International Council for the
Exploration of the Sea

C.M.1963
Symposium on the Measurement
of Abundance of Fish Stocks
No.12

A Review of Methods of Estimating Population Size from Marking Experiments

by

R. Jones
Marine Laboratory, Aberdeen

Introduction

Marking experiments can provide a means of estimating population size in a variety of situations, and these can for convenience be classified in the following way:

1. Situations in which marked animals suffer the same mortality as the unmarked population, both at the time of marking and subsequently. A number of theoretical models have been developed to deal with this type of situation and these can be sub-divided into those that take account of multiple recaptures and those that do not. By "multiple recaptures" is meant the repeated recapture of the same individuals. Multiple recapture models therefore cater for situations where the rate of recapture is comparatively high, while "single recapture" models are more appropriate when the rate of return is low, or when recaptured individuals are not returned to the population.

2. Situations in which marked animals suffer greater mortality than unmarked ones. In these situations, recapture data can sometimes be used for determining either instantaneous total or fishing mortality rates. Given one of these, estimates of population size can then be obtained for a range of values of the other. Two situations of importance occur:-

   (a) When there is mortality due to marking but at the time of marking only. If this happens it is possible to determine an instantaneous total mortality rate, but not an instantaneous fishing mortality rate. Similarly, if there is incomplete reporting of tags, it is still possible to determine a total mortality rate from the decline in the rate of return of marked animals.

   (b) When there is mortality due to marking, but over a period subsequent to the marking operation only. In this situation it is possible to determine an instantaneous mortality rate due to fishing, but not one due to all causes.

Situations in which marked and unmarked animals undergo the same mortality.

A. No account taken of multiple recaptures.

Petersen Method.

The simplest method, which is known as the Petersen or Lincoln Index method consists of marking animals on one occasion, and sampling for recaptures on a single occasion or over a single period of time. Thus, out of a population of N individuals suppose that T are marked. The probability of subsequently recapturing one of these marked individuals will depend, in the first place, on how they are distributed throughout the population and on the way in which the recapture effort is deployed. If one of these is random, the probability that a sampled animal is marked is $\frac{T}{N}$.

Out of a sample of n animals one would therefore expect to get exactly $\frac{nT}{N}$ marked ones.

If this number is denoted by m. Then

$$m = \frac{nT}{N} \text{ and, rearranging terms, one gets}$$

$$N = \frac{nT}{m} \text{ ------------------ } (1)$$

This is a first estimate of population size (N) in terms of the number marked (T), the number recaptured (m) and the number sampled (n) in the process of obtaining these recaptures. A better approximation is obtained from a model in which the number of marked animals per sample is treated as a random variate. This can be done by considering the probability distribution of numbers of marked animals out of a sample of size n and this is the approach used by Bailey (1951), Chapman (1951) and Schaefer (1951). Bailey showed that although the ratio $\frac{m}{nT}$ gives an unbiased estimate of 1/N, its reciprocal is not an unbiased estimate of N. To allow for this, various modifications of equation (1) have been proposed as more suitable for estimating N. These, along with their estimated variances are summarized in Table 1.

Table 1. Formulae for estimating population size (N) by the Petersen method

Reference	Type of Sampling	Estimates of	
		Population size (N)	Variance of (N)
A. Bailey, 1951	Direct	$N = \frac{Tn}{m}$	$\text{var } N = \frac{T^2 n (n - m)}{m^3}$
B. Bailey, 1951	Direct	$N = \frac{T (n + 1)}{m + 1}$	$\text{var } N = \frac{T^2 (n + 1) (n - m)}{(m + 1)^2 (m + 2)}$
C. Chapman, 1951	Direct	$N = \frac{(T + 1) (n + 1)}{m + 1}$	$\text{var } N = N^2 \left[\frac{N}{nT} + 2\left(\frac{N}{nT}\right)^2 + 6\left(\frac{N}{nT}\right)^3\right]$
D. Schaefer, 1951	Direct	$N = \frac{(n + 1) (T + 1)}{m + 1} - 1$	none given
E. (Bailey, 1951) (Chapman, 1952)	Inverse	$N = \frac{n (T + 1)}{m} - 1$	$\text{var } N = \frac{(T - m + 1)(N + 1)(N - T)}{m (T + 2)}$

The first of these equations (A), corresponds to (1) above and is included to show Bailey's estimate of its variance. Equations (B) - (D) correct for the bias in the basic equation.

Equations (A) - (D) are appropriate to "direct" sampling. That is sampling until a predetermined sample size (n) has been obtained. An alternative procedure known as inverse sampling is to continue sampling until a predetermined number of marked animals (m) have been recaptured. It appears (Bailey 1951; Chapman 1951) that the theory of this procedure is simpler than that of "direct" sampling and their equation for estimating N in this situation is given by (E) of Table 1.

Examples of population estimation, using the Petersen method are given by Ricker (1958), Hancock (1961), Le Cren and Kipling (1961), Sato (1938), and Simpson (1961).

A number of assumptions are implicit in the derivation of the equations in Table 1; these are as follows:-

a. The marked animals are distributed representatively throughout the whole population before any recaptures are taken.

b. The marked and unmarked animals are equally liable to capture.

c. The ratio T/N remains constant throughout the period in which recaptures are taken.

The third assumption has a number of consequences of interest. If the rate of recapture is low so that a considerable interval of time has to elapse before a reasonable proportion of the marked individuals has been recaptured, some account must be taken of mortality of emigration. This need not necessarily invalidate the equations in Table 1, however, provided one can assume that the mortality or emigration rates of marked and unmarked animals are the same. If they are, the ratio T/N should, as a first approximation, remain constant. The only danger then is that if recaptures are taken over too long a period, the equations in Table 1 may no longer provide the most efficient estimate of population size. Provided the necessary conditions can be satisfied, it may instead be better to use one of the other methods described below.

If the recapture of marked animals extends over a long enough period, it is necessary to take some account of "dilution", resulting from changes in population size due to recruitment or immigration. The effect of this will be to increase N, but not T, so that the ratio T/N will no longer remain constant, as required. The simplest way of allowing for this arises in those populations in which the recruits or immigrants can be distinguished from the remainder of the population by their size or age, or some morphological characteristic. In that case they can be recorded separately and excluded from the computations. If recruits or immigrants cannot be excluded in this way an alternative procedure due to Parker (1955) may be adopted. This is based on the fact that the effect of dilution, in causing the ratio T/N to decline, must also cause the ratio m/n, the proportion of marked individuals in a sample to decline. If then m/n, or some function of it can be plotted against time and extrapolated to the origin, an estimate will be obtained of m/n before dilution occurred. This method has been used by Hancock (1961) for estimating the size of whelk populations. Other methods of estimating rates of dilution will be referred to below.

The assumption that marked and unmarked animals are equally liable to capture is important and if it does not hold, population estimates will be biased (Carlander & Lewis, 1948; Junge 1961). Andersen & Bagge (1961) describe how plaice marked with Petersen discs became caught up in the material of meshes through which they would otherwise have escaped. Their chances of capture were thereby increased and to allow for this, a different type of tag had to be used.

Schnabel Method

The Schnabel method (Schnabel, 1938) is similar to the Petersen method except that marking as well as recapturing is done on a series of occasions. The fundamental difference is that whereas in the Petersen method the proportion of marked individuals $\left(\frac{T}{N}\right)$ is assumed constant, in the Schnabel method it is the population size (N) that is assumed constant. The number of marked individuals (T) is not constant, but increases as the experiment proceeds. Let T_i be the number of marked individuals in the population immediately prior to taking the i^{th} sample. Let this sample contain N_i individuals of which M_i are marked.

Schnabel gives the following maximum likelihood equation for estimating the population size (N).

$$\sum_i \frac{n_i T_i - m_i N}{N - T_i} = 0$$

This equation can be solved for N, the population size, by numerical methods (De Lury 1951). Alternatively some special cases of interest have been considered by Schnabel. In particular if the number of marked individuals (T_i) is negligible compared with the population size (N), the equation can be simplified to give a direct estimate of N.

$$N = \frac{\sum n_i \; T_i}{\sum \; m_i}$$

Chapman (1952) suggests that a better estimate would be

$$N = \frac{\sum n_i \; T_i}{\sum m_i + 1}$$

whilst Schumacher and Eschmeyer (1943) suggest

$$N = \frac{\sum n_i \; T_i^2}{\sum m_i \; T_i}$$

Examples of the application of this method are given by Ricker (1958), Krumholz (1944), Le Cren & Kipling (1961) and Schaefer (1951).

A method for estimating mortality as well as population size

An extension of the Schnabel method in which mortality is allowed for is given by Chapman (1954). It is assumed that marking and recapture take place on each of a series of occasions and that the survival rate is constant and the same for tagged as for untagged individuals. Using the method of maximum likelihood, a pair of equations are derived to provide estimates by numerical methods of the survival rate and of the number at the time of the first marking.

B. Account taken of multiple recaptures

Methods that take account of multiple recaptures have been described by a number of authors, and many of these accounts have been reviewed by Pope (1961). Instances of multiple recaptures do not often arise in fisheries work but examples have been described by Le Cren & Kipling (1961) for char in Lake Windermere and by Kelly & Barker (1961) for redfish in Eastport, Maine. Theoretical models that take account of multiple recaptures can differ in any of the following ways:-

a. According to whether they allow for survival and dilution rates separately, or together, or not at all.

b. According to whether individuals that have been recaptured and marked more than once are grouped, and if so, what method of grouping is used.

c. According to whether the models are deterministic, or stochastic.

A summary of some of the main papers dealing with multiple capture, recapture analysis is given in Table 2 to show which of the various combinations of treatment have been dealt with by different authors.

Table 2. Showing the scope of some of the main papers dealing with multiple recapture analysis

Author	Method of Grouping$^{x)}$	Parameters estimated			Remarks
		Survival rate	Dilution rate	Size of Population	
Bailey, 1951	earliest mark only	constant	-		Deals with Jackson's "negative" method
Bailey, 1951	earliest mark only	constant	constant		Triple catch method
Leslie & Chitty, 1951	A	constant	-	-	Discusses methods of grouping
	B	constant	-	-	
Moran, 1952	A + B	-	-	-	Discusses methods of grouping
Leslie, 1952	B	constant	variable		
Leslie	A	variable	-		
Leslie	B	variable	-		
Hammersley,1953	-	variable	-		
Darroch, 1958	-	-	-		Discusses whether sample size should be fixed or variable
Darroch, 1959	-	-	variable		
Darroch	-	variable	-		
Darroch	-	variable	variable		

$^{x)}$Methods of Grouping:- A recaptures grouped according to number of marks.
B recaptures grouped according to time since they were previously captured.

With the exception of Bailey's "triple catch method", the methods used leads to equations that can only be solved by numerical methods.

Jackson describes two kinds of census. Firstly, in his "negative" method, individuals are marked on several occasions, but only one sample is taken, at the end of the experiment, for recapture purposes. This method is used by Jackson for estimating population size and survival rate. Secondly, in his "positive" method individuals are marked on one occasion only but samples for recapture purposes are taken on a series of subsequent occasions. Jackson uses this method to estimate population size and birth and immigration rates. Bailey (1951) attempted a maximum likelihood solution of Jackson's "negative" method and, at the expense of a small loss of information grouped recaptures using the earliest mark only.

Various methods of grouping recaptured animals have been used. For example, Jackson (1936, 1939, 1948) and Fisher & Ford (1947) grouped recaptures according to the number of marks, so that an individual was counted as many times as it had marks. An alternative method of grouping was proposed by Leslie & Chitty (1951). This consisted of grouping marked individuals according to the time since they were previously recaptured. Both Leslie & Chitty (1951) and Moran (1952) showed that this method was more efficient than grouping by the numbers of marks.

Hammersley (1953) pointed out that all previous models were deterministic or semi-probabilistic and he developed a partially stochastic model with deterministically operating death rates for estimating death rates and population size by numerical methods. This paper was later criticised by Darroch (1958, 1959) who developed stochastic models for estimating population size, death rates and dilution rates.

Experiments in which marked and unmarked individuals undergo different mortalities

The importance of mortality, or survival rates in the estimation of population parameters can be deduced directly from the basic Petersen type equation.

Since $N = n\,{}^{T}/m$

one can also write

$$N = n \div \left(\frac{m}{T}\right)$$

Now, $\frac{m}{T}$ is the proportion of marked animals that are returned during the period in which the sample of n individuals is collected. If some assumptions are made about the rate of decline of the marked animals, the ratio ${}^{m}/T$ can be expressed as a function of their instantaneous mortality rates. In particular, if the T marked animals are subject to a constant instantaneous total mortality rate Z, due partly to fishing (F) and partly to natural causes (M) it is easily shown that

$$\frac{m}{T} = \frac{F}{Z}\ (1 - e^{-Z}t)$$

where t is the length of time during which the m recapturesare taken. Of special interest is the case when t is infinitely long, in which case

$$\frac{m}{T} = \frac{F}{Z}$$

and

$$N = n.\frac{Z}{F}$$

In this case, n usually refers to the total yield in numbers from a year-class throughout its life which corresponds with the virtual population of Fry (1949). N then becomes an estimate of the initial size of the year-class. Also of interest is the case when t = 1 year, so that

$$\frac{m}{T} = \frac{F}{Z}\,(1 - e^{-Z})$$

and m is then the number of recaptures in the first year only. This ratio is referred to as the "rate of exploitation" (u) by Ricker (1958). In this case the sample size n can be thought of in two ways. If it refers to the number of a single year-class caught during one year, then N becomes an estimate of the size of that year-class at the beginning of the year. If it refers to the numbers of all year-classes caught in one year, then, excluding considerations of recruitment, N becomes an estimate of the population size at the beginning of that year.

The determination of population size from the virtual population using tagging data to determine $F/Z\ (1 - e^{-Zt})$ can therefore be thought of as the application of the Petersen method to the special case where the recaptures are made as the result of the commercial exploitation of the population.

The importance of this way of expressing the problem becomes apparent if the tagging data are subject to certain limitations. In particular:-

a. If there is some mortality of marked animals at the time of liberation, as a result of the marking operation.

b. If there is incomplete reporting of the marks.

c. If as a result of marking the mortality rate of marked individuals subsequent to the marking operation is different from that of unmarked individuals.

Errors arising due to (a) or (b) are referred to by Ricker (1958) as Type A errors, those due to (c) as Type B errors.

Type A errors only

Errors due to (a) above mean that T is unknown, whilst errors due to (b) affect the observed value of m. In either case, therefore, the ratio m/T is biased, so that the quantity $F/Z\ (1 - e^{-Z})$ can no longer be determined from the returns of marked animals alone.

However, Type A errors do not affect the subsequent total mortality rate of marked animals as judged by the rate of decline of the number recaptured per unit time. It is therefore still possible to determine the total instantaneous mortality rate (Z) from the rate of decline of marked animals. Estimates of population size can then be made for a range of likely values of F (or M).

A number of methods have been described for estimating the total mortality (or survival) rate from tag returns.

1. Jackson (1939) gives a formula for estimating the proportion surviving from one year to the next (S) as

$$S = \frac{m_2 + m_3 + m_4 \cdots\cdots\cdots\cdots m_n}{m_1 + m_2 + m_3 \cdots\cdots\cdots\cdots m_{n-1}}$$

where $m_1\ m_2 \cdots\cdots\cdots\ m_n$ refer to the numbers recaptured in successive periods of time.

If the successive periods of time are not equal to 1 year but to a period p say, then this formula gives an estimate of S^p

Examples of the application of this method are given by Ricker (1958) and Cleaver (1961). Given S, Z can be calculated from the equation $Z = -\log_e S$.

2. Method (1) gives an estimate of survival rate that is weighted by the numbers returned in successive periods. An unweighted estimate can be obtained by plotting the natural logarithms of the numbers returned against the period in which they were returned. This gives a relationship with a slope equal to $-Z_p$, from which Z may be determined. This method, which has been used by a number of authors is referred to later in more detail.

Examples are given by Ricker (1958), Cleaver (1961), Dickie (1961), and Andersen & Bagge (1961).

3. In both methods (1) and (2) it is assumed that the rate of decline in recaptures is representative of the rate of decline of the surviving marked individuals. Strictly speaking this will only be true if the mortality rate is constant, and although the effects of changes in fishing effort, for example, can be allowed for by converting the numbers recaptured to numbers recaptured per unit of fishing effort this is only an approximation. A method of estimating survival

rates when both the survival rate and the rate of recapture vary, quite arbitrarily from year to year, is described by Eipper, Forney, and Robson (1961). For its application individuals are marked and recaptured during successive periods, as indicated for 6 periods, for example, in the diagram below.

Period	1	2	3	4	5	6	Total recaptures
	T_1	m_{12}	m_{13}	m_{14}	m_{15}	m_{16}	m_1
		T_2	m_{23}	m_{24}	m_{25}	m_{26}	m_2
			T_3	m_{34}	m_{35}	m_{36}	m_3
				T_4	m_{45}	m_{46}	m_4
					T_5	m_{56}	m_5
Total recaptures		C_2	C_3	C_4	C_5	C_6	

T_1 .... T_5 are the numbers marked in periods 1 - 5 respectively, m_{ij} is the number recaptured in period j out of the number (T_i) marked in period i.

m_i is the total number recaptured out of the number (T_i) marked in period i.

C_i is the total number recaptured in period i. The formula given by Eipper *et al.* for determining the survival rate S_i from period i to period i + 1 is

$$S_i = \frac{T_i + 1}{T_i} \cdot \frac{m_i}{m_i + 1} \quad \frac{\left[(m_1 + m_2 + \cdots\cdots m_i) - (C_2 + C_3 + \cdots C_{i+1})\right]}{\left[(m_1 + m_2 + \cdots\cdots m_i) - (C_2 + C_3 + \cdots C_i)\right]}$$

This is a maximum likelihood estimate, and estimators of variance and co-variance are also given.

4. Another maximum likelihood approach is developed by Gulland (1955) who derives maximum likelihood estimates of the instantaneous fishing and natural mortality rates F and M. He shows that $\frac{\sum t_i}{m}$ is an unbiased estimate of $^1/Z$. As a first approximation, $\frac{m}{\sum t_i}$ could therefore be used as an estimate of Z. Here m is the total number recaptured and $\sum t_i$ is the cumulative time absent of these m individuals.

Type B errors only

If the physical act of marking causes animals to die at a greater rate than they otherwise would do, subsequent to the marking operation, then their total instantaneous mortality rate will be an overestimate of the normal rate.

It is still possible, however, to obtain estimates of F, the fishing mortality rate, free from this bias providing the excess mortality of marked animals is due only to the presence of the marks, and not to a greater vulnerability to capture. Estimates of population size can then be obtained for different values of the natural mortality rate M. There are two methods for estimating F from tagging data.

1. Gulland's (1955) maximum likelihood estimate of F is unaffected by Type B errors and is given by:

$$F = \frac{m^2}{T \sum t_i}$$

2. Beverton & Holt (1956) and Jones (1956) show that by plotting the natural logarithms of the numbers returned against the period of return a line with a slope of -Zp is obtained. The effect of Type B errors is to overestimate Z when estimated in this way. They do not, however, alter the estimate of F that can be made from the intercept of this line on the ordinate at the point corresponding to

zero time. More precisely, if marked animals are returned in successive periods, numbered 0, 1, 2, etc. and each of duration p then m_t, the number returned in period number t is given by

$$m_t = \frac{TFe^{-Ztp}(1 - e^{-Zp})}{Z}$$

so that

$$\log_e m_t = \log_e T + \log_e F + \log_e \frac{(1 - e^{-Zp})}{Z} - Ztp$$

Then when t = 0, the intercept I becomes

$$I = \log_e T + \log_e F + \log_e \frac{(1 - e^{-Zp})}{Z}$$

and, on re-arranging terms, and taking antilogarithms

$$F = \frac{e^I Z}{T(1 - e^{-Zp})}$$

The fact that Z is too large, because of Type B errors does not invalidate this estimate of F, since the intercept I is itself a function of Z.

Paloheimo (1958) gives a modification of this method, an example of which is given by Dickie (1961).

Summary

A summary of the way in which tagging experiments have been grouped in this paper is given in Table 3.

Table 3. Classification of marking experiments

Marked and unmarked individuals experience the same rates of mortality or emigration	no account taken of multiple recaptures account taken of multiple recaptures
Mortality due to marking but at the time of marking only Incomplete reporting of marks	possible to determine instantaneous total mortality rate only
Mortality due to marking, but subsequent to time of marking only	possible to determine instantaneous recapture rate only (i.e. instantaneous fishing mortality rate in most instances)

From this table it will be appreciated that many of the more sophisticated methods of estimating population size usually cannot be applied to fish stocks for the simple reason that the mortality rates of marked and unmarked individuals are rarely the same. Only too often, there is reason to believe that marking can cause mortality not only at the time of liberation but also subsequently. In this situation, estimates of population size from tagging data alone cannot be exact although there may be instances in which useful approximations can be made.

A more encouraging viewpoint is that with the gradual improvement of marking techniques the time may come when this obstacle can be overcome. When this happens some, or all of the more sophisticated techniques will become applicable, and there will be much to be gained by sampling for marked animals according to a special design, instead of relying solely on the commercial exploitation of the stockfor the return of marked individuals.

Abstract

Marking experiments can provide a means of estimating population size in a variety of situations, and these can for convenience be classified in the following way:-

1. Situations in which marked animals suffer the same mortality as the unmarked population, both at the time of marking and subsequently. A number of theoretical models have been developed to deal with this type of situation and these can be sub-divided into those that take account of multiple recaptures and those that do not. By "multiple recaptures" is meant the repeated recapture of the same individuals. Multiple recapture models therefore cater for situations where the rate of recapture is comparatively high, while "single recapture" models are more appropriate when the rate of return is low, or when recaptured individuals are not returned to the population.

2. Situations in which marked animals suffer greater mortality than unmarked ones. In these situations, recapture data can sometimes be used for determining either instantaneous total or fishing mortality rates. Given one of these, estimates of population size can then be obtained for a range of values of the other. Two situations of importance occur:-

   (a) When there is mortality due to marking but at the time of marking only. If this happens it is possible to determine an instantaneous total mortality rate, but not an instantaneous fishing mortality rate.

   (b) When there is mortality due to marking, but over a period subsequent to the marking operation only. In this situation it is possible to determine an instantaneous mortality rate due to fishing, but not one due to all causes.

The fact that many methods of analysis require equal mortality of marked and unmarked individuals means that they cannot be used to estimate the size of many fish populations. It is hoped, however, that with further advances in marking techniques, this obstacle can be overcome and that some or all of the methods referred to in this review may ultimately be of use for estimating the size of fish populations.

References

Andersen, K. P. & Bagge, O.	1961	"The benefit of plaice transportation as estimated by tagging experiments". ICNAF Fish Tagging Symp., Paper no.26, May 1961.
Bailey, N. T. J.	1951	"On estimating the size of mobile populations from recapture data". Biometrika, 38, pp.293-3o6.
Beverton, R. J. H. & Holt, S. J.	1956	"A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling". Rapp.Cons.Explor.Mer, 14o(1), pp.67-83.
Carlander, K. D. & Lewis, W. M.	1948	"Some precautions in estimating fish populations". Progr.Fish.Cult., 1o, pp.134-37.
Chapman, G. C.	1951	"Some properties of the hypergeometric distribution with applications to zoological sample censuses". Univ.Calif.Publ.Statist., 1, pp.131-6o.
Chapman, D. G.	1952	"Inverse multiple and sequential sample censuses". Biometrics, 8, pp.286-3o6.
Chapman, D. G.	1954	"The estimation of biological populations". Ann. math.Statist., 25, pp.1-15.
Clarke, F. N. & Janssen, J. F.		"Results of tagging experiments in California waters on the sardine (*Sardinops caerulea*)". Fish.Bull., Sacramento, 61, pp.1-42.
Cleaver, F. C.	1961	"Bering Sea King Crab (*Paralithodes camtschatica*) tagging experiments". ICNAF Fish Tagging Symp., May 1961, Paper no.1o.

Darroch, J. N.	1958	"The multiple recapture census. I. Estimation of a closed population". Biometrika, 45, pp.343-59.
Darroch, J. N.	1959	"The multiple recapture census. II. Estimation when there is immigration or death". Biometrika, 46, pp.336-51.
Dickie, L. M.	1961	"Estimation of mortality rates of a Gulf of St. Lawrence cod tagging". ICNAF Fish Tagging Symp., May 1961, Paper no.13.
De Lury, D. B.	1947	"On the estimation of biological populations". Biometrics, 3, pp.145-67.
De Lury, D. B.	1951	"On the planning of experiments for the estimation of fish populations". J.Fish.Res.Bd.Can., 8, pp.281-3o7.
Eipper, A. E., Forney, J. L. & Robson, D. S.	1961	"Maximum likelihood estimation of a sequence of annual survival rates from a capture-recapture series". ICNAF Fish Tagging Symp., May 1961, Paper no.56.
Fisher, R. A. & Ford, E. B.	1947	"The spread of a gene in natural conditions in a colony of the moth, *Panaxia dominula* L.". Heredity, 1, pp.143-74.
Fry, F. E. J.	1949	"Statistics of a lake trout fishery". Biometrics, 5, pp.27-67.
Graham, M.	1938	"Rates of fishing and natural mortality from the data of marking experiments". J.Cons.Explor.Mer, 13, pp.76-9o.
Gulland, J. A.	1955	"On the estimation of population parameters from marked members". Biometrika, 42, pp.269-7o.
Hammersley, J. M.	1953	"Capture-recapture analysis". Biometrika, 4o, pp.265-78.
Hancock, D. A.	1961	"Marking experiments with the common whelk (*Buccinum undatum*)". ICNAF Fish Tagging Symp., May 1961, Paper no.28.
Howard, R.	1949	"A study of the tagging method in the enumeration of sockeye salmon population". Bull.int.Pacif. Salm.Fish.Comm., no.2.
Jackson, C. H. N.	1936	"Some new methods in the study of *Glossina monitus*". Proc.zool.Soc.Lond.,1o6, pp.811-96.
Jackson, C. H. N.	1939	"The analysis of an animal population".J.Anim. Ecol., 8, pp.238-46.
Jackson, C. H. N.	1948	"The analysis of a Tsetse-fly population III." Ann.Eugen.,Lond., 14, pp.91-1o8.
Jones, R.	1956	"The analysis of trawl haul statistics, with particular reference to the estimation of survival rates". Rapp.Cons.Explor.Mer, 14o(1), pp.3o-39.
Junge, C. O.	1961	"A quantitative evaluation of the bias in population estimates based on selective samples". ICNAF Fish Tagging Symp., May 1961, Paper no.4.
Kelly, G. F. & Barker, A. M.	1961	"Estimation of population size and mortality rates from tagged redfish *Sebastes marinus* L., at Eastport, Maine". ICNAF Fish Tagging Symp., May 1961, Paper no.31.
Krumholz, L. A.	1944	"A check on the fin clipping method for estimating fish populations".Pap.Mich.Akad.Sci., 29, pp.281-91.
Le Cren, E. D. & Kipling, C.	1961	"Some marking experiments on spawning populations of char (*Salvelinus willughbii*)". ICNAF Fish Tagging Symp., May 1961, Paper no.21.
Leslie, P. H.	1952	"The estimation on population parameters from data obtained by means of the capture-recapture method. II. The estimation of total numbers". Biometrika, 39, pp.363-88.

Leslie, P. H. & Chitty, D.	1951	"The estimation of population parameters from data obtained by means of the capture-recapture method. I. The maximum likelihood equations for estimating the death-rate". Biometrika, 38, pp.269-92.
Moran, P. A. P.	1952	"The estimation of death-rates from capture-mark-recapture sampling". Biometrika, 39,pp.181-88.
Paloheimo, J. E.	1958	"Determination of natural and fishing mortalities of cod and haddock from analysis of tag records off western Nova Scotia". J.Fish.Res.Bd.Can., 15, pp.1371-81.
Parker, R. A.	1955	"A method for removing the effect of recruitment on Petersen type population estimates". J.Fish. Res.Bd.Can., 12, pp.447-5o.
Pope, J. A.	1961	"The design and analysis of capture-recapture experiments". ICNAF Fish Tagging Symp., May 1961, Paper no.58.
Ricker, W. E.	1948	"Methods of estimating vital statistics of fish populations". Ind.Univ.Publ., no.15.
Ricker, W. E.	1958	"Handbook of computations for biological statistics of fish populations". Bull.Fish.Res.Bd.Can.,no.119.
Sato, R.	1938	"On the migratory speed of salmon and the stock of red salmon estimated from the tagging experiments in northern North Pacific". Bull.Jap.Soc.Sci. Fish., 7, no.1, pp.21-23.
Schaefer, M. B.	1951	"Estimation of size of animal populations by marking experiments". Fish.Bull.U.S., 52, pp. 191-2o3.
Schnabel, Z. E.	1938	"The estimation of the total fish population of a lake". Amer.math.Mon., 45, pp.348-52.
Schumacher, F. X. & Eschmeyer, R. W.	1943	"The estimation of fish populations in lakes or ponds". J.Techn.Acad.Sci., 18, pp.228-49.
Simpson, A. C.	1961	"Marking crabs and lobsters for mortality and growth studies". ICNAF Fish Tagging Symp., May 1961, Paper no.29.
