

ESTIMATING POPULATION PARAMETERS FROM CATCHES LARGE RELATIVE TO THE POPULATION

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INTRODUCTION

The estimation of the size and other parameters of populations of animals has long been a central problem for ecologists and several different methods have been used that mostly fall into two categories, (a) mark-recapture experiments (e.g. De Lury 1958; Parker 1963; Seber 1965), and (b) the effect on the population of catches of random size but known effort (e.g. Leslie & Davis 1939; De Lury 1947; Beverton & Holt 1957; Ricker 1958; and many others)—Zippin (1956, 1958) calls this the removal method. The aim of the following paper is to investigate the removal method more fully and, in particular, to consider its application to situations in which it is possible to catch a significant proportion of the population present (see, for example, Junge & Libosvářský 1965).

The method was developed for estimating fish populations in small rivers where capture by electricity was easy but where marking experiments had drawbacks. The method may, however, be found to be useful in quite different situations where it could, for example, provide a check on mark-recapture methods and perhaps in the sorting of animals out of samples of mud, soil or grain. The paper is written throughout in terms that are used in fishing as not only are there few suitable alternatives in non-technical language, but previous work in this subject has been pioneered mostly by fishery biologists.

A description of the method of calculating population size from two catches is first presented, followed by the estimation of its variance, the verification of the method by several repeated catches and the information available from single catches. The estimation of mortality rates from successive population estimates and combined catch and mark-recapture experiments are also discussed. The methods described are illustrated with examples taken from actual fishing experiments. In these examples most numbers are written to just one or two decimal places for simplicity.

THE TWO-CATCH METHOD

The usual Leslie (or De Lury) estimates of total original populations depend upon a large series of data on catch and fishing effort; each individual unit of fishing effort has, by itself, little effect upon the population and is considered to be independent of the others. The errors are considered to be of the Poisson type and population estimates are usually made by fitting a regression line to data of catch-per-unit-effort plotted against accumulated catch (Ricker 1958). Where the individual fishings catch a significant proportion of the population, however, binomial statistics are more appropriate.

Let n = the population size to be estimated (before any fishing), c_1 = the catch taken by the first fishing, c_2 = the second catch, $p = (1 - q)$ = the probability that any one fish is caught (assumed to be the same for both catches), then the joint probability distribution of c_1 and c_2 is given by

$$P[c_1, c_2] = \frac{n!}{c_1! c_2! (n - c_1 - c_2)!} p^{c_1} (qp)^{c_2} (q^2)^{n - c_1 - c_2}$$

By equating c_1 and c_2 with their expected values we obtain the moment estimates

$$\bar{n} = c_1^2 / (c_1 - c_2) \quad \text{and} \quad \bar{p} = (c_1 - c_2) / c_1$$

We note that these are also the maximum likelihood estimates. The means and variances of these estimates can be found using a Taylor expansion, i.e. the so-called δ -method (cf. Darroch 1958, p. 347) or, alternatively, from asymptotic maximum likelihood theory (Zippin 1956, p. 169) and are approximately given by

$$\begin{aligned} E[\bar{n}] &= n + q(1+q)/p^3 = n + b \\ \text{var}[\bar{n}] &= nq^2(1+q)/p^3 + 2q(1-p^2-q^3)/p^5 - b^2 \end{aligned} \quad (2.1)$$

and

$$\begin{aligned} E[\bar{p}] &= p \\ \text{var}[\bar{p}] &= q(1+q)/np \end{aligned}$$

The above variances can be estimated by simply replacing n and p by their estimates. Alternatively it may be easier and more accurate in practice to use the original catch data. Thus

$$\bar{n}\bar{q}^2(1+\bar{q})/\bar{p}^3 = \frac{c_1^2 c_2^2 (c_1 + c_2)}{(c_1 - c_2)^4} \quad (2.2)$$

Second-order terms have been included in $E[\bar{n}]$ and $\text{var}[\bar{n}]$ so that the validity of the large sample approximations can be checked; as a rough rule, the approximations are usually satisfactory if $np^3 > 16q^2(1+q)$. By a simulation method using random numbers and tables of binomial variables, Zippin (1956) showed that \bar{n} is approximately normal and therefore a confidence interval for n can be easily calculated.

For example (Example 1) two successive electric fishings in a section of a small stream yielded seventy-nine and twenty-eight young trout respectively. The population can be estimated as

$$\bar{n} = 79^2 / (79 - 28) = 122,$$

with

$$\bar{q} = 28/79 = 0.35 \quad \text{and} \quad \bar{p} = 0.65$$

Then the variance of the population estimate of 122 is

$$\begin{aligned} \text{var}[\bar{n}] &= 122 \times 0.35^2 \times 1.35 / 0.65^3 \\ &= 77.4 \end{aligned}$$

or, using the equation (2.2),

$$\begin{aligned} \text{var}[\bar{n}] &= \frac{79^2 \times 28^2 \times 107}{51^4} \\ &= 77.4 \end{aligned}$$

and the standard error $SE[\bar{n}] = 8.8$ giving a 95% confidence limit as 122 ± 18 or (104, 140). We note that $\bar{n}\bar{p}^3 = 33 \gg 2.6 = 16q^2(1+q)$ and the bias b is estimated by $0.35 \times 1.35 / 0.65^3$ or roughly 2. The first of the second-order terms in $\text{var}[\bar{n}]$ is estimated by

$$2\bar{q}(1-\bar{p}^2-\bar{q}^3)/\bar{p}^5 = 3.2$$

which is small and is almost cancelled out by b^2 . When $b/SE(\tau) > 0.1$, as is the case here,

it is advisable to allow for this bias in the confidence interval (Cochran 1963, § 1.7) Thus in the above example the final confidence interval would be 120 ± 18 .

The above method depends upon the following conditions:

- (a) that p is large enough to have a significant effect upon n ,
- (b) that p is constant, or, in other words, that the fishing effort is the same for the two catches and the fish remaining after the first fishing are as vulnerable to capture as were those that were caught in the first fishing,
- (c) that there is no recruitment, mortality, immigration or emigration between the times of the two fishings, and
- (d) that the first catch is removed from the population or, if returned alive, the individuals are marked so that they can be ignored in counting the second catch.

In electrical fishing, it is possible that p may vary with the size of fish as it is well known that large fish are influenced more strongly by the electric current than small ones. However, as demonstrated by Junge & Libovárský (1965), the bias in the estimate of the total population size due to this gear selectivity will be small if p is large, e.g. $p > \frac{1}{2}$.

MULTIPLE CATCHES AND THE VERIFICATION OF THE CONSISTENCY OF p

If only two fishings are made, it is impossible to verify the assumption that $p_1 = p_2$. However, if more than two catches are taken, e.g. s catches c_1, c_2, \dots, c_s , then there are three methods available for testing the hypothesis $p_1 = p_2 = \dots = p_s = p$, say.

The first method is basically the Leslie-De Lury method; each catch c_i is plotted against the sum of all previous catches,

$$\sum_{j=1}^{i-1} c_j$$

If the points lie on a straight line, p is consistent. This graph also provides a method for estimating the total population, as the abscissa will be cut by the line at a value of x which is the total population. (Alternatively each catch is plotted against the sum of it and all subsequent catches, and the abscissa will be cut at $-x$ which is the difference between the sum of the catches and the total population.)

The second method is that given by Zippin (1956) and it involves calculating a χ^2 goodness of fit test statistic in which n is replaced by its maximum likelihood estimate \tilde{n} . For s catches, \tilde{n} is a root of a polynomial of degree $s-1$ and Zippin gives graphs for the rapid calculation of \tilde{p} and \tilde{n} . It can be readily shown that these estimates are unique.

A third method is available, since it is often possible to catch the whole population in a finite number of fishings, especially when p is large, and thus n becomes known. Even if not quite all the individuals in the population have been caught the number remaining can be estimated by the graphical method described under the first method above; this will give a value of n accurate to 1 or 2%, if all but 1 or 2% of the individuals have been caught. If n is known, a straight-forward goodness of fit test can be calculated on the first K catches. For catches c_1, c_2, \dots, c_K the maximum likelihood estimate for p is given by Zippin 1956, p. 165.

$$\tilde{p} = r/(Kn-X) \quad (3.1)$$

where

$$r = \sum_{i=1}^K c_i$$

the total catch, and

$$X = \sum_{i=1}^K x_i$$

where

$$x_i = \sum_{j=1}^{i-1} c_j$$

the total number captured prior to the i th catch. The χ^2 goodness of fit statistic is simply

$$T_1 = \sum_{i=1}^K (c_i - E_i)^2 / E_i + (n - r - E_{K+1})^2 / E_{K+1}$$

where $E_i = n\tilde{q}^{i-1}\tilde{p}$ for $i = 1, 2, \dots, K$ and $E_{K+1} = n\tilde{q}^K$. The statistic T_1 is distributed asymptotically as χ^2 with $K-1$ degrees of freedom when the hypothesis that p is constant is true.

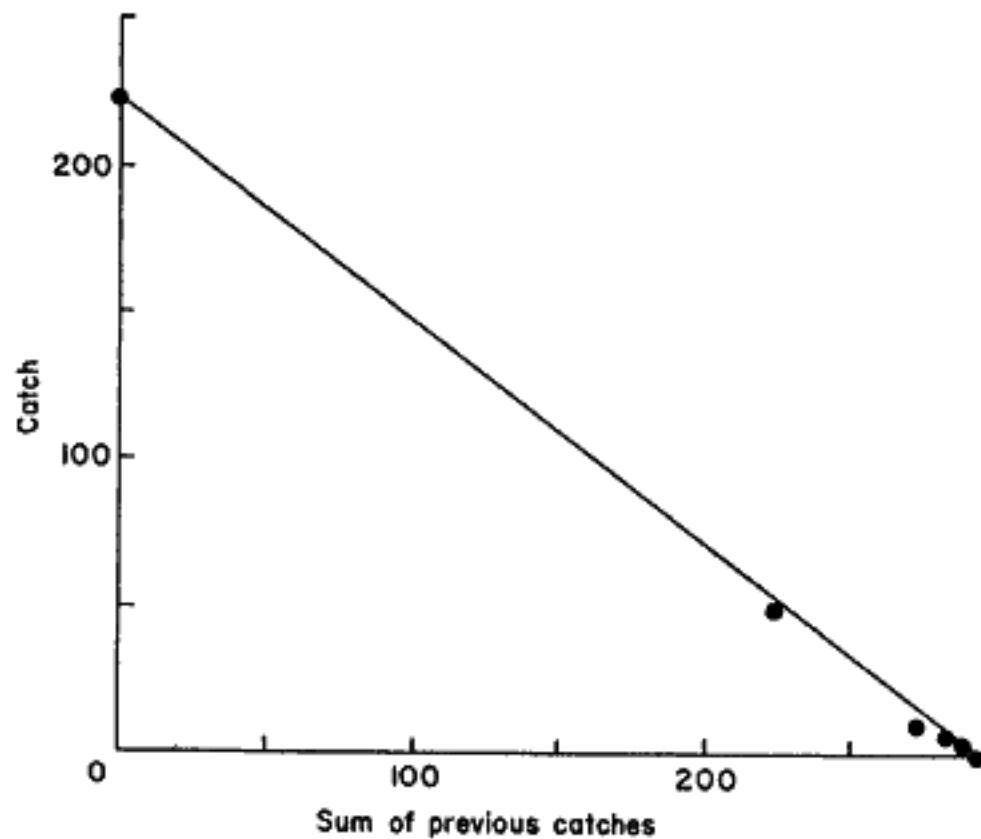


FIG. 1. A graph of successive catches (c_i) against the sum of all previous catches (x_i). The line was drawn by eye and cuts the abscissa at $x = 294$.

As an example (Example 3) of the above method, we take the results of seven successive fishings of a reach of a stream to remove the survivors of an experimental population of young trout. The catches made were successively: 224, 49, 11, 6, 4, 0 and 0. The catches were plotted against the sums of all preceding catches in Fig. 1. It will be seen that a reasonably straight line results, though the second and third points are a little below the line and if only four fishings had been made, a line drawn by eye through the plot would have indicated a population of about 287, though 294 fish were eventually caught. The calculation of T_1 is shown in Table 1 with $K = 4$. Here $T_1 = 6.28$ which is just significant at 10%.

For n known the above χ^2 test would be more powerful than Zippin's test in which one degree of freedom is used for estimating n . We note also that it is not necessary to remove the catches completely from the population—one could use a simple marking procedure in which the unmarked or untagged fish in each catch are marked before returning the whole catch to the population.

When several different populations are being fished, both methods can be generalized for constant p *between* populations as well as for constant p *within* populations. Suppose we have m populations with known sizes n_i ($i = 1, 2, \dots, m$). Let

$$\begin{aligned} K_i &= \text{number of catches used from the } i\text{th population,} \\ c_{ij} &= \text{size of the } j\text{th catch in the } i\text{th population } (j = 1, 2, \dots, K_i), \\ p_{ij} &= \text{probability that a fish in the } i\text{th population is caught in the } j\text{th catch,} \\ r_i &= \sum_{j=1}^{K_i} c_{ij}, \text{ the total number caught in the } i\text{th population,} \\ X_i &= \text{value of } X \text{ for the } i\text{th population (see above for definition) and} \\ \bar{p} &= \sum_{i=1}^m r_i / \sum_{i=1}^m (K_i n_i - X_i). \end{aligned} \quad (3.2)$$

To test the hypothesis that $p_{ij} = P$, we simply calculate an overall estimate \bar{p} by 'pooling' the data (as seen in the above equation), then using this value, the expected catches for each fishing in each population are calculated and the final goodness of fit statistic T_2

Table 1. Calculations to test the consistency of p in a repeated-catch experiment (Example 3)

$K = 4$							
i	c_i	x_i	\bar{q}^{i-1}	$n\bar{q}^{i-1}$	E_i	$ c_i - E_i $	$(c_i - E_i)^2/E_i$
1	224	0	1	294	215.8548	8.1452	0.3073
2	49	224	0.2658	78.1452	57.3742	8.3742	1.2222
3	11	273	0.07065	20.7711	15.2501	4.2501	1.1184
4	6	284	0.01878	5.5213	4.0537	4.4787	3.6329
(5)	4	—	0.004992	1.4676	1.4676		
(6)	0	781					
(7)	0	—					
	294				294.0004		6.2808

$$n = 294; r = 290; \bar{p} = 290/(1176 - 781) = 290/395 = 0.7342; q = 0.2658; T_2 = 6.28.$$

is the sum of the separate goodness of fit statistics from each population. When the hypothesis is true, T_2 will be asymptotically distributed as χ^2 with $\left(\sum_{i=1}^m K_i\right) - 1$ degrees of freedom. We note that if some of the expected catches are less than 5 we may need to pool some of the c_{ij} . This was found to be the case in Table 1 where catch 4 and those uncaught were pooled (see Addendum 1).

POPULATION ESTIMATION FROM SINGLE CATCHES

If p ($= 1/\theta$) has been estimated from a two catch experiment for a population of size n and it is known to have the same value for other populations (or perhaps different areas of the same population), then its estimate \bar{p} can be used to estimate the population size from a single fishing. If N = the population to be estimated and C = the single catch, then the estimate of N is

$$\tilde{N} = C/\bar{p} = C\bar{\theta} \text{ say}$$

As C is asymptotically normally distributed and \bar{p} is a consistent estimate of p , it is

reasonable to assume (Cramér, 1945, § 20.6) that \tilde{N} is asymptotically normal. By the δ -method we have asymptotically

$$\begin{aligned} E[\tilde{\theta}] &= \theta + 2q/np^4 \\ E[(\tilde{\theta} - \theta)^2] &= q(1+q)/np^5 \end{aligned}$$

leading to the approximate formulae

$$E[\tilde{N}] = N + 2qN/np^3$$

and, from equation (4.1), (see below)

$$\text{var}[\tilde{N}] = N^2q(1+q)/np^3 + Nq/p + Nq^2(5+q)/np^4$$

Once again we estimate the bias and $\text{var}[\tilde{N}]$ by replacing N , n and p by their estimates.

Example 2. A fishing in a similar section of the same stream as Example 1 gave a catch of 111 trout. Thus

$$\tilde{N} = 111/0.65 = 171$$

with a bias of 4.

The 95% confidence limits for N are given by $167 \pm 2 \times \text{SE}[\tilde{N}]$ where

$$\begin{aligned} \text{SE}[\tilde{N}]^2 &= 171^2 \times 0.35 \times 1.35/122 \times 0.65^3 + 171 \times 0.35/0.65 + 171 \times 0.35^2 \times 5.35/122 \times 0.65^4 \\ &= 415.7 + 94.4 + 5.4 \\ &= 515.5 \end{aligned}$$

Thus the confidence limits are 167 ± 46 or (121, 213).

We note that the estimate \tilde{N} is not very accurate because of the wide confidence interval. Unfortunately nothing can be done about this without obtaining additional information on p as it follows from the maximum likelihood theory that $\tilde{\theta}$ is asymptotically the most efficient estimate of θ , i.e. asymptotically it is the best estimate we can get from just two previous catches. The reason for the wide confidence interval can be seen roughly as follows. Considering C as a measure of Np , the percentage error in the estimate is $200 \times \text{SE}(C)/E(C)$ which is estimated by $200 \sqrt{(q/C)}$, i.e. approximately 10%. Similarly the percentage error in $\tilde{\theta}$ as an estimate of θ is of the order of 15%. Since C and $\tilde{\theta}$ are independent, the percentage error in the product \tilde{N} is roughly $10 + 15 = 25\%$.

At this point it is of practical interest to consider ways of obtaining more accurate estimates of θ by utilizing additional information, as for example from multiple-catch experiments or different experiments with similar p values. If $\hat{\theta}$ is such an estimate of θ and $N = C\hat{\theta}$ then

$$\begin{aligned} E[\hat{N}] &= NpE[\hat{\theta}] \\ &= N + NpE[\hat{\theta} - \theta] \end{aligned}$$

and

$$\text{var}[\hat{N}] = N^2p^2 \text{var}[\hat{\theta}] + Nq/p + Nq[pE[(\hat{\theta} - \theta)^2] + 2E[\hat{\theta} - \theta]] \quad (4.1)$$

which is approximately

$$(N^2p^2 + Npq)E[(\hat{\theta} - \theta)^2] + Nq/p$$

We shall now briefly consider various alternatives for $\hat{\theta}$. If we estimate p from a multiple catch experiment then from equation (3.1)

$$\hat{\theta}_1 = (Kn - X)/r$$

and using asymptotic maximum likelihood theory (n known) we have

$$\begin{aligned} E[(\hat{\theta}_1 - \theta)^2] &= \left\{ -E \left[\frac{\partial^2 \log(\text{likelihood})}{\partial \theta^2} \right] \right\}^{-1} \\ &= q/np^2(1 - q^K) \end{aligned}$$

If we use several multiple catch experiments (say m for example) then we can use either the pooled estimate (cf. equation 3.2)

$$\hat{\theta}_2 = \frac{\sum_{i=1}^m (K_i n_i - X_i)}{\sum_{i=1}^m r_i}$$

or the average estimate

$$\hat{\theta}_3 = m^{-1} \sum_{i=1}^m \{(K_i n_i - X_i)/r_i\}$$

where

$$E[(\hat{\theta}_2 - \theta)^2] = q \left/ \sum_{i=1}^m \{n_i p^2 (1 - q^{K_i})\} \right.$$

and

$$E[(\hat{\theta}_3 - \theta)^2] = \sum_{i=1}^m \{q/n_i p^2 (1 - q^{K_i}) m^2\}$$

In some situations, however, p could vary within each multiple catch series and yet remain constant as far as the first catch of each series is concerned (one-catch fishings included). One of the authors (Le Cren) had an example of this when a series of six successive catches spread over 3 days gave catches for eels that were obviously too large in the afternoons and too small in the mornings, i.e. p_1, p_3 and p_5 were below expectation and p_2, p_4 and p_6 above expectation. The opposite phenomenon could occur when fish became wary as a result of the morning fishing. In such cases one might have data from a series of multiple catch experiments, each of which estimated n fairly accurately (by eventually removing nearly all the fish) but in each of which only p_1 could be regarded as constant. Let us for a moment consider such a single catch. The usual estimate for p_1 could be c_1/n and we consider

$$\hat{\theta}_4 = (n+1)/(c_1+1)$$

which is an almost unbiased estimate of θ .

Then

$$E[\hat{\theta}_4] = \theta(1 - q_1^{n+1})$$

and

$$E[(\hat{\theta}_4 - \theta)^2] = n p_1 q_1 (n+1)^2 / (n p_1 + 1)^4$$

Utilizing several such experiments (say m) we would obtain m such estimates $\hat{\theta}_{5i}$ and estimate θ by the average

$$\hat{\theta}_5 = \sum_{i=1}^m \hat{\theta}_{5i} / m$$

for which

$$E[(\hat{\theta}_5 - \theta)^2] = \sum_{i=1}^m \{n_i p_1 q_1 (n_i + 1)^2 / (n_i p_1 + 1)^4 m^2\}$$

Thus we see that if m such estimates of θ are averaged the $SE[\tilde{N}]$ is reduced by roughly a factor of $1/\sqrt{m}$.

Finally, if we have a number of estimates $\hat{\theta}_{bi}$ from different experiments the weighted average

$$\hat{\theta}_b = \frac{\sum_i w_i \hat{\theta}_{bi}}{\sum_i w_i}$$

where

$$w_i = \{E[(\hat{\theta}_{bi} - \theta)^2]\}^{-1}$$

has the smallest variance of all linear combinations $\sum_i d_i \hat{\theta}_{bi}$ ($\sum d_i = 1$) including the usual unweighted average. We then have asymptotically

$$E[(\hat{\theta}_b - \theta)^2] = (\sum_i w_i)^{-1}$$

This method can be used to improve on the estimates $\hat{\theta}_3$ and $\hat{\theta}_5$.

THE ESTIMATION OF NATURAL MORTALITY COEFFICIENTS

Estimates of population sizes are rarely ends in themselves and are frequently used in ecology for the study of changes in population numbers. The most important of such changes is often the decrease in a population with time, or mortality; emigration may be considered similar to mortality in this context.

An estimate of the natural mortality coefficient can be found from two-catch data, as follows. Assuming that the survival is Poisson with parameter M , then the probability of surviving for time t is $\phi = \exp\{-Mt\}$. This can be compared with the deterministic model by equating the actual size N_t of the population at time t with its expected value, i.e. $N_t = N_0 \phi = N_0 \exp\{-Mt\}$.

Suppose we carry out two two-sample fishing experiments separated by a time t with N_0 and N_t respectively being the sizes of the populations before each experiment. Let c_1, c_2, c_3 and c_4 be the respective catches and let p_1 and p_2 represent the probabilities of capture for the two experiments; it is assumed that there is no immigration, emigration or birth throughout the whole period. Also after the first experiment the total catch $c_1 + c_2 - d$ is returned to the population; d being the number which die accidentally through handling, etc. Then

$$\tilde{q}_1 = c_2/c_1, \tilde{q}_2 = c_4/c_3$$

$$\tilde{N}_0 = c_1^2/(c_1 - c_2)$$

$$\tilde{N}_t = c_3^2/(c_3 - c_4)$$

and ϕ the fraction surviving at time t is estimated by

$$\tilde{\phi} = \tilde{N}_t/(\tilde{N}_0 - d)$$

Using the δ -method we have approximately (using equation (2.1))

$$E[\tilde{\phi}] = \phi$$

$$\text{var}[\tilde{\phi}] = \frac{N_0 q_1^2 (1 + q_1) \phi^2}{p_1^3 (N_0 - d)^2} + \frac{N_t q_2^2 (1 + q_2)}{p_2^3 (N_0 - d)^2}$$

For example (Example 4) the following catches were observed: 91, 54, 53 and 12 ($d = 0$).

Thus

$$\tilde{q}_1 = 54/91 = 0.59$$

$$\tilde{q}_2 = 12/53 = 0.23$$

$$\tilde{N}_0 = 91^2/37 = 233$$

$$\tilde{N}_t = 53^2/41 = 69$$

and

$$\tilde{\phi} = \frac{53^2 \times 37}{91^2 \times 41} = 0.31$$

Also $\text{var}[\tilde{\phi}] = 0.0037$ and the asymptotic confidence interval for ϕ is 0.31 ± 0.12 .

To obtain a confidence interval for M , the natural mortality coefficient, we note that $\tilde{M} = -(1/t) \log_e \tilde{\phi}$ and we have approximately that $E[\tilde{M}] = M$ and

$$\begin{aligned}\text{var}[\tilde{M}] &= \text{var}[\tilde{\phi}] (dM/d\phi)^2 \\ &= \text{var}[\tilde{\phi}] / t^2 \phi^2\end{aligned}$$

Another parameter of interest is the (mean) survival rate or (mean) fraction surviving, namely

$$\begin{aligned}\tilde{S} &= \exp(-\tilde{M}) \\ &= \tilde{\phi}^{1/t}\end{aligned}$$

for which

$$\text{var}[\tilde{S}] = \text{var}[\tilde{\phi}] S^2 / t^2 \phi^2$$

If $p_1 = p_2 = p$ the joint distribution of the catches becomes

$$P[c_1, c_2, c_3, c_4] = \frac{N_0! N_t!}{\prod_i c_i! (N_0 - c_1 - c_2)! (N_t - c_3 - c_4)!} \times p^{c_1 + c_3} (qp)^{c_2 + c_4} (q^2)^{N_0 + N_t - R}$$

where $R = c_1 + c_2 + c_3 + c_4$. The maximum likelihood estimates of the unknown parameters are given by

$$\begin{aligned}\hat{q} &= (c_2 + c_4) / (c_1 + c_3) \\ \hat{N}_0 &= (c_1 + c_2) / (1 - \hat{q}^2) \\ \hat{N}_t &= (c_3 + c_4) / (1 - \hat{q}^2)\end{aligned}$$

and

$$\hat{\phi} = \hat{N}_t / (\hat{N}_0 - d)$$

In calculating the variance of $\hat{\phi}$ we shall neglect the losses d . Thus we have approximately

$$E[\hat{\phi}] = \phi$$

and

$$\begin{aligned}\text{var}[\hat{\phi}] &= \text{var}[\hat{N}_t / \hat{N}_0] \\ &= \text{var}[(c_3 + c_4) / (c_1 + c_2)] \\ &= q^2 N_t (N_0 + N_t) / N_0^3 (1 - q^2)\end{aligned}$$

If we can assume $p_1 = p_2$ we would expect intuitively that the estimate of ϕ for this model would have a smaller variance than that obtained from the model with $p_1 \neq p_2$, since the information from the catches is shared among fewer parameters, i.e. we would expect $\text{var}[\hat{\phi}] < \text{var}[\tilde{\phi}]$.

One could test the hypothesis that $p_1 = p_2$ by simply using the large sample normal approximation to the binomial distribution as follows. From p. 632, \tilde{p}_1 is asymptotically normally distributed with mean p_1 and variance estimated by

$$\tilde{q}_1 (1 + \tilde{q}_1) / \tilde{N}_0 \tilde{p}_1 = c_2 (c_1 + c_2) / c_1^3$$

Therefore since \tilde{p}_1 and \tilde{p}_2 are statistically independent $(\tilde{p}_2 - \tilde{p}_1)$ is asymptotically normally distributed with mean $(p_2 - p_1)$ and variance

$$c_2 (c_1 + c_2) / c_1^3 + c_4 (c_3 + c_4) / c_3^3$$

and a confidence interval for $(p_1 - p_2)$ can be constructed. Using the data of Example 4

$$\begin{aligned}\tilde{p}_2 - \tilde{p}_1 &= 0.3670 \\ \text{var}[\tilde{p}_2 - \tilde{p}_1] &= 0.0156\end{aligned}$$

and the confidence interval is 0.37 ± 0.26 . As this interval does not contain zero we reject the hypothesis that $p_1 = p_2$ at the 5% level of significance.

Finally, for completeness, we shall consider one further situation which is of lesser importance especially when p is large. Suppose that the catches c_1 and c_2 are not returned to the population after the first experiment. The probability density function is now given by

$$P[c_1, c_2, c_3, c_4] = \frac{n!}{\prod_i c_i! (n-R)!} p_1^{c_1} (q_1 p_1)^{c_2} (q_1^2 \phi p_2)^{c_3} (q_1^2 \phi q_2 p_2)^{c_4} \Psi^{n-R}$$

where $\Psi = q_1^2(1 - \phi(1 - q_2^2))$. Equating random variables to their expected values gives the following moment (and maximum likelihood) estimates.

$$\tilde{q}_1 = c_2/c_1, \quad \tilde{q}_2 = c_4/c_3$$

$$\tilde{n} = c_1^2/(c_1 - c_2)$$

and

$$\tilde{\phi} = c_3^2(c_1 - c_2)/c_2^2(c_3 - c_4)$$

From the δ -method we have

$$E[\tilde{\phi}] = \phi$$

$$\text{var}[\tilde{\phi}] = \phi^2 \left\{ \frac{4}{nq_1^2\phi p_2} + \frac{5}{np_1^2} + \frac{4}{np_1q_1} - \frac{3}{nq_1^2\phi p_2^2} \right\}$$

which will give us a confidence interval for ϕ .

If $p_1 = p_2 = p$ the maximum likelihood estimates now become

$$\hat{q} = (c_2 + c_4)/(c_1 + c_3)$$

$$\hat{n} = (c_1 + c_2)/(1 - \hat{q}^2)$$

$$\hat{\phi} = (c_3 + c_4)/\hat{q}^2(c_1 + c_2)$$

for which we have approximately

$$E[\hat{\phi}] = \phi$$

$$\text{var}[\hat{\phi}] = \frac{\phi^2}{npq} \left\{ \frac{1 - \phi q^2}{\phi q(1 + q)} + \frac{4(1 + q)}{(1 + \phi q^2)} \right\}$$

Once again one would expect intuitively that $\text{var}[\hat{\phi}] < \text{var}[\tilde{\phi}]$.

One can test the hypothesis that $p_1 = p_2$ by calculating a standard goodness of fit test

$$T_3 = \sum_{i=1}^4 (c_i - E_i)^2/E_i$$

where $E_1 = \hat{n}\hat{p}$, $E_2 = \hat{n}\hat{p}\hat{q}$, $E_3 = \hat{n}\hat{\phi}\hat{q}^2\hat{p}$ and $E_4 = \hat{n}\hat{\phi}\hat{q}^3\hat{p}$. Here T_3 is asymptotically distributed as χ^2 with one degree of freedom—one degree of freedom as there are four independent square terms but three parameters estimated.

MARKING EXPERIMENTS

Brief mention should be made of the use of marking in a two-catch experiment. Normally marking would be considered as an alternative to population estimation from two successive catches but the combination of the two procedures allows a test of a necessary assumption.

Suppose c_1 fish are caught in the first catch and are then all marked and returned alive to the population. Let $c_{12} + c_2$ be caught in the second catch of which c_{12} are found to be marked. Let p be the (constant) probability of catching an unmarked fish and p_0 the probability of catching a marked fish, then,

$$P[c_{12}, c_1, c_2] = \frac{n!}{c_1! c_2! (n - c_1 - c_2)!} p^{c_1 + c_2} q^{2n - 2c_1 - c_2} \binom{c_1}{c_{12}} p_0^{c_{12}} q_0^{c_1 - c_{12}}$$

The estimates \tilde{n} , \tilde{p} of n and p will be the same as on p. 632 above, and the estimate of p_0 will be c_{12}/c_1 . However, the advantage of using marked fish is that we can test the hypothesis $H: p = p_0$ which is always a difficult assumption to verify in fishing models. The reason why H can be tested here is because we assume constant probability p for the unmarked fish which gives just sufficient information for the estimation of all the unknown parameters. When H is true the maximum likelihood estimates of n and p_0 are simply

$$\hat{n} = (c_1 + c_2 + c_{12})^2 / 4c_{12}$$

and

$$\hat{p}_0 = 2c_{12} / (c_1 + c_2 + c_{12})$$

and the test statistic is

$$\begin{aligned} T_4 &= (c_1 - c_{12} - E_1)^2 / E_1 + (c_2 - E_2)^2 / E_2 \\ &= 2(c_2 - E_2)^2 / E_2 \end{aligned}$$

where $E_1 = E_2 = \hat{n}\hat{p}_0\hat{q}_0 = \frac{1}{2}(c_1 + c_2 - c_{12})$, the other terms vanish identically.

The statistic T_4 has a χ^2 distribution with one degree of freedom when H is true.

As an example (Example 5) consider the following (hypothetical) data. On the first fishing forty-nine trout were caught, marked and released alive. The next day, fifty trout were caught of which twenty-four were marked and twenty-six unmarked. Thus $c_1 = 49$, $c_{12} = 24$, $c_2 = 26$ giving

$$\begin{aligned} \hat{n} &= (49 + 26 + 24)^2 / (4 \times 24) = 102 \\ \hat{p}_0 &= 2 \times 24 / (49 + 26 + 24) = 0.4848 \\ T_4 &= \frac{2(26 - 25.5)^2}{25.5} = 0.020 \end{aligned}$$

This value of T_4 lies between the 10% and 25% points of χ_1^2 . By the two-catch method alone (if the marked fish had not been returned) $\tilde{n} = 49^2 / (49 - 26) = 104$ with a standard error of 20. By Bailey's (1952) mark-recapture method for small samples $n = 49 \times 51 / 25 = 100$ with a standard error of 14. It will be noticed that the standard error of the mark-recapture method is lower than that of the two-catch method and this will always be the case though the difference may not be very large.

Suppose we take a second example (Example 6) in which $c_1 = 27$, $c_{12} = 10$, $c_2 = 20$, then $\hat{n} = 81$, $\hat{p}_0 = 0.3508$ and $T_4 = 0.24$ which lies between the 25% and 50% points of χ_1^2 . By the two-catch method $\tilde{n} = 104$ and $\tilde{p} = 0.259$ but as $\tilde{n}\tilde{p}^3 < 2$ the asymptotic formulae for the bias and variance of \tilde{n} are no longer valid. In fact the formula for the bias gives a value of 74! One of the authors hopes to give a more robust method of obtaining a confidence interval for n in a later paper.

DISCUSSION

The choice of method of estimating an animal population will usually depend upon practical considerations rather than statistical efficiency, though the latter may be taken

into account. The exploration of the present method arose because the introduction of electric fishing enabled large proportions of the total populations of stream fish to be caught quite easily. There are other methods of fishing that in small confined habitats may catch a significant part of the population and there are doubtless other animal populations where the method might be applied. It could, for example, be used to reduce the time spent in sorting soil, litter, mud or grain samples, by recording the animals sorted out in two successive relatively short periods of time.

The number of fishings carried out for each estimation can be adapted to the accuracy required on that occasion. In investigations on stream fish normally one fishing sufficed, with two fishings periodically and occasional series of four or five fishings to check the reliability of the method.

In some situations marking experiments would be preferred, especially where they could provide information on other aspects of the populations being studied, such as migration. The data from marking experiments can, however, be used in the form of two repeated-catch experiments and this can provide a check on the reliability of the marking method, especially such factors as the comparative survival and susceptibility to capture of marked animals. The two-catch method could be particularly useful where marking is difficult, time-consuming or likely to introduce bias. Although, under ideal conditions, a marking experiment will produce a population estimate with a smaller standard error, in practice the possibilities of marked animals being affected by the marking may make a two-catch estimate more reliable.

Elaborations of the two-catch method are obvious. For instance, it cannot be assumed that all species present, or all sizes or sexes of any one species will be equally liable to capture and have the same value for p ; stratified counting of the catches is thus wise.

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SUMMARY

Where two successive catches, c_1 and c_2 are taken with the same effort from a population, an estimate of the size of the population, \tilde{n} , is given by

$$\tilde{n} = c_1^2 / (c_1 - c_2),$$

with a variance

$$\text{var} [\tilde{n}] = [c_1^2 c_2^2 (c_1 + c_2)] / (c_1 - c_2)^4$$

Estimates from more than two successive catches, from single catches and of mortality rates are discussed and formulae given. Simple mark-recapture experiments can be combined with repeated catch experiments.

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ADDENDA

1. Usually it would be more appropriate to test the hypothesis that $p_{ij} = P$ (see p. 635) given constant p within populations using T_2 minus the sum of the values of T_1 for each population. When the hypothesis is true this statistic is asymptotically χ^2 with $(m-1)$ degrees of freedom.

2. Nees, Helm & Threinen (1957) noted that $n = c_1^2 / (c_1 - c_2)$ and compared some field estimates of fish populations using this formula with those obtained from mark-recapture experiments but did not elaborate the statistics of the repeated catch method.

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