

Bulletin of the  
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**Computation  
and  
Interpretation  
of  
Biological Statistics  
of  
Fish  
Populations**

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now a considerable body of information and a corresponding methodology. Finally, the overall production of a fish stock, in relation to density and to rate of fishing, has interested a number of authors since the middle 1920s, and there is much attention in recent years.

At first the study of reproduction or "year-class strength" was considered mainly in relation to environmental factors, but its relation to stock density has attracted another.

The population he is studying, and he can increasingly use one method to check the investigator now has a number of methods from which to choose one best suited to rate started early but progressed much more slowly. In the past 25 years there has been much activity along theoretical lines, and numerous new applications. An investigation of procedures for estimating population size and survival potential sources of error have received close consideration.

Historically, age and rate of growth were the first of these subjects to receive wide attention, possibly because they require less extensive field work. Most of the methods now in use for estimating growth rate had been evolved by 1910, and their

1. The abundance of the population, usually somewhat restricted as to age or size.
2. The total mortality rate at successive ages, or even within each year.
3. The fraction of the total mortality ascribable to each of several causes. It is possible at times to distinguish (a) deaths caused by fishing, (b) deaths caused by predation other than human, (c) deaths from disease, parasites, or senility; (b) and (c) together comprise "natural" mortality.
4. The rate of growth of the individual fish. In human populations the rate of growth of individuals is not generally regarded as a vital statistic. However growth rate among fishes is much more variable than in man, and it may be even more sensitive than mortality to changes in abundance and to environmental variability.
5. The rate of reproduction, particularly as it is related to stock density.
6. The overall rate of *surplus production* of a stock, which is the resultant of growth plus recruitment less natural mortality.

The topics which can be considered as biological statistics of a fish population include the following:

#### 1.1. THE PROBLEMS

### CHAPTER I.—INTRODUCTION

1.2. DEFINITIONS, USAGES, AND GLOSSARY

The list below includes only a part of the varied terminology which has been used in fish population analysis. More extended descriptions of some terms are given in later sections. If a special symbol is associated with a term, it is shown in parentheses. Terms marked with an asterisk are not used in this book, at any rate not in a context where strict definition is called for.

**ABSOLUTE RECRUITMENT:** The number of fish which grow into the catchable size range in a unit of time (usually a year).

**AGE:** The number of years of life completed, here indicated by an arabic numeral, followed by a plus sign if there is any possibility of ambiguity (age 5, age 5+)<sup>1</sup>. **ANNUAL (or seasonal) GROWTH RATE (h):** The *increase* in weight of a fish per year (or season), divided by the initial weight.

**ANNUAL (or seasonal) TOTAL MORTALITY RATE (A):** The number of fish which die during a year (or season), divided by the initial number. Also called: actual mortality rate, \*coefficient of mortality (Heincke).

**AVAILABILITY: 1. (r):** The fraction of a fish population which lives in regions where it is susceptible to fishing during a given fishing season (Mart 1951). This fraction receives recruits from or becomes mingled with the non-available part of the stock at other seasons, or in other years. (Any more or less completely isolated segment of the population is best treated as a separate stock.)

**2. (C/f or Y/f):** Catch per unit of effort.

**BIOMASS (B):** The weight of a fish stock, or of some defined portion of it.

**CATCHABILITY (q):** The fraction of a fish stock which is caught by a defined unit of the fishing effort. When the unit is small enough that it catches only a small part of the stock — 0.01 or less — it can be used as an instantaneous rate in computing population change. (For fractions taken of various portions of the stock, see "vulnerability.") Also called: catchability coefficient, \*force of fishing mortality (Fry 1949, p. 24; in his Appendix, however, Fry defines the force of fishing mortality as equivalent to our rate of fishing, F).

**CATCH CURVE:** A graph of the logarithm of number of fish taken at successive ages or sizes.

**CATCH PER UNIT OF EFFORT (C/f or Y/f):** The catch of fish, in numbers or in weight, taken by a defined unit of fishing effort. Also called: catch per effort, fishing success, availability (2).

**CONDITIONAL FISHING MORTALITY RATE (m):** The fraction of an initial stock which would be caught during the year (or season) *if* no other causes of mortality were present.

**1** While the above is recommended, other usages exist. Roman numerals are frequently used in North America, but their cumbersome nature seems to outweigh any advantage. Some have used either roman or arabic numerals to indicate year of life, rather than years completed. For anadromous fishes both the actual age and the age at seaward migration are frequently indicated. Several conventions are employed for this purpose, and it seems necessary to specify each time which one is being used.

- operated ( $= 1 - e^{-F}$ ). Also called: annual fishing mortality rate, seasonal fishing mortality rate.
- CONDITIONAL NATURAL MORTALITY RATE ( $n$ ): The fraction of an initial stock that would die from causes other than fishing during a year (or season), if there were no fishing mortality ( $= 1 - e^{-M}$ ). Also called: annual natural mortality rate, seasonal natural mortality rate.
- CRITICAL SIZE: The average size of the fish in a year-class at the time when the instantaneous rate of natural mortality equals the instantaneous rate of growth in weight for the year-class as a whole. Also called: \*optimum size.
- EFFECTIVE FISHING EFFORT ( $F/q$ ): Fishing effort adjusted, when necessary, so that each increase in the adjusted unit causes a proportional increase in instantaneous rate of fishing.
- EFFECTIVENESS OF FISHING: A general term referring to the percentage removal of fish from a stock, but not as specifically defined as either rate of exploitation or instantaneous rate of fishing.
- EQUILIBRIUM CATCH ( $C^E$ ): The catch (in numbers) taken from a fish stock when it is in equilibrium with fishing of a given intensity, and (apart from the effects of environmental variation) its abundance is not changing from one year to the next.
- EQUILIBRIUM YIELD ( $Y^E$ ): The yield in weight taken from a fish stock when it is in equilibrium with fishing of a given intensity, and (apart from effects of environmental variation) its biomass is not changing from one year to the next. Also called: sustainable yield, equivalent sustainable yield. (See also SURPLUS PRODUCTION.)
- EXPLOITATION RATIO ( $E$ ): The ratio of fish caught to total mortality ( $= F/Z$  when fishing and natural mortality take place concurrently). Also called: \*rate of exploitation.
- FISH STOCK: See STOCK.
- FISHING EFFORT ( $f$ ): 1. The total fishing gear in use for a specified period of time. When two or more kinds of gear are used, they must be adjusted to some standard type (see Section 1.7).  
2. Effective fishing effort.  
3. Effectiveness of fishing.
- \*FISHING INTENSITY: 1. Effective fishing effort.  
2. Fishing effort per unit area (Beverton and Holt).  
3. Effectiveness of fishing.
- \*FISHING POWER (of a boat, or of a fishing gear): The relative vulnerability of the stock to different boats or gears. Usually determined as the catch taken by the given apparatus, divided by the catch of a standard apparatus fishing at nearly the same time and place.
- FISHING SUCCESS: Catch per unit of effort.
- INSTANTANEOUS RATES (in general): See Section 1.4. Also called: logarithmic, exponential, or compound-interest rates.

**INSTANTANEOUS RATE OF FISHING MORTALITY (F):** When fishing and natural mortality act concurrently,  $F$  is equal to the instantaneous total mortality rate, multiplied by the ratio of fishing deaths to all deaths. Also called: rate of fishing; instantaneous rate of fishing; \*force of fishing mortality (see under CATCHABILITY).

**INSTANTANEOUS RATE OF GROWTH (G):** The natural logarithm of the ratio of final weight to initial weight of a fish in a unit of time, usually a year. When applied collectively to all fish of a given age in a stock, the possibility of selective mortality must be considered (Section 9.4).

**INSTANTANEOUS RATE OF MORTALITY (Z):** The natural logarithm (with sign changed) of the survival rate. The ratio of number of deaths per unit of time to population abundance during that time, if all deceased fish were to be immediately replaced so that population does not change. Also called: \*coefficient of decrease (Baranov).

**INSTANTANEOUS RATE OF NATURAL MORTALITY (M):** When natural and fishing mortality operate concurrently it is equal to the instantaneous total mortality rate, multiplied by the ratio of natural deaths to all deaths. Also called: \*force of natural mortality (Fry).

**INSTANTANEOUS RATE OF RECRUITMENT (z):** Number of fish that grow to catchable size per short interval of time, divided by the number of catchable fish already present at that time. Usually given on a yearly basis: that is, the figure just described is divided by the fraction of a year represented by the "short interval" in question. This concept is used principally when the size of the vulnerable stock is not changing or is changing only slowly, since among fishes recruitment is not usually associated with stock size in the direct way in which mortality and growth are.

**INSTANTANEOUS RATE OF SURPLUS PRODUCTION:** Equal to rate of growth plus rate of recruitment less rate of natural mortality — all in terms of weight and on an instantaneous basis. In a "balanced" or equilibrium fishery, this increment replaces what is removed by fishing, and rate of surplus production is numerically equal to rate of fishing. Also called: \*instantaneous rate of natural increase (Schaefer).

**MAINTAINABLE YIELD:** "The largest catch that can be maintained from the population, at whatever level of stock size, over an indefinite period. It will be identical to the sustainable yield for populations below the level giving the  $MSY$ , and equal to the  $MSY$  for populations at or above this level" (Gulland).

**MAXIMUM EQUILIBRIUM CATCH (see MAXIMUM SUSTAINABLE YIELD).**

**MAXIMUM SUSTAINABLE YIELD (MSY OR  $Y_s$ ):** The largest average catch or yield that can continuously be taken from a stock under existing environmental conditions. (For species with fluctuating recruitment, the maximum might be obtained by taking fewer fish in some years than in others.) Also called: maximum equilibrium catch (MEC); maximum sustained yield; sustainable catch.

**\*MECHANICAL INTENSITY OF FISHING: Fishing effort (I).**

**NATURAL MORTALITY:** Deaths from all causes except man's fishing, including predation, senility, epidemics, pollution, etc.

**NET INCREASE (OR DECREASE):** New body substance elaborated in a stock, less the loss from all forms of mortality.

**PARAMETER:** A "constant" or numerical description of some property of a *population* (which may be real or imaginary). Cf. statistic.

**PIECES:** Individual items, as in the expression "two dollars a piece" (German *Stück*). Individual fish.

**PRODUCTION:** 1. (sense of Ivlev). The total elaboration of new body substance in a stock in a unit of time, irrespective of whether or not it survives to the end of that time. Also called: \*net production (Clarke et al. 1946); \*total production. 2. \*Yield.

**RATE OF EXPLOITATION ( $u$ ):** The fraction, by number, of the fish in a population at a given time, which is caught and killed by man during the year immediately following (=  $FA/Z$  when fishing and natural mortality are concurrent). The term may also be applied to separate parts of the stock distinguished by size, sex, etc. (See also "rate of utilization.") Also called: \*fishing coefficient (Heincke).

**RATE OF FISHING ( $F$ ):** INSTANTANEOUS RATE OF FISHING MORTALITY.

**\*RATE OF NATURAL INCREASE:** INSTANTANEOUS RATE OF SURPLUS PRODUCTION.

**RATE OF REMOVAL:** An inexactly-defined term that can mean either rate of exploitation or rate of fishing — depending on the context (see Section 1.4.3).

**RATE OF UTILIZATION:** Similar to rate of exploitation, except that only the fish *landed* are considered. The distinction between catch and landings is important when considerable quantities of fish are discarded at sea.

**RECRUITMENT:** Addition of new fish to the vulnerable population by growth from among smaller size categories (Section 11.1).

**RECRUITMENT CURVE, REPRODUCTION CURVE:** A graph of the progeny of a spawning brood has become vulnerable to fishing), plotted against the abundance of the stock that produced them.

**SECULAR:** Pertaining to the passage of time.

**STATISTIC:** The estimate of a parameter which is obtained by observation, and which in general is subject to sampling error.

**STOCK:** The part of a fish population which is under consideration from the point of view of actual or potential utilization.

**SUCCESS (of fishing):** Catch per unit of effort.

**SURPLUS PRODUCTION ( $Y'$ ):** Production of new weight by a fishable stock, plus recruits added to it, less what is removed by *natural* mortality. This is usually estimated as the catch in a given year plus the increase in stock size (or less the decrease). Also called: natural increase, sustainable yield, equilibrium catch (Schaefer).

- SURVIVAL RATE (S): Number of fish alive after a specified time interval, divided by the initial number. Usually on a yearly basis.
- SUSTAINABLE YIELD: Equilibrium yield.
- USABLE STOCK: The number or weight of all fish in a stock that lie within the range of sizes customarily considered usable (or designated so by law). Also called: \*standing crop.
- UTILIZED STOCK, UTILIZED POPULATION (V): The part, by number, of the fish alive at a given time, which will be caught in future.
- VIRTUAL POPULATION: Utilized stock.
- VULNERABILITY: A term equivalent to CATCHABILITY but usually applied to separate parts of a stock, for example those of a particular size, or those living in a particular part of the range.
- YEAR-CLASS: The fish spawned or hatched in a given year. In the northern hemisphere, when spawning is in autumn and hatching in spring, the calendar year of the hatch is commonly used to identify the year-class (except usually for salmon). Also called: brood, generation.
- In the above, only the kinds of "rates" are defined which are most frequently used. In general, for any process there will be an *absolute* rate, a *relative* rate and an *instantaneous* rate (Sections 1.4, 1.5).
- ### 1.3. SYMBOLS
- The symbols used are those of the "international" system (Gulland 1956a) as far as possible, but quite a number of additional ones are required, of which those more frequently used are shown below. The predecessors of this bulletin (Ricker 1948, 1958a) used essentially the system recommended by Widrig (1954a, b), and their symbols are indicated below in square brackets.
- a 1. a coefficient used in the Ricker recruitment curve (Section 11.6.2)  
 2. the multiplier in the functional weight-length relationship (Section 9.3.1)
- b 1. the slope of any line  
 2. the exponent in the functional weight-length relationship (Section 9.3.1)
- e 2.71828 . . .
- f fishing effort
- h annual growth rate
- k 1. Ford growth coefficient (Section 9.6.4)  
 2. a rate; used in various connections
- l length of a fish
- m conditional rate of fishing mortality
- n conditional rate of natural mortality
- q catchability [c]

- r 1. availability (1).  
2. rate of accession (Section 5.3)
- s standard deviation
- t 1. a point in time (often used as a subscript)  
2. an interval of time (also  $\Delta t$ )  
3. age
- u 1. rate of exploitation of a fish stock, or expectation of capture by man ( $\mu$  of Ricker 1948)  
2. the ratio of number of recoveries to number of marked fish released ( $= R/M$ )
- v expectation of natural death ( $v$  of Ricker 1948)
- w weight of a fish
- y instantaneous rate of emigration
- z 1. instantaneous rate of immigration  
2. instantaneous rate of recruitment
- A annual (or seasonal) mortality rate [ $a$ ]
- A' annual (or seasonal) rate of disappearance of fish
- B weight (biomass) of a group of fish; for example of a year-class, or of an entire stock
- C 1. catch, in numbers — usually for a whole year  
2. number of fish examined for tags or marks  
1. escapement (of salmon, etc., past a fishery)
- E 2. number of eggs  
3. exploitation ratio ( $= F/Z$ )  
4. (as subscript) an equilibrium level (see Appendix III)
- F instantaneous rate of fishing mortality [ $p$ ]
- G instantaneous rate of growth [ $g$ ]
- K 1. Brody growth coefficient (Section 9.6.1)  
2. any rate  
3. cumulative catch (Chapter 6)
- L mean length at recruitment, in Baranov's yield equation  
 $L_{\infty}$  asymptotic length, in the Brody-Bertalanffy growth equation
- M 1. instantaneous rate of natural mortality [ $q$ ]  
2. number of fish marked or tagged (also  $M$ )
- N number of fish in a year-class, population, or sample
- P 1. abundance of a parental stock or generation  
2. level of statistical probability
- Q the constant which appears in the integration of Baranov's yield computation





1.4.2. SUBDIVISIONS OF MORTALITY. There can be several causes of death among the fish in a population: removals by man (fishing), predation, disease, accident, etc., each with its own rate. In practice we usually consider a division into only two types: fishing, and natural mortality (which includes everything else). Each kind of mortality has its own instantaneous rate, and the sum of these is the instantaneous total mortality rate. If  $F$  represents the instantaneous rate of fishing mortality, the expression  $e^{-F}$  represents the survival rate if there were no natural mortality, and  $1 - e^{-F}$  corresponds to the conditional mortality rate if no other source of mortality existed, here represented by  $m$ . Similarly, if  $M$  is the instantaneous rate of natural mortality,  $1 - e^{-M}$  is the conditional natural mortality rate. When fishing and natural mortality act concurrently, they are competing for the same fish, so the conditional mortality rates cannot be added. However, an expectation of death can easily be computed for each cause of mortality, as described in Section 1.5.2, and these are additive. The

It has been suggested that mortality should not really be divided up into time periods of less than a day, because of probable diurnal fluctuations in predation, etc., and hence that a calculus of finite differences should be employed. Actually, even 365 divisions of the year is close enough to an "indefinitely large number" to make the exponential relationship between  $Z$  and  $A$  accurate enough for our purposes. A more penetrating consideration is that we are not, after all, interested in dividing up the fish's year into astronomically equal time intervals; for our purpose a physiological time scale would be more appropriate, or perhaps one based on the diurnal and seasonal variation in activity of the fish's predacious enemies. It is only when total mortality is subdivided into components whose effect may vary seasonally in different ways, that time by the sun becomes important.

The concept of an "instantaneous" rate apparently continues to trouble students. Imagine a year of a fish's life to be divided into a large number  $n$  of equal time intervals, and let the quantity  $Z/n$  represent the expectation of death of the fish during each such interval; or, in other words,  $Z/n$  is the fraction of a large population which would actually die during each time interval one- $n$ th of a year long. In such a relationship,  $Z$  is the instantaneous rate of mortality, expressed on a yearly basis. The interval  $1/n$  year is made short ( $n$  made large) so that the change in size of population during each interval will be negligible; that is,  $Z/n$  must be a small fraction. But of course the cumulative effect of the death of  $Z/n$  of the fish over a large number of  $n$ ths of a year is quite important. This can be illustrated by a numerical example. Let  $n = 1000$  and  $Z = 2.8$ . Then during  $1/1000$  of a year  $2.8/1000 = 0.28\%$  of the average number of fish present die. Since this is a very small number of deaths, the difference between average number and initial number can be ignored; and, of a population of, say, 1,000,000 initially, about 2800 will die and 997,200 will remain alive. During the next thousandth of the year  $0.28\%$  of 997,200 = 2793 die and hence 994,407 survive. Repeated 1000 times, this process leaves 1,000,000  $(1 - 0.0028)^{1000} = 60,000$  survivors. The mortality for the year is therefore 940,000 fish, and the annual mortality rate is  $A = 0.940$ , as compared with the instantaneous rate of  $Z = 2.8$ . This relation is not quite exact, because 1000 divisions of the year are scarcely enough to compute the relative sizes of these two rates with 3-figure accuracy. The value appropriate to an indefinitely large number of divisions of the year is given by the relationship:  $(1 - A) = e^{-Z}$  where  $e = 2.71828$ . In this example, for  $Z = 2.8$ ,  $A = 0.9392$ , so that the approximate calculation was not far off. Obviously there is no limit to the possible size of  $Z$ , but  $A$  cannot exceed unity — that is, no more fish can die than are actually present. On the other hand, when  $Z$  and  $A$  are small they approach each other in magnitude. The table of Appendix I shows that when  $Z = 0.1$  there is only 5% difference between them.



For *Type 1 fisheries* it is convenient to start the biological year at the time fishing begins, and to consider that natural mortality occurs after fishing ends. We have then the following relationships, additional to (1.3)-(1.5):

(1.6) Rate of exploitation:  $n = m = 1 - e^{-F}$

(1.7) Conditional natural mortality rate:  $n = 1 - e^{-M}$

(1.8) Expectation of natural death:  $v = n(1 - n)$

For *Type 2 fisheries*, in which fishing and natural mortality operate concurrently, the following relationships hold:

(1.9) Conditional fishing mortality rate:  $m = 1 - e^{-F}$

(1.10) Conditional natural mortality rate:  $n = 1 - e^{-M}$

(1.11) Rate of exploitation:  $n = FA/Z$

(1.12) Expectation of natural death:  $v = MA/Z$

Expressions (1.9)-(1.12) also imply the following:

(1.13) 
$$\frac{Z}{A} = \frac{F}{n} = \frac{M}{v}$$

(1.14) 
$$m + n - mn = A$$

Notice particularly that expressions (1.3)-(1.5) and (1.14) do not require that fishing and natural mortality occur at rates which are proportional within the year. For example, a simple calculation will show that a 50% conditional rate of natural mortality ( $n$ ), combined with a 50% conditional rate of fishing mortality ( $m$ ), gives a 75% total mortality rate ( $A$ ), regardless of whether the two causes of death operate concurrently, or consecutively, or in any intermediate fashion. On the other hand, differences in the seasonal incidence of the two kinds of mortality can cause striking changes in the relative magnitudes of the annual expectations of death ( $n$  and  $v$ ), though the latter always add up to  $A$ . Expression (1.13) pertains only to the situation where fishing and natural mortality are distributed proportionally within the year (though it is not necessary that each be of a constant magnitude on an astronomical time scale.)

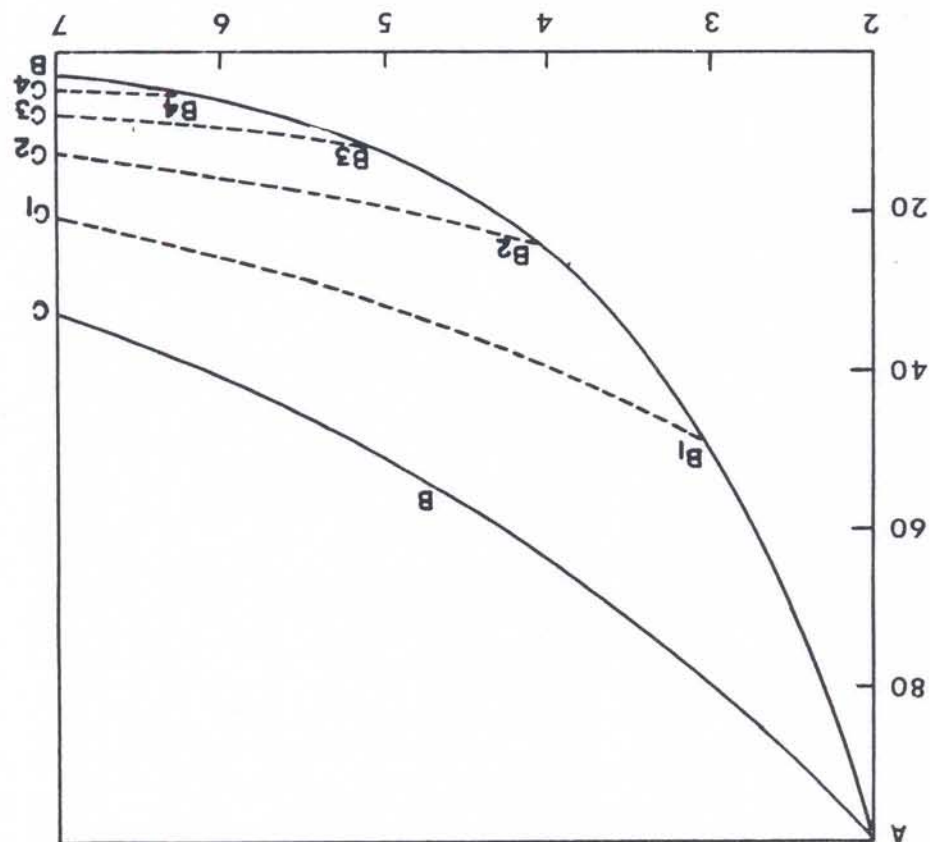
To obtain a good approximation to either the Type 1 or Type 2 fishery it is legitimate to set the limits of the fishery year in as convenient a manner as possible. For example, to increase the resemblance to Type 2 it may be possible to arrange the statistical year so that the mean time of fishing is at the middle of that year, with times of little fishing distributed as symmetrically as possible at the beginning and at the end.

If fishing is so distributed, seasonally, that neither the Type 1 nor Type 2 model is realistic, the year can be divided into two or more parts and separate values of  $F$ ,  $M$ , etc., computed for each.

$$(1.16) \quad \frac{M}{F+M} \times NA = \frac{MNA}{Z} = \underline{MN}$$

The total deaths, which equal NA by definition, are therefore Z times the average fishing in the ratio of F to M, then natural deaths are M/(F + M) = M/Z times NA, or (from 1.15) M times the average population; that is:

Fig. 1.1. Exponential decrease in a stock from an initial abundance of 100 at age 2, when the annual mortality rate is 0.2 (AC) and when it is 0.5 (AB). The broken lines indicate population structure during a period of transition from the smaller to the larger mortality. (Redrawn from fig. 8 of Baranov 1918, by S. D. Gerking.)



$$(1.15) \quad \underline{N} = \int_{t=1}^{t=0} N e^{-Zt} dt = N \left( \frac{e^{-Z}}{-Z} - \frac{1}{-Z} \right) = \frac{N(1 - e^{-Z})}{Z} = \frac{Z}{NA}$$

1.5.3. SINGLE AGE-GROUPS. Consider a single age-group of fish in the recruited (fully vulnerable) part of a stock. Its abundance during a year decreases from N to NS, according to equation (1.2); for example, from the point A to the point B<sub>1</sub> in Fig. 1.1. The average abundance during the year is the area of the figure under AB<sub>1</sub>, divided by the length of the base (which is unity). In our symbols, this is:

which is its least value.

$$(1.20) \quad N = \frac{A}{R e^{-z}} = \frac{A}{RS}$$

Similarly, immediately before the annual influx of recruits the stock would be:

$$(1.19) \quad \begin{aligned} N &= R e^{-0.5z} + R e^{-1.5z} + R e^{-2.5z} + \dots \\ &= R e^{-0.5z} (1 + e^{-z} + e^{-2z} + \dots) \\ &= \frac{A}{R e^{-0.5z}} \end{aligned}$$

For example, at the half year it will be:  
At any other time of year the population will of course be somewhat less than this.

$$(1.18) \quad \begin{aligned} N &= R + R e^{-z} + R e^{-2z} + \dots \\ &= R(1 + S + S^2 + \dots) \\ &= R \left( \frac{1 - S^\infty}{1 - S} \right) = \frac{R}{R - S} = \frac{A}{R} \end{aligned}$$

1.5.5. INSTANTANEOUS RECRUITMENT. Consider R recruits added to the catchable stock of a species each year. Suppose the stock is of Type A, so that the recruits become catchable during a brief interval of time, or for practical purposes all at one instant. With a constant rate of survival, S, the recruits decrease in 1 year to  $R e^{-z}$  or RS, in 2 years to  $R S^2$ , in t years to  $R S^t$ . Under these equilibrium conditions the total population present just after recruitment in any year is found by summing the converging geometric series:

1.5.4. SEVERAL AGE-GROUPS. A few kinds of commercial fish stocks consist of single age-groups, to which the above expressions apply directly. More commonly a stock consists of a mixture of ages, so that in order to obtain expressions for mortality, etc., of whole populations, consideration must be given to the recruits to the stock, and the manner in which recruitment occurs. We will begin by considering the equilibrium situation, first described in detail by Baranov (1918), where recruitment is the same in all years; and with the further simplification that survival rate is the same throughout life.

This is often known as *Baranov's catch equation*. It has also been derived stochastically by Rothschild (1967).

$$(1.17) \quad C = \frac{FN}{NFA} = \frac{Z}{NFA}$$

Similarly the catch is F times the average population:

$$\frac{dN_t}{dt} = -ZN_t + R \quad (1.28)$$

The development of expression (1.27) just given is that of Ricker (1944), Beverton (1954, p. 140) has developed it directly from the differential equation relating size of stock,  $N_t$ , to instantaneous mortality rate,  $Z$ , and to recruitment,  $R$ :

$$R - \frac{Z}{R(A-Z)} = \frac{Z}{RA} \quad (1.27)$$

The number of recruits which survive the year is therefore:

$$\frac{Z}{R(Z-A)} \quad (1.26)$$

Hence the number of recruits which die during their year of recruitment (expression 1.24) can also be written (substituting  $\bar{N} = R/Z$ ):

$$R = \bar{N}Z \quad (1.25)$$

But under equilibrium conditions the annual number of recruits must be the same as the number of deaths, i.e.:

$$\text{Deaths of the year's recruits} = \bar{N}(Z-A) \quad (1.24)$$

The mortality among recruits must therefore be the difference between these two, or:

$$\text{Deaths of "old" fish} = \bar{N}A \quad (1.23)$$

Considering the fish on hand at the start of a year, the number of them that will die during the year is of course:

$$\text{Total deaths} = \bar{N}Z \quad (1.22)$$

1.5.6. CONTINUOUS RECRUITMENT. Consider a fishery of Type 2B, in which  $R$  recruits enter a catchable stock at a steady absolute rate throughout the year, instead of all at once. Suppose further that the stock is in equilibrium at density  $\bar{N}$ , with the number of recruits just balancing the number of deaths at all times. From (1.15), the number of fish that die in the course of a year is the product of the number present times the instantaneous mortality rate:

$$\bar{N} = \frac{R}{A} \int_{t=0}^1 e^{-Zt} dt = \frac{R}{A} \times \frac{Z}{A} = \frac{R}{Z} \quad (1.21)$$

The average size of the stock over the course of a year (unit time), during which it decreases from  $R/A$  to  $RS/A$ , is of course:

$$(1.33) \quad \frac{Z_1}{RA_1} + \frac{Z_1}{RS_2A_1} + \frac{Z_1}{RS_3S_2A_1} + \frac{Z_1}{RS_4S_3S_2A_1} + \dots$$

1.5.7. STOCKS IN WHICH MORTALITY RATE CHANGES WITH AGE. When mortality and survival rate change with the age of the fish, whether because of a variable rate of natural mortality or variation in rate of fishing, no simple expressions for catch, etc., in the whole stock are possible: the contribution of each year-class must be summed separately. For example, with R recruits per year and continuous recruitment, the stock is:

Since (1.32) is the same as (1.21), it appears that, regardless of the manner in which recruitment occurs, under equilibrium conditions the average stock on hand over the course of a year will be equal to  $R/Z$ . A practical corollary is the fact that numerical examples in which recruitment is instantaneous (which are somewhat easier to construct) are for many purposes acceptable models of populations in which recruitment actually occurs along with the fishing.

But since recruitment and mortality are continuous, the population is the same at all times of year, and (1.32) represents the stock continuously on hand,  $N$ .

$$(1.32) \quad \frac{RA}{R} \left( \frac{1-S}{1-S^\infty} \right) = \frac{Z}{RA} \times \frac{A}{1} = \frac{Z}{R}$$

$$N = \frac{Z}{RA} + \frac{Z}{RAS} + \frac{Z}{RAS^2} + \dots$$

as in (1.27) above. During their second year of life the above survivors (expression 1.27) are subject to the full mortality rate A, so that  $RA^2/Z$  die and  $RAS/Z$  survive. The total population of all ages, at the beginning of any year, is therefore found by summing the geometric series:

$$(1.31) \quad \frac{R}{RA} (1 - e^{-Z}) = \frac{Z}{R(1-S)} = \frac{Z}{RA}$$

When  $t = 1$  year, this number of survivors is:

$$(1.30) \quad N_t = \frac{Z}{R} - \frac{Z}{R} e^{-Zt} = \frac{Z}{R} (1 - e^{-Zt})$$

where K is an integration constant. If we consider a stock consisting of a single year's recruits, so that  $N_t = 0$  when  $t = 0$ , the constant K is equal to  $-R/Z$ . Hence the general expression for the number of surviving recruits at time  $t$  becomes:

$$(1.29) \quad N_t = \frac{Z}{R} + K e^{-Zt}$$

where R is the number of recruits which enter at a uniform absolute rate over a unit of time (in this case, a year). Integrating the above gives the expression for number of catchable fish at time  $t$  as:



### CHAPTER 3. — VITAL STATISTICS FROM MARKING: SINGLE SEASON EXPERIMENTS

#### 3.1. GENERAL PRINCIPLES OF POPULATION ESTIMATION BY MARKING METHODS

Attaching tags to fish, or marking them by mutilating some part of the body, was first done to trace their wanderings and migrations. Toward the close of the last century, C. G. J. Petersen (1896, etc.) began the practice of using marked fish to compute, first, rate of exploitation, and, secondly, total population, of fish living in an enclosed body of water. These procedures have been widely adopted. The names usually applied are "sample censusing," "estimation by marked members," the "mark-and-recapture method," the "Petersen method," and the "Lincoln index."

The principle of this method was discovered by John Graunt and used in his "Observations on the London Bills of Mortality," first published in 1662 — a work that marks the starting point of demographic statistics (E. S. Pearson personal communication). Children born during a year were the "marked" individuals, and the ratio of births to population was ascertained from a sample. About 10 years after Petersen's first work, Knut Dahl employed the same procedure to estimate trout populations in Norwegian farms. Applications to ocean fishes started toward the end of the first decade of the century. Sample censusing of wild birds and mammals began rather belatedly with Lincoln's (1930) estimate of abundance of ducks from band returns, while Jackson (1933) introduced the method to entomology.

The principal kinds of estimates which can be obtained from marking studies are:

1. rate of exploitation of the population
2. size of the population
3. survival rate of the population from one time interval to the next; most usefully, between times one year apart
4. rate of recruitment to the population

Of course not all mark-and-recapture experiments provide all this information; often only population size is involved. Since about 1950 there has been much activity in developing a variety of procedures for marking and recovery and, for any given procedure, there may be a variety of statistical estimates suited to different conditions. Some of the more comprehensive papers are by DeLury (1951), Chapman (1952, 1954), and Cormack (1969).

The general types of procedure involved are as follows:

1. *Single census* (Petersen type). Fish are marked only once; subsequently a single sample is taken and examined for marked fish. Whereas the *marking* should ideally be restricted to a short space of time, the subsequent sample may be taken over quite a long period.

If only two points are used, this method is indistinguishable from the Petersen type.

In practice, sampling can be and probably usually is somewhat intermediate between direct and inverse. An experimenter may have time for up to two weeks of census sampling, for example, but would be glad to stop earlier if a reasonable number of recaptures has been taken. However, if he decides to finish at the end of a certain day, rather than at exactly the time the  $n$ th recapture is made, the procedure is most akin to direct sampling.

*b. Inverse census.* In inverse censusing, the number of recaptures to be obtained is fixed in advance, and the experiment is stopped as soon as that number is obtained (Bailey 1951). This procedure leads to somewhat simpler statistical estimates than direct sampling. A more important consideration, possibly, is that since the size of the relative sampling error of any estimate depends mainly on the absolute number of recaptures made, fixing the number of recaptures determines the sampling accuracy of the result within fairly narrow limits. Inverse censusing is likely to be most useful with single censuses, but it can also be applied to multiple censusing (Chapman 1952).

*a. Direct census.* In direct censusing, the type usually done, the size of the sample or samples taken is fixed in advance, or is dictated by fishing success, etc.

With any of the above four methods, there are two or three possible procedures in taking the second or census sample.

In experiments using tags, individual fish can be identified each time they are recaptured. In some insect marking experiments an individual has been given an additional mark each time it is recaptured, which serves to identify its previous recapture history. Methods for estimating population, survival rate, and recruitment from this information have been devised by Jackson (1936, etc.), Dowdeswell et al. (1940), Fisher and Ford (1947), Cox (1949), Leslie and Chitty (1951), Bailey (1951), Chapman (1951, 1952), Leslie (1952), and others. These methods vary with the kind of grouping of recaptures used, and with the mathematical model employed; they often require complicated tabulations and solving complex expressions.

4. "Point" censuses. Samples for marking and for obtaining recoveries are made at three or more "points" in time, these periods being preferably short compared with the intervening periods. The first sample is for marking only, the last for recoveries only, and the intermediate one or ones for marking and recovery. A different mark is used each time, and subsequent sampling takes cognizance of the origin of each mark recovered. This type of census is well adapted to estimating survival rate and recruitment.

3. Repeated censuses. Procedures for estimating survival rate from two successive Petersen or Schnabel censuses were developed by Ricker (1942b, 1945a, b).

2. Multiple census (Schnabel type). Fish are marked and added to the population over a considerable period, during which time (or at least during part of it) samples are taken and examined for recaptures. In this procedure samples should be replaced: otherwise the population is decreasing and the population estimate cannot refer to any definite period of time — unless, of course, the samples are a negligibly small fraction of the total population. There is some computational advantage in marking all fish taken in the samples, but it is not essential.

$$(3.3) \quad \frac{1}{N} = \frac{C}{n} = \frac{MC}{R}$$

Similarly, an unbiased estimate of the reciprocal of population abundance is, by direct proportion:

$$(3.2) \quad V^{(n)} = \frac{M^2C}{R(C-R)}$$

With large numbers of recoveries,  $R/C$  can be used as an approximation for the unknown  $M/N$ , giving:

$$\frac{C}{M} \left(1 - \frac{N}{M}\right)$$

Leslie (1952) shows that this is an unbiased maximum likelihood estimate. Assuming random mixing of marked and unmarked fish, its variance is found from the binomial distribution to be:

$$(3.1) \quad \frac{R}{n} = \frac{M}{M}$$

An estimate of rate of exploitation of the population is given by:

$n$  rate of exploitation of the population  
 $N$  size of population at time of marking

We wish to know:

$M$  number of fish marked  
 $C$  catch or sample taken for census  
 $R$  number of recaptured marks in the sample

We have:

3.2.1. SIMPLE PETERSEN ESTIMATES. A number of tagged or marked fish are put into a body of water. Record is then kept of the total number of fish caught out of it during a year or other interval, and of the number of marked ones among them.

### 3.2. PETERSEN METHOD (SINGLE CENSUS)

Only the better-known, easier, or more practical of the above procedures will be presented here. The simple Petersen situation is described first, followed by a review of possible systematic errors, then a description of other procedures.

d. *Sequential censuses*. If the problem is to find whether a population is greater or less than some fixed number, sampling can be done by stages and terminated whenever this point is settled, at any desired degree of confidence. Suitable formulae are given by Chapman (1952).

c. *Modified inverse sampling*. A procedure described by Chapman (1952) works toward a predetermined number of *unmarked* fish in the sample, but here the only advantage appears to be statistical convenience.

That a best estimate does not remain a best estimate when inverted is one of the uncomfortable facts of statistical life. The same is true between a statistic and *any* function of it, other than a linear one. For analogous examples see Sections 2.1 and 11.4.2.

Again, however, it is better to obtain approximate confidence intervals from charts or tables appropriate to the binomial or Poisson distributions, using  $R$  as the entering variable (cf. Example 3.1).

$$V(N^*) = \frac{(M+1)^2(C+1)(C-R)}{(R+1)^2(R+2)} = \frac{(C+1)(R+2)}{N^2(C-R)} \quad (3.8)$$

approximately equal to:

The large-sample sampling variance for  $N^*$  in (3.7) is given by Chapman as with large values of  $R$  there is little difference.

It is usually worthwhile to use (3.7) in place of (3.5) in direct sampling, even though

$$N^* = \frac{R+1}{(M+1)(C+1)} \quad (3.7)$$

3.2.2. ADJUSTED PETERSEN ESTIMATE. Although expression (3.5) is a consistent estimate of  $N$ , in that it tends to the correct value as sample size is increased, it is not quite the best estimate<sup>2</sup>. This is true whether sampling is direct or inverse. Bailey (1951) and Chapman (1951) have shown that with ordinary "direct" sampling (3.5) tends to overestimate the true population. They proposed modified formulae which give an unbiased estimate in most situations. Chapman's version is as follows (omitting  $-1$ , which is of no practical significance):

Confidence limits can be obtained more simply, however, by treating  $R$  as a Poisson or binomial variable (whichever is appropriate), obtaining limits for it directly from a chart or table (Appendix II), and substituting these in (3.5).

This is expression (2.6) of Bailey (1951). However, values of  $MC/R$  are not symmetrically distributed, whereas those of  $R/MC$  are; thus if the normal curve of error is used to calculate limits of confidence, it is best to calculate them for  $1/N$  using (3.4), and then invert them to obtain limits for  $N$ .

$$V(N) = \frac{R^3}{M^2C(C-R)} \quad (3.6)$$

with a sampling variance of:

$$N = \frac{MC}{R} = \frac{R}{C} \quad (3.5)$$

The reciprocal of (3.3) is a consistent estimate of  $N$ ; that is,

$$V(1/N) = \frac{R(C-R)}{M^2C^3} \quad (3.4)$$

The large-sample sampling variance of (3.3) is:

3.2.4. SAMPLING ERROR AND SAMPLE SIZE. Sampling errors for Petersen estimates are most easily obtained from tables or charts of fiducial limits for the binomial, Poisson, or normal approximations to the hypergeometric distribution. Suitable charts have been published by Clopper and Pearson (1934), Adams (1951), and Davis (1964), while Ricker (1937 and Appendix II here) tabulates limits for the Poisson distribution: the latter can be used as an approximation for the others, since they will never give too favorable a picture. The observed number of recaptures  $R$  is entered in the  $x$  column of Appendix II, and the 95% or 99% confidence limits read off. The latter are then substituted for  $R$  in (3.5) or (3.7), and corresponding

Similar statistical bias exists when very small numbers of recaptures are made with other kinds of estimates of population, survival rate, and rate of exploitation, described in the sections and chapters to follow.

Since true  $N$  is unknown it is more convenient to have a rule based on an observed statistic, the number of recaptures ( $R$ ). For the Poisson situation (i.e. when  $M/N$  is small) the lower confidence limits in Appendix II will indicate the probability of  $R = 0$  for any observed  $R$ , and thus whether systematic bias of this type is likely. For 95% confidence, true  $R$  will not be less than 1 if observed  $R = 3$  or more; and for 99% confidence this is true when observed  $R = 4$  or more. If  $M/N$  is not small, these limits are somewhat more severe than is necessary. Thus the probability of statistical bias can be ignored if recaptures number 3-4 or more.

Therefore, in practice, a less stringent condition can be used: that  $MC$  be greater than four times the true population  $N$ , in which event the probability of bias will be less than 2% (Robson and Regier 1964).

(3.11)

$$-N e^{-MC/N}$$

bias is close to:

3.2.3. STATISTICAL BIAS IN PETERSEN ESTIMATES. Expression (3.7) provides an unbiased estimate of  $N$  if  $(M + C) > N$ , so that there is no chance that  $R$  might be zero because of sampling variability (Chapman 1951, Robson and Regier 1964). If this condition is not met the estimate  $N^*$  has negative bias. Provided  $N > 100$  this

(3.10)

$$N = \frac{R}{C(M+1) - 1}$$

and his expression for the variance is similarly adjusted, but practically these are indistinguishable from Chapman's formulae.

For "inverse" sampling — which ceases when a predetermined  $R$  has been taken — (3.5) is close to being an unbiased estimate of  $N$ . Nevertheless, a modified formula is slightly better (Bailey, p. 298):

(3.9)

$$N = \frac{M(C+1)}{R+1}$$

Bailey's (1951) expression corresponding to (3.7) differs slightly:

Expressions (3.3)-(3.8) are applicable whether the fish captured are removed from the population or whether they are returned to it (Chapman 1952, p. 300).

$$V(S_1) = S_1^2 \left( \frac{1}{R_{12}} + \frac{1}{R_{22}} - \frac{1}{M_1} - \frac{1}{M_2} \right) \quad (5.2)$$

The large-sample variance of (5.1) can be obtained by substituting the estimates in Seber's (1972) more general expression (see Section 5.1.3), as follows:

This is the large-sample formula of Ricker (1945a, 1948). Notice that it is not essential that all the marked fish recaptured be reported. It is only necessary that during year 2, the marks put on at the start of year 1 be reported as completely as those put on at the start of year 2.

$$S_1 = \frac{R_{12}M_2}{M_1R_{22}} \quad (5.1)$$

We may reason as follows: the number of fish,  $M_2$ , marked at the start of the second year, yields  $R_{22}$  recaptures that year; thus the rate of exploitation in year 2 is  $u_2 = R_{22}/M_2$ . Of the  $M_1$  fish marked in year 1,  $R_{12}$  are caught in year 2. The number of first-year marked fish still at large at the start of year 2 should be  $R_{12}/u_2$ , or  $R_{12}M_2/R_{22}$ . The latter number must be compared with the number of marked fish at large at the start of year 1,  $M_1$ , to obtain the survival rate over that period:

$S_1$  survival rate during year 1 (from time of marking in year 1 to time of marking in year 2)

We wish to know:

$M_1$  number of fish marked at the start of the first year  
 $M_2$  number of fish marked at the start of the second year  
 $R_{11}$  recaptures of first-year marks in the first year  
 $R_{12}$  recaptures of first-year marks in the second year  
 $R_{22}$  recaptures of second-year marks in the second year

5.1.1. NATURAL MORTALITY THE SAME AT ALL AGES. The most direct approach to an estimate of survival by marking is to run similar marking experiments in two successive years (or other interval), using different marks for each. When marking is all done right at the start of the fishing season, we have the following:

5.1. POPULATION AND SURVIVAL RATE WHEN MARKING IS DONE AT THE START OF FISHING IN TWO CONSECUTIVE YEARS — RICKER'S METHOD

## CHAPTER 5.—POPULATION STATISTICS FROM MARKING EXPERIMENTS EXTENDING THROUGH TWO OR MORE TIME INTERVALS, WITH VARIABLE SURVIVAL RATE

Expression (5.1) can be modified for small numbers of recaptures by analogy with expressions (3.7) and (5.12):

$$S_1 = \frac{R_{12}M_2}{M_1(R_{22} + 1)} \tag{5.3}$$

Expression (5.2) can be used for the variance of this estimate also.

The estimate of  $S_1$  from (5.1), rather than (5.3), has the advantage that it can be transformed directly to  $A_1$  and  $Z_1$ ; hence  $F_1$  and  $M$  can be computed using (5.28) provided the recaptured marks are reported completely. The value of  $F_2$  is also available, if acceptable data of the type shown by equation (5.27) are at hand.

5.1.2. NATURAL MORTALITY VARIES WITH AGE. The method above can also be made to take care of any changes in natural mortality rate associated with age which may occur among the fish. If such are important, the fish marked in the second year,  $M_2$ , should have a minimum size greater than that of the fish marked in the first year,  $M_1$ , by one year's growth (Ricker 1945a). Still better, the computation can be made to apply to one or more definite year-classes or length-groups of fish in two successive years of their existence by using different marks, or merely by advancing the boundary between the groups as the fish increase in size, as in Example 3.2 above.

EXAMPLE 5.1. SURVIVAL RATE OF BLUEGILLS IN MUSKELLUNGE LAKE, FROM MARKINGS DONE AT THE START OF TWO CONSECUTIVE YEARS. (From Ricker 1948.)

The procedure of Section 5.1 was the principal one used during the 1940's to estimate vital statistics of fish populations in small Indiana lakes. An example concerning bluegills (*Lepomis macrochirus*) of Muskellunge Lake will be described; the data are from Ricker (1945a, p. 383-384).

Of  $M_1 = 230$  bluegills marked before the start of the 1942 fishing season,  $R_{12} = 13$  were captured in 1943. Of  $M_2 = 93$  marked before the start of the 1943 fishing season,  $R_{22} = 13$  were recaptured in 1943. The survival rate in the first year is therefore, from (5.3):

$$S_1 = \frac{13 \times 93}{230 \times 14} = 0.37546$$

From (5.2), the variance of  $S_1$  is:

$$V(S_1) = 0.37546^2 \left( \frac{1}{1} + \frac{13}{1} - \frac{1}{230} - \frac{1}{93} \right)$$

$$= 0.14097 \times 0.13874 = 0.01956$$

The standard error is the square root of this, or 0.1398.