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ESTIMATION OF SIZE OF ANIMAL POPULATIONS BY MARKING EXPERIMENTS

By Milner B. Schaefer

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ESTIMATION OF SIZE OF ANIMAL POPULATIONS BY MARKING EXPERIMENTS

By MILNER B. SCHAEFER, *Fishery Research Biologist*

Determination of population numbers is basic to studies of changes in populations of animals and of the causes of the changes, such as the effects of fishing on a population of fishes. For many animals this cannot be accomplished by direct enumeration, and recourse must be had to indirect methods. One technique which has been employed in the study of fishes, and other organisms as well, and which is still in course of development, is the use of marked members to estimate population numbers.

SIMPLE CASE

THE PROBLEM

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

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

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

If, for example, we know there are 100 marked members in the population, and a sample of 500 contains 50 marked members, we would estimate the population by this equation to be

$$N=\frac{500\times 100}{50}=1{,}000$$

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

Laplace determined from a sample the ratio of births in a year to the population producing those births, and then ascertained the number of births in a year in each urban and rural district of France; by multiplying the number of births by the ratio of population to births determined from the sample, he arrived at an estimate of the total population. Laplace was led to consider also the error inherent in his estimate. This problem, as restated by Pearson (1928), but using my notation, is as follows: "A population of unknown size N is known to contain T affected or marked members. It is desired to ascertain—on the hypothesis of inverse probabilities—a measure of the error introduced by estimating N to be $n\frac{T}{t}$, where t is the number of marked individuals in a sample of size n." Laplace treated this problem as an urn problem, with an infinite number of black and white balls representing marked and unmarked members. On the basis of an extension of Bayes' theorem, he predicted from a first sample of t and n observed what a second sample with known T but unknown N might produce. He found that the mean value of N would be equal to $\frac{Tn}{t}$ if T, n, and t are all large. He also took the distribution of N to be normal about $\frac{Tn}{t}$ as mean with standard deviation estimated by

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

where the numbers are all large.

For the preceding example, where $T=100$, $n=500$, and $t=50$, Laplace's solution would give an estimate of standard deviation

$$\sigma_N=\left(\frac{100\times450\times150\times500}{50^3}\right)^{\frac{1}{2}}=164$$

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

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

$$\tilde{N}=u+T+\frac{u(T-t)}{t}=\frac{nT}{t} \quad \ldots\ldots \quad (3)$$

the mean value is

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

and the variance is

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

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

$$\bar{N}=\tilde{N}=\frac{nt}{t} \quad \ldots\ldots \quad (6)$$

and

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

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

For the example employed before, with $T=100$, $n=500$, $t=50$, formula 7 would give

$$\sigma_N=\left(\frac{100\times450\times50\times500}{50^3}\right)^{\frac{1}{2}}=95$$

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

SOME APPLICATIONS IN THE LITERATURE

Formula 1 has been applied to the estimation of diverse animal populations. One of the best known of these applications is the so-called Lincoln index of the duck population of North America developed by Lincoln (1930), and mentioned in the textbook of Leopold (1935), the monograph of Kendeigh (1944), the manual of Wright (1939), and elsewhere. Lincoln used the ducks banded at stations in North America as his marked members, and the kill by hunters as his sample of the population. The inaccuracies of kill records and the incomplete return of bands were recognized as sources of errors. No attempt was made to estimate the statistical error.

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

Jackson (1933) developed a method of computing the population of tsetse flies in a closed area by marking flies with colored paint and taking a sample to determine the ratio of marked to unmarked. In a later paper (1936) Jackson states that he discovered this method independently in 1930, but meanwhile became cognizant of Lincoln's work and hastens to credit Lincoln with the method.

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

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

> 2. The stock (S) of red salmon may be estimated by the formula:
>
> $$Y:X=S:Z,$$
>
> where Y is the number of tagged fishes, X, the number of recaptured fishes, and Z, the total catch of the fish.

His estimate of 94.7×10^6 individuals in 1936 was made from 1,358 marked fish and 177 recaptures among a sample of $12{,}339\times10^3$. He made no attempt to estimate the reliability of the result. It may be seen from formula 7, however, that the sampling error is actually quite large.

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

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

and compute the number of "other (unmarked) hares present in precensus period," and add it to the number of marked hares to get the total population. This may be illustrated by the simple example we have employed before, where we have a population containing 100 marked members and draw a sample of 500 containing 50 marked members. Green and Evans would compute "other hares present in precensus period," as follows:

$$\frac{100}{X}=\frac{50}{450} \qquad X=900$$

and add the 100 marked hares to get the population estimate of 1,000.

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

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

p = proportion of hares trapped in census period that were not banded (trapped) in precensus period.
P = number of the hares trapped in census period that were not trapped (banded) in precensus period.
N = total number of hares trapped in the census period.
$p=\frac{P}{N}$

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

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

where $q=1-p$. Taking $P\pm2\sigma_pN$, and employing these values in place of the second quotient in their formula (8), they arrive at an estimate of range of the error due to sampling. They conclude that—

> If we use $2\sigma_p$ as our range on either side of the figure obtained . . . we are almost certain to include the correct figure for p, since twice the standard deviation on either side of the mean includes 95 percent of a normal distribution curve.

While this estimate of the reliability of the population estimate is better than none and, indeed, will give an idea of limits within which the population may be expected to fall, it suffers from a lack of precision. The method of computation may be illustrated by the simple numerical example we have employed before. Here $P=450$, $N=500$, and $p=0.90$. Formula 9 then yields

$$\sigma_p=\sqrt{\frac{.9\times.1}{500}}=.01342$$

and $2\sigma_p N=13.42$. The corresponding values of 463.4 and 436.6 may be employed in the second quotient of formula 8 in place of 450 for P to obtain estimates of 927 and 873 for limits of the estimate of "other hares present in precensus period." Corresponding values of total population are 1,027 and 973.

Formula 9 gives the standard deviation of p in repeated samples of size N from a population of infinite size. Since in the present case the population is finite, and N is large with respect to it, the formula for the standard deviation of p should be

$$\sigma_p^2=\frac{P-N}{P-1}\frac{p\cdot q}{N}$$

where P=the number in the population (Cramer 1946, p. 516; Kendell 1944, p. 203). Thus Green and Evans' limits for p would tend to be too broad. For the same simple example used above, this formula gives us

$$\sigma_p^2=\frac{(1000-500)}{(1000-1)}\frac{0.9\times0.1}{500}=.0000901$$

$$\sigma_p=.00949$$

Green and Evans' estimate also has, however, the same objection that Pearson raised to Laplace's solution, rather important in this instance, that this treats the problem of a further sample from a population in which the value of p is known, which is not the same thing as determining the error of the estimate of the population from the single sample available.

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

Knut Dahl (1943, pp. 139–143), has applied the method of marked members to enumeration of trout in a lake. In a small lake on the west coast of Norway, of 250,000 square meters, trout were captured by beach seine and marked. During a second fishing 8 to 14 days later he determined the number of marked and unmarked fish captured. From the number of marked fish liberated, divided by the number of marked fish recaptured, he computed a "Gjenfangstkvotient" by which the total fish taken in the second fishing was multiplied to obtain the total population. This is, of course, the same as formula 1, where $\frac{T}{t}$ is the "Gjenfangstkvotient."

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

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

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

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

SOME FURTHER CONSIDERATIONS

An alternative derivation

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

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

whence

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

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

This means that

$$\frac{(n+1)(T+1)}{(t+1)}-1\ \ldots\ldots\ (12)$$

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

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

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

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

Confidence limits on the population estimate

The method of confidence intervals, due to Neyman (1934), may be employed to determine the range of values within which we may expect N to lie. A discussion of the theory of confidence intervals is beyond the scope of this paper, and reference is made to the original paper of Neyman or to the discussion of Cramer (1946, p. 507 et seq.) or that of Kendall (1946, p. 62 et seq.).

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

> Suppose we have a population consisting of a finite number N of individuals, Np of which possess a certain attribute A, while the remaining $Nq=N-Np$ do not possess A. It is now required to estimate the unknown proportion p . . . Let us draw a random sample of n individuals *without replacement*, and observe the number v of individuals in the sample possessing the attribute A. In current text-books on probability, it is shown that we have
>
> $$E\left(\frac{v}{n}\right)=p \qquad D^2\left(\frac{v}{n}\right)=\frac{N-n}{N-1}\cdot\frac{pq}{n}$$
>
> Further the variable $p^*=\frac{v}{n}$ is approximately normally distributed, when n and $N-n$ are large. Taking p^* as an estimate of p, we now assume as above that the error of approximation in the normal distribution can be neglected. The probability that p^* lies between the limits $p\pm\lambda\sqrt{\frac{N-n}{N-1}\frac{pq}{n}}$ is then equal to ϵ, where λ has the same significance as in the preceding example. (Note: where λ was stated to be the $100\epsilon\%$ value of a normal deviate, and ϵ is the confidence level.)

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

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

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

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

where

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

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

$$N=\frac{T}{p^*} \quad \ldots\ldots\ldots\ldots \quad (14)$$

which is the same as formula 1, of course.

A numerical example may make this clear. Suppose that in a given experiment we have placed 1,000 tagged fish in the population and plan to draw a sample of 2,000 fish for determining the tag ratio. By formula 13 we can compute for values of population tag ratio, p, the limits within which p^* will be expected to fall in, say, 95 percent of the cases ($\epsilon=0.95$). In figure 1, we have calculated and plotted these limits for part of the range of p for this example. The ordinates on this graph are values of p, and the abscissae are values of p^*. Going horizontally across the graph for a given value of p we come to the values of p^* within which samples of 2,000 from a population having a true tag ratio of p would be expected to fall in 95 percent of the cases. By the theory developed by Neyman the loci of such points for various values of p form the 95-percent confidence limits for values of p^*. For a given value of p^* we go along the vertical to the intersections with these loci to find the confidence limits for that value of p^*. Thus, suppose that we draw our sample of 2,000 and find that it contains 100 tagged fish. Our estimate of the tag ratio in the population is 0.05, and from figure 1 we find that for this value of p^* the 95-percent confidence limits are 0.042 and 0.059. Since we know there are 1,000 tagged fish in the population, our estimate of the population by formula 14 is 20,000 with 95-percent confidence limits 16,950 and 24,800. On the right-hand edge of the graph we have plotted the values of N corresponding to tag-ratio values of the same ordinates on the left-hand edge, in order to exhibit graphically the relation between the two.

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

For values of n which are small with respect to N, so that $\frac{N-n}{N-1}$ approaches 1, formula 13 approaches the form appropriate for the binomial. Clopper and Pearson (1934) have computed and charted the confidence limits of the binomial for a large number of values of n for 95 percent and 99 percent confidence levels. Since the limits for the binomial fall in every case outside the limits given by formula 13, these charts may be used to obtain upper and lower limits on the sample value of p^* even where n is not small in relation to N. This involves, of course, a considerable loss of efficiency when n is not small in relation to N, so that the employment of formula 13 would seem to be generally preferable in such cases.

Chapman (1948) has considered the Poisson approximation to the distribution of expected numbers of tag recoveries where the tag ratio is low, in addition to the normal, normal-binomial, and normal-hypergeometric approximations, as bases for confidence-interval estimates of N. He has tabulated useful confidence limits for the Poisson distribution, and discusses practical criteria for judging which distribution to choose as a basis of estimation for various values of n and $\frac{t}{n}$.

As is shown by Chapman's example on page 81 of his paper, for experiments involving numbers of tagged fish, T, and subsequent samples, n, of the magnitude of the example we have employed, and which is of the approximate magnitude of most practical tagging experiments, the differences in confidence limits resulting from the several distributions which might be employed are not very great. In practice it would make little difference which we chose. He recommends which distribution to employ for various situations; for values of $n>1{,}000$ and $\frac{t}{n}>0.05$ he recommends the normal hypergeometric, which has been employed by me in the example above.

REPEATED SAMPLING OF A CONSTANT POPULATION

Where the population of an area remains constant over an appreciable period of time, it is possible to arrive at an estimate based on repeated sampling and marking.

In order to estimate the population by this method, a sampling station or group of stations is established that will result in a random sample of all parts of the population. Samples are drawn at intervals and the fish are tagged and replaced. Records are kept, for each sample, of the number of fish caught and the number of recaptures. Schnabel (1938) provided a solution to the problem of estimating the population from the resulting data.

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

$$\sum_{i=1}^{k} \frac{u_i T_i}{N-T_i} = \sum_{i=1}^{k} t_i \quad \ldots\ldots\ldots (15)$$

which can be expanded in the form

$$\sum_{i=1}^{k} \frac{u_i T_i}{N} \left(1+\frac{T_i}{N}+\frac{T_i^2}{N^2}+\ldots\right) = \sum_{i=1}^{k} t_i \quad \ldots (16)$$

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

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

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

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

$$\frac{\sum_{i=1}^{k} n_i T_i}{\sum_{i=1}^{k} t_i} \quad \ldots\ldots\ldots\ldots (18)$$

This is the formula which has been employed by fisheries workers in practice. Its application will be clear from the example given in table 1, the data for which are from a marking experiment by Krumholz (1944).

TABLE 1.—*Schnabel's method of computing a fish population by repeated sampling and marking*

[Data from Krumholz (1944) table I]

Date (1941)	Number of fish examined	Number of marked fish in lake	Product	Sum of products	Number of returns	Sum of returns	Estimated population
	n_i	T_i	n_iT_i	Σn_iT_i	t_i	Σt_i	$\Sigma n_iT_j/\Sigma t_i$
July 30	53	-----	-----	-----	-----	-----	-----
31	55	53	2,915	2,915	2	2	1,458
Aug. 1	67	106	7,102	10,017	3	5	2,003
2	59	170	10,030	20,047	2	7	2,864
4	85	225	19,125	39,172	6	13	3,013
5	94	297	27,918	67,090	3	16	4,193
6	53	376	19,928	87,018	1	17	5,119
7	115	426	48,990	136,008	5	22	6,182
8	59	520	30,680	166,688	4	26	6,411
9	53	573	30,371	197,059	4	30	6,569
11	53	609	32,277	229,336	5	35	6,552
12	68	604	41,074	270,410	2	37	7,308
13	45	666	29,970	300,380	4	41	7,326
14	38	705	26,790	327,170	-----	41	7,980
15	45	742	33,390	360,560	3	44	8,195
16	28	742	20,776	381,336	-----	44	8,667
18	40	741	29,640	410,976	2	46	8,934
19	20	741	14,820	425,796	-----	46	9,256
20	30	741	22,230	448,026	5	51	8,785
21	27	741	20,007	468,033	1	52	9,001
22	42	741	31,122	499,155	1	53	9,418
23	20	741	14,820	513,975	-----	53	9,698

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

$$N = T\frac{\Sigma n_i}{\Sigma t_i} \quad \ldots\ldots\ldots (19)$$

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

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

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

Underhill (1941) applied this method and formula 18 to the computation of a chub-sucker population of a pond in New York, and Roach

(1943) has done the same in estimating the white-bass population of an Ohio lake.

Schumacher and Eschmeyer (1943) have devised an estimate of N from repeated samplings which is different from that of Schnabel. They assume that the weight, or value, of each sample is proportional to the number of fish in the sample. Under this assumption, an estimate of N is arrived at by minimizing the sum of the squares of the weighted discrepancies of the $\frac{T_i}{N}$ from their estimates $\frac{t_i}{n_i}$. This leads to the formula

$$N=\frac{\sum_{i=1}^{k}T_i^2n_i}{\sum_{i=1}^{k}T_it_i} \quad \text{. . . . . (20)}$$

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

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

$$\frac{N^3s^2}{\sum_{i=1}^{k}T_it_i} \quad \text{. . . . . (21)}$$

where

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

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

In table 2 is recapitulated a numerical example from Schumacher and Eschmeyer (1943), pertaining to the estimation of a population of bullheads in Yellow Creek Pond, Tennessee. Substituting the appropriate sums from this table in formulae [20] and [21], we obtain the following estimates for N and its standard error (σ_N):

$$N=\frac{49{,}598{,}907}{35{,}121}=1{,}412$$

$$s^2=\frac{1}{14}\left(27.992263-\frac{35{,}121}{1412}\right)=0.2228$$

$$\sigma_N=\sqrt{\frac{(1{,}412)^3(0.2228)}{35{,}121}}=134$$

TABLE 2.—*Schumacher and Eschmeyer's method of computing a fish population by repeated sampling and marking*

[Data from table 2 of Schumacher and Eschmeyer (1943)]

Date (1941)	Number of marked fish in pond	Number of fish in sample	Number of marked fish in sample	$T_i^2n_i$	T_it_i	$\frac{t_i^2}{n_i}$
	T_i	n_i	t_i			
Oct. 3	23	39	4	20, 631	92	0. 410256
Oct. 6	57	49	4	159, 201	228	. 326531
Oct. 7	102	51	4	530, 604	408	. 313725
Oct. 8	149	28	5	621, 628	745	. 892857
Oct. 9	172	79	19	2, 337, 136	3, 268	4. 569620
Oct. 10	232	43	8	2, 314. 432	1. 856	1. 488372
Oct. 11	267	49	7	3, 493, 161	1, 869	1. 000000
Oct. 12	309	22	2	2, 100. 582	618	. 181818
Oct. 13	329	38	11	4, 113, 158	3, 619	3. 184211
Oct. 14	356	22	5	2, 788. 102	1, 780	1. 136364
Oct. 15	372	15	4	2, 075, 760	1, 488	1. 066667
Oct. 16	383	4	1	586, 756	383	. 250000
Oct. 17	383	25	7	3, 667. 225	2, 681	1. 960000
Oct. 18	383	98	30	14, 375, 522	11, 490	9. 183673
Oct. 19	383	71	12	10, 414, 919	4, 596	2. 028169
Total				49, 598, 907	35, 121	27. 992263

Ricker (1945b) has investigated the relative efficiency of Schumacher's estimate (20) and Schnabel's formula (18). He states:

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

Krumholz (1944) has made a practical check of the accuracy of estimation of a fish population by repeated sampling, marking by clipped fins, and the application of Schnabel's formula (18). He computed the population of fish over 45 millimeters in length in the north basin of Twin Lake, Mich., in this manner and then poisoned the area with rotenone and counted the fish poulation directly. He concluded:

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

ESTIMATION OF A CHANGING POPULATION

Some fishes, such as salmon spawning in a given stream or lake, do not always form a single, homogeneous, completely mixed population. There may be a tendency for the fish which migrate to the spawning grounds earliest to complete their spawning and die earliest; there results a positive correlation between time of migration past a point below the spawning grounds and the time of appearance on, and of death at, the spawning grounds. If, now, we are tagging fish below the spawning grounds, or even on these grounds, and later sampling for tag ratios, the "mixing" of the fish between tagging and sampling is not complete, and this may need to be taken into consideration in our estimation of the population. Similar situations may occur among other migratory animals.

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

Presented here is a method of estimating the population by which these errors may be reduced when the tagging is done by means of numbered tags, so that the relation between time of tagging and time of recovery may be estimated. I am indebted to Dr. S. Lee Crump of the Iowa State College Statistical Laboratory for much assistance with the mathematics involved.

If our tagged fish have been marked by numbered tags, we know both the date of tagging and date of recovery for each one recovered. This makes it possible to tabulate the recoveries by time of tagging and time of recovery, using as a time interval a convenient period of days. Our notations for the elements involved in the discussion of this section, in addition to those introduced before, are as follows:

Let

N_α=the total number of fish passing the point of tagging during the α^{th} period of tagging. ($\alpha=1, 2, 3, \ldots a$).

T_α=the number of these fish which are tagged during the α^{th} tagging period.

$n_{\alpha i}$=the number of fish out of the $N\alpha$ that are subsequently recovered during the i^{th} recovery period.

$T_{\alpha i}$=the number of fish out of the T_α that die and are thus available to be recovered during the i^{th} recovery period.

$m_{\alpha i}$=the number of tagged fish tagged during the α^{th} period of tagging and recovered during the i^{th} period of recovery ($i=1, 2, 3, \ldots s$).

$m'_{\alpha i}$=the number of untagged fish passing the point of tagging during the α^{th} tagging period and recovered during the i^{th} recovery period.

The following summation conventions are employed:

$$\sum_i m_{\alpha i}=m_{\alpha\cdot} \qquad \sum_\alpha m_{\alpha i}=m_{\cdot i} \qquad \sum_\alpha\sum_i m_{\alpha i}=m_{\cdot\cdot}$$

$$\sum_i m'_{\alpha i}=m'_{\alpha\cdot} \qquad \sum_\alpha m'_{\alpha i}=m'_{\cdot i}$$

$$\sum n_{\alpha i}=n_\alpha.$$

Obviously,

$$m_{\alpha\cdot}+m'_{\alpha\cdot}=n_\alpha.$$

Also let:

$$m_{\cdot i}+m'_{\cdot i}=C_i$$

N_i=the number of fish dying on the spawning grounds during the i^{th} recovery period.

$$q\alpha=\frac{\sum_i n_{\alpha i}}{N_\alpha}$$

$$Pi=\frac{\sum_\alpha T_{\alpha i}}{N_i}$$

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

	Period of tagging (α)			Total tagged fish recovered	Total fish recovered
	1	2	3 . . . a		
Period of recovery (i):					
1	m_{11}	m_{21}	m_{31} . . . m_{a1}	$m_{.1}$	C_1
2	m_{12}	m_{22}	m_{32} . . . m_{a2}	$m_{.2}$	C_2
3	m_{13}	m_{23}	m_{33} . . . m_{a3}	$m_{.3}$	C_3
. . .	. . .	. . .	. . . . . .	. . .	. . .
. . .	. . .	. . .	. . . . . .	. . .	. . .
. . .	. . .	. . .	. . . . . .	. . .	. . .
S	m_{1s}	m_{2s}	m_{3s} . . . m_{as}	$m_{.s}$	C_s
Total tagged fish recovered	$m_{1.}$	$m_{2.}$	m_3 . . . m_a	$m_{..}$ $(=t)$	
Total fish tagged	T_1	T_2	T_3 . . . T_a		

Of course, $\sum_\alpha T_\alpha=T$ and $\sum_i C_i=n$.

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

$$n^*_{\alpha i}=\frac{m_{\alpha i}}{P_{\alpha i}} \quad \text{. . . . .} \quad (22)$$

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

If the samples drawn for tagging and the samples later drawn for tag ratios are representative of the parts of the population from which they are drawn, Pi and q_α may be estimated from the data as follows:

$$q^*_\alpha=\frac{m_{\alpha.}}{T_\alpha}$$

$$\text{. . . . .} \quad (23)$$

$$Pi^*=\frac{m_{.i}}{C_i}$$

The estimate of $n_{\alpha i}$ is, then, given by

$$n^*_{\alpha i}=\frac{m_{\alpha i}}{q^*_\alpha P^*_i}$$

which is equivalent to

$$n^*_{\alpha i}=m_{\alpha i}\frac{T_\alpha}{m_{\alpha.}}\frac{C_i}{m_{.i}} \quad \text{. . . . . .} \quad (24)$$

The estimate of the total population is obtained by summing all these $n^*_{\alpha i}$, thus

$$N^*=\sum_\alpha\sum_i m_{\alpha i}\frac{T_\alpha C_i}{m_{\alpha.}m_{.i}} \quad \text{. . . . .} \quad (25)$$

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

The problem is to estimate the $n_{\alpha.}$ and the q_α. if we can do this we can take as our estimate of N,

$$N^*=\sum_\alpha\frac{n_{\alpha.}^*}{q_\alpha^*}$$

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

$$P(\alpha/i)=\frac{P(i/\alpha)P(\alpha)}{\sum_\alpha P(i/\alpha)P(\alpha)} \quad \text{. . . . .} \quad (26)$$

we have the problem of estimating the $P(i/\alpha)$ and the $P(\alpha)$.

Now,

$$P(\alpha)=\frac{\sum_i n_{\alpha i}}{n}$$

and we may estimate $P(\alpha)$ by

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

To estimate $P(i/\alpha)$ we may use

$$P^*(i/\alpha)=\frac{m_{\alpha i}}{m_{\alpha.}} \quad \text{. . . . .} \quad (28)$$

Then our estimate of $P(\alpha/i)$ becomes

$$P^*(\alpha/i)=\frac{\frac{m_{\alpha.}m_{\alpha i}}{m_{..}m_{\alpha.}}}{\sum_\alpha\frac{m_{\alpha}\cdot m_{\alpha i}}{m_{..}m_{\alpha.}}}=\frac{\frac{m_{\alpha i}}{m_{..}}}{\frac{m_{\cdot i}}{m_{..}}}=\frac{m_{\alpha i}}{m_{.i}} \quad \text{. .} \quad (29)$$

This gives us for an estimate of n_α.

$$n^*_{\alpha i}=\sum_i C_i P^*(\alpha/i)=\sum_i C_i\frac{m_{\alpha i}}{m_{.i}} \quad \text{. .} \quad (30)$$

TABLE 3.—*Data from a tagging experiment on migrating adult sockeye salmon*

	Week of tagging (α)								Total tagged fish recovered	Total fish recovered	$C_i/m_{\cdot i}$
	1	2	3	4	5	6	7	8			
Week of recovery (i):									$m_{\cdot i}$	C_i	
1	1	1	1						3	19	6.33
2		3	11	5					19	132	6.95
3	2	7	33	29	11				82	800	9.76
4			24	79	67	14			184	2,848	15.48
5			5	52	77	25			159	3,476	21.86
6			1	3	2	3			9	644	71.56
7				2	16	10	1	1	30	1,247	41.57
8			1	7	7	6	5		26	930	35.77
9				3	3	2			8	376	47.00
Total tagged fish recovered $m_{\alpha\cdot}$	3	11	76	180	183	60	6	1	520		
Total fish tagged T_α	15	59	410	695	773	335	59	5			
$T_\alpha/m_{\alpha\cdot}$	5.00	5.36	5.39	3.86	4.22	5.58	9.83	5.00			

$\Sigma C_i = 10{,}472$.
$\Sigma T_\alpha = 2{,}351$.

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

$$N^* = \sum_\alpha \frac{n^*_{\alpha i}}{q^*_\alpha} \quad \text{. . . . .} \quad (31)$$

we have, then,

$$N^* = \sum_\alpha \sum_i C_i \frac{m_{\alpha i}}{m_{\cdot i}} \frac{T_\alpha}{m_{\alpha.}} \quad \text{. . . . .} \quad (32)$$

which is the same result as obtained in formula 25.

Application of this method of population estimation may be illustrated by the data from a tagging experiment conducted by me on a migrating population of adult sockeye salmon in British Columbia. A total of 2,351 fish were tagged in a certain river, on the way to their spawning grounds, over an 8-week period. Later, tag-ratio samples were drawn regularly over a 9-week period as the fish spawned and died on the spawning grounds farther upstream: 10,472 fish, of which 520 had been tagged, were recovered in these samples. In table 3 are tabulated, in the same form as the table on page 200, tag recoveries by week of tagging and week of recovery, with data on total numbers tagged and recovered for each week. From these data are computed values of $T_\alpha/m_{\alpha.}$ and $C_i/m_{.i}$ tabulated along the margins. From these computed values and the tag-recovery data tabulated in the body of the table has been computed the estimate of the population, as shown in table 4, according to formulae 24 and 25 (or 32). The values in the body of this table are values of $n^*_{\alpha i} = m_{\alpha i} \frac{T_\alpha}{m_{\alpha.}} \frac{C_i}{m_{.i}}$ which sum to the estimate of N, 47,860 fish.

TABLE 4.—*Computation of population estimate by formulae 24 and 25 from the data of table 3*

	Week of tagging (α)								Total
	1	2	3	4	5	6	7	8	
Week of recovery (i):									
1	32	34	34						100
2		112	412	134					658
3	98	366	1,736	1,093	453				3,746
4			2,002	4,720	4,377	1,209			12,308
5			589	4,388	7,103	3,049			15,129
6			386	829	604	1,198			3,017
7				321	2,807	2,320	409	208	6,065
8			193	967	1,057	1,198	1,758		5,173
9				544	595	525			1,664
Total	130	512	5,352	12,996	16,996	9,499	2,167	208	47,860

From formula 25 (or 32) it may be seen that where the tagging or the sampling is uniform, this estimate reverts to the simple case first discussed. For, if the probability of being tagged is constant for all i, the expected value of $\frac{C_i}{m_{\cdot i}} = \frac{n}{m_{\cdot\cdot}}$, a constant. Then,

$$N^* = \sum_\alpha \sum_i m_{\alpha i} \frac{T_\alpha}{m_{\alpha\cdot}} \frac{n}{m_{\cdot\cdot}} = \frac{T_n}{m_{..}} \quad \text{. . .} \quad (33)$$

which is identical with formula 1 since $m_{..} \equiv t$ in formula 1.

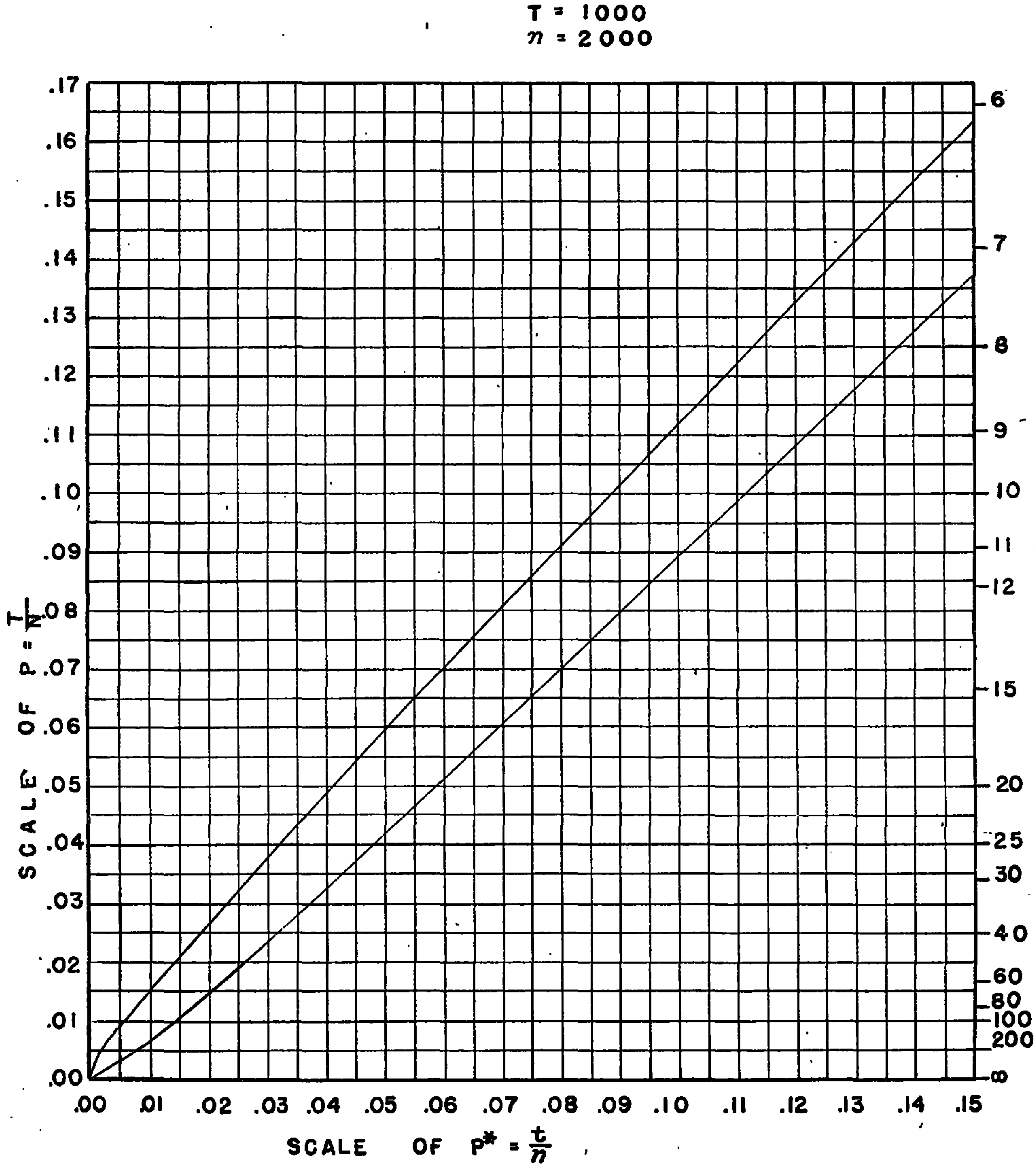
Likewise, if the probability of being recovered is constant, the expected value of $\frac{T_\alpha}{m_{\alpha i}}$ is $\frac{T}{m_{..}}$, a constant. Then,

$$N^* = \sum_\alpha \sum_i m_{\alpha i} \frac{C_i}{m_{.i}} \frac{T}{m_{..}} = \frac{T_n}{m_{..}} \quad \text{. . . .} \quad (34)$$

The tagging experiment illustrated in table 3 is a practical situation of this sort. Although the probability of a fish being recovered, estimated from $C_i/m_{.i}$, changed very much during the course of the season, the probability of being tagged, judged from T_α/m_α. was fairly even over most of the season. In consequence, the estimate from the simple formula (1)

$$N=\frac{(10,472)\,(2,351)}{520}=47,345$$

is practically identical with the estimate from formula 25 (or 32).



Confidence limits on sample tag ratios and on estimated population numbers, at a confidence level of 95 percent, for experiments involving 1,000 tagged individuals and samples of 2,000.

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