INTERNATIONAL PACIFIC SALMON
FISHERIES COMMISSION

BULLETIN II

PROBLEMS IN ENUMERATION OF POPULATIONS OF SPAWNING SOCKEYE SALMON

1. A STUDY OF THE TAGGING METHOD IN THE ENUMERATION OF SOCKEYE SALMON POPULATIONS

BY

GERALD V. HOWARD

2. A MATHEMATICAL STUDY OF CONFIDENCE LIMITS OF SALMON POPULATIONS CALCULATED FROM SAMPLE TAG RATIOS

BY

D. G. CHAPMAN

NEW WESTMINSTER, B. C.
CANADA
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FOREWORD

When the International Pacific Salmon Fisheries Commission undertook the investigation of the Fraser River sockeye, one of the first problems encountered was the development of a method of determining the numbers of sockeye spawning in the different tributaries. Most of these streams were too large and swift to lend themselves to the use of time-honored weirs except at heavy cost. Such expenditures were beyond the means of the Commission. Moreover, weirs were of doubtful value until the distribution of spawning fish in the rivers had been determined. The possibility of adapting tagging to determining the size of the spawning stocks was therefore explored and under field conditions the method seemed to provide an excellent answer.

Many questions arise in the application of such a method which involves the random sampling of a population at least twice and requires adequate distribution of the marks used. The experiments reported in paper number one of this bulletin were initiated by Dr. J. L. Kask in 1938 at Cultus Lake and were repeated in 1939. Their principal objective was to determine if a tag ratio could be established in a population of spawning sockeye and if samples of the dead fish would yield an accurate estimate of that ratio. The experiments were successful in this regard and on the basis of a preliminary report by Dr. Kask the tagging method was widely adopted in the Commission's work.

Owing to changes in personnel a final report was not written and when the writer took the position of Chief Biologist the material was still in a preliminary stage of analysis.

The wide use of the method in the Commission's work and the many problems that have arisen through its application in different types of streams indicated that the original material had to be studied carefully with a view to determining as far as possible the limits of accuracy of the population measurements obtained by tagging. Accordingly, the data were subjected to a statistical analysis commensurate with their basic accuracy. The resulting paper is published herewith.

Dr. Kask in the meantime had spent several years at the California Academy of Sciences and one year with the United States Army of Occupation in Japan and unfortunately had lost contact with the work. Because of this, upon returning from Japan, he requested that his name be withdrawn from authorship. The paper originally planned to appear under the joint authorship of Dr. Kask and Mr. Howard is therefore published under Mr. Howard's name only. Dr. Kask's part in initiating the experiment, carrying through the field work and in writing up the preliminary report must therefore be acknowledged in this manner. Great credit is due him for his excellent work.

With the use of tagging under the many different conditions encountered in the Fraser River system, problems have arisen which could not be foreseen when the original experiments were devised. These problems, discussed in the paper, have to do with the location of tagging and with the recovery of the dead fish and tags. The original experiments were not designed to study differences in accuracy of results due to differences in methods and conditions of tagging or in the conditions of recovery of the dead fish. A new experiment was executed at Cultus Lake in the fall of 1947 which should solve some of these problems. In the latter experiment, control was exercised at the weir by tagging every fifth fish of each sex and size group (jacks and 4- and 5-year-olds), as well as by tagging every fifth fish that passed through, regardless of sex or size. A uniform density of tags was thus maintained in the population as a whole as it passed the weir, and in each size and sex group.

Dead fish were examined on the spawning grounds in 1947 as far as possible *in situ* and upon the first examination were marked with a numbered aluminum cattle tag fastened to the tail. Where it was necessary to disturb dead fish to read the tag numbers they were returned as closely as possible to the position in which they were found. In this way each coverage of an area formed an independent sample of the dead fish and the recoveries for the entire season are thus subject to an analysis which should indicate the limits of error of individual samples as well as the extent to which the errors are affected by modifying the time and area of sampling. A report upon this experiment is in preparation.

The effect of tagging in different locations relative to the spawning grounds cannot be studied at Cultus Lake except in an indirect manner. It was studied in the South Thompson area in 1946.

Solution of the problems of tagging and the use of tagging for determining the size of spawning populations forms a preliminary step in the program of the study of spawning stocks. The final objective must be to develop a simple yet accurate method of observation for determining the size of populations in each spawning area. The use of indices such as live fish counts, or widespread density counts, is now being developed. These indices are calibrated against tagging experiments or where possible against weir counts. Ultimately calibrated indices will be developed for each stream which should reduce the cost and labor of spawning population counts to a minimum. A constant watch must be maintained, however, to insure the continuity and accuracy of such observations and this can be accomplished by periodic checks with accurate methods of enumeration. Determination of the limitations of the tagging method is fundamental to the development of this program. The present paper is the first publication of the Salmon Commission dealing with this problem.

The accuracy of the estimated sizes of populations may be studied either through direct experimentation such as the Cultus Lake experiments or through a theoretical study of the mathematical characteristics of the formulae involved. Both approaches must be used, since direct experimentation when properly designed can show the range of accuracy of a method, but the measures involved are always conditioned by the particular environment under which the work is carried out.

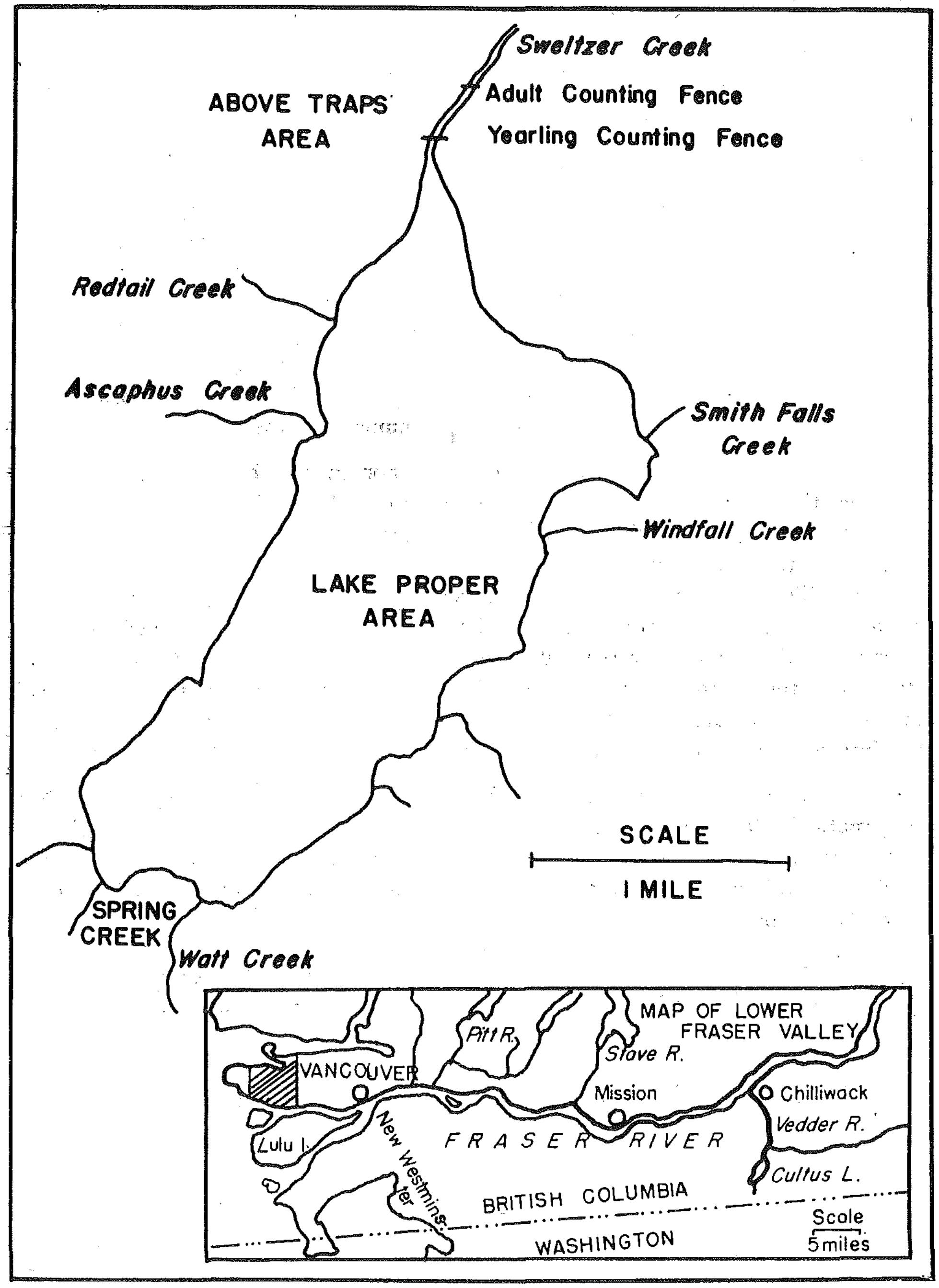
No two streams are alike and it is impossible to apply such results obtained on one stream directly to another. The theoretical basis of the method must therefore be established, and from this foundation the practical results can be interpreted and extended.

Professor Chapman of the Department of Mathematics of the University of British Columbia was engaged early in 1947 as consultant to the Commission in mathematical statistics and one of the first problems presented to him concerned the mathematical background of the various measurements of accuracy of calculated populations. Superficially, Pearson's formula (see Ref. in Chapman) for the standard error of population sizes calculated from the recovery of marked individuals seemed to be a valid solution of the problem. However, as shown by Professor Chapman (paper No. 2 of this bulletin), this formula has a dubious mathematical foundation which makes its use basically unsound. Examination of the limits outlined by Garwood and later extended by Ricker (Refs. Chapman's paper) showed them to be too asymmetrical under certain circumstances. Professor Chapman has worked out a new solution which presents the advantages of a sound mathematical background as well as greater symmetry in the results.

In the course of his work Professor Chapman has brought together and compared the other methods that have been developed for determining confidence limits and in doing so has clarified many points left obscure in previous applications by defining the conditions under which different methods of calculation should be used. The application of the formulae to the determination of the number of tags that should be put out and size of sample that should be examined to obtain an estimate of the size of a population within given confidence limits is of special interest to the Commission's biological staff. Comparison of this theoretical approach with actual results obtained under experimental conditions of varied sampling will be made in the analysis of the 1947 Cultus Lake work.

The Commission is indebted to Professor Chapman for his assistance in mathematical statistics. It is also indebted to Professor J. Neyman of the University of California for his interest in this paper. Proper acknowledgment of others who have assisted with criticisms of the two manuscripts is made in each of the two papers.

R. VAN CLEVE,
Chief Biologist.



Map of Cultus Lake with inset to show lower Fraser Valley.

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A Study of the Tagging Method in the Enumeration of Sockeye Salmon Populations

by

GERALD V. HOWARD

INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION

A STUDY OF THE TAGGING METHOD IN THE ENUMERATION OF SOCKEYE SALMON POPULATIONS

By GERALD V. HOWARD

INTRODUCTION

A run of salmon returning to a river system as adults in a given year consists ultimately of three portions, the catch, the escapement and the loss due to natural causes. The numbers of sockeye taken by the fishery can be determined by a system of catch statistics. Evaluation of the various losses resulting from natural mortality is a difficult problem that is not considered in this paper.

The accurate determination of the numbers which escape to the spawning grounds in the Fraser River system has presented a variety of problems due to the many different types of streams involved. On some tributaries of the Fraser such as Cultus, Bowron, Seton Creek and some streams in the Stuart area, weirs have been built and these runs have been counted. However, this method is not practical in most of the other spawning areas in the Fraser system since the streams are too large. In lieu of weirs, a system of tagging has been studied and applied to calculate the size of the spawning populations in such tributaries.

The tagging method involves the release of a varying number of live tagged fish on or below the spawning grounds. Subsequently, samples of the dead fish are examined, and on the assumption that the ratio of tagged to untagged fish found in these samples is the same as the ratio of tagged to untagged in the population, the total number of fish in that population is calculated from the following equation:

$$\frac{\text{Total number tagged}}{\text{Total population}} = \frac{\text{Number of tagged carcasses examined}}{\text{Total number of carcasses examined}}$$

This hypothesis requires the assumption that either the tagged fish released are distributed randomly in the population so that any sample taken from that population would be representative of the whole, or that the sampling of the dead fish is thorough enough to give an accurate picture of the over-all tag ratio regardless of whether or not the tagged fish are distributed randomly. If neither of these conditions is fulfilled, the probability of obtaining an accurate estimate of the population from the experiment would be small.

Estimates of the errors of such calculated populations were made on theoretical bases by Pearson (1928) and others, but the problems encountered in handling a population of spawning sockeye in this manner were unknown. Therefore, these estimates could not be accepted without some study of the extent to which the necessary assumptions were applicable. Such an investigation was possible only in a population over which complete control was exercised by means of a weir. This condition was met admirably at Cultus Lake where accurate counts of the migrating population are made as the fish pass through a counting fence located below the spawning grounds. In 1938 and 1939 the International Pacific Salmon Fisheries Commission conducted tagging experiments at this locality. It was hoped that the results of these experiments would be useful in estimating the accuracy with which the method could be applied in other areas.

The superficial results of these experiments showed that the ratio of tagged to untagged fish could be determined with a fair degree of accuracy even when the relative number of tags was as small as two in one hundred, or two per cent. Therefore, this method has been widely applied in the Commission's work. However, its use under field conditions over a period of years has brought to light a number of problems which could not be foreseen when the original experiments were undertaken. These problems limit the extent to which the results of the original Cultus Lake experiments can be applied (see page 11).

Cultus Lake (*Frontispiece*) is a small body of water with a surface area of approximately 2½ square miles and a maximum depth of 130 feet (Ricker, 1937a). It is connected with the Fraser River by Sweltzer Creek and the Vedder River. The lake is approximately 70 miles by water from the mouth of the Fraser River. Four small streams flow into the lake. An accurate count of all sockeye entering the lake can be made through a weir which is located on Sweltzer Creek about a quarter mile below the outlet of the lake.

Most of the sockeye salmon that spawn in the Cultus Lake area each year are 4-year-old fish (Foerster, 1929). No natural spawning was permitted in 1934, the cycle year of the 1938 run. The fish were spawned artificially and 5½ million eyed eggs were planted in four streams tributary to Cultus Lake in the spring of 1935 (Foerster, 1937). The Fisheries Research Board of Canada marked all of the downstream migrants from this planting by removing both ventral fins (Foerster, 1944). In 1938, a total of 13,342 sockeye were counted through the weir. Spawning occurred only in Sweltzer Creek above the weir, in the Lake and in Spring Creek. No sockeye returned to the other three tributary streams. With the data at hand it is impossible to determine the origin of the fish spawning in the different parts of the area or to determine what happened to the fish which presumably returned from plants made in the three streams which were barren in 1938. In 1939 the run to Cultus Lake of 73,189 sockeye was the progeny of the natural spawning of 10,174 females and 5,615 males in 1935 (Foerster, 1944).

METHODS

COUNTING AND TAGGING THE FISH

In 1938 all the fish that arrived at the counting weir were lifted over the fence with dip nets. During this procedure the sex and size category (see page 12) of each fish was determined. In 1939 all fish, except those tagged, were counted through an escape gate designed so that only one sockeye at a time could get through. The fish passed over a white flashboard and it was assumed that the sex of each could be noted. This speeded up counting but the small fish were not separated from the large ones.

The tagging procedure was the same for both years. Each fish was tagged with two white celluloid discs. A nickel pin was used to hold these discs on either side of the back at the base of the dorsal fin (MacKay, Howard and Killick, 1944). Only one of these discs was numbered. The tags were attached firmly and were clearly visible on the spawning grounds.

EXAMINATION OF THE DEAD FISH

To find the ratio between the number of tagged and untagged dead sockeye, all of the spawning areas were patrolled as frequently as possible. Tributary streams and some parts of the lake were visited daily. The district was divided into three statistical areas (*Frontispiece*), namely:

1. "Above Traps Area"—referred to as "Traps", between the adult counting fence and the outlet of the lake marked by a foot bridge across Sweltzer Creek.
2. "Lake Proper Area"—referred to as "Lake", the main lake area, excluding "Above Traps Area".
3. "Spring Creek".

The water is shallow in the Traps so that the number of fish collected represented approximately all of the fish that died there. In the Lake, however, only those fish could be recovered that spawned and died in, or drifted into the shallow water along the shoreline. Spring Creek is a small stream 1½ miles long, 6 to 9 feet wide, with a depth of 6 to 16 inches. It was possible to recover practically all of the carcasses from this stream.

Significant numbers of fish were recovered in all three areas in 1938. During 1939 only a small number of sockeye spawned in Spring Creek, and so few recoveries were made there that they were included with those in the Lake. The following data were recorded for each dead fish: date, statistical area, sex, condition of carcass, degree spawned, tag number or presence of tag scar. All dead fish recovered were examined and recorded and were removed from the water to preclude duplication of data.

LIMITATIONS OF THE DATA

As noted above, the experience gained through the use of tagging for enumerating spawning populations of sockeye has revealed many problems that could not be foreseen at the time the Cultus Lake experiments were undertaken. These problems are derived from two sources. One source is the location and time of tagging. An error has been found to occur where tagging is conducted too far below the spawning grounds. The results of such experiments indicate that the tag ratios obtained from dead fish tend to be too low; hence, the estimated populations tend to be large. The error increases directly with the distance between the tagging location and the redds. The present experiments give no measure of the errors involved when tagging is not conducted immediately downstream from the spawning grounds.

In some tributaries of the Fraser it has been found impractical to tag fish below the spawning areas and in these localities tagging has been conducted on the redds themselves. In such cases there has been some question as to the random distribution of the tagged fish within the population and it has been impossible to determine whether or not the sampling of dead fish has compensated for any errors that might have arisen from non-random distribution. The present experiment can shed no light on this problem. It is probable that the errors deriving from this source will vary with each spawning ground and an assessment of these errors may have to be made for each stream before the accuracy of the population estimate involved can be determined.

The second group of problems arises in the recovery of the dead fish. In large runs this requires a great amount of effort if a significant proportion of the run is to be examined, and the cost of recovery can be prohibitive. Reduction in the number of recoveries required, in the area which must be examined and in the period over which recovery of dead fish must be carried out (if possible), is fundamental to an economical and practical operation. The present work indicates the effect upon the accuracy of the results when sampling is confined to one of several large areas. It was not designed to show the effect of reducing the time of sampling or the numbers sampled.

The data obtained from the Cultus Lake work also yield information as to the extent to which the relative number of tagged fish can be reduced and they indicate the extent to which a reduction of the period of tagging during the course of the run will affect the distribution of tags on the spawning grounds and among the dead fish. The reduction of both the number of tags and the period of tagging is important in reducing the cost of the programs.

RESULTS

TAGGING IN 1938

The numbers of sockeye tagged in each sex and size category each week during 1938 are shown in Table I with the numbers of untagged counted through the weir. In 1938 all sockeye without clipped fins could be identified as 3- or 5-year olds and the 3-year olds could be separated arbitrarily from the 5-year olds on the basis of size.

A total of 13,342 sockeye passed through the weir between September 27 and December 21. Of the total number entering the lake that year 58.7 per cent were females, of which approximately 6 per cent were "jacks" or 3-year olds; 71 per cent of all males were 3-year olds. It was noted that the females increased gradually from 30.7 per cent during the first week of migration to over 90 per cent on some days at the end of the run. Similar changes of sex ratio in the course of a run have been noted in other streams of the Fraser River watershed.

A total of 4,416 sockeye or one-third of the run entering the lake was tagged in 1938. Apparently by the end of the run the distribution of tags between the different categories was close to the actual proportion that each group formed of the run. However, the number of fish tagged did not form a constant proportion of the migrants entering the lake in each week. The average tag ratio for all the live fish passing the weir during the season was 1 tagged to 2.02 untagged. This ratio varied from 1 tagged to 2.22 untagged for the large males to 1 to 1.94 for small females. Application of the Chi-square test indicated that the differences in tag ratios from week to week within the different categories of live fish, as well as between the categories, were statistically significant.

TAGGING IN 1939

The numbers of the two sexes tagged in successive weeks during 1939 are shown in Table II. Of the 73,189 sockeye counted into the lake between October 10, 1939, and January 20, 1940, 51,565 or 70.5 per cent were females. Eight sockeye were tagged without determining their sex. A small proportion, probably less than 5 per cent, were 3-year olds but these small fish were not segregated from the large ones at the counting fence. As in 1938, the females increased in proportion as the migration progressed.

One-twentieth of the total run was tagged, corresponding to a tag ratio of 1 tagged to 19 untagged sockeye. The distribution of tags was practically constant throughout the season for each sex. The average tag ratio for the season was 1 to 16.6 for the males and 1 to 20.6 for the females. When tested by Chi-square for variation during the season, no significant differences were found between the tag ratios established each week within the two sexes.

RECOVERY OF THE DEAD

The dead fish recoveries are shown in Table III. The numbers of tagged and untagged fish recovered were divided according to sex and size for each area. Altogether, 35.5 per cent of all fish that passed through the weir was recovered in 1938 and 13.4 per cent in 1939. The smaller proportion examined in 1939 was largely because few sockeye entered Spring Creek where the recovery of carcasses was easy. Also, the magnitude of the run in 1939 was such that with the help available it was impossible to examine all fish and to cover all parts of the lake as frequently in that year as in 1938.

NATURE OF THE RUNS

Tables IV to VIII show the number of tagged sockeye of each size and sex category recovered in the three areas each week throughout the two seasons, separated according to the week in which these fish were tagged at the counting fence. Tags are lost sometimes from the fish but the tag scars on these individuals are recognized easily. It was necessary to omit them from the tables, however, since the dates of tagging were not known. There were 53 such scars found in 1938 and 2 in 1939. Only 6 male jacks and 2 female jacks were found in Spring Creek in 1938 and they were not included in the analysis.

1938 Run

The numbers in the various cells of Tables IV to VI represent the tagged fish which were recovered in 1938. Since the tagging throughout the 1938 migration was not uniformly proportional to the number of migrants and since tagging may have had some effect on the length of time the fish lived after passing the weir, the tables can not be accepted as being representative of the whole population. However, a comparison of the success of spawning of the females in each area indicated that the tagged fish recoveries differed significantly from the untagged recoveries only in the Traps area (see below). Analysis of the time that the tagged fish, recovered in each area, passed through the weir indicated that there was no marked difference in period of migration of either males or females into the different areas. However, the proportion of each category migrating past the weir to all areas varied. The females dominated the end of the run in each area. More fish destined for Spring Creek moved through the counting fence later than fish going to the other two areas.

Inconsistencies were noted in the distribution in the three areas of the tag recoveries from successive weeks of tagging. For the Lake and Spring Creek, the fish tagged during a particular week tended to distribute themselves throughout successive weeks of the dead recovery (see Tables V and VI). However, for the Traps it was noted that only one late recovery was made of large fish from tags that were put on before the middle of November (see Table IV). This will be discussed later when it will be shown that some fish, which may be assumed to be the weaker ones, died earlier than the others immediately above the tagging locality (see below). Only 4 males were recovered in Spring Creek after December 19 while 72 females were examined after that date, the last one during the last week in January.

The large females were examined for the degree spawned and each dead female was recorded as having deposited 100, 75, 50, 25, or 0 per cent of its eggs. For the tagged females in the three areas the average degree spawned of all those recovered in each week is given by the week of recovery. Similar information is given for corresponding samples of untagged females. Approximately 95 per cent of the females examined in all three areas prior to November 15 were unspawned. The success of spawning after that time was better in the Lake than in the other two areas. Comparison of the average per cent spawned in tagged and untagged fish showed no statistically significant differences between the two groups through the heaviest part of the dead recovery period in both the Lake and Spring Creek. Significant discrepancies seen in the Traps were associated with the early death of fish which must have been injured in tagging, and died unspawned. With reference to the Spring Creek population, these fish were the progeny of eyed eggs planted in that stream and therefore were an introduced run. Few sockeye returned to this stream in the following cycle year (1942). The poor spawning of the 1938 run in this area may have been due to the fact that the introduced run was not adapted to this environment, the 1938 run was too large to permit normal spawning in Spring Creek, or the creek is not a suitable sockeye spawning ground. Successful spawning of smaller numbers of sockeye in the creek since that time rules out the last possibility and leaves only the first two as tenable explanations.

The entire period during which the fish died extended over 16 weeks from October 11 to January 30 (see Tables IV to VI and IX). The majority of the tagged sockeye were recovered during the seven-week period from November 15 to January 8, with the exception of the small females in the Traps where only 7 of these fish were found. Of the total number of tagged fish recovered in the Traps, 150, or 74 per cent, were recovered during the designated 7 weeks. In the two remaining areas, the Lake and Spring Creek, 81 per cent and 97 per cent respectively were recovered in this period. In the Traps a larger percentage of the tagged fish died prior to November 15 than in the other two areas. The Traps and Lake had a larger percentage of the total number of tagged fish dying after January 8 than was the case for Spring Creek. It was noted that 69.5 per cent of the recoveries from Spring Creek were tagged before November 1, whereas 81.1 per cent of the recoveries in the other two areas were tagged before this time.

The average number of days out for tagged fish is given in Table IX. In each area it was seen that the males were recovered after a longer period than the females; and in the Lake the 3-year old sockeye were recovered after a longer period than the 4-year olds. Apparently the Spring Creek sockeye passed through the weir later than most of the Lake and Trap fish and the run was more narrowly defined. With all the spawning areas accessible to examination the period of dead recovery was more restricted than in the other two areas. The relatively high percentage of unspawned females in Spring Creek throws doubt as to the validity of the recovery period as a measure of the normal spawning period in Spring Creek. The recovery period in the Lake may have been extended because of the possibility that some fish became accessible to recovery some time after death. The tagged fish in the Traps died and were recovered sooner on the average than the fish in the other two areas.

1939 RUN

Since tagging throughout the 1939 migration was uniform, that is, since a constant tag ratio was maintained, the data shown in Tables VII and VIII may be considered to be approximately representative of the run except insofar as tagging affected the length of time the fish survived after passing the weir. As in 1938 there was no marked difference in the period of migration to the two areas. The samples from the Traps did not have late recoveries from the earlier weeks of tagging. In the Lake, fish tagged during each week after October 26 tended to distribute themselves throughout successive weeks of the recovery, overlapping recoveries from earlier and later tagging. Only 200 fish were tagged during the first three weeks ending October 26 and recoveries were too few to give a clear picture of the distribution of these early fish. Only one of these tags (a female) was recovered after December 21.

As in 1938, the average success of spawning of tagged females, shown in Tables VII and VIII, did not differ significantly from the untagged fish during the period of heaviest recoveries. Differences, especially in the Traps, were found in the small number of early recoveries and in the single recovery during the week ending January 25. The differences found in the first two weeks' recoveries in the Lake were not as marked as in the other area and were probably due to the small number of fish involved. The fish spawned more successfully in the Lake than in the Traps and spawning was better in both areas after December 1.

The 1939 data show that the majority of the tagged fish were recovered during a seven-week period from December 1 to January 18 and a larger percentage of the tagged fish died in the Traps prior to the beginning of this period than was the case in the Lake (see Table IX). Tagged fish were recovered after a longer period of time in the Lake and the males lived longer after tagging than the females did.

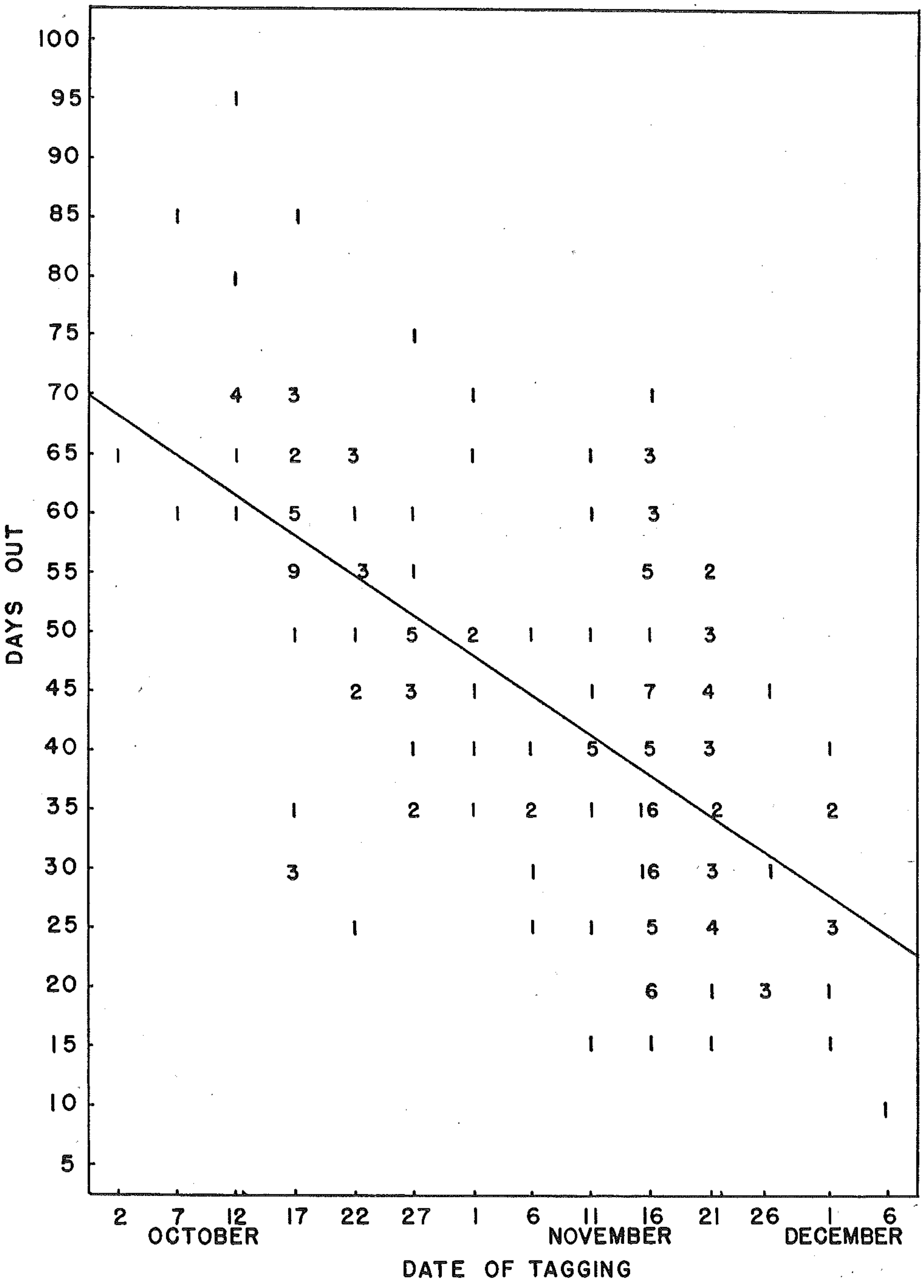

FIGURE 1

Number of tagged females spawned between 50 and 100 per cent and recovered in the Lake Proper Area from successive five-day tagging periods. The number of days elapsing between tagging and examination in the dead state (days out) is shown for each of these recoveries. A regression line ($y=a+bx$) is fitted to these recoveries where y=days out and x=number of days after tagging. (See Table X).

Date of Tagging and Time of Death

Each female tag recovered in the three areas was plotted according to the date of tagging and the number of days elapsing before death for the different years. The recoveries were separated into two groups in 1938, those which had spawned from 0 to 25 per cent of their eggs and those 50 to 100 per cent spawned (see page 14). Straight lines were fitted to the recoveries as in Figure 1. The slopes obtained are shown in Table X. There were not sufficient unspawned recoveries in the Lake in 1938 to fit a line to the data for this category. A slope significantly different from zero was found in each instance except for the 0 to 25 per cent spawned fish recovered in the Traps. The earlier migrants into the other areas lived a longer time, according to the negative slopes obtained, than the later entries did. However, for the poorly spawned females in the Traps, the calculated slope indicated that there was no significant change in survival time during the run. These fish died soon after passage through the weir, apparently as a result of handling during the tagging procedure. The unspawned females in Spring Creek showed a significant slope and it may be concluded that they were not adversely affected by the handling.

Since the number of tagged females recovered in 1939 was small no attempt was made to segregate the spawned from the unspawned. The samples from the two areas had significant negative slopes. The earlier entries into the Lake lived a longer period after tagging than did the ones tagged later in the season, but the calculated slope was lower for the Lake than it was for the Traps. This condition is the opposite to that noted for the two areas in 1938. It is impossible to state whether the lack of slope in the 1938 Traps data was due to rougher handling during tagging than in 1939 or to other differences between the two runs. The data were too limited to draw further conclusions from this particular analysis.

It was pointed out that the major portion of the tagged fish died in a seven-week period in both years. The recoveries of untagged fish followed the same pattern. The interesting feature of this situation was that it might have been possible to tag samples of the population just prior to the beginning of the seven-week period, and still obtain approximately the same results as were obtained by tagging throughout the season. Investigation of this hypothesis suggests that the length of time spent on both tagging and sampling of dead fish might be reduced. However, the recoveries of tagged fish indicate that tagging should take place during the first part of the migration if it is desired to have the tags distributed throughout the dead recovery. Under these circumstances the tagging period will be determined by the time that the major portion of the run begins to die. The efficiency of such an abbreviated program in determining the size of the total run is examined in a later section of the paper.

DISTRIBUTION OF TAGGED SOCKEYE IN THE DEAD

Application of the Chi-Square Test

It is possible to calculate, from a sample, the magnitude of unknown animal populations containing a known number of marked individuals, providing the ratio of marked to unmarked in the sample is representative of the entire population.

Theoretically, if the sampling is uniform throughout the population, the average tag ratio obtained from a composite of all samples will be the same as the average for the whole population, regardless of whether or not the tags are uniformly distributed.

Tagging was not uniform in the 1938 experiment, whereas the procedure the following year was designed to assure a uniform distribution of tags at the weir. An analysis was made by the Chi-square test of the distribution of the tagged fish in the dead fish samples to ascertain the effect of variations in distribution of the tags and the associated variations in the tag ratio upon the populations calculated from them. The same statistical procedure was utilized, along with other methods, to study possible differences in the reactions of tagged and untagged fish.

In the analysis of data that would be obtained in the course of an ordinary experiment designed to determine a population by tagging, it would be logical to use the Chi-square test to study the degree to which tags disperse in the population. This test would measure the extent to which the data follow the hypothesis required for the calculation of the population from samples of tagged and untagged fish when the total number of tagged fish in a population is known. In order to determine the utility of the Chi-square tests of uniformity in measuring the reliability of the tag ratios in the data, these tests were applied to the experimental data in the same manner they would be used in ordinary tagging experiments. With the view to accepting the uniformity of the tag ratio samples, Chi-square values corresponding to probabilities lower than 5 per cent were considered significant.

The dead fish samples were grouped into two-week periods in 1938 and weekly periods in 1939 because daily samples were small. Where samples from these periods were still too small they were themselves grouped. Typical examples for each step in the procedure are shown. When extensive tables are not included, the Chi-square value, the number of degrees of freedom and the *P*-value are given in a summary table or are stated in the text.

DISTRIBUTION OF TAGGED FISH IN 1938

The dead fish samples, each covering a two-week period, were grouped according to sex and size within each area of recovery. These samples were tested by Chi-square against the border totals for the consistency of the tag ratio throughout the period of recovery (see Tables XI to XIV). The limited numbers of small sockeye (32) in Spring Creek, and of small females (2), in the Traps, made it impossible to include these groups.

With the exception of the small males in the Traps and the large females in Spring Creek, the sex and size categories in each of the areas had consistent tag ratios throughout the recovery period. The large values of Chi-square in both cases resulted from discrepancies in the tag ratios found in the first samples where the relative number of tagged fish was much higher than in subsequent periods. The same tendency was seen in the earliest recoveries of both the large males and females in the Traps although the discrepancies were not large enough to make the total Chi-square significant. This situation may be ascribed to tagging injury causing the early death of a small number of fish tagged at the beginning of the season (see Table VII). The high value of Chi-square obtained for the large females in Spring Creek was due to a "large" recovery of tags in the first sample (see Table XXII).

Tests were made to determine whether or not there were inconsistencies in the tag ratio when the samples from the three areas were combined (see Table XIV). The unevenness was maintained for the small males and still resulted from the earlier death of a few small males in the Traps. The other three categories in the combined area had tag ratios which according to the Chi-square test were stable throughout the period of recovery, although the Chi-square values for large males and large females were high owing to the recovery of a relatively large number of tags early in the season when samples were small.

An examination was made to determine whether or not the various size and sex categories showed consistent tag ratios when grouped together within their respective areas (see Table XV). Although the Lake samples were the least uniform, it was found that in each area the recoveries of tagged and untagged from the four categories showed no inconsistencies and the Chi-square values in all cases were not significant. The same uniformity existed when the three areas were combined. There was no statistically significant difference between the tag ratios of the sexes or sizes, either within areas or within all areas grouped together.

Tests were made to learn whether or not there was any unevenness in the tag ratio during the period of recovery when the sexes and sizes of each area were grouped together (see Tables XVI to XVIII). Only the two-week samples from the Traps showed inconsistencies in the tag ratio and this condition obviously resulted from the group of tagged small males mentioned above. When the samples from the three areas were combined, the same group of small males and the high values calculated for the first samples of the other categories gave a cumulative effect and resulted in a significant Chi-square (see Table XIX).

In this experiment the actual or true tag ratio was known for the total population as well as for the individual sex and size components. Chi-square tests were calculated again, substituting the known ratio for the border total hypothesis to determine the agreement between the tag ratio existing in the dead recoveries and the true tag ratio established at the weir. The interaction or heterogeneity Chi-square (Snedecor, 1946) was also calculated to measure the degree to which positive and negative deviations were concentrated in different parts of the distribution under examination.

The results of the analysis with the true tag ratio are summarized in Table XX in which the total Chi-square measures the discrepancy between the number of tagged and untagged fish recovered in each two-week period and the number of tagged and untagged fish that could be expected from the tag ratio established at the weir. The pooled Chi-square measures the difference between the total numbers of tagged and untagged recovered in the entire season and the numbers of each that could be expected. The interaction Chi-square is the difference between these two values. The Chi-square values did not differ greatly from those obtained with the border totals except that there was a tendency for the values to be higher (see Tables XI to XIV). This was to be expected because the percentage of tagged sockeye present in the Lake and Spring Creek was less than the percentage tagged at the counting fences. Conversely, there was a higher percentage of tagged fish in the Traps. The tests with the known ratios showed that the inconsistencies for the small male samples in the Traps and all three areas combined were due to interaction. This was an expression of the fact that the tag ratio was too high in the Traps during the first part of the sampling. The large females in Spring Creek had a significant Chi-square value as was the case with the border hypothesis tests. This also was due to interaction, i.e. a tag ratio too high in the early samples which was balanced, when all recoveries were grouped, by a lower tag ratio later in the season. The large males in the Traps showed a significant Chi-square value which did not exist with the former test and was the result of a high tag ratio in the early sampling.

The pooled Chi-square values showed that the small males in the Traps may be regarded as being drawn from a population with the known tag ratio (see Table XX). On the other hand, despite the fact that the two-week tag ratio samples for the small males in the Lake were in agreement, the pooled Chi-square value showed that the total sample in that area was significantly lower than the actual tag ratio. This situation held throughout the period of recovery. The pooled Chi-square value for the over-all sample of the small males was significant because of the recovery of fewer tagged fish in this category than was expected. With reference to the large males in both the Traps and the Lake, the pooled Chi-square values showed that both total samples of this category differed significantly from the known ratio. For the Traps there were more tagged fish than expected during the first two recovery periods, however, for the Lake which was a borderline case ($P = .04$), no particular period could be blamed for the high value of Chi-square resulting in general from the consistent recovery of too few tags except in the first two periods when a slight excess occurred.

The Spring Creek sample including all sizes and both sexes showed no inconsistencies in the tag ratio throughout the dead recovery and the over-all sample or total of the two-week samples agreed with the known tag ratio in the population (see Table XXI). The lumped samples from the Lake had a constant proportion of tags in relation to time, but the over-all ratio in this area was lower than expected. It was determined that the two-week lumped samples from both the Traps and the combined areas had inconsistent tag ratios but that the over-all ratio in each case was not statistically different from the known tag ratio in the population (see Table XXI). For a further discussion of the significance of these data see page 21.

DISTRIBUTION OF TAGGED FISH IN 1939

The statistical measures applied to the 1939 data were similar to those utilized in 1938 but they differed in two respects; first, the samples were grouped by weekly periods instead of two-week periods; and secondly, they were segregated by sex alone instead of both sex and size, because the few small sockeye present were not distinguished in the weir counts. The weekly dead fish samples were grouped according to the area of recovery and sex. Each of these groups was subjected to the Chi-square test to determine the consistency of the tag ratios. A summary of the results is given in Table XXII.

The male and female samples from each of the two areas showed tag ratios which did not vary significantly through the period of recovery. When the two areas were combined, however, the excessive early recovery of tagged females in the Lake resulted in a significant Chi-square value. Despite this inconsistency, when the total female sample was compared with the total male sample the Chi-square test showed that they might be considered as being drawn from the same population ($P = .26$).

When the weekly samples of males and females were combined in each of the two areas, the tag ratio was consistent throughout the recovery period (see Table XXIII). When the two areas were combined, however, the weekly samples gave a Chi-square value with a probability of less than 1 per cent again as a result of the high density of tagged females in the Lake during the early part of the sampling.

Similar tests were conducted for these weekly samples in each area, using the actual tag ratio as determined at the counting fences. A summary of these tests is given in Table XXIV in which the same values are calculated as in Table XX (see page 19). The weekly female samples in the Traps (Total Chi-square) could not be considered as being drawn from a population with the known tag ratio. The pooled Chi-square value indicated that interaction was not responsible for this situation as the total sample was not representative of the actual or known female population. The tag ratios from the weekly male samples in this area were in agreement but the total sample did not conform to the known ratio. The discrepancies in each instance were due to the higher proportion of tagged fish dying in the Traps immediately above the tagging location. For the Lake, the Chi-square tests showed that the weekly samples of both the males and females had similar tag ratios throughout the season and that the total sample of females agreed with that ratio known to exist in the population, but the male sample did not. When the two areas were combined the females alone showed a high value of Chi-square as a result of interaction. The pooled Chi-square value indicated that the total sample of females as well as males agreed with the known tag ratio.

Referring to Table XXV, it was seen that although the weekly samples of sockeye, in both the Traps and the Lake, showed small Chi-square values according to the border total hypothesis (Col. 9), neither could be considered as being drawn from the population with the known ratio (Col. 7). In contrast, the reverse condition was in effect when the two areas were combined.

COMPARISON OF THE TWO EXPERIMENTS

It was seen that certain samples had a uniform distribution of tagged fish with respect to time and yet the summation of the samples did not have a tag ratio conforming to that known to exist in the population. Conversely, some samples had an uneven distribution of the tagged fish throughout the period of recovery and the over-all sample had a tag ratio which agreed with the known. Others conformed in both instances.

The discrepancies encountered in the two experiments were of similar origin. They centered chiefly around the fact that a higher proportion of tagged fish was found in the Traps than in the remaining parts of the district. This situation was particularly true during the early part of each season. These discrepancies appeared to arise whether or not the fish were tagged in proportion to the number entering the Lake.

The tag ratio samples could not be discarded on the basis that they did not have the tagged fish uniformly distributed with respect to time. The dead fish samples from the statistical areas showed that the tag ratio was usually lower than expected during the latter part. The weekly distribution of the tagged and untagged fish indicated that the untagged fish lived for a longer period of time than the tagged fish.

Conversely, the tag ratio samples could not always be accepted solely on the basis that they had a uniform distribution of the tagged fish with respect to time, because the over-all sample might not be representative of the population with the actual tag ratio. In cases where inconsistencies exist in tag ratios the data should be examined carefully in an effort to discover the cause. This was done for certain samples from the 1938 data and the small males were found to cause the disagreement. It was discovered that despite this disparity the total samples were reliable. A close analysis of similar discrepancies may explain non-conformities.

The examination and analysis of the dead fish recoveries in the determination of the tag ratio have revealed certain limitations that must be imposed with respect to the use of these samples. In general, the recoveries from individual areas should not be used to calculate the population for the entire area. This point is illustrated by the fact that the over-all tag ratio in the Traps was higher than expected in each season and that in the Lake was lower. As a result the tag ratio from the two areas combined approximates more nearly that in the population. The various conditions encountered in these experiments demonstrate that the dead recovery should be distributed over the entire spawning area, the entire period of dying, and that unless some reason can be found for differences, such as a differential rate of tagging or recovery in a particular category, all tags and recoveries should be grouped to obtain the best estimate of the population.

Samples of dead fish which are tested for uniformity of tag ratios with respect to time are sometimes found to be inconsistent, but consistency or inconsistency of tag ratio in dead fish samples does not always indicate whether they represent the true ratio.

REDUCTION OF THE TAGGING PERIOD AND THE NUMBER OF TAGS

THEORETICAL CONSIDERATIONS

The proportions of fish tagged and recovered in both years are much greater than can be handled usually under field conditions, especially when the runs of fish are great and the available personnel is limited. A more important consideration is the realization that it is not always possible to tag salmon that are entering a spawning area throughout the migration as was done in the two experiments at Cultus Lake. Floods often make it impossible to operate a trap or weir and may destroy such structures during tagging operations. Under these or similar circumstances, or because of lack of funds, it may be possible to tag only during a limited period of the migration. It is of considerable interest to see just how far the period of tagging and the numbers of fish to be tagged can be reduced without impairing the accuracy of the results.

The tagging period may be reduced arbitrarily in the present study while the number of carcasses examined remains constant. Unfortunately, it was impossible to reduce the number of dead fish examined by reducing the period of recovery. All recoverable fish were removed from the water and there was no way to estimate the number that would have been recovered at any time if the dead fish had not been disturbed. When only those fish tagged within a specified period were considered and all the other tagged fish were presumed to be untagged, it was possible to examine the results that would have been obtained had no sockeye been tagged during other parts of the season.

In the present analysis the tagging was reduced into three periods for both years. The three which were chosen were the first half, middle half and last half of each of the two seasons designated as the first, second, and third periods. In 1938 they were: September 27 to November 8, October 21 to November 23, and November 9 to December 23, while in 1939 they became: October 10 to November 16, November 1 to December 3, and November 17 to December 29. For the three successive periods in 1938, there were 2,346, 2,754 and 2,070 fish tagged. In the following year, there were 1,701, 3,043 and 1,922 fish tagged in the respective periods.

In separating the data into three periods, two of which began sometime after the fish had started spawning, the problem arose of how to handle dead fish that had been examined before the first tag had been put on at the weir. Under field conditions tagging would almost always be carried out, or at least would be started, before any dead fish were recovered. If fish die before recovery begins some may be lost before the area is covered. Since the treatment of these data in periods necessarily placed the number of recoveries on a purely artificial basis, all fish recovered before tagging began were omitted.* Fortunately, the numbers involved were small. For the middle half of the season in 1938 there were only 14 dead sockeye examined prior to October 21; and for the second half there were 88 sockeye examined before November 9. These numbers are small in comparison to the total number of 4,735 sockeye examined and the fact that they were omitted from the calculations did not materially affect the results. In 1939 a total of 13 fish was omitted in the second period and in the third period 55 fish. These may be compared with a total recovery of 9,819 and 9,777 respectively in the two periods.

REDUCTION OF THE TAGGING PERIOD IN 1938

Chi-square tests were applied to the dead fish samples from each of the three arbitrary periods in a similar manner to those applied to the samples from tagging throughout the migration. First, the size and sex categories in each area were examined in two-week samples in order to determine the nature of the distribution of the tagged fish. Then, the total number of each of the categories in each of the three areas was tested against the sum of all recoveries in the different areas to see whether or not they had significantly different tag ratios. Subsequently, Chi-square tests were applied to the two-week samples of the grouped categories

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*In practice these recoveries should be included but the numbers here are small enough to have little influence on the results.

in each area. Summary tabulations of the results of these tests are given in Tables XXVI to XXVIII. In addition, the total sample from each of these areas was tested to discover the relationship between the tag ratio existing and that known to exist in the population (see Table XXI).

Chi-square values calculated for the tag ratios in the two-week samples from the first period were significant in all categories from the Traps although the discrepancies were largest in the large males and large females (see Table XXVI). These two categories also showed significant Chi-squares in the Lake and Spring Creek. Only the small male and small female recoveries in the Lake showed uniformity in their tag ratios throughout the season. When all recoveries were lumped by categories for the season (see Table XXVII), and the tag ratios of the various categories compared within each area, none of the resulting Chi-squares were significant though that for the Traps shows a P of .07. Apparently, the differences in time were compensatory to some extent. The latter effect did not hold when the categories were grouped over all areas and compared. The Chi-square P of .03 is significant. When the two-week samples of the categories were grouped together in each area and also when the samples from all areas were combined, the Chi-square value was significant in every case in this period (see Table XXVIII). The inconsistencies resulted from the fact that the tag ratio was higher than expected especially for the large fish during the first part and too low during the latter part of the dead recovery. This was more apparent when all categories were grouped in the two-week periods within the areas and was demonstrated by the high Chi-squares noted in Table XXVIII.

Finally, a comparison of the tag ratio obtained from the total sample from each area and the combined areas against the known tag ratio was made (see Table XXI). This showed that the Lake had an over-all tag ratio conforming approximately with the known, but the other areas did not. In each instance it was noted that the tag ratio observed was too low.

Results from the second tagging period showed that the tagged fish in all categories except the large females and the small males in the Traps were distributed uniformly within their two-week samples (see Table XXVI). The tag ratio in the large female recoveries in the Traps corresponded closely with the border totals during the early part of the recovery period, but relatively small excesses of tags in the height of the season resulted in a high expectation of tags in the latter part. The small number of tags recovered during this part of the period made the principal contribution to Chi-square. On the contrary, the small males in the Traps showed an excess of recovered tags in the early recoveries combined with a defect of tags in the late recoveries which was the same type of distribution that caused most of the discrepancies observed in the recoveries from the first tagging period. The total samples of each of the categories were significantly different in the Lake as well as in the combined areas (see Table XXVII). This condition resulted from the recovery of a larger number of tags than expected in both large and small females and a lower number in both large and small males. This seems to have been due to a differential time of migration into the lake. With tagging being carried on during the middle part of the season when the number of females entering the lake was higher than the males in contrast with the early part of the run, the number of females tagged was higher than the number of males. With a large reservoir of untagged males in the lake before tagging commenced the recoveries could not be expected to show comparable tag ratios.

When the two-week samples were examined according to area of recovery without regard for sex and size, the tag ratios were in agreement throughout the season in all areas but the Traps (see Table XXVIII). This variation resulted principally from a low tag ratio in the recovery period ending January 2. The excess tags were distributed through the early part of the recovery period.

A comparison of the tag ratio obtained from the total sample in each area with the known tag ratio showed the sample from Spring Creek to be the only one not conforming (see Table XXI). Inconsistencies occurring in the distribution of tags by time in the dead fish samples for this period were caused predominantly by interaction. The interaction resulted from the differential time of migration of the two sexes as well as from the early death of injured tagged fish. It was eliminated usually when the sexes were grouped.

Finally, results from the third tagging period showed that all categories in the Traps and in the Lake had tags uniformly distributed within the two-week samples (see Table XXVI). The Spring Creek recoveries were not uniform in character however. The male recoveries showed a low tag ratio in the early fish and an excess in the late ones. With a $P = .05$, this may be considered of doubtful significance. The females showed a similar high Chi-square. Apparently tagging started too late to sample the first of the run.

As was the case for the second tagging period, the Chi-squares for the total samples (see Table XXVII) of each of the categories were significant in the Lake and the combined areas as a result of the differential time of migration. Examination of the two-week samples (see Table XXVIII) according to area of recovery without regard for sex or size showed the effect of the similar variations of tag ratios in males and females in Spring Creek. These deviations were sufficient to affect the tag ratio for all areas combined, and Chi-squares for both the Creek and all areas were significant. Comparisons of the over-all tag ratios in each area with the known show significant Chi-square values in all cases but the Lake (see Table XXI).

The analysis conducted for the three reduced tagging periods showed that the tagged fish from the second tagging period were distributed more uniformly in the dead fish samples than those from the other two periods. In addition, the over-all tag ratios obtained from this period approached the known tag ratio more closely than did those from the other periods. Tagging in the second period commenced before the major portion of the fish began to die. The distribution from this reduced period was more uniform than that obtained from the first period because a larger number of untagged fish were dying at the time the tagged fish were, and as a result a differential time of death, if present, was masked. The distribution of tags was also more uniform than that of the third period. For the third period tagging commenced after the major portion of the run began to die. In this case the tag ratio was low at the beginning of the season and high during the latter part. Due to the relation of the period of tagging to the runs there would be greater likelihood of obtaining an uneven distribution of tags from such early and late tagging periods than would be the case if tagging were placed more symmetrically with respect to the run.

The present analysis shows that when tagging takes place over a limited period of the migration the sex and size categories should not be utilized for calculating the total population, especially when Chi-square tests indicate marked absence of agreement in the returns. The differential time of migration of these groups would cause them to be tagged in proportions which would not correspond to the proportions in the population. The sex and size groups were recovered in this experiment in approximately the same proportion that they were present in the total population.

Reduction of the Tagging Period in 1939

Sockeye were tagged from October 10 to December 29 in 1939. The tagging was arbitrarily reduced into three periods in exactly the same manner as for the 1938 data. These periods were: October 10 to November 16, November 1 to December 3, and November 17 to December 29. The statistical treatment used on the samples of dead fish was identical with that applied to the 1938 data.

The Chi-square tests of the one-week samples from the first reduced period showed significant values for the females in both areas and the males in the Lake which were the result of the differential time of death between the tagged and untagged sockeye (see Table XXIX). The tag ratio from the total samples of each of the sexes in the Traps and the combined areas was not in agreement (see Table XXX). The weekly samples of the sexes grouped together showed variable tag ratios resulting from a higher tag ratio at the beginning of the recovery, giving a high Chi-square value (see Table XXXI). The total sample in the Lake and in the areas combined was representative of the population with the known tag ratio (see Table XXV), but that for the Traps gave a Chi-square with a P of .07 which approaches significance.

In the second period the one-week samples of the dead, both males and females, in the two areas had consistent tag ratios and the over-all samples did not have significant Chi-square values (see Tables XXIX and XXX). The weekly samples of the sexes grouped had consistent tag ratios in each area and when the areas were combined (see Table XXXI). However, neither the total sample from the Traps nor that from the Lake conformed with that known to exist in the population (see Table XXV). The tag ratio was too high in the Traps and too low in the Lake. When the two were combined, the discrepancies counterbalanced each other and the resulting sample had a tag ratio which agreed with the known.

In the third tagging period the one-week samples of the females in the Lake showed inconsistencies in the tag ratio, and the males were a borderline case, $P = .06$ (see Table XXIX). This condition originated from commencing tagging about the time the major portion of the run began to die, at which time a large pool of untagged fish was already in the Lake. The total samples of each sex in each area did not vary significantly with respect to the tag ratios in the different areas (see Table XXX). Only the Traps showed a uniform tag ratio for the weekly samples of the males and females combined (see Table XXXI). The Lake showed a tag ratio which was much higher than expected during the early part of the recovery and with the larger number recovered, these dominated the tag ratios when the two areas were combined. Chi-square tests with the known ratio as the hypothesis demonstrated that neither area had an over-all tag ratio consistent with the known (see Table XXV). There were too many tagged fish in the Traps and too few in the Lake. Since the discrepancies were compensatory, the sample obtained by combining the two areas had a tag ratio which agreed with that known to exist.

COMPARISON OF THE REDUCED PERIODS

Results obtained for the reduced tagging periods in 1939 were in agreement with the 1938 data. Inconsistencies in the distribution of tags from the second and third tagging periods were as apparent in the 1939 data as they were in the former year. The reasons for these inconsistencies were the differential time of migration of the sexes and the relation of the beginning of tagging to the beginning of the run (see Tables I and II). Operations for the third period in 1939 commenced two weeks prior to the seven-week period during which the major portion of the run began to die. The third period of tagging in 1938 commenced about the same time that the major portion of the run started to die.

It is seen that samples with consistent tag ratios throughout the recovery can not be considered to agree necessarily with the population with the known tag ratio. The reverse situation may be true. The former condition was particularly apparent in the Traps in both experiments.

The data in each case showed that when tagging takes place over a limited period of the migration the sexes and sizes should not be segregated in calculating the population. Differential times of migration between these categories may cause them to be tagged in proportions unequal to those in the population. In addition, tagging should commence before the major portion of the population begins to die, to increase the probability of obtaining a good estimate of the true tag ratio. At the same time, the difficulties involved in measuring this ratio apparently will not be increased if tagging is delayed long enough after the migration starts to overcome the irregularities brought about by the differential time of death between tagged and untagged. An uneven distribution of the tagged fish in the dead samples is more likely to occur when tagging is conducted either early or late in the migration. If the different sexes and sizes are tagged and recovered in widely varying proportions which are not compensating, it would probably be best to calculate the population of the categories individually. Then, the categories could be added together to obtain the total populations.

MEASUREMENT OF TAG RATIOS

The present analysis gives some basis upon which to judge the relationship between the distribution of tags in the dead fish recoveries and the validity of the tag ratios established. The variations in tag ratios were the result of many factors. The sex proportions varied throughout the migration in a fairly regular manner for the cases illustrated. This variation resulted in different proportions of the two sexes being tagged when tagging was confined to a limited period. In general, the tagged fish died sooner than the untagged ones and more of them died closer to the point of tagging. The first of these two factors resulted in a high tag ratio early in the recovery period and a low one toward the end. The over-all ratio immediately above the tagging location tended to be too high while it was too low in the upper reaches of the recovery area. Added to these factors were differences that seemed to result from different reactions of both the two sexes and the two size groups to tagging as well as differences in the actual proportions of the different sexes and sizes that could be recovered after death.

It was apparent from the Chi-square analysis that consistency of a tag ratio in a particular area throughout the period of recovery did not mean that the over-all ratio had been measured accurately for the entire population. Moreover, significant differences existed in the tag ratio with time and between sexes as well as areas, yet when lumped together, the over-all ratio gave an accurate measure of the population.

In short, the various causes of variations in the numbers of tags recovered tend to compensate for one another providing recoveries are made over the entire period of dying and over-all areas in which dead fish were found. After such widespread effort the recoveries of all sexes and sizes should be lumped together, unless there is definite evidence that the different sexes and sizes have been tagged and recovered in widely different proportions which are not compensatory. In such an event, the populations for the different categories may have to be calculated separately.

Under no circumstances can accurate quantitative results be expected if tagging is carried on some distance below the spawning grounds where recoveries can not be made immediately above the tagging location as well as over all areas above it. These conditions of accuracy will become clearer in the following sections.

POPULATION CALCULATIONS

Under ordinary conditions the data shown in Table III would be the basis upon which the populations would be calculated. Tag ratios were established for each size and sex group in each area and for all fish in these areas. Accordingly, with the formula given on page 9, the number of fish belonging to each category and the total number of fish present were determined (see Table XXXII). The total number calculated from the total sample within each area is shown in column 6 and the sum of the calculated number of sockeye in the individual categories is shown in column 7. These estimates may be compared with the total number calculated from all areas combined and with the actual size of the runs (1938 — 13,342; 1939 — 73,189).

The calculated population (see Tables XXI and XXV) for both 1938 and 1939 indicated an inverse relationship between the Traps and the Lake. The tag ratio in the Traps was too high and the Lake tag ratio was too low in both years with the exception of the small females in 1938. In the latter case the small female population calculated from the Traps samples was slightly higher than that for the Lake. The differences between the tag ratios in these two areas were greater in 1939. In that year the population calculated from the total Lake recoveries was approximately 15 per cent too high and was 38 per cent too low when calculated from the Traps recoveries. In 1938, the population calculated from all the recoveries in the Traps was 9 per cent too low and was 11 per cent too high when calculated from the Lake recoveries. The population calculated from all the Spring Creek recoveries in 1938 had an error of less than 2 per cent.

It was interesting to note that the mean of the estimates from the three areas in 1938 was 13,528, which was closer to the actual number of fish counted into the Lake than was the population calculated from all recoveries. The standard deviation of the three estimates was 1,346, while the standard error of the mean was calculated to be 777, giving a coefficient of variation of about 5.7 per cent. In contrast with 1938, the mean of the 1939 populations calculated from the tag ratios in the two areas showed an error of 13 per cent as compared with an error of only 3 per cent from the population calculated from all recoveries made in that year.

Comparison of the populations in the last two columns of Table XXXII revealed that no material improvement was made in the estimated populations by calculating the sex and size categories separately. Although these categories were tagged in different proportions, they were examined in approximately the same proportion that they occurred in the population. The latter situation explained why there was little difference in the results of the two estimates.

The determination of the limits of confidence for individual populations calculated from tag ratios has not received a great deal of attention in the past. The formula developed by Pearson (1928) for determining the standard error of a population calculated from marked individuals is not entirely valid principally because of the use of the theory of inverse probability in its derivation, and the fiducial limits utilized by Garwood (1936) and Ricker (1937b), give limits of error that are too asymmetrical. A recent paper (Chapman, 1948) was used as a guide in determining the limits of confidence for the populations estimated in the present study. According to Chapman (page 82), the method used in determining the confidence limit is governed by the size (n) of the sample examined and the number (s) of tagged individuals found in the sample.

The 95 per cent confidence interval was calculated for the populations determined from the tag ratio samples in each of the areas and in the district as a whole for tagging throughout the season and for each of the reduced tagging periods in 1938 and 1939 (see Tables XXI and XXV). The arbitrary tagging periods automatically reduced the number of fish tagged as well as the period of tagging. However, the proportion of the run tagged in each case was of such a magnitude that it would not materially affect the estimates. A discussion of the reduction of the numbers tagged follows in a later section and will illustrate this. In each experiment a number of fish were recovered with the tags missing. In those estimations of the population which were calculated by making use of all the tags placed it was possible to include these tag scars. However, the use of any of the reduced tagging periods necessitated the discarding of those individuals with tag scars because it was impossible to ascertain when these fish were tagged. The omission of these fish resulted in the estimations for the reduced periods being somewhat higher than they would have been if these tags had not been lost.

Intervals or limits of confidence are based upon the assumption of either a perfectly random distribution of the marked individuals in the population, or a uniform sampling of the population to obtain the ratio of marked to unmarked individuals. Whether or not the confidence limits include the true population, depends on the extent to which the samples comply with the conditions upon which the confidence intervals are derived.

An examination of Table XXI shows that of the 16 estimates of the population in 1938 only 8 had confidence intervals within which the true population fell. Table XXV showed the same situation for only 6 of the 12 estimates in 1939. The number of tag scars recovered in each year was not sufficient to have brought those calculated confidence limits which did not include the true populations within its range. The observed errors were caused by the non-random distribution of tags between areas. This, in turn, was due to many different factors discussed above. In 1938 it was more apparent in the early and late parts of the season and was least apparent in the recoveries from the middle half of the tagging period. In 1939 the errors were most apparent in the recoveries from the middle and second halves of the tagging period. The first half of the tagging in 1939 corresponded with the middle half in 1938 in relation to the pattern of the run. In 1939 the total recoveries from all periods of tagging resulted in confidence limits that included the true population. This did not hold in 1938 for the first and third periods of tagging.

The danger in the use of an abbreviated tagging program to estimate a population is demonstrated adequately in this section. It is seen that the true population may not fall within the limits of confidence applied to the estimate. The results of the 1938 and 1939 experiments indicate that to insure the best estimate of the population it is necessary to conduct the sampling over both the entire district and the whole period of spawning and that if the tagging period is to be abbreviated it should be carried out through the heaviest part of the run. The real effect of reducing the period of recovery will be examined in an experiment that was conducted at the same locality in 1947.

RETURNS FROM GROUPS OF 100 TAGS PUT OUT DURING LIMITED PERIODS

It is of interest to examine the returns from successive one hundred tags put out during the season in a further study of the reduction of the number of tags used. Of the total number placed in the two experiments 34.4 per cent and 13.0 per cent were recovered in 1938 and 1939 respectively. The number or percentage returned in each area from successive hundreds tagged during 1938 is given in Table XXXIII. The numbers recovered in the three areas combined from each one hundred tagged varied widely with greater numbers recovered during the second half of the season. The reverse situation might have been expected because those tags put on at the beginning of the season would be recoverable over a longer period of time. It was shown that the tag ratio was usually higher during the first part of the dead recovery. This situation should not be confused with the lower return of tags from the early successive groups of one hundred tags put out. The groups of one hundred tags were subject to recovery throughout the spawning period. Different proportions of the run migrated to the three areas during the first and second halves of the season (see page 14). More of the late fish spawned in Spring Creek. Since nearly all fish that spawned in Spring Creek were examined it would be expected that a greater number of each successive one hundred tags placed during the latter part of the season would be recovered.

In order to determine statistically whether or not there was any significant difference between the mean number of tags redeemed from the various groups of one hundred tags in each of the three portions of the 1938 season *t*-tests were applied. The mean number of tags recovered from the successive groups of one hundred tags placed during the first period was significantly different from the mean number of tags recovered in the other two periods. There was no significant difference between the means of the recoveries of the groups of one hundred tags put out during the second and the third periods of the season.

The asymmetrical distribution of tags in the recoveries from the different parts of the season was further demonstrated by tests of randomness applied to the recoveries in Table XXXIII. Using a method outlined by Kendall (1946) and suggested by D. G. Chapman, the number of runs of various numbers of positive and negative deviations from the median was compared with numbers calculated on the basis of chance variation. Using Chi-square to measure the significance of the differences, it was found that only the recoveries from the Traps could be considered random. The trend from negative deviations in recoveries from the earlier tag groups to positive deviations in the later ones dominated both the Lake and Spring Creek recoveries. The larger number of recoveries in the latter areas were sufficient to give the same trend to the totals.

The populations calculated from the average number of tags redeemed from each successive one hundred placed during the first (tag nos. 1 to 2,200), second (tag nos. 1,301 to 4,000) and third periods (tag nos. 2,201 to 4,400) of the season gave estimates of 16,857, 13,138 and 12,596 sockeye respectively.

These data indicate the danger of tagging during a limited period to obtain the population in a district which has distinct populations passing by the tagging location in varying proportions during the migration and which spawn in areas where such great differences exist in the relative proportions which can be recovered after death.

The number returned from each successive one hundred fish tagged in 1939 is given in Table XXXIV. The number recovered in the two areas combined from each one hundred successive tagged fish varied as in 1938 but the *t*-test showed that there was no appreciable difference between the numbers recovered in the first, second or third periods of the season. The population calculated from the mean number of tags recovered from the groups of one hundred tags placed during the first part of the season was 69,879. The third part of the season gave a population of 81,933 while for the second period of the season the population was 79,290.

The variations in the calculated populations in each year with only one hundred tags are shown in Tables XXXIII and XXXIV. The upper extreme in 1938 was obtained with 16 tag recoveries giving a population of 29,594 with a 95 per cent confidence interval between 16,573 and 48,297. The corresponding lower extreme (46 recoveries) gave a population of 10,293 with an interval between 7,434 and 13,694. The mean number of recoveries (33.2) indicated a population of 14,262 with a confidence interval between 9,759 and 20,124.

For 1939 the minimum number of 6 tag recoveries gave an estimate of 163,867 with the confidence interval between 59,680 and 389,999. The maximum number of 37 recoveries showed a population of 36,415 with an interval between 18,514 and 176,142. The mean number of 12.8 recoveries gave an estimate of 76,813 with a corresponding confidence interval between 40,901 and 133,519.

An examination of Tables XXXIII and XXXIV shows that the use of one hundred tags will not necessarily give good estimates for a population of the magnitude present in 1938 even when recoveries are made over the entire period of dying. However, the groups put out during the peak of the migration gave results that did not vary unreasonably. On the other hand, the same number of tags gave extremely wide variations when the population was of the 1939 magnitude and these variations occurred irregularly throughout the period of tagging.

REDUCTIONS IN NUMBERS TAGGED THROUGHOUT SEASON

Another way of considering reduced numbers of tags was to use only every one hundredth or two hundredths or any other fraction of the fish tagged. In this way the limited number of tags was distributed throughout the migration. A summary of this study is shown in Table XXXV.

For 1938 a minimum of 27 tags was used which were distributed through the season and a maximum of 216 tags. In the first instance it was possible to get 160 groups of 27 tags and in the second case there were 20 groups of 216 tags placed during the migration. For these cases and the intervening two cases the population calculated from the mean number of recoveries is shown along with those obtained from the maximum and minimum number of recoveries. The 95 per cent confidence limits indicated are calculated from the number of tag recoveries obtained by taking 1.96 times the standard deviation of the tag recovery distribution on either side of the mean number of recoveries. In other words, assuming normality, these intervals include 95 per cent of the distribution.

The same procedure was applied to the 1939 data (see Table XXXV). The numbers involved varied from 160 groups of 22 tags used during the season to 20 groups of 176 tags.

The results of this analysis showed that when 108 tags were used, representing 0.8 per cent of the 1938 run, there were 95 chances in 100 that the error in the estimate would not be more than 49 per cent. When 216 fish or 1.6 per cent of the total run were used, there were 95 chances in 100 that the error was not more than 17 per cent. The data for 1939 showed that the numbers of tags utilized were not sufficient to obtain samples containing enough tags to derive results comparable with those of 1938. The twenty groups of 176 tags each of which represented 0.24 per cent of the run, gave 95 per cent confidence limits of 148,000 to 54,000, or a possible maximum error of 100 per cent. One series actually gave a population of 173,000, or an error of 136 per cent. Obviously, the reduction of the number of tags to or below 1 per cent cannot be expected to yield dependable results. If the number of tags released is kept above 2 per cent the results can be accepted with some confidence, providing sufficient care is taken to obtain an adequate sample of the dead fish.

SUMMARY AND CONCLUSIONS

Experiments were conducted at Cultus Lake by the International Pacific Salmon Fisheries Commission in the years 1938 and 1939 for the purpose of determining the feasibility of estimating the size of a population of spawning sockeye by tagging a portion of the migrants as they moved into the spawning area. The tag ratio in the population was established from the examination of samples of dead fish. Complete control was exercised at Cultus Lake by making an accurate count through a weir of all sockeye entering the area. Tagging was conducted throughout two years' migrations. In 1938, 4,416 fish, or one-third, were tagged of the 13,342 sockeye counted through the weir between September 27 and December 27; and 3,660 sockeye, or one-twentieth of the 73,189 fish entering the lake between October 10, 1939, and January 20, 1940 were tagged.

The tags were not distributed between the individual sex and size categories in the proportions that they occurred in the population in either year. In addition, the number tagged during successive weeks in 1938 was not uniformly proportional to the number of fish entering the lake. The proportion tagged each week in 1939 did not vary significantly from the over-all proportion tagged.

The numbers of dead fish examined were 4,735 or 35.4 per cent of the fish present in 1938, and 9,832 or 13.4 per cent of the 1939 run. The entire area was patrolled as often as possible throughout the spawning period. For the purposes of the investigation three sub-areas (Traps, Lake and Spring Creek) were defined. Few fish spawned in Spring Creek in 1939 and these fish were included with the Lake recoveries.

The two runs were not characterized by the same sex ratios or age groups. There was a higher proportion of males during the first part of each season than there was during the latter part of the migrations. No differences could be detected in the time of migration of the two sexes into the different spawning areas. However, different proportions of the run migrated to the three areas during the first and second halves of the 1938 season.

The major portion of each run died within a seven-week period, despite the fact that the entire spawning period covered more than twice this length of time. Tagged fish lived for a shorter period after passing through the counting fence than the untagged fish. The period between tagging and death varied in different individuals; on the average the males lived longer than the females and 3-year olds lived longer than 4- and 5-year olds. A higher ratio of tagged fish died in the Traps immediately above the tagging location than in the other areas. Apparently, handling during tagging caused some of the tagged fish to remain in the area immediately above the tagging location rather than to continue their migration. There was a negative correlation between the date of tagging and the length of time to recovery; the earlier migrants lived longer than the later ones. This difference was more pronounced in the Lake and Spring Creek. No differences were noted in the degree spawned between tagged and untagged females in the Lake and Spring Creek. Differences noted in the Traps in this regard were probably the result of injuries. Tagged fish from particular weeks of tagging usually distributed themselves through all successive weeks of the recovery in the Lake and Spring Creek but probably as a result of injuries this was not true for the Traps.

The proportions of fish tagged and recovered in both years was much greater than can be handled usually under regular field conditions and it is not always possible to tag throughout the migration. Due to the method of recovering dead fish, it was impossible to reduce either the period of recovery or the number of carcasses. The tagging period for each year was reduced arbitrarily into three periods in the present study. The periods corresponded to the first, middle and second halves of the season. An examination was made also of the returns from successive one hundred tags put out and the recoveries from groups of a limited number of tags put out over the entire migration. The latter study was of interest in a further examination of the reduction of the number of tags used.

With the aid of Chi-square test, distribution of the tagged fish in the dead samples throughout the season was examined in detail to determine the relationship between this distribution and the validity of the tag ratios obtained. The dead fish samples were grouped into two-week periods in 1938 and weekly periods in 1939 because daily samples were too small. The study was made for tagging throughout the season and for each of the three reduced tagging periods.

Many factors were responsible for variations which were found to occur in the tag ratios both according to time of tagging as well as of recovery and between recovery areas. When tagging operations commenced with the beginning of the migration, the early dead fish samples nearly always had a higher tag ratio than expected and the later samples a lower ratio than expected. This situation was a result of the differential time of death between tagged and untagged fish, and in such samples the tagged fish were not distributed uniformly. On the contrary, it was also found that in other sections of the experiment where tags were uniformly distributed by time in the dead fish recoveries, the over-all tag ratio was significantly different from the tag ratio established at the weir. The reverse situation was found to exist also.

Differences in the relative numbers of the various size and sex categories migrating past the tagging location caused the dead fish samples from these groups to have different tag ratios. As a result the tag ratios obtained by grouping these categories were usually closer to the known tag ratio than those obtained from the samples of the individual categories. However, this improvement would not have occurred if the various categories had not been examined in the dead fish recoveries in approximately the same proportions that they existed in the population.

Over-all tag ratios varied between areas whether or not the tagged fish were distributed uniformly in each of them. Included among the factors causing this variability were the higher density of tagged fish in the area immediately above the tagging location and different proportions of the run migrating to the three areas during the season. Sampling of the dead over the entire spawning area compensated to a large degree for discrepancies in tag ratios between areas and gave the most reliable results.

It was possible to reduce the period of tagging without loss of accuracy in estimating the tag ratio. Tagged fish were distributed more uniformly throughout the dead recovery when the tagging operation began prior to the time the major portion of the run began to die. This period corresponded to the peak of the migration. When operations were limited and commenced before this time the differences in the tag ratio were emphasized; the early recoveries showed a high tag ratio and the late samples showed a low tag density. The reverse situation was illustrated when tagging started after the peak of the migration.

Various estimates of the sockeye populations were made from the tag ratios in the different dead fish samples. The 95 per cent limits of confidence were calculated for these estimates; the method used to obtain them depended upon both the size of the dead fish samples and the proportion of tagged fish contained therein. The populations, when all tags and all recoveries were considered, were calculated to be 13,765 in 1938 and 75,441 in 1939. The limits of confidence were between 14,475 and 13,090 in the first year and between 85,523 and 68,966 in the second.

Examination of the results obtained from the returns of successive groups of one hundred tags put out during the season proved that accurate estimates of the population could not be obtained from such a small number of tags distributed in that manner. Different proportions of the run migrating to different areas during the run resulted in the tags being distributed asymmetrically in the population. However, the most accurate population estimates were obtained from the groups of one hundred tags released during the peak of the migration.

A study of the results obtained by distributing small numbers of tags throughout the period of migration indicated that the reduction of the number of tags below 2 per cent of the total population present could not be expected to yield dependable estimates. If the numbers of tags released were kept above 2 per cent the results could be accepted with some confidence.

From the analysis presented in this paper the following conclusions have been reached based upon the criterion that sampling of the dead fish is conducted throughout the spawning period in as uniform a manner as possible with a constant degree of effort.

1. The tagging location should be situated immediately below the spawning area.
2. A continuous and uniform effort should be exercised to recover dead fish over the entire area above the tagging locality. If it is possible for the fish to move below the tagging location, all areas thus accessible should be examined.
3. Tagging operations should commence immediately before the major portion of the run begins to die.
4. If an abbreviated tagging program is conducted, the best results will be obtained when these operations take place during the peak of the migration.
5. For populations of the magnitudes studied, population calculations with less than 2 per cent of the total number tagged could not be expected to yield accurate results.

6. All recoveries should be lumped regardless of sex or size in order to obtain the ratio of tagged to untagged, unless definite evidence is available to indicate the categories were tagged and recovered in proportions varying widely from those in the population.
7. Uniformity of the tag ratio throughout the period of recovery in any area as indicated by Chi-square tests does not necessarily prove that the tag ratio is accurately measured. The reverse situation may be true also. Comparison of recoveries from various spawning areas may indicate the reasons for discrepancies of this nature.
8. It was not possible to study the effect of a reduction of the time or extent of the dead recovery upon the accuracy of the tag ratio estimates, and neither the effects of tagging some distance below the spawning area nor the effects of releasing the tagged fish in the area of spawning can be measured.

The conclusions may not be entirely applicable to other spawning areas. However, the results should be of assistance in both the planning and analysis of similar enumeration experiments.

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TABLE I

NUMBER OF SOCKEYE TAGGED AND THE NUMBER UNTAGGED PASSING THROUGH THE WEIR EACH WEEK DURING THE 1938 SEASON.

One-week Period Ending	LARGE MALES			LARGE FEMALES			SMALL MALES			SMALL FEMALES			TOTAL			
	Tagged	*Un-tagged*	*Total*	*Tagged*	*Un-tagged*	*Total*	*Tagged*	*Un-tagged*	*Total*	*Tagged*	*Un-tagged*	*Total*	*Tagged*	*Un-tagged*	*Total*	*Per cent Females*
October 3	21	36	57	25	52	77	48	59	107	5	7	12	99	154	253	35
" 10	61	67	128	77	82	159	113	98	211	8	26	34	259	273	532	36
" 17	98	315	413	213	783	996	220	734	954	17	108	125	548	1,940	2,488	45
" 24	98	55	153	379	238	617	362	201	563	46	15	61	885	509	1,394	49
" 31	26	57	83	191	385	576	93	209	302	10	24	34	320	675	995	61
November 7	13	65	78	97	536	633	56	352	408	9	29	38	175	982	1,157	58
" 14	44	104	148	169	401	570	63	151	214	9	7	16	285	663	948	62
" 21	112	293	405	843	1,934	2,777	298	578	876	33	69	102	1,286	2,874	4,160	69
" 28	2	11	13	238	276	514	3	19	22	6	3	9	249	309	558	94
December 5	19	98	117	174	235	409	64	164	228	8	6	14	265	503	768	55
" 12	3	5	8	18	24	42	9	12	21	4	2	6	34	43	77	62
" 19	0	0	0	7	0	7	1	0	1	3	0	3	11	0	11	91
" 26	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0
TOTALS	497	1,106	1,603	2,431	4,946	7,377	1,330	2,578	3,908	158	296	454	4,416	8,926	13,342	75

TABLE II

NUMBER OF SOCKEYE TAGGED AND THE NUMBER UNTAGGED EACH WEEK DURING THE 1939 SEASON.

One week Period Ending		MALES			FEMALES			SEX UNKNOWN		TOTAL			
		Tagged	*Un-tagged*	*Total*	*Tagged*	*Un-tagged*	*Total*	*Tagged*	*Total*	*Tagged*	*Un-tagged*	*Total*	*Per cent Females*
October	12	14	311	325	16	275	291			30	586	616	47
"	19	48	600	648	26	740	766			74	1,340	1,414	54
"	26	48	727	775	48	1,084	1,132			96	1,811	1,907	59
November	2	53	976	1,029	92	2,012	2,104			145	2,988	3,133	67
"	9	82	1,404	1,486	144	3,137	3,281	2	2	228	4,541	4,769	69
"	16	442	6,171	6,613	684	13,589	14,273	2	2	1,128	19,760	20,888	68
"	23	225	4,883	5,108	600	11,894	12,494	1	1	826	16,777	17,603	71
"	30	172	3,132	3,304	405	8,991	9,396	3	3	580	12,123	12,703	74
December	7	110	1,700	1,810	331	5,833	6,164			441	7,533	7,974	77
"	14	24	420	444	62	1,230	1,292			86	1,650	1,736	74
"	21	2	54	56	19	268	287			21	322	343	84
"	28	0	14	14	0	51	51			0	65	65	78
January	4	1	3	4	4	23	27			5	26	31	87
"	11	0	0	0	0	6	6			0	6	6	100
"	18	0	0	0	0	1	1			0	1	1	100
TOTALS		1,221	20,395	21,616	2,431	49,134	51,565	8	8	3,660	69,529	73,189	70

TABLE III

NUMBER OF TAGGED AND UNTAGGED SOCKEYE RECOVERED IN EACH AREA IN 1938 AND 1939

AREA	LARGE MALES		LARGE FEMALES		SMALL MALES		SMALL FEMALES		TOTAL		*Total*
	Tagged	*Untagged*	*Tagged*	*Untagged*	*Tagged*	*Untagged*	*Tagged*	*Untagged*	*Tagged*	*Untagged*	*Dead*
1938											
Above Traps	36	44	85	156	76	144	7	13	204	357	561
Lake Proper	44	139	240	503	140	367	16	29	440	1,038	1,478
Spring Creek	166	394	701	1,403	6	17	2	7	875	1,821	2,696
TOTALS	246	577	1,026	2,062	222	528	25	49	1,519	3,216	4,735
1939											
Above Traps	48	521	59	700					107	1,221	1,328
Lake Proper	112	2,384	258	5,750					370	8,134	8,504
TOTALS	160	2,905	317	6,450					477	9,355	9,832

TABLE IV

NUMBER OF TAGS RECOVERED IN EACH SIZE AND SEX CATEGORY IN THE ABOVE TRAPS AREA EACH WEEK, SEGREGATED ACCORDING TO THE WEEK OF TAGGING. THE PERCENTAGE SPAWNED OF TAGGED AND UNTAGGED LARGE FEMALES IS SUMMARIZED FOR EACH WEEK OF RECOVERY IN 1938.

Date of tagging One week period ending:		DATE OF RECOVERY — ONE WEEK PERIOD ENDING																
		October				November				December				January				
		10	17	24	31	7	14	21	28	5	12	19	26	2	9	16	23	30
Large Males																		
October	3								1									
"	10	—																
"	17		—					1	2									
"	24			2	3				1		2							
"	31				1													
November	7					—	1					1						
"	14						—			1	1							
"	21							—		1	3	4		1	2			
"	28								—	1								
December	5									—			1	1	1			
"	12										—		1	1				
"	19											—						
TOTALS				2	4		1	1	4	3	6	5	2	3	3			
Large Females																		
October	10	—	1			1				1								
"	17		—		1						1			1				
"	24			2	4			1										
"	31				—	1					1							
November	7					1		1	1	1	2		1					
"	14						—			1		1						
"	21							—	4	6	6	11	3	1			1	
"	28								1		1	6	1	1	1			
December	5									—	2	4	5	1	1		1	
"	12										1				1			
"	19											—	1					
TOTALS			1	2	5	3		2	6	9	14	22	11	4	3		2	
% spawned (tagged)			0	0	0	0		0	0	5.6	44.6	38.6	50.0	75.0	100.0		100.0	
% spawned (untagged)			0	0	16.7	0	0	0	4.5	16.2	52.3	53.9	55.9	94.1	100.0	100.0	100.0	
Small Males																		
October	3									1								
"	10	—									1							
"	17		—	2	3							2			1			
"	24			5	2			1	2			1		2			1	
"	31				3			1						1				
November	7					—						2						
"	14						—			1	1			1	1			
"	21							—		3	7	11	4	1	2			
"	28								—									
December	5									—	1	5	4	2				
"	12										—							
"	19											—		1				
TOTALS				7	8			2	2	5	10	21	8	8	4		1	
Small Females																		
October	3																	
"	10	—	1															
"	17		—															
"	24			1	1	1						1	1					
"	31				—													
November	7					—												
"	14						—								1			
"	21							—										
"	28								—									
December	5									—								
"	12										—							
"	19											—						
TOTALS			1	1	1	1						1	1		1			

TABLE V

NUMBER OF TAGS RECOVERED IN EACH SEX AND SIZE CATEGORY IN THE LAKE PROPER AREA EACH WEEK, SEGREGATED ACCORDING TO THE WEEK OF TAGGING. THE PERCENTAGE SPAWNED OF TAGGED AND UNTAGGED LARGE FEMALES IS SUMMARIZED FOR EACH WEEK OF RECOVERY IN 1938.

Date of tagging One week period ending:	DATE OF RECOVERY — ONE WEEK PERIOD ENDING																
	October				November				December				January				
	10	17	24	31	7	14	21	28	5	12	19	26	2	9	16	23	30
Large Males																	
October 3									1			1					
" 10	—								2	1	1	1	2		1		
" 17		—			1	2	1	2		1	2			1			
" 24			—			2	1	2		1							
" 31				—		1	2										
November 7					—												
" 14						—			1								
" 21							—	1				3		3			
" 28								—		1							
December 5									—		1						
" 12										—							
" 19											—						
TOTALS					1	5	4	5	4	4	4	5	2	4	1		
Large Females																	
October 3								1	1								
" 10	—					1			1	1			1				
" 17		—			1	1			2	6	6	6	1			1	
" 24			—	1		2	1			9	10	3	2	1	1		
" 31				1	1	3	2	1	3	5	6	1		1			
November 7					—				1		3	2	1	1	1		
" 14						—			3	3	2	3	1				
" 21							1	5	13	12	31	12	8	5	7	2	
" 28								—	1	1	4	4	3	7	2	1	
December 5									—		4	4	1	3			
" 12										—	1						
" 19											—						
TOTALS				2	2	7	4	7	25	37	67	35	18	18	11	4	
% spawned (tagged)				0	0	0	0	17.9	55.0	91.9	93.7	95.7	100.0	100.0	100.0	100.0	
% spawned (untagged)					0	0	3.3	15.9	52.2	84.6	95.3	95.8	96.5	92.2	96.4	66.7	
Small Males																	
October 3							1		2	1	1	1					
" 10	—										1	4	1	1		1	
" 17		—				1	1			3	5	9	2	4	2		
" 24			—			1		1	1	4	9	9	2	4			
" 31				—						4	2	1		1			
November 7					—		1				1	1			1	1	
" 14						—		1		1	3	1	2		1		
" 21							—		2	1	7	17	1	1	1	1	
" 28								—									
December 5									—					1			
" 12										—		1					1
" 19											—						
TOTALS						2	3	2	5	14	29	44	8	12	5	3	1
Small Females																	
October 3						1											
" 10	—																
" 17		—											2				
" 24			—							1	3		2				
" 31				—													
November 7					—							1					
" 14						—											
" 21							—				1	2			1		
" 28								—			1						
December 5									—								
" 12										—							
" 19											—						
TOTALS						1				1	5	3	4		1		

TABLE VI

NUMBER OF TAGGED LARGE MALES AND FEMALES RECOVERED IN SPRING CREEK EACH WEEK, SEGREGATED ACCORDING TO THE WEEK OF TAGGING. THE PERCENTAGE SPAWNED OF TAGGED AND UNTAGGED FEMALES IS SUMMARIZED FOR EACH WEEK OF RECOVERY IN 1938.

Date of tagging One week period ending:		DATE OF RECOVERY — ONE WEEK PERIOD ENDING																
		October				November				December				January				
		10	17	24	31	7	14	21	28	5	12	19	26	2	9	16	23	30
Males																		
October	3							2	1	1								
"	10								6	4	2	3						
"	17					1		3	7	6	1	1						
"	24							1	13	13	4	1						
"	31							1	4	2								
November	7								1	1	1	1						
"	14							1	4	6	8	6						
"	21								4	10	12	15	1					
"	28																	
December	5											4	1	1	1			
"	12																	
"	19																	
TOTALS						1		8	40	43	28	31	2	1	1			
Females																		
October	3								3	2								
"	10							1	9	3	2	3	1					
"	17						1	16	21	14	6	3						
"	24							12	41	38	23	9	3		1			
"	31							9	22	19	3	3					2	
November	7							4	7	12	2	2						
"	14							5	12	19	11	4	2		2			
"	21							2	27	64	51	53	16	5	3		2	
"	28								1	4	16	25	10	3	6		1	
December	5									1	14	18	10	2				
"	12											2			1			
"	19													1				1
TOTALS							1	49	143	176	128	122	42	11	13		5	1
% spawned (tagged)							0	35.9	18.9	25.6	36.7	55.3	46.4	61.4	55.8		0	0
% spawned (untagged)							50.0	30.4	21.3	19.5	36.0	53.5	53.5	73.5	27.4	0	0	0

TABLE VII

NUMBER OF TAGGED MALES AND FEMALES RECOVERED IN THE ABOVE TRAPS AREA EACH WEEK, SEGREGATED ACCORDING TO THE WEEK OF TAGGING. THE PERCENTAGE SPAWNED OF TAGGED AND UNTAGGED FEMALES IS SUMMARIZED FOR EACH WEEK OF RECOVERY IN 1939.

Date of tagging One week period ending:		DATE OF RECOVERY — ONE WEEK PERIOD ENDING																
		October		November					December				January				February	
		19	26	2	9	16	23	30	7	14	21	28	4	11	18	25	1	8
Males																		
October	12																	
"	19	—				1		1		1								
"	26		—								1							
November	2			—					1									
"	9				—					1								
"	16					—		1	4	1	5	4	3					
"	23						—		2	1		3	1					
"	30							—		3	4	1	3					
December	7								—			3		2				
"	14									—					1			
"	21										—							
"	28											—						
January	4												—					
TOTALS						1		2	7	7	10	11	7	2	1			
Females																		
October	12																	
"	19	—								1								
"	26		—			1												
November	2			—			3	1										
"	9				—	1	1	2	1									
"	16					—		1	1	1	2	1						
"	23						—	1	5	4	1			1				
"	30							—		2	4	3						
December	7								—	3	5							
"	14									—	4	1	1					
"	21										—	1	1					
"	28											—						
January	4												4					
TOTALS						2	4	5	7	11	16	6	6	1				
% spawned (tagged)						0	0	0	35.7	31.8	51.6	33.3	33.3	100.0				
% spawned (untagged)				16.7	0	0	3.6	3.6	23.6	32.9	64.5	29.5	34.7	56.0	0	0		

TABLE VIII

NUMBER OF TAGGED MALES AND FEMALES RECOVERED IN THE LAKE PROPER AREA EACH WEEK, SEGREGATED ACCORDING TO THE WEEK OF TAGGING. THE PERCENTAGE SPAWNED OF TAGGED AND UNTAGGED FEMALES IS SUMMARIZED FOR EACH WEEK OF RECOVERY IN 1939.

Date of tagging One week period ending:		DATE OF RECOVERY — ONE WEEK PERIOD ENDING																
		October		November					December				January				February	
		19	26	2	9	16	23	30	7	14	21	28	4	11	18	25	1	8
Males																		
October	12																	
"	19	—						1		3								
"	26		—							1								
November	2			—			1		1	1			1					
"	9				—				2	2	2	2	1	1				
"	16					—			1	5	9	12	6	6	6			
"	23						—			1	3	5	5	1	3			
"	30							—				2	2	5	1			
December	7								—			2	2	1	6			1
"	14									—	2		2	1	1	1		
"	21										—				1			
"	28											—						
January	4																	
TOTALS							1	1	4	13	16	23	19	15	18	1		1
Females																		
October	12								1									
"	19	—							1	1	1				1			
"	26		—						1	1	1							
November	2			—			1	1	2	3	2	1	1					
"	9				—		2	2	1	8	6	4	3					
"	16					—		1	2	23	24	12	8	5	2	1		
"	23						—	1	2	3	6	12	12	4	7			
"	30							—		2	8	8	11	3	5			
December	7								—	2	2	5	9	10	10			
"	14									—	3	3	1	1	2			
"	21										—		1					
"	28											—	1					
January	4												—					
TOTALS							3	5	10	43	53	45	47	23	27	1		
% spawned (tagged)							100.0	60.0	80.0	83.7	84.0	83.3	97.3	89.1	98.1	100.0		
% spawned (untagged)							42.9	84.3	79.7	81.0	84.5	89.1	80.8	93.7	97.7	99.5	100.0	100.0

TABLE IX

COMPARISON OF THE NUMBER AND PER CENT OF TAGS RECOVERED FROM DEAD FISH OF EACH SEX AND SIZE IN EACH AREA DURING THREE SUCCESSIVE SEGMENTS OF THE RECOVERY PERIOD IN 1938 AND 1939. AVERAGE NUMBER OF DAYS OUT AFTER TAGGING IS SHOWN.

	NUMBER RECOVERED				PER CENT RECOVERED			
1938	*Before Nov. 15*	*Nov. 15 to Jan. 8*	*After Jan. 8*	*Total*	*Before Nov. 15*	*Nov. 15 to Jan. 8*	*After Jan. 8*	*Av. days out*
Above Traps								
Large Males	7	24	3	34	20.6	70.6	8.8	28
Large Females	11	68	5	84	13.0	81.0	6.0	23
Small Males	15	56	5	76	19.7	73.7	6.6	29
Small Females	4	2	1	7	57.1	28.6	14.3	21
Lake Proper								
Large Males	6	28	5	39	15.4	71.8	12.8	47
Large Females	11	193	33	237	4.7	81.4	13.9	40
Small Males	2	105	21	128	1.6	82.0	16.4	54
Small Females	1	13	1	15	6.6	86.7	6.6	49
Spring Creek								
Large Males	1	153	1	155	0.6	98.8	0.6	36
Large Females	1	671	19	691	0.1	97.1	2.8	31
1939	*Before Dec. 1*	*Dec. 1 to Jan. 18*	*After Jan. 18*	*Total*	*Before Dec. 1*	*Dec. 1 to Jan. 18*	*After Jan. 18*	
Above Traps								
Males	3	45	0	48	6.2	93.8	0.0	32
Females	11	47	0	58	19.0	81.0	0.0	19
Lake Proper								
Males	2	108	2	112	1.8	96.4	1.8	41
Females	8	248	1	257	3.1	96.5	0.4	37

TABLE X

SLOPES (b) and y INTERCEPTS (a) (AVERAGE NUMBER OF DAYS TO RECOVERY AT BEGINNING OF TAGGING FOR FEMALES) CALCULATED FROM LINES FITTED TO THE POINTS OBTAINED BY PLOTTING THE DATES OF TAGGING AGAINST THE NUMBER OF DAYS ELAPSING BETWEEN TAGGING AND DEATH.

Year and Area of Recovery	Degree Spawned				All Degrees	
	0 –25 per cent		*50–100 per cent*			
	a	*b*	*a*	*b*	*a*	*b*
1938						
Above Traps	10.67	–0.0845	14.96	–0.5053		
Lake Proper			15.01	–0.6694		
Spring Creek	13.88	–0.8401	15.60	–0.9693		
1939						
Above Traps					13.76	–0.8664
Lake Proper					14.09	–0.6892

TABLE XI

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS WITHIN THE TWO SIZE CLASSES OF EACH SEX IN THE ABOVE TRAPS AREA. ALL FISH RECOVERED ARE INCLUDED (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
Large Males						
October 24	0	2	2			
November 7	4	4	8			
" 21	0	2	2			
December 5	6	7	13	13.75	11.25	2.2727
" 19	20	13	33	18.15	14.85	0.4190
January 2	12	5	17	12.10	9.90	0.6630
" 16	2	3	5			
TOTALS	44	36	80	44.00	36.00	3.3547
	Chi-sq. = 3.3547		*df* = 2	*P* = .19		
Large Females						
October 24	2	3	5			
November 7	10	9	19			
" 21	7	2	9	15.54	8.46	2.2877
December 5	28	15	43	33.66	18.34	0.1513
" 19	63	36	99	64.08	34.92	0.0516
January 2	34	15	49	31.72	17.28	0.4647
" 16	9	3	12	11.00	6.00	0.2576
" 30	3	2	5			
TOTALS	156	85	241	156.00	85.00	3.2129
	Chi-sq. = 3.2129		*df* = 4	*P* = .52		
Small Males						
October 24	2	7	9			
November 7	2	8	10			
" 21	2	2	4	12.43	6.57	16.5338
December 5	5	7	12	10.47	5.53	3.3274
" 19	61	31	92	60.22	31.78	0.0716
January 2	58	16	74	48.44	25.56	5.4624
" 16	8	4	12	12.44	6.56	0.5070
" 30	6	1	7			
TOTALS	144	76	220	144.00	76.00	25.9022
	Chi-sq. = 25.9022		*df* = 4	*P* <.01		

TABLE XII

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS WITHIN THE TWO SIZE CLASSES OF EACH SEX IN THE LAKE PROPER AREA. ALL FISH RECOVERED ARE INCLUDED (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
Large Males						
October 24	–	–	–			
November 7	2	1	3			
“ 21	14	10	24	20.51	6.49	4.1258
December 5	28	9	37	28.10	8.90	0.0011
“ 19	45	9	54	41.02	12.98	1.6066
January 2	30	9	39	29.62	9.38	0.0203
“ 16	19	6	25	19.75	6.25	0.1185
“ 30	1	0	1			
TOTALS	139	44	183	139.00	44.00	5.8723
	Chi-sq. = 5.8723		*df* = 4	*P* = .20		
Large Females						
October 24	–	–	–			
November 7	2	4	6			
“ 21	24	11	35	27.76	13.24	0.3456
December 5	56	32	88	59.57	28.43	0.6622
“ 19	216	107	323	218.67	104.33	0.1009
January 2	124	53	177	119.83	57.17	0.4493
“ 16	73	29	102	77.17	36.83	0.5884
“ 30	8	4	12			
TOTALS	503	240	743	503.00	240.00	2.1464
	Chi-sq. = 2.1464		*df* = 4	*P* = .72		
Small Males						
October 24	–	–	–			
November 7	1	0	1			
“ 21	10	5	15	11.58	4.42	0.7804
December 5	24	7	31	22.44	8.56	0.4447
“ 19	131	49	180	130.30	49.70	0.0137
January 2	136	57	193	139.70	53.30	0.1237
“ 16	54	18	72	62.98	24.02	0.2347
“ 30	11	4	15			
TOTALS	367	140	507	367.00	140.00	1.5972
	Chi-sq. = 1.5972		*df* = 4	*P* = .83		
Small Females						
October 24	–	–	–			
November 7	–	–	–			
“ 21	1	1	2			
December 5	4	0	4			
“ 19	10	7	17	14.83	8.17	0.0054
January 2	10	7	17	14.17	7.83	0.0037
“ 16	4	1	5			
“ 30						
TOTALS	29	16	45	29.00	16.00	0.0091
	Chi-sq. = 0.0091		*df* = 1	*P* = .98		

TABLE XIII

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS WITHIN THE TWO SIZE CLASSES OF EACH SEX IN THE SPRING CREEK AREA. ALL FISH RECOVERED ARE INCLUDED (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
Large Males						
November 7	0	1	1			
" 21	23	8	31	22.51	9.49	0.0360
December 5	182	89	271	190.67	80.33	1.3298
" 19	163	62	225	158.31	66.69	0.4687
January 2	24	5	29	22.51	9.49	1.8247
" 16	2	1	3			
" 30	0	0	0			
TOTALS	394	166	560	394.00	166.00	3.6592
	Chi-sq. = 3.6592		*df* = 3	*P* = .30		
Large Females						
November 7	–	–	–			
" 21	60	51	111	74.02	36.98	7.9708
December 5	715	326	1041	694.16	346.84	1.8779
" 19	518	252	770	513.46	256.54	0.1204
January 2	77	53	130	86.69	43.31	3.2511
" 16	21	13	34	22.67	11.33	0.3692
" 30	12	6	18	12.00	6.00	0.0000
TOTALS	1403	701	2104	1403.00	701.00	13.5894
	Chi-sq. = 13.5894		*df* = 5	*P* = .02		

TABLE XIV

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS WITHIN THE TWO SIZE CLASSES OF EACH SEX IN ALL THE AREAS. ALL FISH RECOVERED ARE INCLUDED (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
Large Males						
October 24	0	2	2			
November 7	6	6	12	9.81	4.19	4.9442
" 21	37	20	57	39.96	17.04	0.7335
December 5	216	105	321	225.06	95.94	1.2198
" 19	228	84	312	218.74	93.26	1.3114
January 2	66	19	85	59.59	25.41	2.3065
" 16	23	10	33	23.84	10.16	0.0036
" 30	1	0	1			
TOTALS	577	246	823	577.00	246.00	10.5190
	Chi-sq. = 10.5190		*df* = 5	*P* = .06		
Large Females						
October 24	2	3	5			
November 7	12	13	25	20.03	9.97	5.4622
" 21	91	64	155	103.50	51.50	4.5437
December 5	799	373	1172	782.60	389.40	1.0344
" 19	797	395	1192	795.95	396.05	0.0042
January 2	235	121	356	237.72	118.28	0.0936
" 16	103	45	148	98.83	49.17	0.5295
" 30	23	12	35	23.37	11.63	0.0177
TOTALS	2062	1026	3088	2067.00	1026.00	11.6853
	Chi-sq. = 11.6853		*df* = 6	*P* = .07		
Small Males						
October 24	2	7	9			
November 7	3	8	11	14.08	5.92	19.7782
" 21	13	7	20	14.08	5.92	0.2798
December 5	30	14	44	30.98	13.02	0.1048
" 19	206	84	290	204.15	85.85	0.0567
January 2	195	75	270	190.08	79.92	0.4302
" 16	62	22	84	59.14	24.86	0.4673
" 30	17	5	22	15.49	6.51	0.4974
TOTALS	528	222	750	528.00	222.00	21.6144
	Chi-sq. = 21.6144		*df* = 6	*P* <.01		
Small Females						
October 24	0	2	2			
November 7	2	2	4			
" 21	3	2	5			
December 5	8	1	9	13.24	6.76	0.0129
" 19	17	8	25	16.56	8.44	0.0346
January 2	10	8	18	19.20	9.80	0.0429
" 16	8	2	10			
" 30	1	0	1			
TOTALS	49	25	74	49.00	25.00	0.0904
	Chi-sq. = 0.0904		*df* = 2	*P* = .95		

TABLE XV

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION OF TAG RATIOS BETWEEN FISH OF DIFFERENT SIZES AND SEXES USING ALL FISH RECOVERED IN EACH OF THE AREAS (1938).

Area, sex and size	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-Sq.*
Above Traps						
Large Males	44	36	80	50.91	29.09	2.5793
Small Males	144	76	220	140.00	80.00	0.3143
Large Females	156	85	241	153.36	87.64	0.1249
Small Females	13	7	20	12.73	7.27	0.0157
TOTALS	357	204	561	357.00	204.00	3.0342
	Chi-sq. = 3.0342		$df = 3$	$P = .39$		
Lake Proper						
Large Males	139	44	183	128.52	54.48	2.8706
Small Males	367	140	507	356.07	150.93	1.1270
Large Females	503	240	743	521.81	221.19	2.7777
Small Females	29	16	45	31.60	13.40	0.7184
TOTALS	1,038	440	1,478	1,038.00	440.00	7.4937
	Chi-sq. = 7.4937		$df = 3$	$P = .06$		
Spring Creek						
Large Males	394	166	560	378.24	181.76	2.0232
Small Males	17	6	23	15.54	7.46	0.4229
Large Females	1,403	701	2,104	1,421.14	682.86	0.7134
Small Females	7	2	9	6.08	2.92	0.4291
TOTALS	1,821	875	2,696	1,821.00	875.00	3.5886
	Chi-sq. = 3.5886		$df = 3$	$P = .31$		
All Areas						
LargeMales	577	246	823	558.98	264.02	1.8109
Small Males	528	222	750	509.40	240.60	1.9896
Large Females	2,062	1,026	3,088	2,097.36	990.64	1.8582
Small Females	49	25	74	50.26	23.74	0.0985
TOTALS	3,216	1,519	4,735	3,216.00	1,519.00	5.7572
	Chi-sq. = 5.7572		$df = 3$	$P = .12$		

TABLE XVI

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS OF ALL FISH RECOVERED IN THE ABOVE TRAPS AREA (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
October 24	4	14	18	11.45	6.55	13.3209
November 7	18	23	41	26.09	14.91	6.8981
" 21	9	6	15	9.55	5.45	0.0872
December 5	41	29	70	44.55	25.45	0.7781
" 19	148	81	229	145.72	83.28	0.0981
January 2	104	37	141	89.73	51.27	6.2412
" 16	23	11	34	29.91	17.09	0.8779
" 30	10	3	13			
TOTALS	357	204	561	357.00	204.00	28.3015
	Chi-sq. = 28.3015		*df* = 6	$P < .01$		

TABLE XVII

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS OF ALL FISH RECOVERED IN THE LAKE PROPER AREA (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
November 7	5	5	10			
" 21	49	27	76	60.39	25.61	2.2705
December 5	112	48	160	112.37	47.63	0.0041
" 19	402	172	574	403.13	170.87	0.0107
January 2	300	126	426	299.18	126.82	0.0075
" 16	150	54	204	143.27	60.73	1.0619
" 30	20	8	28	19.66	8.34	0.0198
TOTALS	1,038	440	1,478	1,038.00	440.00	3.3745
	Chi-sq. = 3.3745		*df* = 5	$P = .63$		

TABLE XVIII

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS OF ALL FISH RECOVERED IN THE SPRING CREEK AREA (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
November 7	0	1	1			
" 21	86	60	146	99.29	47.71	5.4809
December 5	900	416	1,316	888.89	427.11	0.4279
" 19	698	318	1,016	686.25	329.75	0.6199
January 2	102	60	162	109.42	52.58	1.5503
" 16	23	14	37	24.99	12.01	0.4882
" 30	12	6	18	12.16	5.84	0.0065
TOTALS	1,821	875	2,696	1,821.00	875.00	8.5737
	Chi-sq. = 8.5737		*df* = 5	*P* = .13		

TABLE XIX

CHI-SQUARE TEST OF SIGNIFICANCE OF VARIATION WITH TIME OF RECOVERY OF TAG RATIOS OF ALL FISH RECOVERED IN ALL THE AREAS (1938).

Two week recovery period ending	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*
October 24	4	14	18	12.23	5.77	17.2771
November 7	23	29	52	35.32	16.68	3.5255
" 21	144	93	237	160.97	76.03	5.5767
December 5	1,053	493	1,546	1,050.04	495.96	0.0260
" 19	1,248	571	1,819	1,235.46	583.54	0.3968
January 2	506	223	729	495.13	233.87	0.7438
" 16	196	79	275	186.78	88.22	1.4187
" 30	42	17	59	40.07	18.93	0.2898
TOTALS	3,216	1,519	4,735	3,216.00	1,519.00	29.2544
	Chi-sq. = 29.2544		df = 7	*P* <.01		

TABLE XX

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED IN SUCCESSIVE TWO WEEK PERIODS IN FISH OF DIFFERENT SIZES AND SEXES RECOVERED IN EACH AREA AND THE KNOWN TAG RATIO ESTABLISHED FOR THE WHOLE SEASON AT THE COUNTING WEIR FOR CORRESPONDING SIZES AND SEXES (1938).

		TOTAL CHI-SQ.			POOLED CHI-SQ.			INTERACTION CHI-SQ.		
Area of recovery	*Category*	*Value*	*df*	*P*	*Value*	*df*	*P*	*Value*	*df*	*P*
Above Traps	Large males	12.2120	3	.01	7.3304	1	<.01			
	Large females	3.9965	5	.55	0.6128	1	.42			
	Small males	26.2503	5	<.01	0.0194	1	.90	26.2309	4	<.01
Lake Proper	Large males	10.8403	5	.06	4.1337	1	.04			
	Large females	1.9483	5	.86	0.1414	1	.74			
	Small males	10.3605	5	.06	9.1406	1	<.01			
	Small females	0.0248	2	.99	0.0106	1	.90			
Spring Creek	Large males	4.0654	4	.39	0.4821	1	.47			
	Large females	13.7926	6	.03	0.1215	1	.70	13.6711	5	.02
All Areas	Large males	8.4698	5	.13	0.4827	1	.47			
	Large females	11.8602	7	.10	0.1021	1	.74			
	Small males	26.6439	7	<.01	6.5696	1	.01	20.0743	6	<.01
	Small females	0.0262	3	.99	0.0334	1	.57			

TABLE XXI

CHI-SQUARE TESTS OF DIFFERENCES BETWEEN TAG RATIOS OBSERVED IN FISH RECOVERED ON THE SPAWNING GROUNDS IN THE DIFFERENT AREAS USING ALL TAGS PUT OUT (LINES 1-4) AND ALSO USING ONLY THOSE TAGS PUT OUT IN THE THREE REDUCED TAGGING PERIODS (LINES 5-16). THE DIFFERENT RATIOS ARE COMPARED WITH THE KNOWN SEASON TAG RATIO FOR ALL FISH AT THE COUNTING WEIR (COLUMN 7) AND WITH THE BORDER TOTALS OF THE TWO WEEK PERIODS (COLUMN 9). THE PROBABILITIES OF THE CHI-SQUARES OCCURRING THROUGH CHANCE ALONE ARE SHOWN IN COLUMNS 8 AND 11. THE TOTAL POPULATION ABOVE THE WEIR CALCULATED FROM THE DEAD RECOVERIES IN DIFFERENT AREAS AND DURING DIFFERENT PERIODS OF THE SEASON ARE SHOWN (COLUMN 12) WITH THE 95 PER CENT CONFIDENCE LIMITS (COLUMN 13) (1938).

Period of tagging and area of recovery	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*	*P*	*Chi-sq. from 2-week periods*	*df*	*P*	*Cal. Pop.*	*Confidence limits 95 per cent point*	
All season													
Above Traps	357	204	561	375.32	185.68	2.7017	.10	28.3015	6	<.01	12,144	14,000	10,600†
Lake Proper	1,038	440	1,478	988.80	489.20	7.3963	<.01	3.3745	5	.63	14,834	16,284	13,510*
Spring Creek	1,821	875	2,696	1,803.64	892.36	0.5048	.22	8.5737	5	.13	13,606	14,538	12,734*
All Areas	3,216	1,519	4,735	3,167.79	1,567.21	2.2167	.13	29.2544	7	<.01	13,765	14,475	13,090*
Sept. 27—Nov. 8													
Above Traps	484	77	561	462.36	98.64	6.3050	.015	142.3730	4	<.01	17,092	24,500	13,500†
Lake Proper	1,255	233	1,478	1,218.11	259.89	3.3758	.07	33.2548	4	<.01	14,881	15,769	13,089*
Spring Creek	2,274	422	2,696	2,221.95	474.05	6.9343	<.01	159.4505	3	<.01	14,988	16,488	13,624*
All Areas	4,013	722	4,735	3,902.42	832.58	17.8202	<.01	294.2499	6	<.01	15,385	16,550	14,304*
Oct. 21—Nov. 23													
Above Traps	423	124	547	434.09	112.91	1.3726	.24	19.2312	4	<.01	12,149	16,200	10,400†
Lake Proper	1,201	277	1,478	1,172.92	305.08	3.2567	.06	2.2167	5	.82	14,695	16,514	13,079*
Spring Creek	2,077	619	2,696	2,139.50	556.50	8.8451	<.01	1.4150	4	.85	11,995	12,978	11,087*
All Areas	3,701	1,020	4,721	3,746.51	974.49	2.6782	.10	11.5206	6	.07	12,747	13,555	11,977*
Nov. 9—Dec. 3													
Above Traps	374	127	501	423.27	77.73	36.9655	<.01	2.9822	3	.39	8,166	11,800	7,500†
Lake Proper	1,249	202	1,451	1,225.88	225.12	2.8104	.09	5.5119	3	.14	14,869	17,066	12,955*
Spring Creek	2,196	499	2,695	2,276.72	418.28	18.4393	<.01	97.1141	4	<.01	11,180	12,204	10,241*
All Areas	3,819	828	4,647	3,926.02	720.98	18.8030	<.01	48.3033	5	<.01	11,618	12,436	10,853*

*Normal distribution

†Binomial distribution—Clopper and Pearson (1934) table

TABLE XXII

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED IN SUCCESSIVE ONE WEEK PERIODS FOR MALES AND FEMALES RECOVERED IN EACH AREA (1939).

Area of recovery	*Category*	*Chi-Sq.*	*df*	*P*
Above Traps	Males	2.6689	4	.61
	Females	3.5278	6	.75
Lake Proper	Males	1.0654	5	.96
	Females	11.7776	6	.10
All Areas	Males	6.4172	6	.39
	Females	24.8074	7	<.01

TABLE XXIII

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED FOR ALL FISH RECOVERED IN EACH AREA (1939).

Area of recovery	*Chi-sq.*	*df*	*P*
Above Traps	2.0458	6	.92
Lake Proper	9.9281	6	.13
All Areas	26.9903	8	<.01

TABLE XXIV

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED IN SUCCESSIVE ONE WEEK PERIODS IN FISH OF DIFFERENT SEXES RECOVERED IN EACH AREA AND THE KNOWN TAG RATIO ESTABLISHED FOR THE WHOLE SEASON AT THE COUNTING WEIR FOR CORRESPONDING SEXES (1939).

		TOTAL CHI-SQ.			POOLED CHI-SQ.			INTERACTION CHI-SQ.		
Area of recovery	*Category*	*Value*	*df*	*P*	*Value*	*df*	*P*	*Value*	*df*	*P*
Above Traps	Males	9.2282	4	.09	8.3465	1	<.01			
	Females	20.2351	1	<.01	15.7964	1	<.01			
Lake Proper	Males	7.0402	6	.32	6.3203	1	.01			
	Females	8.0939	7	.32	2.4226	1	.12			
All Areas	Males	6.9632	7	.43	1.0137	1	.32			
	Females	24.7350	8	<.01	0.0107	1	.75	24.7243	7	<.01

TABLE XXV

CHI-SQUARE TESTS OF DIFFERENCES BETWEEN TAG RATIOS OBSERVED IN FISH RECOVERED ON THE SPAWNING GROUNDS IN THE DIFFERENT AREAS USING ALL TAGS PUT OUT (LINES 1-3) AND ALSO USING ONLY THOSE TAGS PUT OUT IN THE THREE REDUCED TAGGING PERIODS (LINES 4-12). THE DIFFERENT RATIOS ARE COMPARED WITH THE KNOWN SEASON TAG RATIO FOR ALL FISH AT THE COUNTING WEIR (COLUMN 7) AND WITH THE BORDER TOTALS OF THE ONE WEEK PERIODS (COLUMN 9). THE PROBABILITIES OF THE CHI-SQUARES OCCURRING THROUGH CHANCE ALONE ARE SHOWN IN COLUMNS 8 AND 11. THE TOTAL POPULATION ABOVE THE WEIR CALCULATED FROM THE DEAD RECOVERIES IN DIFFERENT AREAS AND DURING DIFFERENT PERIODS OF THE SEASON ARE SHOWN (COLUMN 12) WITH THE 95 PER CENT CONFIDENCE LIMITS (COLUMN 13) (1939).

Period of tagging and area of recovery	*Untagged*	*Tagged*	*Total*	*Exp. Untagged*	*Exp. Tagged*	*Chi-sq.*	*P*	*Chi-sq. from week periods*	*df*	*P*	*Cal. Pop.*	*Confidence limits 95 per cent point*	
All Season													
Above Traps	1,221	107	1,328	1,261.59	66.41	26.1146	<.01	2.0458	6	.92	45,425	54,886 54,775	37,599* 36,755†
Lake Proper	8,134	370	8,504	8,078.74	425.26	7.5587	<.01	9.9281	6	.13	84,121	93,080	76,035*
All Areas	9,355	477	9,832	9,340.33	491.67	0.4607	.49	26.9903	8	<.01	75,441	82,523	68,966*
Oct. 10—Nov. 16													
Above Traps	1,287	41	1,328	1,296.91	31.09	3.2345	.07	13.1103	3	<.01	55,096	74,545	39,147†
Lake Proper	8,315	189	8,504	8,304.91	199.09	0.6340	.42	69.2772	6	<.01	76,536	88,253	66,375*
All Areas	9,602	230	9,832	9,601.82	230.18	0.0002	.99	99.4585	7	<.01	72,714	82,738	63,907*
Nov. 1—Dec. 3													
Above Traps	1,235	80	1,315	1,260.33	54.67	12.2451	<.01	4.3145	6	.63	50,019	58,206 62,144	42,984* 39,475†
Lake Proper	8,207	297	8,504	8,150.43	353.57	9.4436	<.01	7.1260	7	.42	87,130	97,619	77,721*
All Areas	9,442	377	9,819	9,410.76	408.24	2.4943	.12	12.8758	8	.12	79,255	87,670	71,648*
Nov. 17—Dec. 29													
Above Traps	1,207	66	1,273	1,238.93	34.07	30.7473	<.01	3.2736	4	.51	37,785	47,159 47,063	29,142* 28,521†
Lake Proper	8,323	181	8,504	8,276.38	227.62	9.8111	<.01	27.4241	6	<.01	92,041	104,451	78,070*
All Areas	9,530	247	9,777	9,515.31	261.69	0.8473	.17	12.9347	6	.03	76,092	86,176	67,164*

*Normal distribution
†Poisson distribution—Chapman (1948) table

Table XXVI

CHI-SQUARES CALCULATED FOR TAG RATIOS ESTABLISHED WITHIN THE DIFFERENT SIZE AND SEX CATEGORIES OF DEAD FISH IN EACH AREA DURING SUCCESSIVE TWO WEEK PERIODS USING TAGS PUT OUT DURING THE THREE REDUCED TAGGING PERIODS AND THE BORDER TOTAL HYPOTHESIS (1938).

Area of recovery and category	Reduced Tagging Periods								
	Sept. 27–Nov. 8			*Oct. 21–Nov. 23*			*Nov. 9–Dec. 23*		
	Chi-sq.	*df*	*P*	*Chi-sq.*	*df*	*P*	*Chi-sq.*	*df*	*P*
Above Traps									
Large males	24.2521	1	<.01	0.7288	2	.70	1.2586	1	.26
Large females	19.0573	1	<.01	8.0767	3	.05	1.5147	2	.47
Small males	5.3859	1	.02	15.5927	2	<.01	2.2248	1	.14
Lake Proper									
Large males	9.5079	2	<.01	1.4632	1	.22	2.4768	1	.11
Large females	23.7643	4	<.01	3.8989	4	.42	2.0609	3	.57
Small males	1.1866	3	.75	1.1093	3	.77	3.8065	2	.15
Small females	2.2821	1	.13	0.1851	1	.88	1.5290	1	.22
Spring Creek									
Large males	54.1224	3	<.01	5.0874	3	.16	6.0723	2	.05
Large females	136.1216	3	<.01	1.8821	4	.76	89.0980	4	<.01

Table XXVII

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED FOR ALL FISH RECOVERED IN EACH AREA USING TAGS PUT OUT DURING THE THREE REDUCED TAGGING PERIODS AND THE BORDER TOTAL HYPOTHESIS (1938).

Area of recovery	Reduced Tagging Periods								
	Sept. 27–Nov. 8			*Oct. 21–Nov. 23*			*Nov. 9–Dec. 23*		
	Chi-sq.	*df*	*P*	*Chi-sq.*	*df*	*P*	*Chi-sq.*	*df*	*P*
Above Traps	7.0322	3	.07	5.4904	3	.14	3.5411	3	.32
Lake Proper	6.2770	3	.10	34.1490	3	<.01	41.4597	3	<.01
Spring Creek	2.2416	3	.53	6.0159	3	.11	4.0795	3	.25
All Areas	9.3139	3	.03	27.8884	3	<.01	14.1697	3	<.01

TABLE XXVIII

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED IN SUCCESSIVE TWO WEEK PERIODS FOR ALL FISH RECOVERED IN EACH AREA USING TAGS PUT OUT DURING THE THREE REDUCED TAGGING PERIODS AND THE BORDER TOTAL HYPOTHESIS (1938).

	REDUCED TAGGING PERIODS								
Area of recovery	*Sept. 27–Nov. 8*			*Oct. 21–Nov. 23*			*Nov. 9–Dec. 23*		
	Chi-sq.	*df*	*P*	*Chi-sq.*	*df*	*P*	*Chi-sq.*	*df*	*P*
Above Traps	142.3730	4	<.01	19.2312	4	<.01	2.9822	3	.39
Lake Proper	33.2548	4	<.01	2.2167	5	.82	5.5119	3	.14
Spring Creek	159.4505	3	<.01	1.4150	4	.82	97.1141	4	<.01
All Areas	294.2499	6	<.01	11.5206	6	.07	48.3033	5	<.01

TABLE XXIX

CHI-SQUARES CALCULATED FOR TAG RATIOS ESTABLISHED WITHIN THE DIFFERENT SEXES OF DEAD FISH IN EACH AREA DURING SUCCESSIVE ONE WEEK PERIODS USING TAGS PUT OUT DURING THE THREE REDUCED TAGGING PERIODS AND THE BORDER TOTAL HYPOTHESIS (1939).

	REDUCED TAGGING PERIODS								
Area of recovery and sex	*Oct. 10–Nov. 16*			*Nov. 1–Dec. 3*			*Nov. 17–Dec. 29*		
	Chi-sq.	*df*	*P*	*Chi-sq.*	*df*	*P*	*Chi-sq.*	*df*	*P*
Above Traps									
Males	1.4948	2	.47	2.2104	4	.70	1.2410	2	.55
Females	12.0928	1	<.01	2.2952	4	.68	5.9100	4	.20
Lake Proper									
Males	12.8322	5	.03	4.0394	5	.55	9.5224	4	.06
Females	61.4196	4	<.01	6.5781	6	.37	19.4988	5	<.01

TABLE XXX

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED FOR ALL FISH RECOVERED IN EACH AREA USING TAGS PUT OUT DURING THE THREE REDUCED TAGGING PERIODS AND THE BORDER TOTAL HYPOTHESIS (1939).

	REDUCED TAGGING PERIODS								
Area of recovery	*Oct. 10–Nov. 16*			*Nov. 1–Dec. 3*			*Nov. 17–Dec. 29*		
	Chi-sq.	*df*	*P*	*Chi-sq.*	*df*	*P*	*Chi-sq.*	*df*	*P*
Above Traps	4.2490	1	.04	2.2982	1	.13	1.4744	1	.22
Lake Proper	2.3703	1	.12	0.2366	1	.63	1.0230	1	.32
All Areas	6.1202	1	.015	2.6650	1	.10	0.7083	1	.42

TABLE XXXI

CHI-SQUARES CALCULATED FOR DIFFERENCES BETWEEN TAG RATIOS ESTABLISHED IN SUCCESSIVE ONE WEEK PERIODS FOR ALL FISH RECOVERED IN EACH AREA USING TAGS PUT OUT DURING THE THREE REDUCED TAGGING PERIODS AND THE BORDER TOTAL HYPOTHESIS (1939).

	REDUCED TAGGING PERIODS								
Area of recovery	*Oct. 10–Nov. 16*			*Nov. 1–Dec. 3*			*Nov. 17–Dec. 29*		
	Chi-sq.	*df*	*P*	*Chi-sq.*	*df*	*P*	*Chi-sq.*	*df*	*P*
Above Traps	13.1103	3	<.01	4.3145	6	.63	3.2736	4	.51
Lake Proper	69.2772	6	<.01	7.1260	7	.42	27.4010	5	<.01
All Areas	99.4585	7	<.01	12.8758	8	.12	12.9347	6	<.01

TABLE XXXII

POPULATIONS OF THE VARIOUS SEX AND SIZE CATEGORIES AS CALCULATED FROM DEAD FISH RECOVERED IN DIFFERENT AREAS IN 1938 AND 1939.

Year and Area	*Large Males*	*Large Females*	*Small Males*	*Small Females*	*All *Categories*	*†Summation of Categories*
1938						
Above Traps	1,104	6,893	3,850	451	12,144	12,298
Lake Proper	2,067	7,526	4,817	444	14,834	14,854
Spring Creek	1,677	7,296	5,098	711	13,606	14,782
All Areas	1,663	7,317	4,414	468	13,765	13,862
1939						
Above Traps	14,284	31,479			45,425	45,763
Lake Proper	26,854	56,983			84,121	83,837
All Areas	23,083	52,236			75,441	75,319

* Population calculated from the tag ratio in all fish recovered in each area.

† Population derived by adding numbers of each sex and size category calculated for each area.

TABLE XXXIII

NUMBER OF TAGGED SOCKEYE RECOVERED IN EACH AREA FROM SUCCESSIVE ONE HUNDRED TAGGED DURING 1938. THE DEVIATION FROM THE MEAN NUMBER OF RECOVERIES PER HUNDRED IS SHOWN IN EACH CASE.

TAG NOS.	ABOVE TRAPS		LAKE PROPER		SPRING CREEK		ALL AREAS		ALL AREAS
	No. of Rec.	*Dev. from mean*	*No. of Rec.*	*Dev. from mean*	*No. of Rec.*	*Dev. from mean*	*No. of Rec.*	*Dev. from mean*	*Calculated Population*
1–100	2	—2	11	+1	10	—9	23	—10	20,587
200	1	—3	8	—2	7	—12	16	—17	29,594
300	3	—1	6	—4	16	—3	25	—8	18,940
400	1	—3	6	—4	14	—5	21	—12	22,548
500	2	—2	13	+3	18	—1	33	0	14,348
600	5	+1	4	—6	18	—1	27	—6	17,537
700	1	—3	16	+6	13	—6	30	—3	15,783
800	1	—3	11	+1	12	—7	24	—9	19,729
900	3	—1	15	+5	15	—4	33	0	14,348
1000	3	—1	9	—1	20	+1	32	—1	14,797
1100	3	—1	9	—1	14	—5	26	—7	18,212
1200	6	+2	5	—5	10	—9	21	—12	22,548
1300	6	+2	9	—1	17	—2	32	—1	14,797
1400	3	—1	11	+1	17	—2	31	—2	15,274
1500	2	—2	7	—3	20	+1	29	—4	16,328
1600	2	—2	9	—1	24	+5	35	+2	13,529
1700	6	+2	4	—6	21	+2	31	—2	15,274
1800	2	—2	11	+1	15	—4	28	—5	16,911
1900	3	—1	8	—2	13	—6	24	—9	19,729
2000	4	0	13	+3	27	+8	44	+11	10,761
2100	2	—2	13	+3	20	+1	35	+2	13,529
2200	5	+1	10	0	19	0	34	+1	13,926
2300	6	+2	6	—4	21	+2	33	0	14,348
2400	3	—1	6	—4	37	+18	46	+13	10,293
2500	4	0	9	—1	21	+2	34	+1	13,926
2600	1	—3	10	0	28	+9	39	+6	12,141
2700	2	—2	14	+4	22	+3	38	+5	12,460
2800	6	+2	10	0	23	+4	39	+6	12,141
2900	6	+2	9	—1	17	—2	32	—1	14,797
3000	3	—1	11	+1	20	+1	34	+1	13,926
3100	5	+1	14	+4	16	—3	35	+2	13,529
3200	14	+10	10	0	17	—2	41	+8	11,549
3300	6	+2	12	+2	16	—3	34	+1	13,926
3400	5	+1	15	+5	19	0	39	+6	12,141
3500	4	0	8	—2	27	+8	39	+6	12,141
3600	1	—3	18	+8	23	+4	42	+9	11,274
3700	8	+4	8	—2	18	—1	34	+1	13,926
3800	10	+6	4	—6	22	+3	36	+3	13,153
3900	3	—1	12	+2	30	+11	45	+12	10,522
4000	6	+2	9	—1	27	+8	42	+9	11,274
4100	3	—1	12	+2	25	+6	40	+7	11,837
4200	14	+10	3	—7	23	+4	40	+7	11,837
4300	11	+7	8	—2	14	—5	33	0	14,348
4400	8	+4	6	—4	18	—1	32	—1	14,797

TABLE XXXIV

NUMBER OF TAGGED SOCKEYE RECOVERED IN EACH AREA FROM SUCCESSIVE ONE HUNDRED TAGGED DURING 1939. THE DEVIATION FROM THE MEAN NUMBER OF RECOVERIES PER HUNDRED IS SHOWN IN EACH CASE.

TAG NOS.	ABOVE TRAPS		LAKE PROPER		ALL AREAS		ALL AREAS
	No. of Rec.	*Dev. from mean*	*No. of Rec.*	*Dev. from mean*	*No. of Rec.*	*Dev. from mean*	*Calculated Population*
1–100	3	0	9	—1	12	—1	81,933
200	3	0	4	—6	7	—6	140,457
300	4	+1	11	+1	15	+2	65,547
400	5	+2	11	+1	16	+3	61,450
500	2	—1	13	+3	15	+2	65,547
600	0	—3	20	+10	20	+7	49,160
700	3	0	11	+1	14	+1	70,229
800	1	—2	12	+2	13	0	75,631
900	1	—2	7	—3	8	—5	122,900
1000	3	0	13	+3	16	+3	61,450
1100	4	+1	17	+7	21	+8	46,819
1200	1	—2	8	—2	9	—4	109,244
1300	6	+3	14	+4	20	+7	49,160
1400	0	—3	11	+1	11	—2	89,382
1500	1	—2	8	—2	9	—4	109,244
1600	2	—1	8	—2	10	—3	98,320
1700	2	—1	11	+1	13	0	75,631
1800	4	+1	9	—1	13	0	75,631
1900	2	—1	10	0	12	—1	81,934
2000	3	0	12	+2	15	+2	65,547
2100	3	0	4	—6	7	—6	140,457
2200	2	—1	6	—4	8	—5	122,900
2300	2	—1	6	—4	8	—5	122,900
2400	0	—3	8	—2	8	—5	122,900
2500	3	0	7	—3	10	—3	98,320
2600	3	0	7	—3	10	—3	98,320
2700	0	—3	6	—4	6	—7	163,867
2800	2	—1	7	—3	9	—4	109,244
2900	3	0	8	—2	11	—2	89,382
3000	4	+1	10	0	14	+1	70,229
3100	8	+5	10	0	18	+5	54,622
3200	4	+1	9	—1	13	0	75,631
3300	2	—1	11	+1	13	0	75,631
3400	4	+1	10	0	14	+1	70,229
3500	3	0	12	+2	15	+2	65,547
3600	6	+3	21	+11	27	+14	36,415

TABLE XXXV

MEAN NUMBERS AND EXTREMES OF TAGS RECOVERED FROM DIFFERENT GROUPS OF TAGS PUT ON THROUGHOUT THE SEASON AND THE CORRESPONDING POPULATION CALCULATIONS FOR THESE RECOVERIES.

No. of Groups	*No. of tags in each group*	*Range in no. of recoveries*	*Calculated population extremes*		*Mean no. of tag recoveries*	*Population from mean no. of recoveries*	*Stand. dev. of tag recoveries*	*Calculated populations 95 per cent confidence limits**	
1938									
160	27	1 - 16	127,845	7,990	8.98	14,236	2.43	30,295	9,305
80	54	9 - 29	28,410	8,817	17.82	14,373	3.55	23,544	10,318
40	108	26 - 47	19,668	10,880	35.65	14,344	5.04	19,844	11,232
20	216	56 - 92	18,264	11,117	72.30	14,146	8.66	15,655	11,457
1939									
160	22	0 - 9		24,034	2.73	79,232	1.62		26,612
80	44	0 - 11		39,232	5.46	79,232	2.06	304,654	45,538
40	88	4 - 17	216,304	50,895	10.95	79,015	2.93	166,068	51,840
20	176	10 - 31	173,043	55,820	21.85	79,196	5.20	148,408	54,008

* Calculated on basis of 1.96 times standard deviation.

A Mathematical Study Of Confidence Limits Of Salmon Populations Calculated From Sample Tag Ratios

by

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INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION

A MATHEMATICAL STUDY OF CONFIDENCE LIMITS OF SALMON POPULATIONS CALCULATED FROM SAMPLE TAG RATIOS

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An important problem in all fisheries work is the estimation of populations. Tagging programs have been used increasingly in recent years in an attempt to obtain a scientific solution of this problem. Such a program involves tagging some members of the population and subsequently obtaining a sample of the population which is random with respect to tagged and untagged fish. The evidence available from experiments designed to test this assumption of randomness is considered elsewhere.

In this paper procedures for finding point and interval estimates of the population are considered; in particular confidence limits are found for the estimate of the population which form an interval estimate that is optimum in a certain sense.

The following notations will be used:

N: Total number in the population;
t: Number of tagged or marked fish;
n: Number subsequently sampled;
s: Number of tagged fish in the sample.

Here t, n, s are known while N is the unknown to be estimated. The usual practice is to take as an estimate of N

$$\hat{N} = \frac{nt}{s} \qquad (1)$$

The basis for this estimate will be considered; further it is desirable to find an interval $(\underline{N}\ \overline{N})$, such that it may be said with (say) 95 per cent confidence that $(\underline{N}\ \overline{N})$ includes the true value of N.

Consideration of the problem from a statistical viewpoint appears to go at least as far back as Laplace (1786) with his essay on the problem dealing with the population of France. The first mathematical attack upon the problem in modern times is due to Pearson (1928) who used the method of inverse probabilities to obtain his results. The basis of this method is to combine with the initial probability distribution of N, the information obtained from the sample and derive by means of Bayes Theorem, what is usually called the *"a posteriori"* probability distribution of N.

Actually, N is a fixed, though unknown number and in this situation cannot be regarded as a random variable with a probability distribution. Moreover, nothing is known concerning N initially, except that it must be at least as large as the number of the fish already counted through tagging or sampling. In this situation it was necessary for Pearson to assume that all values of N above this limit are equally likely. This is a questionable assumption and should different values be assigned as an *"a priori"* upper bound of N, different results would be obtained. A further discussion of the modern statistical viewpoint with regard to the use of inverse probability in problems of this type may be found in Neyman (1942) and Cramer (1946).

A POINT ESTIMATE FOR *N*

The number of tagged fish (s) actually counted in any sample is subject to sampling fluctuations, i.e. it is a random variable; consequently, it is the frequency distribution of s which is of interest. Since the sampling occurs without replacement and since the initial proportion of tagged fish is $\frac{t}{N}$, the distribution of s is hypergeometric (Kendall, 1945, p. 126-128). The probability of s tags, where s is any integer from 0 to n is given by:

$$P\,\{s\} = \frac{n!}{s!(n-s)!}\;\frac{t(t-1)\cdots(t-s+1)(N-t)(N-t-1)\cdots(N-t-n+s+1)}{N(N-1)\cdots(N-n+1)} \tag{2}$$

$$= \frac{n!}{s!(n-s)!}\;\frac{t!(N-t)!\,(N-n)!}{N!(t-s)!\,(N-t-n+s)!} \tag{3}$$

In actual fact, s and not N is known. The question may be asked: what value or values of N would most probably have given the actually observed s. We proceed then to find what values of N (there may be more than one) make $P\,\{s\}$ a maximum.

Denote by N_0 the largest of the values of N which make $P\,\{s\}$ a maximum. By the definition of N_0

$$P\,\{s/N_0-1\} \leqq P\,\{s/N_0\} \tag{4}$$

$$P\,\{s/N_0+1\} < P\,\{s/N_0\} \tag{5}$$

Inserting the appropriate probabilities from (3) and simplifying, these equations become

$$\frac{(N_0-1-t)!\,(N_0-1-n)!}{(N_0-1)!\,(N_0-1-t-n+s)!} \leqq \frac{(N_0-t)!\,(N_0-n)!}{N_0!\,(N_0-t-n+s)!} \tag{6}$$

$$\frac{(N_0+1-t)!\,(N_0+1-n)!}{(N_0+1)(N_0+1-t-n+s)!} < \frac{(N_0-t)!\,(N_0-n)!}{N_0!\,(N_0-t-n+s)!} \tag{7}$$

These, in turn, may be easily simplified and combined to:

$$\frac{nt}{s} - 1 < N_0 \leqq \frac{nt}{s} \tag{8}$$

Consequently, the value of N which is most probable on the basis of the samples is $\frac{nt}{s}$, or if $\frac{nt}{s}$ is fractional, the integer immediately below $\frac{nt}{s}$. This is the maximum likelihood estimate of N usually denoted by $\hat{N}$.

It is known that any maximum likelihood estimate of a parameter is also a consistent estimate: that is, the probability of the estimate differing from the true value may be made as small as desired, provided n is taken sufficiently large. When a method of estimation furnishes a consistent estimate of a parameter (such as N in this problem), it is possible to obtain an estimate with any desired degree of accuracy.

INTERVAL ESTIMATES FOR N

While a maximum likelihood estimate gives some clue as to the population size, no information is provided as to how far the actual value of N may differ from the estimate. In particular, it is frequently desirable to be able to use the sample information to determine some interval which may be said to include with a reasonable degree of confidence, the true value of N. The confidence interval approach (Neyman, 1937) enables us to formulate this problem precisely and to solve it.

Let c denote the desired degree of confidence—usually one of 0.90, 0.95 or 0.99. If corresponding to each possible sample result there can be determined a pair of numbers $\overline{N}$ and $\underline{N}$ such that

$$P\,\{(\overline{N}\,\underline{N}) \text{ includes } N\} \geqq c \qquad (9)$$

then, such a set of number pairs constitutes a set of confidence limits for N. Then, it may be said with confidence c, that the interval associated with any sample value s includes the true population values with the following probability basis: if a large number of independent samples were taken from the population of size N, and the confidence limits for N determined for each observed value of s, then the statement that N is included between the appropriate confidence limits would be correct not less than 100 c per cent of the time.

The terms confidence limits and fiducial limits are frequently used interchangeably. However, there is a basic conceptual difference. While the two methods frequently give coincident limits in elementary problems, there are situations where they differ. The conceptual basis underlying a fiducial approach to this problem would involve considering the hypothetical set of all possible population sizes. If possible, a quantitative interpretation of statistical results is desirable. The confidence interval estimate may be interpreted quantitively by means of the probability or frequency equation (9). However, unless fiducial limits happen to coincide with confidence limits, it is impossible to make a probability or frequency statement concerning the interval estimate.

As a result, no emperical verification of fiducial limits is satisfactory logically while there is no difficulty in performing experiments to verify that confidence intervals have the properties ascribed to them. This may be done by performing several tagging experiments upon the same population. Data were already available in this connection from the tagging experiments carried out by the International Pacific Salmon Fisheries Commission at Cultus Lake in 1938-39 (Howard, 1948).

The probability distribution of s is known exactly, i.e., it is the hypergeometric distribution (3), and since the distribution involves only one unknown parameter N, in theory it is possible to determine the appropriate confidence limits corresponding to any value of s. Writing

$$P\,\{x \leqq s/n\} = \sum_{x=0}^{s} \frac{n!}{x!(n-x)!} \; \frac{t!(N-t)!\,(N-n)!}{N!(t-x)!\,(N-t-n+x)!} \tag{10}$$

then $\underline{N}$ and $\overline{N}$ are solutions of the equation

$$P\,\{x \leqq s/\underline{N}\} + P\,\{x \geqq s/\overline{N}\} \leqq 1-c \tag{11}$$

To show this, it may be observed first that as N increases for any fixed value of t, the *proportion* of tagged fish decreases and the expected number of tagged fish per sample will be smaller. Consequently, small values of s will be more probable and large values less so. In mathematical terms, as N increases for fixed values of s and t, $P\{x \leqq s/N\}$ increases while $P\{x \geqq s/N\}$ decreases.

Hence, when $\underline{N} > N$ (12)

$$P\,\{x \leqq s/\underline{N}\} \geqq P\,\{x \leqq s/N\} \tag{13}$$

and when $\overline{N} < N$ (14)

$$P\,\{x \geqq s/\overline{N}\} \geqq P\,\{x \geqq s/N\} \tag{15}$$

Now, if the interval $(\underline{N}\ \overline{N})$ does not include N, either (12) or (14) must be true. These inequalities will hold when s is such that either (13) or (15) is true. Since the sum of the left hand sides of equations (13) and (15) are less than 1-c, the sum of the probabilities on the right hand sides of (13) and (15) must be less than 1-c. In other words, the values of s which give rise to confidence intervals that do not include the true value N, occur with a probability less than 1-c; consequently, (9) is satisfied.

It is necessary to use inequalities in (9) and (11) since the hypergeometric distribution is discrete; and in general, it would not be possible to find integer values of $\underline{N}$ and $\overline{N}$, such that the left hand side of (11) would equal 1-c exactly.

There are two unknowns in equation (11) and consequently there will be an infinite number of solutions for $\overline{N}$ and $\underline{N}$. This may be emphasized by writing (11) in a slightly different form. Let c_1, be any non-negative number not greater than 1-c. Then, (11) may be written

$$P\{x \leqq s/\underline{N}\} \leqq 1-c-c_1\ ;\ P\{x \geqq s/\overline{N}\} \leqq c_1 \tag{16}$$

In general, each choice of c_1 will give rise to a different pair of confidence limits. This difficulty may be resolved by choosing

$$c_1 = \frac{1}{2}(1-c) \tag{17}$$

This choice will frequently reduce the computational difficulties. However, particularly for skewed distributions, other choices of c_1 will give rise to a much shorter confidence interval than is provided by the solution of (16) and (17). If it is possible to find for each s a confidence interval of minimum length L, (i.e., $L = \overline{N} - \underline{N}$) then, this set of confidence intervals is optimum in a certain sense. We now consider this problem.

Because the hypergeometric distribution is awkward to handle and because the parameter appears in the distribution in a complex manner, any solution of (16) is virtually impossible even by trial and error methods. Consequently, it is necessary to find some simpler approximate distribution. The binomial, normal or Poisson distributions may be used to approximate the hypergeometric distribution. The one which furnishes the best approximation will depend on the relative and absolute sizes of n, t and N. These three possibilities are considered successively.

THE POISSON APPROXIMATION

In many tagging experiments the tag ratio is low and in such cases the distribution of s is most closely approximated by the Poisson distribution

$$P\ \{s\} = \frac{e^{\frac{-nt}{N}}}{s!}\left(\frac{nt}{N}\right)^{s} \tag{18}$$

It is more convenient to write

$$\frac{nt}{N} = m \tag{19}$$

and put (16) in the more usual form

$$\mathrm{P}\ \{s/m\} = \frac{e^{-m}}{s!}\ m^{s} \tag{20}$$

If confidence limits $\underline{m}$ and $\overline{m}$ are determined for the parameter m, by the use of (19), confidence limits for N can be immediately calculated. By an argument similar to the one given for N, the confidence limits m and $\overline{m}$ are solutions of the equation:

$$P\ \{x \geqq s/\underline{m}\} = c_1\ ;\ \ P\ \{x \leqq s/\overline{m}\} = 1 - c - c_1 \tag{21}$$

As in equations (9), (11) and (16), inequalities should be written in (21), rather than equalities. However, it will be convenient to use the equality now since we are going to solve for the values of $\underline{m}$ and $\overline{m}$ which most nearly satisfy the equality of (21).

Confidence limits for the parameter m in the Poisson distribution have been studied extensively for the case where the restriction (17) is imposed. Garwood (1936) has calculated confidence limits for the confidence coefficients 0.90 and 0.98. Ricker (1937) computed the limits for the confidence coefficient 0.95 and 0.99, while the upper limits for the confidence coefficient 0.99 have been published also by Przyborowski and Wilenski (1935).

Using equation (19) any of these limits for m can be converted into confidence limits for N but the upper limits are very large. For example, using Ricker's table when $n=500$, $t=100$ and $s=5$ the 95 per cent confidence limits for N are:

$$\underline{N} = 4{,}274 \qquad \overline{N} = 31{,}250 \text{ while } \hat{N} = 10{,}000.$$

By a more suitable choice of c_1 this interval can be reduced. We turn to the determination of c_1 in order to make

$$L = \overline{N} - N = \frac{1}{nt}(\overline{m} - \underline{m}) \tag{22}$$

a minimum, where $\underline{m}$ and $\overline{m}$ are the solutions of (21).

Differentiating L with respect to c_1

$$\frac{dL}{dc_1} = nt\left(-\frac{1}{\underline{m}^2}\frac{d\underline{m}}{dc_1} + \frac{1}{\overline{m}^2}\frac{d\overline{m}}{dc_1} \right) \tag{23}$$

Replacing the probabilities of (21) by their appropriate values, the equations become

$$P\,\{x \geqq s/\underline{m}\} = \sum_{x=s}^{\infty} e^{-\underline{m}}\frac{\underline{m}^x}{x\,!} = c_1 \tag{24}$$

$$P\,\{x \leqq s/\overline{m}\} = \sum_{x=0}^{s} e^{-\overline{m}}\frac{\overline{m}^x}{x} = 1-c-c_1 \tag{25}$$

Differentiating (24) and (25) with respect to c_1 gives:

$$\sum_{x=s}^{\infty}\left[e^{-\underline{m}}\frac{\underline{m}^{x-1}}{(x-1)\,!} - e^{-\underline{m}}\frac{\underline{m}^{x}}{x\,!} \right]\frac{d\underline{m}}{dc_1} = 1 \tag{26}$$

$$\sum_{x=0}^{s}\left[e^{-\overline{m}}\frac{\overline{m}^{x-1}}{(x-1)\,!} - e^{-\overline{m}}\frac{\overline{m}^{x}}{x\,!} \right]\frac{d\overline{m}}{dc_1} = -1 \tag{27}$$

or upon simplification

$$e^{-\underline{m}}\frac{\underline{m}^{s-1}}{(s-1)\,!}\frac{d\underline{m}}{dc_1} = 1 \tag{28}$$

$$-e^{-\overline{m}}\frac{\overline{m}^{s}}{s\,!}\frac{d\overline{m}}{dc_1} = -1 \tag{29}$$

Solving for the derivatives of $\underline{m}$ and $\overline{m}$ with respect to c_1 from (28) and (29) and substituting them in (23) gives:

$$\frac{dL}{dc_1} = nt\left[-\frac{1}{\underline{m}^2}\frac{(s-1)\,!}{e^{-\underline{m}}\underline{m}^{s-1}} + \frac{1}{\overline{m}^2}\frac{s\,!}{e^{-\overline{m}}\overline{m}^{s}} \right] \tag{30}$$

Now put $\frac{dL}{dc_1} = 0$ and obtain the equation

$$se^{-\underline{m}}\underline{m}^{s+1} = e^{-\overline{m}}\overline{m}^{s+2} \tag{31}$$

Equations (24), (25) and (31) are the fundamental equations for the determination of the three unknowns: c_1, $\underline{m}$ and $\overline{m}$. The equations cannot be solved explicitly but only by repeated trials and suitable interpolation.

It is to be noted now that c_1 will vary for each s: no one value of c will make all confidence intervals a minimum. However, for any m

$$P\,\{\underline{m}\;\overline{m}\ \text{does not include}\ m\} = P\,\{\underline{m} > m\} + P\,\{\overline{m} < m\}. \tag{32}$$

The reasoning here is exactly similar to that following equation (16). If s_1 is the last value of s such that $\overline{m} < m$ (or $\underline{N} > N$) and s_2 is the first value of s such that $\underline{m} > m$ (or $\overline{N} < N$) then

$$\begin{aligned} P\,\{\overline{m} < m\} &= P\,\{x \leqq s_1\} \leqq P\,\{x \leqq s_1/\overline{m}\} = 1 - c - c_1(s_1) \\ P\,\{\underline{m} > m\} &= P\,\{x \geqq s_2\} \leqq P\,\{x \geqq s_2/\underline{m}\} = c_1\,(s_2) \end{aligned} \qquad (33)$$

$$P\,\{(\underline{m}\ \overline{m}) \text{ does not include } m\} \leqq 1 - c + c_1\,(s_2) - c_1\,(s_1) \qquad (34)$$

Now in solving equations (24), (25) and (31) it is found that $c_1\,(s)$ decreases as s increases. Since s_1 is less than m, s_2 greater than m, it follows that:

$$c_1(s_2) < c_1(s_1) \text{ i.e. } c_1(s_2) - c_1(s_1) < 0 \qquad (35)$$

and hence

$$P\,\{(\underline{m}\ \overline{m}) \text{ does not include } m\} < 1 - c \qquad (36)$$

Consequently, the solutions $\underline{m}$ $\overline{m}$ of these equations when inverted and multiplied by nt form confidence limits for N such that the interval $(\overline{N}\ \underline{N})$ is of minimum length.

That $c(s)$ is a decreasing function of s is due to the fact that as m increases the Poisson distribution becomes less skewed. Thus to prevent $\underline{m}$ from being too close to zero (and consequently $\overline{N}$ too large) when s is small it is necessary to make c_1 large. As s, and hence also $\underline{m}$, $\overline{m}$, increases the minimum confidence interval is attained by choosing c_1 progressively closer to being equal to $1 - c - c_1$.

In order to make the limits easily available, a table of 95 per cent confidence limits for $\frac{N}{nt}$ has been calculated from these equations for values of s from 0 to 50. It is only necessary to multiply the tabulated values by nt to determine the desired confidence limits. Referring to the example for which confidence limits were given previously, where $n = 500$, $t = 100$ and $s = 5$, it is found that: $\underline{N} = 3{,}290$ and $\overline{N} = 25{,}750$. The length of the confidence interval is reduced in this particular case from 26,977 to 22,460. However the gain will be less significant for larger values of s because the Poisson distribution becomes less skewed as m increases. It may be pointed out that if Pearson's σN were used to obtain an interval estimate for N, i.e., taking $N \pm 1.96\ \sigma N$ as the limits, the result would be $\underline{N} = 595$, $\overline{N} = 32{,}557$ (the actual lower limit from the formula is negative but the tagging and sampling indicate that N must be as large as 595). Such limits are not confidence limits.

TABLE I.

95 Per Cent Confidence Limits for $\frac{N}{nt}$

s	*Lower Limit*	*Upper Limit*	*s*	*Lower Limit*	*Upper Limit*
0	0.0885	....			
1	0.0720	19.489	26	0.02478	0.0563
2	0.0767	2.821	27	0.02408	0.0539
3	0.0736	1.230	28	0.02342	0.0516
4	0.0690	0.738	29	0.02279	0.0495
5	0.0644	0.513	30	0.02221	0.0475
6	0.0600	0.388	31	0.02165	0.0457
7	0.0561	0.309	32	0.02112	0.0440
8	0.0526	0.256	33	0.02061	0.0425
9	0.0495	0.217	34	0.02014	0.0410
10	0.0468	0.188	35	0.01968	0.0396
11	0.0443	0.165	36	0.01925	0.0384
12	0.0420	0.147	37	0.01883	0.0372
13	0.0400	0.133	38	0.01843	0.0360
14	0.0382	0.121	39	0.01805	0.0350
15	0.0365	0.111	40	0.01769	0.03396
16	0.0350	0.1020	41	0.01733	0.03300
17	0.03362	0.0945	42	0.01700	0.03210
18	0.03233	0.0880	43	0.01668	0.03124
19	0.03114	0.0823	44	0.01636	0.03043
20	0.03004	0.0773	45	0.01606	0.02966
21	0.02901	0.0729	46	0.01578	0.02892
22	0.02806	0.0689	47	0.01550	0.02822
23	0.02716	0.0653	48	0.01523	0.02755
24	0.02632	0.0620	49	0.01498	0.02691
25	0.02552	0.0591	50	0.01475	0.02625

TABLE II

Values of a and b to be used in Equations (43), (44) and (46) and 95 per cent Confidence Limits for selected larger values of s.

s	a	b	*Lower Limit*	*Upper Limit*
50	1.802	2.192	0.01475	0.02625
60	1.815	2.164	0.01263	0.02140
80	1.834	2.129	0.009865	0.01553
100	1.844	2.112	0.008105	0.01214

Using limits given in Table I and a table of the Poisson distribution, it is possible to represent graphically the properties of confidence limits (see Figure 1). The top graph is a histogram of the Poisson distribution for which $\frac{nt}{N} = m = 4$, while the lower graph shows the confidence intervals corresponding to each value of s. Here $nt = 100{,}000$ and the true value of N is 25,000. It is seen that the confidence intervals fail to include the true value of N when s is zero, and when it is larger than or equal to 9. The total probability of such values given that $m = 4$ is 0.0264 so that the confidence intervals include the true N certainly more than the required 95 per cent of the time.

It may be noted also that 0 and 9 are the values of s_1 and s_2, defined above (33), for this particular case.

In calculating the limits shown in Tables I and II, it was necessary to determine the probabilities of equations (24) and (25). For smaller values of s, these were determined (as Ricker did) from Tables LI and LII in Pearson (1930).

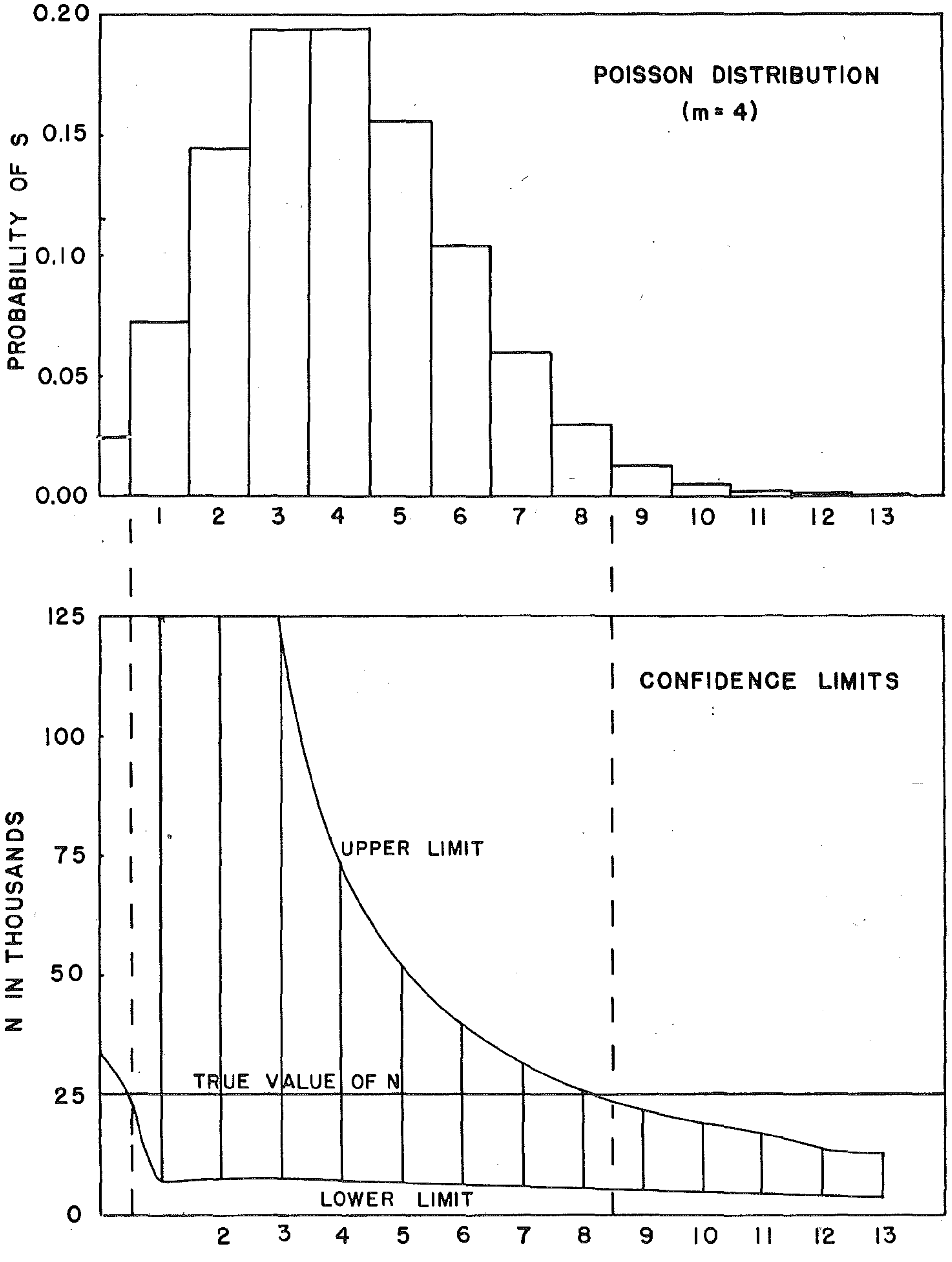

FIGURE 1.

For larger values of s the probabilities were determined by means of the Wilson-Hilferty approximation to the X^2 integral. Garwood (1936) was responsible for this approach to the problem. He showed by simple transformations that

$$P\,\{x \leqq s/m\} = 1 - \int_0^m e^{-t}\,\frac{t^s}{s\,!}\,dt \tag{37}$$

$$= 1 - \frac{1}{2^{s+1}\,s\,!}\int_0^{2m} e^{\frac{-u}{2}}\,u^s\,du \tag{38}$$

$$\doteq 1 - \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{K} e^{\frac{-t^2}{2}}\,dt \tag{39}$$

where

$$K = \left[\left(\frac{m}{s+1}\right)^{1/3} + \frac{1}{9s+9} - 1\right]\sqrt{9s+9} \tag{40}$$

Similarly,

$$\mathrm{P}\,\{x \geqq s/m\} \doteq \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{K^1} e^{\frac{-t^2}{2}}\,dt \tag{41}$$

$$\text{With } K^1 = \left[\left(\frac{m}{s}\right)^{1/3} + \frac{1}{9s} - 1\right]\sqrt{9s} \tag{42}$$

It may be recalled that Garwood (1936) showed that the Poisson distribution may be accurately evaluated by the use of the Wilson-Hilferty approximation for the range of values of s and m here considered. The author verified this by comparisons between terms of the Poisson distribution calculated in this manner and those tabulated in Pearson's tables cited above.

Using this method, the procedure was to estimate c_1 and determine a and b, so that the area under the normal curve to the right of a and b is c_1 and $1-c-c_1$ respectively; then determine $\underline{m}$ and $\overline{m}$ from the equations:

$$\underline{m} = s\left[1 - \frac{1}{9\mathrm{s}} - a\,(9s)^{\frac{-1}{2}}\right]^3 \tag{43}$$

$$\overline{m} = (s+1)\left[1 - \frac{1}{9s+9} + b\,(9s+9)^{\frac{-1}{2}}\right]^3 \tag{44}$$

Finally, the values of $\underline{m}$ and $\overline{m}$ obtained in (43) and (44) were substituted in (36). In general, (36) was satisfied only after repeated steps and interpolations.

Equations (43) and (44) may be used to calculate the appropriate confidence limits for values of s larger than 50. Table II gives the values of a and b for different values of s. By interpolation in this table, the appropriate values of a and b may be found for any value of s. Substituting these values in (43) and (44) the required confidence limits may be determined.

Alternatively, the normal approximation to the Poisson distribution may be used to determine confidence limits for larger values of s. This procedure which was used in Ricker's paper (1937, p. 352), is based on the fact that $\frac{s-m}{\sqrt{m}}$ is distributed approximately normally. Hence, with a and b as defined above, approximate 95 per cent confidence limits are found for m by solving the equations:

$$\frac{s-\underline{m}}{\sqrt{\underline{m}}} = a \qquad \frac{s-\overline{m}}{\sqrt{\overline{m}}} = b \qquad (45)$$

These are easily solved to yield:

$$\underline{m} = s + \frac{a^2}{2} - a\sqrt{s + \frac{a^2}{4}}\,; \quad \overline{m} = s + \frac{b^2}{2} + b\sqrt{s + \frac{b^2}{4}} \qquad (46)$$

If a and b are put equal to 1.96, these equations are exactly those of Ricker. The confidence limits found are those for which restriction (17) is valid. However, choosing a and b as suggested above, i.e. by interpolating in Table II, a slightly shorter confidence interval will be obtained. Equations (46) are slightly easier to use than equations (43) and (44) but the result will be slightly less accurate since the Wilson-Hilferty approximation is better than the normal approximation.

THE BINOMIAL APPROXIMATION

If $\frac{t}{N}$ is not small, either the binomial or normal distributions will furnish a better approximation to the hypergeometric distribution than the Poisson distribution. Confidence limits have been calculated for the binomial distribution (Clopper and Pearson, 1934). From the graphs in their paper, upper and lower limits for $\frac{t}{N}$ (p in their notation) may be found and by inversion limits for N. These limits are calculated under the restriction of (17). It would be possible to calculate new limits which would form minimum confidence intervals for N. However, the improvement would be somewhat less than in the case of the Poisson limits and the work would appear to be even greater. In addition, other approximations appear to be more useful in zoological work and these calculations have not been attempted. A more important limitation of the Clopper-Pearson limits is the inaccuracy in interpolation from the graph particularly because the limits obtained must be inverted and multiplied by t to determine confidence limits for N.

THE NORMAL APPROXIMATION

It is well known that under certain conditions the binomial distribution may be accurately approximated by the normal distribution. It may be shown that the hypergeometric distribution possesses the same property (Cramer, 1946, p. 516). The random variable s has the hypergeometric distribution (3); the mean of this distribution is $\frac{nt}{N}$ and its variance,

$$\sigma^2 = \frac{N-n}{N-1}\,\frac{nt}{N}\left(1 - \frac{t}{N}\right) \qquad (47)$$

Consequently,

$$\frac{s - \dfrac{nt}{N}}{\sqrt{\dfrac{N-n}{N-1}\,\dfrac{nt\,(N-t)}{N^2}}} \tag{48}$$

is distributed approximately normally for both n and $N-n$ sufficiently large.

Since 95 per cent of the normal distribution with zero mean and unit variance lies between -1.96 and 1.96, confidence limits for N may be found by solving the equation

$$\frac{|Ns-nt|\sqrt{N-1}}{\sqrt{(N-n)\,nt\,(N-t)}} = 1.96 \tag{49}$$

which can be reduced by simple algebra to:

$$s^2 N^3 - (2\,nts + 3.8416\,nt + s^2)N^2 + (n^2t^2 + 3.8416\,nt^2 + 3.8416\,n^2t + 2\,nts)N - 4.8416\,n^2t^2 = 0 \tag{50}$$

Such an equation must be solved by some approximate method, e.g. Newton's or Horner's, which are treated in any college algebra text. The equation will have three positive real roots but one of these will be very small so that no difficulty exists in deciding which two roots give the desired confidence limits.

Since the solution of the cubic equation (50) will be tedious for n and t large, a simpler approximation may be desirable. If N is much larger than n, it may be assumed that the hypergeometric distribution (3) differs little from the binomial distribution with the same mean. Since the variance of the binomial distribution is

$$n\frac{t}{N}\left(1 - \frac{t}{N}\right) \tag{51}$$

it follows that for large n

$$\frac{s - n\dfrac{t}{N}}{\sqrt{n\,\dfrac{t}{N}\left((1 - \dfrac{t}{N}\right)}} \tag{52}$$

is distributed approximately normally.

Using this approximation, confidence limits for N are given by the solutions of the equation

$$\frac{Ns - nt}{\sqrt{nt\,(N-t)}} = 1.96 \tag{53}$$

which can be reduced to

$$s^2N^2 - 2N(nts + 1.9208\,nt) + n^2t^2 + 3.8416\,nt^2 = 0 \tag{54}$$

The roots of this equation are:

$$(\overline{N}, \underline{N}) = \frac{nt}{s^2}\left[s + 1.9208 \pm \sqrt{(s + 1.9208)^2 - s^2\left(1 + \frac{3.8416}{n}\right)}\right] \tag{55}$$

These are the required limits.

Two observations may be noted concerning the above procedure. In setting up equation (53) we are using the approximation

$$P\{s \leqq a\} = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{K} e^{\frac{-t^2}{2}} d\,t \text{ with } K = \frac{a - n\frac{t}{N}}{\sqrt{\frac{nt}{N}\left(1 - \frac{t}{N}\right)}} \tag{56}$$

rather than the more usual

$$P\{s \leqq a\} = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{K^1} e^{\frac{-t^2}{2}} d\,t \text{ with } K^1 = \frac{a + \frac{1}{2} - n\frac{t}{N}}{\sqrt{\frac{nt}{N}\left(1 - \frac{t}{N}\right)}} \tag{57}$$

The latter approximation seriously over-estimates the binomial probability in the tails and while the first method does not entirely correct this situation, it does give somewhat better results. Similar considerations apply to equation (49).

The confidence limits (55) or those obtained by solving (50) are the ones for which the restriction (17) holds. If this restriction of "equal tails" is eliminated, shorter confidence intervals can be obtained. The problem of determining these intervals has been solved for the quadratic case. Since the gain is slight, it appears doubtful whether this refinement would serve any practical purpose here. This will be seen from the following example.

Taking the particular case, $n = 1{,}000$, $t = 1{,}000$ and $s = 100$, the confidence limits and confidence intervals obtainable by the different methods of approximation are set down in Table III for comparison purposes.

TABLE III

COMPARISON OF CONFIDENCE INTERVALS

Method of Approximation	$\underline{N}$	$\overline{N}$	L
Binomial (Clopper-Pearson Graph)....	8,100	12,400	4,300
Poisson (Table I)................................	8,105	12,140	4,035
Normal-Binomial (55)	8,322	12,062	3,740
Shortest Normal-Binomial	8,229	11,946	3,717
Normal-Hypergeometric (50)	8,145	11,999	3,584

The numbers in brackets in Table III refer to the equations used in the determination of the confidence limits. The limits in the fourth line were obtained by eliminating the "equal tails" restriction; as asserted above the gain is insignificant.

It is to be noted that two problems are involved in our present approach; first finding the best approximation to the hypergeometric distribution and, second, finding the shortest confidence intervals when given the appropriate approximation. The approximation to be used depends on the relative and absolute sizes of n, t and N. The method of approximation cannot be chosen solely because it yields the shortest confidence interval.

The question of the various approximations to the binomial and more especially to the hypergeometric distribution have been inadequately studied. However, the normal approximation to the binomial gives relatively poor results when $p \left(\frac{t}{N}\right)$ is small, particularly for the tails of the distribution. Without a complete study of the approximation to the hypergeometric distribution, no final conclusions can be laid down as to which approximation should be used in a given circumstance. Consequently, the following suggestions must be taken as tentative guiding rules rather than absolute principles.

Criteria to determine the best method to use in finding a confidence interval estimate for N:

$n \leqq 500$	$\frac{s}{n} \leqq 0.1$	Poisson Approximation—Tables I and II.
	$\frac{s}{n} > 0.1$	Binomial—Clopper-Pearson Graph.
$500 < n \leqq 1{,}000$	$\frac{s}{n} \leqq 0.075$	Poisson Approximation—Tables I and II.
	$\frac{s}{n} > 0.075$	Normal Approximation—(55).
$n > 1{,}000$	$\frac{s}{n} \leqq 0.05$	Poisson Approximation—Tables I and II.
or	$s \leqq 100.$	
	$\frac{s}{n} > 0.05$	Normal Approximation—(55), or preferably Normal-Hypergeometric (50).
and	$s > 100.$	

The number in brackets refer to the equations to be used to compute the confidence limits. When the Poisson approximation is to be used and s is larger than 50, equations (43) and (44) or (46) will be necessary.

The normal-hypergeometric approximation, i.e., the solutions of the cubic equation (50) will be preferable for larger values of n, say 5,000 - 10,000 or larger.

APPLICATIONS TO THE DESIGN OF TAGGING EXPERIMENTS

The results obtained may be used as a guide to the design of tagging experiments. There are several possibilities depending on the information desired. Here, one solution is outlined in which the number of fish tagged is small in relation to the total population. As a result, the Poisson approximation is the appropriate method for the determination of confidence limits.

When no "a priori" information exists and only one sample is to be taken, there is no solution to the question as to how large n and t should be in order to obtain an interval estimate of N of preassigned length. If some upper bound can be estimated for the population either from a preliminary sample or by some other means, an answer can be found to the following problem. Find the smallest value of nt, so that even if the population attains the upper bound, the interval estimate will exceed a preassigned value no more than a certain percentage of the time. An example explains the procedure.

Example: A population is believed not to exceed 10^6 and it is desired to obtain an interval estimate of less than 6×10^5. Try $nt = 40 \times 10^6$. If N were to equal the upper bound 10^6, then $m = \frac{nt}{N} = 40$. Then, s will be greater than or at least equal to 40 in slightly more than half the cases. Referring to Table I it is found that for $s = 40$, $nt = 40 \times 10^6$ and the length of the confidence interval is 650,800. This is larger than desired. After a few more such trials, it will be found that when $nt = 47 \times 10^6$ for $s = 47$ the length of the confidence interval is 597,800. Consequently, if nt is chosen as indicated and even if N is as large as the estimated upper bound, the interval estimate will have the desired property more than half the time (whenever $s \geqq 47$). Moreover, if N is smaller than 10^6 the interval estimate will be in general much smaller than 6×10^5. Thus, if the actual population were only 470,000, the most probable value of s would be 100 with a corresponding interval of 190,000.

In the foregoing example the size of the product nt was determined. The separate choice of n and t will be dependent upon other factors. If there is no difference in effort between tagging and sampling, then the most favorable choice is to have $n = t$. In the above example if $nt = 47 \times 10^6$, n and t would be each approximately 6,850. More generally, if it requires b times as much effort to place a tag as to sample a fish, then if the aim of the program is to minimize the effort (E) expended, n and t may be determined as follows:

Putting $E = c\ (n + bt)$ and $nt = K$ where c is a constant of proportionality, it is a routine calculus problem to show that E will be a minimum if

$$n = \sqrt{b\,K} \text{ and } t = \sqrt{\frac{K}{b}}$$

In general, it will not be possible to design a tagging program in such a simple manner. In particular, the availability of the fish will play a dominant role. Moreover, the relative effort expended in tagging and sampling will vary from region to region, for different times of the migration, for different relative sizes of n and t, etc. However, the principles discussed here may be a useful guide in certain circumstances. For example, where it is known that the dead recovery (sampling) will be difficult, the same results may be achieved by increasing the number of fish tagged. On the other hand, if the tagging program is complete, the size of the sample of dead fish may be determined so that the product nt may be of a desired magnitude.

In this paper various estimates of the population have been considered with a view to making the optimum use of the information obtained from a tagging program. Methods of procedure have been outlined for various cases and the circumstances under which each should be used have been considered. It may be pointed out that there are other methods of utilizing the information from such experiments which will yield information concerning the accuracy of population estimates. Also, it should be emphasized again that the results here obtained are based upon the assumption that the sampling process is random with respect to tagged and untagged fish.

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