Population Size Estimation

Fish populations are dynamic units; that is, they are characterized by changes with time. Monitoring and estimation of the numerical changes in population or stock size are critical to a fundamental understanding of fishery biology, production, yield, and the establishment of rational management practices. Measures of absolute or relative abundance are indicators of population status and, hence, provide information on the net result of environmental interactions and exploitation activities. In turn, abundance estimates are used to evaluate management impacts on fish stocks through derivation of mortality and exploitation rates. Care should be taken in any use of abundance measures that the simplest, most efficient method is chosen consistent with the requisite needs and applications for such measures.

The development of techniques for fish population enumeration started in the last century but progressed slowly. The inaccessibility of fishes in their natural habitats to direct observation constrained the use of the highly developed sample census techniques employed on human populations. In the past 25 years, however, a large body of theory and techniques has evolved for assessing animal (particularly fish) numbers, in both "closed" and "open" populations (depending on whether or not the population remains unchanged during the investigation period). Hence, a variety of methods now exist to delineate population size, often enabling the use of one estimation technique to validate another.

Absolute Abundance - Direct Enumeration Methods, Total Counts

In some fishery situations, population size can be estimated by direct count of a whole or selected portion of a population. This technique may be utilized when one or more life history stages are sufficiently confined to permit an actual tally of the individuals composing the population. A variety of methods have been employed:

1) Draining bodies of water and recovering fish - often used in small ponds

2) Trapping of migratory species - widely used with anadromous or adfluvial species such as salmon, alewives, and shad in streams passing by a counting device or an observer

3) Visual sitings in clear water - SCUBA observations in lakes and ponds (with or without cameras) or visual observations at sea with whales, either by ship or airplane. Also deep-sea submersibles or counting towers streamside

4) Recording with electronic gear - employed in weirs or streams equipped with passage devices (pipes, fish ladders) where passage is automatically recorded on a counter, TV, or video-tape

5) Counts of natural or man-induced mass mortalities - used in events such as red tide, strandings, or natural disasters with alewives (Great Lakes), pond fishes (summerkill), or marine species (squid, lobster, menhaden). The use of toxicants (poisoning) in lakes and ponds has also been widely accomplished

6) Fishing to the point of "no return" - angling, trapping, and netting of populations until none are left. Seining in small ponds has frequently been used. The completeness of this method has generally not been treated adequately.

Direct enumeration is one of the simplest methods of population estimation and, if properly done, the most accurate. If all individuals are tallied, there is no further statistical analysis involved. However, the application of several of the methods are severely limited and some possess inherent errors or implausible assumptions. Expenses can also be quite high, especially when sophisticated equipment is employed. The total count method is often time-consuming and may result in considerable disturbance of the population and/or its environment.

Absolute Abundance - Direct Enumeration Methods, Partial or Incomplete Counts

Often, a complete direct tally of a population is not possible due to noncontinuous monitoring during all counting periods or incomplete census of all habitats. In these instances, a partial or incomplete population estimation methodology may be practical. Like the total tally method, this technique depends upon enumeration but depends also on representative sampling. In its simplest form, the partial count technique enables total population size to be estimated by the expansion of fish counts in randomly selected units of area (or randomly selected units of time during stream counting periods) occupied by the population. Often, the sampling environment is stratified into areas of similar habitat (pools, riffles, and deadwater in streams; geographical zones based on depth and latitude in the ocean) and each area sampled randomly in proportion to its area. Summation of the expanded area-density (or area-swept) estimates results in a determination of total population size.

The partial count technique requires sufficient knowledge of the size of habitat units (for expansion of counts), and/or area effectively sampled. Within habitat units (strata), random sampling is requisite to produce unbiased abundance indices of known precision. Grid patterns and transect sampling designs, while widely used in partial count methods, do not employ randomization and hence are incapable of providing valid estimates of the sampling error (variance) associated with the population size estimate.

Incomplete count methods have been best employed for areal population estimation for nonmigratory species, particularly for benthic (bottom-dwelling) and nonschooling species such as groundfish and invertebrates (clams, mussels, and certain crabs). The Northeast Fisheries Center's research bottom trawl and shellfish assessment surveys are examples of the application of incomplete census efforts to delineate population sizes of marine organisms (although these have been generally used to derive relative abundance indices because of the difficulty in assessing catchability coefficients).

For migratory species, partial count methods can only be used by simultaneously sampling throughout the population range.

Tables 1 and 2 provide examples of the use of partial count methods (non-stratified and stratified) in estimating population size.

Absolute Abundance - Marking and Recapture Methods

Estimating population size through the marking, release, and subsequent recovery of marked individuals has long been used in freshwater fish species, particularly in small lake and stream habitats. The underlying rationale is based on the principle that the proportion of marked fish recovered in the total catch is the same as the proportion of total marked fish in the total population. There exist three basic estimation methodologies: single census, multiple census, and multiple recapture.

A. Single census - the simplest and often most practical technique in population estimation using marked individuals in the Petersen or Lincoln method. A recorded number of fish is captured, marked, and released, and then, at a later time, a single sample is taken and marked recaptures and unmarked fish are counted. The simplest estimator is

$$\hat{N} = \frac{MC}{R}$$

where $\hat{N}$ = population size at the time of release of marked fish

M = number of individuals originally captured and marked

C = total number of fish caught in the second census sample (total marked and unmarked)

R = number of marked fish (recaptured) in the second sample

To derive an unbiased population size estimate, the following assumptions need to be satisfied: (1) marks are not lost during the experiment; (2) marks are recognized and reported on recovery; (3) marked fish are as likely to be caught as unmarked fish; (4) marked fish mix randomly with unmarked, or sampling effort is proportional to the density of fish in different ports of the body of water; (5) loss by natural mortality or emigration is proportionately the same for marked and unmarked fish; and (6) during the experiment period, recruitment is negligible or can be estimated.

Violations of the assumption result in the following effects: (1) loss of marks or reduction of marked fish through excessive mortality reduces R and results in overestimation of $\hat{N}$; (2) incomplete reporting of unmarked fish reduces R and results in overestimation of $\hat{N}$; (3) higher or lower vulnerability of marked fish results in under- or overestimation of $\hat{N}$, respectively; (4) nonrandom mixing may result in an unexpectedly high or low proportion of R in C and hence in under- or overestimation of $\hat{N}$; and (5) unknown recruitment results in a reduced proportion of R in C and thus overestimation of $\hat{N}$.

To assure statistical unbiasedness of $\hat{N}$, M and C should be chosen such that the product MC is larger than 4N. This, obviously, requires a rough, initial estimate of N. Sample sizes for M and C can be chosen to obtain a population estimate of predetermined reliability (statistical precision) if the basic assumptions are not seriously violated, and a reasonable guess concerning the population size can be made. Hence, the relationship between experimental costs and precision level of the population estimate can be evaluated _a priori_, and financial sources and sampling-recapture efforts allocated accordingly.

In taking the second or census samples in a mark-recapture population estimation activity, two possible alternatives, aside from fixing sample size in advance or being dictated by fishing success, are available. These are _inverse censusing_ and _sequential censusing_. In inverse sampling, the number of _recaptures_ to be obtained is determined in advance and the experiment terminated when that number is achieved. Fixing the number of recaptures determines the sampling accuracy of the result within fairly narrow limits and is therefore an important consideration. Sequential sampling is sampling performed in stages to determine whether a population is greater or less than a specified number. Sampling is stopped whenever this number is settled, at any degree of statistical confidence.

The single-census Peterson estimation method is attractive since it is generally simple, quick, and possesses wide applicability. Equally, it is particularly useful when fishing effort is absent or minimal. Unfortunately, the assumptions for application of the technique are difficult or often impossible to meet.

Table 3 presents an example of a Peterson population estimate.

B. Multiple census - this is a modification of the single census estimator in which fish are captured, marked and released over a considerable period (hence repeatedly added to the population), during which time samples are taken and examined for recaptures. All samples should be replaced, otherwise the population is decreasing, particularly if the samples compose a large portion of the total population. As the number of marked individuals increase, the variance of the population estimate decreases. Each interval between sampling periods yields an independent estimate of population size.

A simple multiple census estimator is the Schnabel expression in which:

$$\hat{N} = \frac{\Sigma\ (C_t M_t)}{\Sigma\ R_t}, \text{ where}$$

$\hat{N}$ = estimate of population present throughout the experiment

C_t = number of fish in sample caught on day t

M_t = total number of fish marked prior to day t

R_t = number of recaptured marked fish in sample C_t

An example of a Schnabel multiple census estimate is given in Table 4.

The assumptions of the Schnabel estimator are identical to those for the Peterson method. The multiple census technique is a more efficient procedure, however, than the single census method, and provides an estimate of population size throughout the experiment, rather than at the beginning of the period. The statistical precision of the population estimate using multiple census is generally better than single census as well, since the proportion of marked fish at large is successively increased, creating even better data for the estimation of population size. Systematic errors, however, such as due to recruitment, instant mortality, and fishing mortality, are more likely to affect multiple census estimates than single census estimates.

Schnabel estimates are better when the period of recoveries are as short as possible (such that mortality in the population is negligible). Too short a period, though, will make it difficult to meet the assumption of having a random distribution of marked fish.

Other multiple census estimators available are those of Schumacher-Eschmeyer, Chapman, and Schaefer. The Schumacher-Eschmeyer and Chapman methods are modifications of the Schnabel estimator, while the Schaefer method is a technique for estimating population size in migratory or diadromous species which can be marked at one place and recovered at another.

C. Multiple Recapture - in situations in which a closed population cannot be assumed (and hence in which single or multiple census techniques cannot be used), multiple recapture methods are often employed to estimate population size. The best known of these are Bailey's triple catch method and the Jolly-Seber method. The general multiple recapture procedure (triple catch method) involves securing three "point" samples, usually taken at rather short time intervals. During the first occasion, the fish are marked; in the second sampling effort, recaptures are recorded and released, and the remaining fish are marked but in a different manner from the original markings. In the final (third sample),recaptures exhibiting marks of either category are enumerated, as well as noting the number of unmarked fish. The Bailey population size estimator is

$$N_2 = \frac{M_2(C_2+1)(R_{13})}{(R_{12}+1)\ (R_{23}+1)}$$

where N_2 = population size at time 2 (second sampling effort)

M_2 = number of fish newly marked at time 2

C_2 = number of fish examined for marks at time 2

R_{12} = number of recaptures from 1st marking taken at time 2

R_{13} = number of recaptures from 1st marking taken at time 3(third sample)

R_{23} = number of recaptures from 2nd marking taken at time 3

An example of the Bailey multiple recapture estimate is given in Table 5.

The accuracy of the Bailey population estimate depends primarily on the magnitude of the three sets of recaptured fish. A well-designed experiment should seek to have the size of each of the recaptured set of fish nearly equal; this may usually be attained if the first sample of newly marked individuals is made larger than the second marked sample, and the sample caught for examination of recaptures in the final (third) occasion is larger than the second sample examined for marked fish.

Absolute Abundance - Population Estimation Based on Catch Composition Methods

Estimation of population size can often be derived indirectly from appraisal of catch composition. If a population can be characterized in two or more ways (i.e., year-old fish and older fish, male and female, marked and unmarked) and the harvest from the population is selective with regard to the classification or "dichotomy", then a population estimate can be obtained given knowledge of the original composition, final composition, and composition of the harvested catch. Such a procedure is called a change of composition, dichotomy, or survey-removal technique. Samples are taken at the beginning and end of a "harvest" period (n_1 and n_2), and the ratios (relative abundance of the two categories in the samples to the total fish in the samples are noted ($P_1 = X_1/n_1$; $P_2 = X_2/n_2$). Additionally, the harvested catch is analyzed for the number of both categories of fish taken between sampling periods. The change of composition estimators are

$$\hat{N} = \frac{C_x - P_2 C}{P_1 - P_2} \; ; \quad \hat{N}_x = \frac{P_1 (C_x - P_2 C)}{P_1 - P_2} \; ; \quad \hat{N}_y \text{ is obtained by difference}$$

where $\hat{N}_x$ = number of fish of one type at initial sampling time

$\hat{N}_y$ = number of fish of other type at initial sampling time

$\hat{N}$ = $N_x + N_y$ or total population at initial sampling time

P_1 = decimal fraction of fish of one type in initial sample

P_2 = decimal fraction of fish of one type in second sample

C_x = number of fish of one type caught during the harvest period

C_y = number of fish of other type caught during the harvest period

C = $C_x + C_y$ or total fish taken in the harvested catch

An example of the change of composition population estimate is given in Table 6.

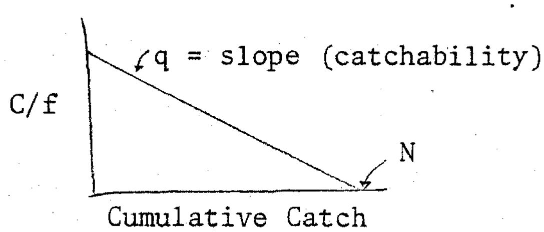
To derive unbiased population estimates using catch composition methods, the following conditions must be satisfied: (1) no natural mortality, recruitment, or migration occurs during the sampling or harvest periods; (2) both categories or types of individuals randomly mix together in the environment and are equally vulnerable to the sampling gear, both before and after harvesting; (3) both types of fish are always distinguishable; (4) the two kinds of individuals must be <u>unequally</u> vulnerable to the harvest between sampling periods; and (5) the total catch (harvest) can be accurately estimated.

The merits of the dichotomy method over marked-fish techniques is that it avoids potential mortality and changes in vulnerability that are often inherent in marking and handling fish. However, estimates of total catch may either be difficult to obtain or very costly.

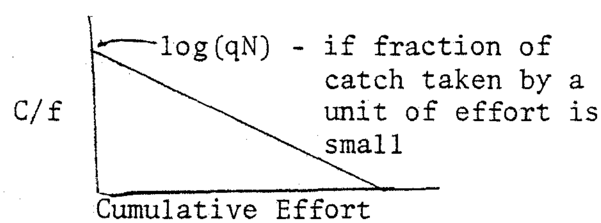
Since a pre-harvest sample has to be taken in the dichotomy method, a concurrent Petersen or Schnabel experiment can be conducted if fish of both types are marked and released. This is desirable since it would permit another check on the population estimated in the dichotomy technique.

<u>Absolute Abundance - Depletion Methods Based on the Relationship Between Catch and Effort</u>

In populations in which fishing removes enough individuals to significantly reduce the catch per unit effort, depletion methods (Leslie, DeLury, and regression techniques)may be employed for population estimation. All are based on the principle that a decrease in catch per unit effort (C/f) as the population is reduced or depleted is directly related to the extent of population decrease. The population size is estimated by sampling over a number of time intervals and plotting either a regression line of C/f on cumulative catch (Leslie Method) or a regression line of C/f against cumulative effort (DeLury Method). The regression line is then projected to the intercept, the initial population size.



Leslie Method



DeLury Method

Population size can be derived directly without plotting by determining the intercept using a least squares regression analysis.

In the Leslie method, the relationship between catch per unit effort and population size is defined by

$C_t/f_t = qN_t$ where t = time period under consideration

q = catchability

N_t = initial population size

The population at any time t, is equal to the initial population less what has been caught up to time t (cumulative catch),

$$N_t = N_o - \Sigma C$$

By substituting N_t from the catch per unit relationship into the above expression, a linear relationship is obtained:

$$C_t/f_t = q(N_o - \Sigma C)$$

This relationship implies if catch per unit is plotted against cumulative catch, a straight line should result with slope equal to catchability and an X intercept equal to the initial population size.

An example of a Leslie population estimate is provided in Table 7.

The generalized DeLury method assumes that the relationship between catch per unit effort and population size is of the form

$$C_t/f_t = qN_o \ (N_t/N_o)$$

or

$$\log_e \ (C_t/f_t) = \log_e(qN_o) + \log_e(N_t/N_o)$$

If the fraction of the population taken per unit effort is small (i.e., 0.02 or less), then

$$N_t/N_o \cong e^{-qE_t}$$

where E_t = cumulative effort units

By substitution, $\log_e(C_t/f_t) = \log_e(qN_o) - qE_t$

or

in common logarithms, $\log_{10}(C_t/f_t) = \log_{10}(qN_o) - 0.4343qE_t$

Thus, a plot of $\log_e(C_t/f_t)$ against cumulative effort up to time period t yields a straight line with slope equal to catchability (q) and intercept equal to $\ln(qN_o)$. The initial population size can therefore be derived from

$$\hat{N}_o = e^{\text{intercept value}}/\text{slope (q)}.$$

An example of a DeLury population estimate is provided in Table 8.

Both the Leslie and DeLury methods depend upon the following assumptions: (1) fishing (or sampling) must take a significant proportion of the population causing a depletion and the decrease in catch per unit effort is proportional to the reduction in the population; (2) catchability of fish remains constant; (3) units of effort (or fishing gear) do not compete with one another; (4)

the entire population is available to the fishery; and (5) there is no recruitment, natural mortality, immigration or emigration in the population.

To reduce error in depletion population experiments through violation of the assumptions, it is advantageous to restrict fishing effort to the shortest time period practicable to minimize recruitment and natural mortality. Also units of efforts should be carefully defined and, if possible, constant sampling effort applied during the experiment. A concurrent analysis of a group of known marked fish in the same population using the depletion method should also be conducted since this will serve as a check on the population estimate. The results of the marked fish estimation can permit a correction to the total population estimate on the basis of the discrepancy between the estimated and actual (known) number of marked individuals.

Although it is often difficult in many populations to meet the assumptions for Leslie or DeLury estimation procedures, the methods have proved useful in those fisheries in which fishing considerably reduces the population size. The Leslie method is generally preferred over the DeLury procedure since measures of fishing effort tend to be less accurate than catch statistics.

Absolute Abundance - Minimum Population Estimation, Virtual Population Analysis

A minimum estimate of the number of fish in a population can be derived given knowledge of the catch in numbers, at each age, of all year classes in the population, given the known or assumed natural mortality rate, and given the known or assumed fishing mortality rate on the oldest age group. Since the analysis is performed on a year-class basis (all fish hatched in a given year), the catch data must be taken over an extended period of years (at least equal to the number of years a year-class significantly contributes to the fishery). The population estimate determined from virtual population analysis is minimal in that it is based on the reported catches from the fishery. Population removals other than those reported (aside from natural losses which are accounted for in the natural mortality rate), if present, are not considered in the analysis and hence the estimated population size will thus be an underestimate or minimal estimate.

In its simplest form, virtual population estimation is accomplished using two equations:

$$N_{i+1} = N_i e^{-(F_i+M)} \qquad (1)$$

and

$$C_i = N_i \frac{F_i(1-e^{-(F_i+M)})}{F_i+M}. \qquad (2)$$

where N_i = size of population of a year class at beginning of year i

N_{i+1} = size of population of a year class at beginning of year i+1

F_i = instantaneous fishing mortality rate of a year class at age i

M = instantaneous natural mortality rate

C_i = catch of a year class at age i

By division, it follows that

$$\frac{N_{i+1}}{C_i} = \frac{(F_i + M)e^{-(F_i + M)}}{F_i \; (1-e^{-(F_i + M)})} \qquad (3)$$

Hence, if C_i and M are known, and an estimate of F_i(the fishing mortality on the oldest age group fished of the year class) is available (or assumed), then N_t (population size of the oldest age group fished) can be derived from equation 2 above. Once N_t is obtained, the equation 3 may be used to derive F_{i-1} and subsequently N_{i-1} from equation 1, and so on.

Equation 3 does not yield an analytical solution for F and thus the expression has to be solved by iteration, which is time consuming unless done by computer. The accuracy of the initial choice of F_i, however, is not critical, in general, to the accuracy of F or N for most younger ages, particularly when cumulative fishing mortality (sum of fishing mortality from year i to year t-1) is high (i.e., >2.0), since estimates of F computed for younger age groups converge asymptotically to their true values for a given M.

An example of a virtual population estimate is given in Table 9.

A simplified approximate form of virtual population analysis known as cohort analysis has been developed which makes the computations of F and N easy without a computer. The simplicity of cohort analysis also makes it easier to determine the effects of systematic and random errors in the sequential computations. Details of these procedures are enumerated in Pope (1972).

Virtual population analysis is most useful in deriving population size on exploited populations in which a good time series of catch-at-age data is available. Although such data require much time and effort to obtain, the virtual population analysis technique obviates the need to incorporate fishing effort in deriving population size. This is especially beneficial when units of effort are extremely difficult to standardize, or when catch per unit effort does not adequately reflect population abundance.

Absolute Abundance - Correlated Population Methods

In certain populations, a statistical correlation may exist with other populations (or objects) which may be more readily estimable than the original population itself. For example, fish population number may be derived, in certain cases, from estimates of fecundity, total numbers of eggs spawned, and size and sex composition of the population. Similarly, adult population size can be forecast in some species (i.e., Pacific salmon) based on a relationship between pre-emergent fry abundance and subsequent adult return.

Often, a relationship between relative abundance of an age group (catch per tow at age in a research survey) and absolute abundance (virtual population analysis) may exist such that the size of a year class at a given age may be ascertained from a predictive regression. In North Sea cod stocks, for example, a relation between the average number of age 1 cod caught per hour fished in the International Young Herring Surveys and year class size estimates from virtual population analysis has been documented. In this case, the relationship is of the form

$$Y = 90 + 3.08\ X \qquad r = 0.95$$

where Y = estimated year class size (VPA estimate) in millions of fish.
X = catch per effort of age 1 cod (mean number of fish per hour fished) in research vessel surveys.

Thus, in the 1976 survey in which 11 age 1 cod were taken per hour, the year-class size was estimated to be 124 million fish.

Correlation population methods are attractive for several reasons: (1) generally they are inexpensive relative to other estimation techniques; (2) estimates can usually be derived over a relatively short time period; (3) handling and/or marking of fish is absent or minimal; and (4) population size can be forecasted in certain conditions. Correlation techniques, however, are limited in their application and often require complex sampling, analysis, and statistical interpretation.

Table 1. Example of incomplete count population estimation, with no stratification.

A. Area occupied by total population as divided into A equal units

Formulae: $\hat{N} = \frac{A\Sigma N}{a}$,

where $\hat{N}$ = estimated total population

N = counts in individual units sampled

a = number of units sampled

$$\text{variance } (\hat{N}) = \frac{A^2 - aA}{a} \times \text{ variance } (N)$$

$$\text{variance } (N) = \frac{a\Sigma N^2 - (\Sigma N)^2}{a\ (a-1)}$$

Example: A 15 acre lake is divided into 15 one-acre sections. Five sections are randomly selected and sampled. The results are:

$a_1 = 10;\ a_2 = 15;\ a_3 = 25;\ a_4 = 30;\ a_5 = 5$

$\hat{N} = (15/5)\ (10+15+25+30+5)$

$\hat{N} = 255$

$$\text{Variance } (N) = \frac{5\ [10^2+15^2+25^2+30^2+5^2]-[10+15+25+30+5]^2}{5(4)}$$

Variance $(N) = 107.5$

$$\text{Variance } (\hat{N}) = \frac{(15)^2 - 5(15)}{5} \times 107.5$$

Variance $(\hat{N}) = 3225$

Table 2. Example of incomplete count population estimation, with stratification

A. Area occupied by total population is divided into k units of different area.

<u>Formulae</u>: $\bar{y}_{st} = 1/N \sum_{h=1}^{k} [N_h \bar{y}h]$

where $\bar{y}_{st}$ = stratified mean catch per effort or per area

N_h = area of the h^{th} unit

N = total area of all units

$\bar{y}_h$ = mean catch per effort or per area in the h^{th} unit

k = number of units in N

$\hat{N} = N \times \bar{y}_{st}$ Where $\hat{N}$ = estimated total population

Example: A stream is divided into 3 sections - riffles (150 square yards), pools (250 square yards), and deadwater (200 square yards). 3 fish were taken per square yard in the riffles, 4 fish were taken per square yard in the pools, and 2 fish per square yard in the deadwater

Hence, $N = 600$ square yards; $k = 3$; $N_1 = 150$; $N_2 = 250$; $N_3 = 200$; $\bar{y}_1 = 3$; $\bar{y}_2 = 4$; $\bar{y}_3 = 2$

$$\bar{y}_{st} = 1/600\ [(3)(150) + (4)(250) + (2)(200)]$$

$$\bar{y}_{st} = 3.08$$

$$\hat{N} = (600)\ (3.08) = 1850 \text{ fish}$$

$$\text{Variance } (\hat{N}) = 1/N\ [\sum_{h=1}^{k} [N_h\ \bar{y}_h^{\,2}] - N\ \bar{y}_{st}^{\,2} + \sum_{h=1}^{k} s_h^{\,2}$$

$$[(N_h - 1) + \frac{(N_h - N)}{N}\ \frac{(N_h - n_h)}{n_h}]\ ]$$

where variance $(\hat{N})$= estimated population variance

n_h = number of standard sampling efforts in the h^{th} unit

$s_h^{\,2}$ = variance within the h^{th} unit, and

$\bar{y}_{st1}\ N_1\ N_h,\ \bar{y}_n$ as defined as before.

Table 3. Peterson, single-census, population estimate

Example: In a small lake, 340 trout are captured in two days with hoop nets. All are marked and returned in good condition back into the lake. During the next three weeks, 2200 trout are taken by angling, of which 85 were marked.

$\hat{N} = \frac{MC}{R}$ where $\hat{N}$ = population size at the time of release of marked fish

M = number of fish marked

C = the catch taken for census

R = the number of recaptured marked fish in the census

Hence, M = 340; C = 2200; R = 85

$\hat{N} = \frac{(340)(2200)}{85} = 8800$ Note MC >>4N

"Rough" 95% confidence limits on $\hat{N} = \hat{N} \pm 2$ standard errors, where standard error is:

$$\sqrt{\frac{M^2C\ (C-R)}{R^3}}$$

For above example:

$$\text{standard error} = \sqrt{\frac{(340)^2(2000)(2115)}{85^3}} = 892.32$$

95% confidence limit = 8800 $\pm$ 1785

Table 4. Schnabel, multiple census, population estimate

Example: Fish are sampled on four occasions by trawling. Thirty-five fish are caught the first day, all are marked and returned. Eighty-five fish are captured in the second sample (5 have marks, the remaining 80 fish are marked and released). In the third sample, 120 fish are taken (12 possess marks, the remaining 108 are marked and released). In the final sample, 90 individuals are captured, of which 20 exhibit marks.

Formula: $\hat{N} = \dfrac{\Sigma\,(C_t M_t)}{\Sigma R_t}$, where $\hat{N}$ = estimate of population present throughout the experiment

C_t = number caught on day t

M_t = total number marked prior to day t

R_t = recaptures in C_t

Sample	C_t	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	R_t	ΣR_t	$\hat{N}$
1	35	0	0	0	0	0	-
2	85	35	2,975	2,975	5	5	595
3	120	115	13,800	16,775	12	17	987
4	90	223	20,070	36,845	20	37	996

When R is small, confidence limits can be derived (based on the assumption of random mixing) by considering R as a Poisson variable. For medium to large R, a normal approximation can be used to compute confidence limits.

Table 5. Bailey Triple Catch Multiple Recapture Population Estimate

Example: Fish are sampled on three occasions by trapping. Two hundred individuals are caught in the first sample; all are marked and released. In the second sample, 350 fish are captured (50 possess marks, the remaining 300 fish are marked, but differently than the original marked fish). In the third (final sample), 425 fish are taken; 40 are recaptures from the first marking and 60 are recaptures from the second sampling.

Formula: $$\hat{N}_2 \frac{M_2\ (C_2+1)\ (R_{13})}{(R_{12}+1)\ (R_{23}+1)}$$

where $\hat{N}_2$ = population size at time of second sample

M_2 = number of fish newly marked from second sample

C_2 = number of fish examined for marks in second sample

R_{12} = number of recaptures from 1st marking taken in second sample

R_{13} = number of recaptures from 1st marking taken in third sample

R_{23} = number of recaptures from 2nd marking taken in third sample

Sample	Fish Newly marked	Fish Examined for marks	Recapture from 1st marking	Recapture from 2nd marking
1	200 (M_1)	-	-	-
2	300 (M_2)	350 (C_2)	50 (R_{12})	-
3	-	425 (C_3)	40 (R_{13})	60 (R_{23})

$$\hat{N}_2 = \frac{(300)(351)(40)}{(51)(60)} = 1376$$

Variance $(\hat{N}_2)$ $$\hat{N}_2^2 - \frac{M_2^2\ (C_2+1)\ (C_2+2)\ R_{13}\ (R_{13}-1)}{(R_{12}+1)(R_{12}+2)\ (R_{23}+1)\ (R_{23}+2)}$$

Variance $(\hat{N}_2)$ = 163,871

Table 6. Change of Composition Population Estimate

Example: An initial sample of 40 largemouth bass from a lake consisted of 24 males and 16 females. A month later, a second sample of 60 bass consisted of 28 males and 32 females. The angling harvest during the month consisted of 200 bass, of which 140 were males and 60 were females.

Formulae: $\hat{N} = \dfrac{C_x - P_2 C}{P_1 - P_2}$; $N_x = \dfrac{P_1 (C_x - P_2 C)}{P_1 - P_2}$

where $\hat{N}$ = total population size at beginning of initial sampling period
P_1 = proportion of male fish in initial sample
P_2 = proportion of male fish in second sample
C = total harvested catch
C_x = number of male fish in harvested catch
$\hat{N}_x$ = total population size of males at beginning of initial sampling period
$\hat{N}_y$ = total population size of females at beginning of initial sampling period

Hence, $P_1 = 0.60$; $P_2 = 0.47$; $C = 200$; $C_x = 140$

$$\hat{N} = \frac{(140) - (0.47)(200)}{0.60 - 0.47} = 354 \text{ fish}$$

$$\hat{N}_x = \frac{(0.60)(140 - (0.47)(200)}{0.60 - 0.47} = 212 \text{ fish}$$

$$\hat{N}_y = 142 \text{ fish}$$

$$\text{Variance } (\hat{N}) \cong \frac{N^2 \hat{V} (P_1) + (\hat{N}-C)^2 \hat{V} (\hat{P}_2)}{(\hat{P}_1 - \hat{P}_2)^2}$$

Table 7. Depletion technique - Leslie Method of Population Estimation

Example: Three samples are taken during a week using an otter trawl. Effort is expressed in hours of trawling in a specified area. In the first sample, 300 fish are caught in four hours. In the second sample, 406 fish are caught in six hours. In the final sample, 172 fish are caught in three hours.

Formulae: $C_t/f_t = q\ (N_o - \Sigma C)$ where

where C_t = number of fish caught at time t

f_t = effort expended in taking C_t

C_t/f_t = catch per unit effort at time t

N_o = initial population size

q = catchability

ΣC = accumulated catch

Sample	Catch (C)	Effort (f)	C/f	Accumulated Catch (ΣC)
1	300	4	75.0	0
2	406	6	67.7	300
3	172	3	57.3	706

Regression parameters: slope (catchability) = q = 0.0251

Y intercept = qN_o = 75.084

Hence $\hat{N}_o = q\ N_o/q = 75.084/0.0251 = 2991$

Initial population size = 2991 fish

Table 8. Depletion Technique - DeLury Method of Population Estimation

Example: Four samples are taken during twenty days using an otter trawl. Effort is expressed in hours of trawling in a specified area. In the first sample, 3000 fish are caught in 40 hours. In the second sample, 4060 fish are caught in 60 hours. In the third sample, 1720 fish are caught in 30 hours. In the final sample, 3175 fish are caught in 60 hours.

Formula: $\log_e (C_t/f_t) = \log_e(qN_o) - qE_t$

where C_t = number of fish caught at time t

f_t = effort expended in taking C_t

q = catchability

N_o = initial population size

E_t = cumulative effort

Sample	Catch (C_t)	Effort (f_t)	C_t/f_t	E_t	$\log_e(C_t/f_t)$
1	3000	40	75.0	0	4.3175
2	4060	60	67.7	40	4.2151
3	1720	30	57.3	100	4.0483
4	3175	60	52.9	130	3.9687

Regression parameters: slope (q) = 0.0027

Y intercept = 4.3196

$$\hat{N}_o = e^{\text{intercept value}}/\text{slope} = e^{4.3196}/0.0027 = 27{,}837$$

Initial population size = 27,837 fish

Table 9. Virtual Population Analysis - Population Estimation

Example: The following table lists the catch at age for a single year-class of fish during 12 years in which the year-class was in the fishery.

Age	1	2	3	4	5	6	7	8	9	10	11	12
Catch (#'s of fish)	100	600	1000	500	200	100	50	25	10	5	2	1

Formulae:

$$N_{i+1} = N_i e^{-(F_i+M)}$$

$$C_i = N_i \frac{F_i(1-e^{-(F_i+M)})}{F_i + M}$$

$$\frac{N_{i+1}}{C_i} = \frac{(F_i + M)e^{-(F_i+M)}}{F_i(1-e^{-(F_i+M)})}$$

where N_i = size of population of a year class at beginning of year i

N_{i+1} = size of population of a year class at beginning of year i+1

F_i = instantaneous fishing mortality rate of a year class at age i

M = instantaneous natural mortality rate

C_i = catch of a year class at age i

Assume M = 0.2 and F_{12} = 0.5. Hence, by iteration:

Age	1	2	3	4	5	6	7	8	9	10	11	12
F	.024	.191	.555	.602	.518	.535	.565	.622	.547	.588	.497	.500
N	4745	3795	2568	1207	541	264	127	69	26	12	6	3

Application of the VPA technique to all year classes in the population will provide estimates of stock size (and fishing mortality) at all ages in each year. Summation of the stock sizes, by age, in each year with this yield total population size in each year.