by tagging very close to the spawning grounds, preferably at the mouth of the spawning stream. Due to mortality during migration of tagged fish, and perhaps of untagged ones

also, as one goes further away from the spawning grounds to conduct the tagging, the calculated population is increased, and at some distance below the spawning grounds the error becomes so large that the estimate is useless by any criterion. In the case of the Birkenhead population, for example, one may tag at the Skookumchuck and arrive at an estimate, by means of subsequent samples in the Birkenhead, only slightly higher than that obtained from experiments conducted entirely on the Birkenhead, the error amounting to not over 20%. Tagging at the mouth of the Harrison, on the other hand, yields estimates high out of all reason. Similarly, tagging at the site of our Harrison Trap may be expected to yield estimates of the Weaver Creek population about 25% higher than obtained from tagging at the mouth of the stream. How much of this sort of error can be tolerated will depend a good deal, of course, on to what use the results are to be put, and perhaps on the relative costs involved in tagging at different places.

Estimating the major sockeye salmon populations of the Harrison River and similar streams by means of tagging at the mouth of the river and subsequently sampling for tag-ratios on the far distant spawning grounds is definitely not practicable; such estimates of the Upper Lillooet (Birkenhead) populations are useless. Tagging at points closer to a spawning ground, (such as at the Skookum-chuck in the case of the Birkenhead population) which are for physical reasons easy places to tag and are yet close enough so that possible mortality effects are small, offers a rapid and inexpensive method of obtaining estimates of a fairly high order of accuracy. Indeed, it may be found by further study that, as in the case of the two years during which we have conducted experiments at the Skookumchuck and Birkenhead, the "discrepancy" is fairly constant from year to year. If so, this would offer a very simple method of obtaining highly accurate comparative estimates. In any case, estimates of the indicated order of accuracy are certainly far superior to the estimates formerly available. Where estimates of a high degree of accuracy are required, tagging on, or preferably just below, the spawning ground is recommended.

Estimates of tag-ratios from live fish counts on the spawning grounds, while easy to obtain and reasonably accurate, are less dependable than similar estimates from dead fish samples.

In final summary, it may be said that the estimation of sockeye salmon populations by means of marked members, following the methods developed herein, is practicable, but must be applied cautiously with careful consideration being given to the interpretation of the data in each instance. Given careful study and analysis of the results of every experiment, the tagging method is believed to offer a means of measuring salmon populations with a degree of accuracy not heretofore obtained except by counting weirs.

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