BULLETIN No. 119

Handbook of computations for biological statistics of fish populations

By W. E. RICKER

Fisheries Research Board of Canada
Nanaimo, B. C.

PUBLISHED BY THE FISHERIES RESEARCH BOARD OF CANADA UNDER THE CONTROL OF THE HONOURABLE THE MINISTER OF FISHERIES

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W. E. RICKER
N. M. CARTER
Editors

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FOREWORD

Most scientific studies of animal population dynamics have taken place in the twentieth century. This was really a new approach to classical biology and required a certain competence in mathematics. It is not a simple study. Fish populations do not lend themselves readily to direct count and thus introduce even further complications.

About three decades ago, some of the more aggressive minds began to separate out the effects of births, deaths and growth on fish populations, and how a population responds to changes in these variables. In the guise of a Handbook of Computations, the present work reviews the major contributions to date in this field, and arranges within a logical framework the independent but interrelated approaches of different investigators. The author of the Handbook has himself been among the leaders in this complex field.

The scientific study of fisheries has not yet been developed into a separate discipline. A work such as the present one, which it is a privilege to introduce, is proof that this field is fast becoming an independent science.

J. L. KASK, *Chairman*,
Fisheries Research Board of Canada.

Ottawa,
February 14, 1958.

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PREFACE

This Bulletin has been prepared to meet a need for a summary of the computations used in estimating statistics of population size and exploitation—particularly those most applicable to fishes. Contributions to this field have appeared rapidly in recent years, and a review should help to relate the ideas and procedures of the various workers. I have included most of the basic procedures and important variants which have come to my attention through 1956. Worked examples are given of those which have been most used, or which seem to offer promise of wide usefulness.

The arrangement of material is primarily generic. Methods which seem conceptually similar are presented in the same chapter, proceeding from the simpler to the more complex as far as possible. Some attention is given also to the historical development of each topic. Some things, of course, did not fit very well into the arrangement adopted, or into any other that was considered.

The amount of space that each topic receives varies with its importance and with its availability. Procedures recently described in standard western journals are not, as a rule, given detailed development: usually only the formulae most useful for estimating population statistics are quoted, together with their asymptotic variance (when available), and a discussion of the necessary conditions which make them usable. More extended treatment is given to methods taken from obscure sources and from my 1948 study (now out of print), and to occasional new developments or new aspects of existing methods. This plan does not give ideal balance within the Handbook, but it does perhaps make for maximum usefulness within a limited compass. Unfortunately it has been impossible to consider fully and assess some of the recent work, particularly from Japan and the USSR. References to some of these papers are included in the bibliography. For those familiar with the Japanese language much has been summarized recently by Kubo and Yoshihara (1957), while contemporary theory and practice in the USSR are exemplified in the works of Moiseev (1953), Monastyrsky (1940, 1952) and Nikolsky (1953). The outstanding contribution to fish population dynamics by Beverton and Holt (1957) became available only during revision of the proof of this Bulletin, but much of its basic material was available in earlier publications of these authors.

In selecting illustrative examples, no attempt has been made to give representation to effort in fishery research on a geographical basis: rather, examples close at hand have usually been selected. The examples from "borrowed" data involve risks of misinterpretation, and are used here to illustrate methodology rather than as a factual treatment of the situations concerned; although, at the same time, I have tried to be as realistic as possible.

This Handbook is of course not intended as a complete text book for fishery biologists. Methods of measuring fish, determining their age, marking, tagging, collecting and tabulating catch statistics—all these are mentioned only incidentally, although they provide the data from which the vital statistics of a stock must be estimated. Nor are we concerned here with the other animals and plants of the environment, or with the flow of nutrient energy which maintains a fish population.

From the point of view of fishery management, information from computations of the kinds described in this Handbook provide only a part of the basic information upon which policy can be based. Sometimes, to be sure, they can provide the greater part of the necessary information. In other situations they have as yet given only equivocal answers to important questions. This is particularly true where several species are possible occupants of and competitors for an important environment, and their relative abundance may vary with the intensity of the fishery or with physical changes. The fishery administrator has also the problem (often not an easy one) of selecting an objective which his regulations are designed to serve, and this involves questions of economics and public policy which are not touched on here. However, there is no question that the increase of biological information has already improved, and will continue to improve, the precision and effectiveness of fishery management.

Some attempt has been made to meet the needs of the beginning student of fishery biology by working out certain examples in detail, even where this consists largely of standard mathematical procedures. To be used as an introductory text book, however, this Handbook should be "cut down" by omitting less frequently used methods and by choosing one among several alternative procedures where these exist. The choice would depend partly on local problems and interests; however, a generalized selection could be as follows:

Chapter 1; a good deal of Chapter 2, not omitting 2I; Chapter 3, A-H; Chapter 4, A, C and D; Chapter 5, A; Chapter 6, A, B and E; Chapter 7, B and C; Chapter 9, A-E; Chapter 10, A, B, C, E and F; Chapter 11, A, C and D; and Chapter 12, A and C.

Some examples have been simplified for presentation here, and others have been invented, in order to keep the text within bounds. However, the practising biologist quickly discovers that the situations he has to tackle tend to be more complex than those in any Handbook, or else the conditions differ from any described to date and demand modifications of existing procedures. It can be taken as a general rule that experiments or observations which seem simple and straightforward will prove to have important complications when analyzed carefully—complications which stem from the complexity and variability of the living organism, and from the changes which take place in it, continuously, from birth to death. Two general precautions are to divide up any body of data in relation to the size, age, sex and history of the fish involved, and in relation to time of the observations (successive hours, days or seasons).

About a third of the text of this Handbook is taken or adapted from "Methods of Estimating Vital Statistics of Fish Populations", published in 1948 by Indiana University as one of its Science Series of Publications. I am indebted to Dr. R. E. Cleland, Dean of the School of Graduate Studies of Indiana University, for permission to quote largely from this work. This 1948 material is for the most part in Chapters 2-5 of the present Bulletin. It proved impractical to use specific references to the 1948 publication, but everything substantial in it appears here.

Finally, I wish to thank the numerous individuals who have assisted in this project in various ways. Among these are F. H. Bell, R. J. H. Beverton, Yvonne Bishop, M. D. Burkenroad, K. D. Carlander, D. W. Carr, N. M. Carter, D. G. Chapman, Frances N. Clark, L. R. Day, D. B. DeLury, L. M. Dickie, A. W. Eipper, R. E. Foerster, N. P. Fofonoff, R. A. Fredin, F. E. J. Fry, S. D. Gerking, Michael Graham, J. L. Hart, D. W. Hayne, Ralph Hile, S. J. Holt, E. C. Jones, J. L. Kask, W. A. Kennedy, K. S. Ketchen, L. A. Krumholz, P. A. Larkin, E. D. LeCren, W. R. Martin, R. B. Miller, D. J. Milne, Garth Murphy, Ferris Neave, A. W. H. Needler, Tamio Otsu, J. E. Paloheimo, D. S. Robson, G. A. Rounsefell, M. B. Schaefer, F. X. Schumacher, D. C. Scott, M. P. Shepard, R. P. Silliman, G. F. M. Smith, L. L. Smith Jr., J. C. Stevenson, Bruce Taft, C. C. Taylor, F. H. C. Taylor, A. L. Tester, K. E. F. Watt, D. A. Webster, W. P. Wickett, T. M. Widrig and D. E. Wohlschlag. Some of the above had pointed out errors or inadequacies in the 1948 study, and many have assisted by reading and criticizing a first draft of Chapters 1 and 6-12 of the present Handbook, which was circulated in 1955. From so large a group a certain number of contradictory opinions were to be expected, but all comments have proved very helpful.

CHAPTER 1.—INTRODUCTION

1A. THE PROBLEMS

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

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.

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 potential sources of error have received close consideration.

The development of procedures for estimating population size and survival rate started early but progressed much more slowly. In the past 10 years there has been much activity along theoretical lines, and numerous new applications. An investigator now has a number of methods from which to choose one best suited to the population he is studying, and he can increasingly use one method to check another.

The study of reproduction or "year-class strength" has been considered mainly in relation to environmental factors, but some work on its relation to stock density has begun.

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 1920's, and there is now a considerable body of information and a corresponding methodology.

1B. 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 in this Handbook, it is shown here in brackets. Terms marked with an asterisk are not used in this Handbook, at any rate not in a context where strict definition is called for.

Absolute rate of 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, usually indicated by a roman numeral, or an arabic numeral followed by a plus sign (e.g., age V, age 5+)[1]. In the northern hemisphere a useful convention is to use the end of the calendar year as a cut-off time, so that a fish is considered to become age I at the first New Year's following its hatching. In temperate regions most fish do not grow in winter, so this convention avoids breaking up growing seasons.

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) mortality rate (m or n): The fraction of an initial stock which *would* die during the year (or season) from a given cause, if no other causes of mortality operated.

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: *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. 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.

Catchability (c): The fraction, *of the whole fish stock under consideration*, which is caught by a defined unit of the fishing effort actually used. This fraction is nearly always small—say, less than 0.01—so it can be used as an instantaneous rate in computing population change. (For fractions taken of various portions of the stock, see "vulnerability".)

Catch curve: A graph of the logarithm of number of fish taken at successive ages or sizes.

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[1] While the above are recommended, other usages exist. Arabic numbers almost have to be used, instead of roman, when fractions follow: e.g., age $2\frac{1}{3}$. On the west coast of North America the age of salmon is usually given in terms of the year of life in progress, while the year of its seaward migration is indicated by a subscript. Thus a "5_3" salmon went to sea when age II (in its third year of life) and returned when age IV (in its fifth year). Russian and some Japanese investigators, however, would designate the same fish as "4_2" or "4_2+". In situations such as this, the advantages of uniformity of usage within a long temporal sequence of data may outweigh the advantage of conforming with some continent-wide or world-wide standard. I have also seen ages designated as 2−, 3−, etc., particularly when the fish are caught shortly before the birthdays indicated.

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).

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): 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: (Y_E): The catch (by weight) 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 density is not changing from one year to the next. (See also "surplus production".)

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 1G).

2. Effective fishing effort.

***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 1D. Also called: logarithmic, exponential or compound-interest rates.

Instantaneous rate of fishing mortality (p): 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 (Fry).

Instantaneous rate of growth (g): The natural logarithm of the ratio of final weight to initial weight, for a unit of time. It is usually computed on a yearly basis, and may be applied either to individual fish, or collectively to all fish of a given age in a stock.

Instantaneous rate of mortality (i): 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 (q): 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 which 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 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 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 ($g + z - q$): Equal to rate of growth plus rate of recruitment less rate of natural mortality—all 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).

MAXIMUM EQUILIBRIUM CATCH (OR YIELD): The largest average catch which can continuously be taken from a stock under current 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 sustained yield; sustainable catch.

*MECHANICAL INTENSITY OF FISHING: Fishing effort.

NATURAL MORTALITY: Deaths from all causes except man's fishing, including 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 a specified time interval immediately following (usually a year). The term may also be applied to separate parts of the stock which are distinguished by size, sex, etc. (See also "rate of utilization".) Also called: *fishing coefficient (Heincke).

RATE OF FISHING (p): Instantaneous rate of fishing mortality.

*RATE OF NATURAL INCREASE: Instantaneous rate of surplus production.

RATE OF REMOVAL: An inexactly-defined term which can mean either rate of exploitation or rate of fishing—depending on the context (see Section 1D, last paragraph, p. 26).

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. The size at which a fish becomes "vulnerable" must often be specified more or less arbitrarily, since recruitment is commonly accomplished by way of vulnerability increasing over a fairly wide range of sizes. A "decruitment" may also occur in some fisheries where large individuals leave the fishing area or become uncatchable, but in computations this has rarely been treated separately from natural mortality.

RECRUITMENT CURVE: A graph of the progeny of a spawning at the time they reach a specified age (for example, the age at which half of the brood has become vulnerable to fishing), plotted against the abundance of the spawning stock which produced them. (A reproduction curve is a special case of this.)

REPRODUCTION CURVE: A graph having abundance of spawners on the abscissa, and on the ordinate the density of mature stock resulting from those spawners, *expressed in comparable units.*

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.

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: equilibrium catch (Schaefer). I prefer to reserve the latter term for situations where the equilibrium catch is actually being caught.

SURVIVAL RATE (s): Number of fish alive after a specified time interval, divided by the initial number. Usually on a yearly basis.

USABLE STOCK: The weight of all fish in a stock which lie within the range of sizes customarily considered usable (or designated so by law). Also called: *standing crop.

VIRTUAL POPULATION (V): The part, by number, of the fish alive at a given time, which will be caught in future.

VULNERABILITY: A term equivalent to catchability but 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. 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 1D, 1F).

1C. SYMBOLS

The principal symbols used are listed below. More detailed definitions of some of the terms were given in Section 1B, and various derivations and interrelationships are in Sections 1D-1G.

The symbols adopted are mainly those listed by Widrig (1954a, b). The principal difference is that his symbol Q, for catchability, which should preferably be a lower case letter, is replaced by the *c* used by Beverton (1954), Tester (1955) and Beverton and Holt (1956). The quantities designated by Widrig's symbols *b* and *c* are not referred to here, and his definitions for them are omitted.

To facilitate comparisons with original accounts, the symbols used by the originator or popularizer of a method of analysis are usually given in the section where it is described. Widrig (1954a) has a table comparing the symbols of a number of authors, as has Gulland (1956a). In addition, symbols proposed for use by certain international fishery organizations are shown where appropriate, using the latest version of the list at hand (Report of the 1957 Lisbon meetings sponsored by FAO/ICNAF/ICES); these are preceded by "*int.*".

a	1. annual (or seasonal) mortality rate 2. the ratio P_r:P_m (see Appendix I)
b	1. the exponent in the length-weight relationship 2. the complement of catchability $(1 - c)$
c	catchability (*int.*, q)
e	2.71828...
f	effective fishing effort (*int.*, f or X)
g	instantaneous rate of growth
h	annual growth rate
i	instantaneous rate of (total) mortality (*int.*, Z)
k	a rate; used in various connections
l	length of a fish (*int.*, l)
m	annual (or seasonal) rate of fishing mortality
n	annual (or seasonal) rate of natural mortality

p	instantaneous rate of fishing mortality (*int.*, F)
q	instantaneous rate of natural mortality (*int.*, M)
r	1. availability (of Marr) 2. rate of accretion (Section 5C)
s	1. rate of survival (*int.*, S) 2. standard deviation
t	time or age, often used as a subscript (*int.*, t)
u	1. rate of exploitation of a fish stock (μ of Ricker, 1948) 2. the ratio of number of recoveries to number of marked fish released (= R/M)
v	expectation of natural death (ν of Ricker, 1948)
w	weight of a fish (*int.*, w)
x	any variable
y	instantaneous rate of emigration
z	1. instantaneous rate of immigration 2. instantaneous rate of recruitment
A	average population in successive years
B	number of natural deaths
C	1. catch, in numbers—usually for a whole year (*int.*, C) 2. number of fish examined for tags or marks
D	total deaths (= B + C)
F	size of a progeny or filial generation
K	a rate; used in various connections, but particularly in von Bertalanffy's growth formula
L	length at recruitment
M	number of fish marked or tagged
N	number of fish in a year-class or population (*int.*, N)
P	1. size of a parental stock or generation 2. level of statistical probability
Q	1. the yearly number of individuals which reaches the minimum reference age, t_Q, used in a yield computation (*int.*, R, approximately) 2. the constant which appears in the integration of Baranov's production computation
R	1. number of recruits to the vulnerable stock 2. number of recaptures of marked or tagged fish
T	an interval of time
V	1. virtual population 2. variance
W	1. weight of a group of fish; for example, of a year-class, or of an entire stock (*int.*, P) 2. size of adult stock divided by the size which produces the "replacement" number of recruits (see Appendix I)
Y	catch or yield, by weight (*int.*, Y)
Z	recruits to a stock, divided by the "replacement" number of recruits (see Appendix I)

A bar over a symbol indicates that it is an average value, and a circumflex (^) indicates that it is an estimate rather than the true value.

1D. NUMERICAL REPRESENTATION OF MORTALITY

The mortality in a population, resulting from any given cause, can be expressed numerically in three different ways.

(a) Simplest and most realistic perhaps is the *annual expectation of death* of an individual fish from a given cause, expressed as a fraction or percentage. This is the fraction of the fish present at the start of a year which actually die during the year from that cause.

(b) There is also an *annual mortality rate* associated with each cause of death, which is the fraction of the fish present at the start of a year which would die during the year from the given cause, *if* no other causes of death existed.

(c) If the number of deaths in a small interval of time is at all times proportional to the number of fish present at that time, the fraction which remains at time t, of the fish in a population at the start of a year ($t = 0$), is:

$$\frac{N_t}{N_0} = e^{-it} \tag{1.1}$$

The parameter i is called the *instantaneous mortality rate.* If the unit of time is 1 year, then at the end of the year (when $t = 1$):

$$\frac{N_1}{N_0} = e^{-i} \tag{1.2}$$

But $N_1/N_0 = s = (1 - a)$; hence $(1 - a) = e^{-i}$, or $i = -\log_e(1 - a)$; hence the instantaneous mortality rate is equal to the natural logarithm (with sign changed) of the complement of the annual (actual) mortality rate.

The instantaneous rate i also represents the number of fish (including new recruits) which would die during the year if recruitment were to exactly balance mortality from day to day, expressed as a fraction or multiple of the steady density of stock.

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 i/n represent the expectation of death of the fish during each such interval; or, in other words, i/n is the fraction of a large population which would actually die during each time interval one-nth of a year long. In such a relationship, i 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, i/n must be a small fraction. But of course the cumulative effect of the death of i/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 $n = 1{,}000$ and $i = 2.8$. 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 2,800 will die and 997,200 will remain alive. During the next thousandth of the year 0.28% of 997,200 = 2,793 die and hence 994,407 survive. Repeated 1,000 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 $i = 2.8$. This relation is not quite exact, because 1,000 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: $(1-a)=e^{-i}$ where $e=2.71828$. In this example, for $i=2.8$, $a=0.9392$, so that the approximate calculation was not far off. Obviously there is no limit to the possible size of i, but a cannot exceed unity—that is, no more fish can die than are actually present. On the other hand, when i and a are small they approach each other in magnitude. The table of Appendix II shows that when $i=0.1$ there is only 5% difference between them.

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 i 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 predaceous 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.

In practice, sources of mortality are usually divided into the two categories, "fishing" and "natural", so that the three kinds of rates described above can be listed as follows:

	Symbol
I. Instantaneous mortality rates—	
1. Total	i
2. From fishing ("rate of fishing")	p
3. From natural causes	q
II. Annual mortality rates—	
1. Total	a
2. From fishing	m
3. From natural causes	n
III. Annual expectations of death—	
1. Total	a
2. From fishing ("rate of exploitation")	u
3. From natural causes	v

The fundamental relationships among these quantities, as described above, can be summarized as follows:

$$p + q = i \tag{1.3}$$

$$a = 1 - e^{-i} \tag{1.4}$$

$$m = 1 - e^{-p} \tag{1.5}$$

$$n = 1 - e^{-q} \tag{1.6}$$

$$a = m + n - mn \tag{1.7}$$

$$\frac{i}{a} = \frac{p}{u} = \frac{q}{v} \qquad (1.8)^2$$

$$u + v = a \tag{1.9}$$

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[2] The conditions which make this expression applicable are given in the paragraph following. The other relationships of the group (1.3)—(1.9) are not restricted.

To use the concepts under I and II above it is not necessary that fishing and natural mortality occur at rates which are proportional within the year. For example, a simple calculation will show that a 50% annual rate of natural mortality (n), combined with a 50% annual 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 (u and v), though the latter always add up to equal a. Expression (1.8) above pertains, strictly speaking, only to the situation where fishing and natural mortality are distributed proportionately within the year. (As noticed earlier, it is not necessary that each be of a constant magnitude on an astronomical time scale.) If it appears that this condition will be violated in an actual fishery, it is sometimes possible to arrange the statistical year for the population 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, so that the error in using (1.8) is minimized.

If fishing is so distributed, seasonally, that this treatment is not realistic, the year can be divided into two or more parts and separate values of p, q, etc., computed for each.

In popular descriptive usage, the relative usefulness of u and p—rate of exploitation and rate of fishing—will depend partly upon the kind of fishery. If fishing occurs at a time when there is little or no recruitment, then a rate of exploitation of, say, 65% shows the fraction of the vulnerable stock being utilized each year; and to say that the rate of fishing is 105% means little to the layman. The situation is different, however, when fishing, recruitment and natural mortality take place throughout the same period of time: in that event, for example, with a 65% rate of exploitation and 10% natural mortality, the year's catch equals 1.21 times the stock on hand at any given time. In such a case the rate of fishing, 121%, seems the more concrete and realistic description of the effectiveness of the fishery.

1E. RECRUITMENT, STOCK AND CATCH IN NUMBERS

TYPES OF IDEAL FISH POPULATIONS. A classification of fish populations in use for some years (Ricker, 1944) is shown below:

IA. Natural mortality and recruitment occur during a time of year other than the fishing season. The population decreases during the fishing season because of catch removals.

IB. Natural mortality occurs along with the fishing, and each occurs at a constant instantaneous rate, or the two rates vary in parallel fashion. Recruitment occurs at some other time of year.

IIA. Natural mortality and fishing mortality take place continuously and at constant instantaneous rates, or else vary in parallel fashion, and are balanced at all times by recruitment, so that the population is in equilibrium.

IIB. Population may either increase or decrease. Recruitment is at an even absolute (linear) rate through the season. Natural and fishing mortality occur at a rate proportional to population present at any moment.

The qualifications of these categories will of course usually be approximated rather than rigidly met, and intermediate types must often be considered.

Single year-classes. Consider a single brood (year-class) 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_1 in Figure 1.1. The *average* abundance during the year is the area of the figure under AB_1, divided by the length of the base (which is unity). In our symbols, this is:

$$\bar{N} = \int_{t=0}^{t=1} Ne^{-it}\,dt = N\left(\frac{e^{-i}}{-i} - \frac{1}{-i}\right) = \frac{N(1-e^{-i})}{i} = \frac{Na}{i} \qquad (1.10)$$

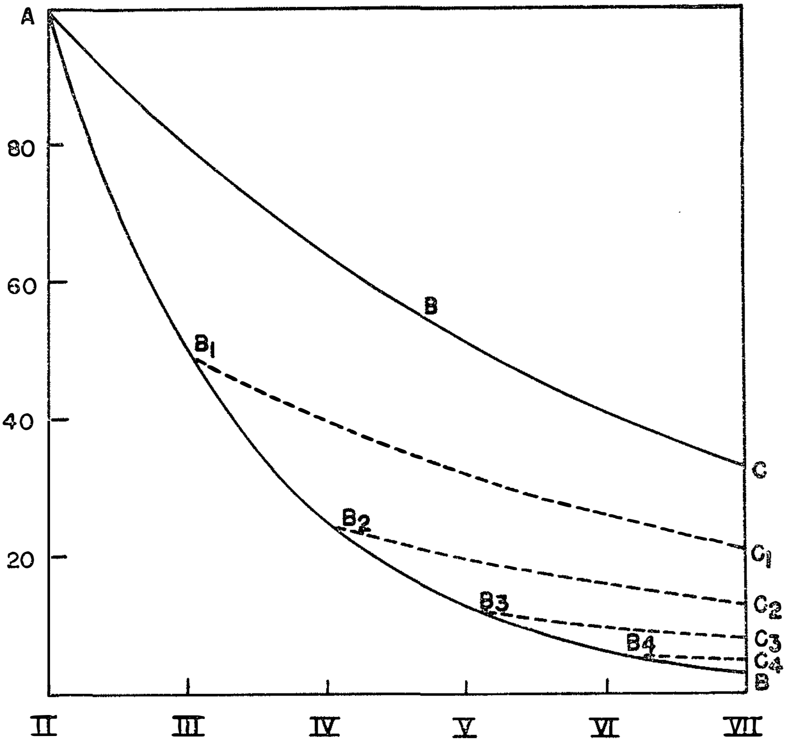

Figure 1.1 Exponential decrease in a stock from an initial abundance of 100 at age II, when the annual mortality rate is 0.2 (AC) and when it is 0.5 (AB). The dotted lines indicate population structure during a period of transition from the smaller to the larger mortality. (Redrawn from figure 8 of Baranov,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

The total deaths, which equal Na by definition, are therefore i times the average population. Since the mortality is at each instant divided between natural causes and fishing in the ratio of p to q, then natural deaths, B, are $q/(p+q) = q/i$ times Na, or q times the average population:

$$B = \frac{q}{p+q} \cdot Na = \frac{qNa}{i} = q\bar{N} \qquad (1.11)$$

Similarly the catch is p times the average population:

$$C = \frac{pNa}{i} = p\overline{N} \tag{1.12}$$

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.

INSTANTANEOUS RECRUITMENT. Consider R recruits added to the catchable stock of a species each year. Suppose the stock is of type IA or IB, 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 one year to Re^{-i} or Rs, in two years to Rs^2, in t years to Rs^t. Under these equilibrium conditions the total population present just after recruitment in any year is found by summing the converging geometric series:

$$\begin{aligned} N &= R + Re^{-i} + Re^{-2i} + \ldots . \\ &= R(1 + s + s^2 + \ldots .) \\ &= R\left(\frac{1 - s^{\infty}}{1 - s}\right) = \frac{R}{(1 - s)} = \frac{R}{a} \end{aligned} \tag{1.13}$$

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

$$\begin{aligned} N &= Re^{-0.5i} + Re^{-1.5i} + Re^{-2.5i} + \ldots . \\ &= Re^{-0.5i}\,(1 + e^{-i} + e^{-2i} + \ldots .) \\ &= \frac{Re^{-0.5i}}{a} \end{aligned} \tag{1.14}$$

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

$$N = \frac{Re^{-i}}{a} = \frac{Rs}{a} \tag{1.15}$$

which is its least value.

The average size of the stock over the course of a year (unit time), during which it decreases from R/a to Re^{-i}/a, is of course:

$$\overline{N} = \frac{R}{a}\int_{t=0}^{t=1} e^{-it}\, dt = \frac{R}{a}\cdot\frac{a}{i} = \frac{R}{i} \tag{1.16}$$

CONTINUOUS RECRUITMENT. Consider a fishery of type IIA, in which R recruits enter a catchable stock at a steady absolute rate throughout the year, instead of all at once; and the stock is in equilibrium at density $\overline{N}$, with the number of recruits just balancing the number of deaths at all times. The number of fish which die in the course of a year is the product of the number present times the instantaneous mortality rate:

$$\text{Total deaths} = \overline{N}i \tag{1.17}$$

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

$$\text{Deaths of ``old'' fish} = \overline{N}a \tag{1.18}$$

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

$$\text{Deaths of the year's recruits} = \overline{N}(i - a) \tag{1.19}$$

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

$$R = \overline{N}i \tag{1.20}$$

Hence the number of recruits which die during their year of recruitment (expression 1.19) can also be written as (substituting $\overline{N} = R/i$):

$$\frac{R(i - a)}{i} \tag{1.21}$$

The number of recruits which survive the year is therefore:

$$R - \frac{R(i - a)}{i} = \frac{Ra}{i} \tag{1.22}$$

The development of expression (1.22) 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, i, and to recruitment, R:

$$\frac{dN_t}{dt} = -iN_t + R \tag{1.23}$$

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:

$$N_t = \frac{R}{i} + Ke^{-it} \tag{1.24}$$

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 $-R/i$. Hence the general expression for the number of surviving *recruits* at time t becomes:

$$N_t = \frac{R}{i} - \frac{R}{i}e^{-it} = \frac{R}{i}(1 - e^{-it}) \tag{1.25}$$

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

$$\frac{R}{i}(1 - e^{-i}) = \frac{R(1 - s)}{i} = \frac{Ra}{i} \tag{1.26}$$

as in (1.22) above.

During their second year of life the above survivors (expression 1.22) are subject to the full mortality rate a, so that $\mathrm{R}a^2/i$ die and $\mathrm{R}as/i$ survive. The total population of all ages, at the beginning of any year, is therefore found by summing the geometric series:

$$\begin{aligned} \mathrm{N} &= \frac{\mathrm{R}a}{i} + \frac{\mathrm{R}as}{i} + \frac{\mathrm{R}as^2}{i} + \ldots . \\ &= \frac{\mathrm{R}a}{i}\left(\frac{1 - s^{\infty}}{1 - s}\right) = \frac{\mathrm{R}a}{i} \cdot \frac{1}{a} = \frac{\mathrm{R}}{i} \qquad (1.27) \end{aligned}$$

But since recruitment and mortality are continuous, the population is the same at all times of year, and (1.27) represents the stock continuously on hand, $\overline{\mathrm{N}}$.

Since (1.27) is the same as (1.16), 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/i. 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.

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:

$$\frac{\mathrm{R}a_1}{i_1} + \frac{\mathrm{R}s_2a_1}{i_1} + \frac{\mathrm{R}s_3s_2a_1}{i_1} + \frac{\mathrm{R}s_4s_3s_2a_1}{i_1} + \ldots . \qquad (1.28)$$

and the catch is:

$$\frac{p_1\mathrm{R}a_1}{i_1} + \frac{p_2\mathrm{R}s_2a_1}{i_1} + \frac{p_3\mathrm{R}s_3s_2a_1}{i_1} + \ldots . \qquad (1.29)$$

If, in addition, the number of recruits varies, the R terms too would have to carry separate subscripts. Numerical calculations where these parameters vary are most easily carried out in tabular form (e.g., Tables 8.2-8.4) though general formulae have been given for the situation when i changes once (Ricker, 1944, p. 32).

1F. GROWTH AND YIELD IN WEIGHT

From the time they are hatched, the individual fish in a brood increase in size, at the same time as they are reduced in numbers. The mass of the whole brood, at a given time, is determined by the resultant of the forces of growth and of mortality. Since man is usually interested in the weight, rather than the number, of fish which he can catch, the individual rate of increase in weight must be balanced against the rate of decrease in numbers in order to obtain an expression from which to compute weight yields.

USE OF OBSERVED AVERAGE WEIGHTS. Possibly the simplest way to take growth into account in constructing such a population model is to combine schedules of age distribution with observed information on the average size of fish at successive ages. An example is shown in Table 10.1 of Chapter 10. This procedure presents a difficulty when any considerable deviation from the existing mortality rate is being examined. For example, as mortality rate increases, the fish caught of a given age will be smaller, on the average, because they decrease in numbers more quickly and fewer survive to the larger sizes reached later in the year. (This is distinct from any actual change in rate of growth that may occur.)

RATE OF GROWTH. When growth is exponential, it may be treated in the same manner as mortality. There is a *relative rate of growth*, h, and a corresponding *instantaneous rate of growth*, g. If w_t is the weight of a fish at time t, and w_0 is its weight at $t = 0$, then the equation of exponential growth is:

$$\frac{w_t}{w_o} = e^{gt} \tag{1.30}$$

If the initial weight is taken as unity, at the end of a unit of time the weight is e^g, and it has increased by $e^g - 1$; hence:

$$h = e^g - 1$$

and

$$\begin{aligned} g &= \log_e(h+1) \\ &= \log_e(w_t/w_o) \text{ when } t = 1 \end{aligned} \tag{1.31}$$

For example, a fish which grew from 2 to 5 lb. in unit time (say a year) would have an absolute growth of 3 lb. per year. Its relative or annual growth rate is $h = 3/2 = 1.5$ or 150% per year. Its instantaneous rate of growth is $g = \log_e(5/2) = 0.916$ (on a yearly basis). Pairs of values of h and g are shown in columns 12 and 13 of Appendix II. It is customary to estimate the rate of growth of a year-class from that of its individual members, though selective mortality is a possible source of error (Section 9A).

In practice, growth is not usually exponential over any very long period of the life of a fish, but any growth curve can be treated in this way if it is divided up into segments of suitable length.

CHANGE IN STOCK SIZE WITHIN A YEAR. The simplest way to relate growth to mortality is to calculate the instantaneous rate of growth for each year separately, and combine it with the instantaneous mortality rate, i, to give the instantaneous rate of change in bulk, $g - i$. Putting W_o for the initial weight of the year-class, and W_t for the weight at time t:

$$\frac{W_t}{W_o} = e^{(g-i)t} \tag{1.32}$$

provided that the rates of growth and mortality do not change with the seasons. If the proviso holds, the average weight of the year-class during the year can be found from:

$$\overline{W} = \int_{t=0}^{t=1} We^{(g-i)t}\, dt$$

$$= \frac{W(e^{g-i} - 1)}{g - i} \text{ or } \frac{W(1 - e^{-(i-g)})}{i - g} \qquad (1.33)$$

When $g - i$ is negative, this expression can be evaluated from column 4 of Appendix II, putting $i - g$ for the i of column 1. When $g - i$ is positive, the required values are given in column 5, and i of column 1 is equated to $g - i$.

If growth and mortality are not constant, but vary seasonally *in parallel fashion,* then (1.33) can be used to compute an average stock size, which can be thought of as based on the fish's physiological and ecological time scale instead of on astronomical time. Whatever time scale is used, the average bulk of the year-class, $\overline{W}$, can be multiplied by any instantaneous rate or combination of rates, to show the mass of fish involved in the activity in question, just as with mean numbers in Section 1E. For example:

$i\overline{W}$ = total mortality, by weight (1.34)

$p\overline{W}$ = weight of catch (1.35)

$q\overline{W}$ = weight of fish which die "naturally" (1.36)

$g\overline{W}$ = production, or total growth in weight of fish during the year, including growth in the part of the population which dies before the year is finished (1.37)

$(g-q)\overline{W}$ = excess of growth over natural mortality (1.38)

$(g-i)\overline{W}$ = net increase in weight of a year-class during the year (a negative value of course indicates a decrease) (1.39)

The restriction on seasonal incidence of growth and mortality may sometimes be serious, but the above expressions will be useful, at least as an approximation, in most cases. There is often some tendency for the two opposed effects to vary in a parallel fashion; for example, both growth and mortality may tend to be less in winter than in summer. During their first year of life both growth and mortality of a fish tend to change rapidly. Sometimes a quantitative seasonal breakdown can be obtained for both, and can be used to calculate production more accurately (Example 10B; see also Ricker and Foerster, 1948).

CHANGE IN STOCK SIZE FROM YEAR TO YEAR. The restriction that seasonal incidence of growth and mortality be proportional is not necessary for computing the mass of the stock *from one year to the next.* That is, the weight of a year-class at age $t + 1$ is related to that at age t as follows:

$$W_{t+1} = W_t\, e^{g-i} \qquad (1.40)$$

regardless of how growth and mortality are distributed during the year.

In general, in the life history of a brood there will be one to several years during which $g - i$ is positive and total bulk is increasing, followed by several years in which $g - i$ is negative and bulk is decreasing. In an unfished population, the mean size of the fish in a year-class when $g = i$ (growth just balancing mortality) will be called the *critical size.* The same term is applied to the fish in exploited populations at the point where $g = q$, that is, where the instantaneous rate of growth is equal to the instantaneous rate of natural mortality (Ricker, 1945c).

1G. FISHING EFFORT AND CATCH PER UNIT OF EFFORT

For greatest ease in estimating biological statistics, a fishery should ideally be prosecuted exclusively by one kind of gear, which should be strictly additive in effect—that is, each additional unit should increase the instantaneous rate of fishing by the same amount. Further, the investigator should have a record of all gear fished, and it should preferably fish only for one kind of fish. It usually happens that these conditions are not satisfied, and much ingenuity has been devoted to obtaining the best representative figure from incomplete or otherwise unsatisfactory data. Good reviews of some of the problems are by Widrig (1954a), Gulland (1955) and Beverton and Parrish (1956).

INCOMPLETE RECORD OF EFFORT. If records of catch are complete but records of effort are incomplete, a good plan is to compute the catch per unit effort for as much of the data as possible. This catch/effort, divided into the residual catch, will give an estimated effort figure for the latter, which can be added to the known effort to obtain a total. Sometimes effort records are complete and catch records incomplete, permitting the same procedure in reverse.

DIFFERENT KINDS OF FISHING GEAR. When different kinds of fishing are conducted on the same stock, the effort and catch taken by each is tabulated separately. For an overall picture, it is necessary to relate all kinds of effort to some standard unit. This is best done from a comprehensive series of fishing comparisons of the different gears under the same conditions. However, sometimes the gears are so unlike that this is impossible. If one kind of gear predominates over the others in a fishery, it may be sufficient to proceed as in the paragraph above: the effort of all other gears is scaled to terms of the dominant gear by dividing their gross catch by the catch/effort of the dominant gear. This has been done for many years for the Pacific halibut, for example (Thompson, Dunlop and Bell, 1931). When two or more very different gears are in extensive use—gill nets and traps, for example—it may be impossible to obtain a really satisfactory comparative measure of total effort from year to year, particularly if the two gears tend to select different sizes of fish, or if they are operated at different times of year.

VARIATION IN EFFICIENCY OF GEAR, AND GEAR SATURATION. With most kinds of gear, the fishing effort depends on the length of time it is in use, though "fixed" gears like traps often fish continuously. However, from the time they are set to the time they are lifted, some kinds of gear decrease in efficiency. For example, baits can be eaten off hooks by trash fish or invertebrates, nets can become fouled and so are more easily avoided by the fish, etc. Also, the mere fact that some fish are already caught can reduce efficiency: the fish already hooked leave fewer vacant hooks on a set-line; in most kinds of traps, fish can leave as well as enter, and a point of saturation may even be reached, so that effort depends partly on how often they are emptied; in a gill net, the presence of some fish already caught tends to scare others away, so that saturation may be reached long before the net is full of fish (Van Oosten, 1936; Kennedy, 1951). The extra time needed to lift or clear a net, when fish are abundant, may appreciably decrease the time it is in the water and fishing, hence decrease the effectiveness of a "net-day" or "trap-day". Thus the catch per unit time, for many kinds of gear, tends to decrease from the time they are set to the time they are lifted, and the speed of this decrease is partly a function of the abundance of the fish.

The reverse phenomenon is also sometimes encountered: for example, in trapping for sunfishes near their spawning beds, the presence of fish in a trap appears to attract others to it, so that dozens of fish may be taken in one small trap while adjacent ones are nearly empty. Some Mississippi River fishermen are said to "bait" their traps with a mature female during the spawning season.

All such effects demand care in assessing the fishing power of a unit of gear, and standardizing it in some way.

VARIATION IN VULNERABILITY OF THE STOCK. Statements so far have concerned only the simple situation where the whole of a fish stock is equally vulnerable to the fishing in progress. In large-scale fisheries this is unlikely to be the true situation, for several possible reasons.

No trouble arises if a portion of a species lives completely outside the range of fishing operations and never mingles with or contributes recruits to the fished population. In that event consideration can be restricted to the vulnerable part of the stock, and the rest is ignored for purposes of current vital statistics. Other possibilities present greater problems:

1. Different portions of a fish stock, even one which is uniformly abundant throughout its range, may be fished at differing intensities in different places because of economic considerations or legal restrictions. If the various portions of the stock intermingle at any time of year, it is necessary somehow to compute average statistics of mortality, etc.

2. A situation similar to but more extreme than the above is where some parts of the range of a population contain fish too sparsely concentrated, in too deep water, or too remote from a harbour to be fished at all, yet these fish mingle with the fished stock at times of year other than the fishing season. For example, in trawl fisheries, and particularly in Danish seining, some parts of the fishing grounds are too rough to be fished without loss of gear, and these areas provide "refuges" where a part of the stock is not accessible.

Where a stock can be divided fairly sharply into a vulnerable and an invulnerable portion, each year, the fraction which is exposed to fishing is called the *availability* of the population that year (Marr, 1951).

3. Catchability can also vary within a year because of seasonal physiological or behaviour changes, and if a short fishing season is not exactly synchronized with this behaviour each year, the result is between-year differences in catchability.

4. Fish of different sizes may be caught with varying efficiency—either as a result of selectivity of gear or because of differences in distribution or habitat. As they grow, their vulnerability to the gear in use changes.

The feature which is common to all the above effects is that different parts of the stock are subjected to different rates of removal by the fishery; that is, they differ in vulnerability. This complicates the estimation of vital statistics, and introduces errors which may be difficult to detect.

If these stocks are treated as though the fishery were directed against a single compact population, the effects above give to estimated vital statistics a somewhat fictitious character. One can't be sure that they are really what they seem to be. For example, some fisheries attack only the part of a stock which is fairly densely aggregated at the edge of a bank, or along a temperature boundary. Decline in catch per unit effort during a season can give an estimate of the stock *in that area* (Chapter 6), but the total population on which such fishing can draw, over the years, is considerably greater because of replenishment of the area in the off season. Again, if fish of certain sizes are more vulnerable than others, a Petersen tagging experiment (Section 3B) is apt to overemphasize the vulnerable ones both in respect to tags put out and recaptures made; hence the estimate of rate of exploitation is too high and the population estimate is too low. However, for some purposes systematic bias of such kinds is not too great a handicap, provided it does not vary from year to year. It is secular *changes* in vital statistics which are of most interest, and changes will show up even in the biased statistics.

When there are year-to-year variations in the distribution of the fishing, or in the distribution and availability of the stock, or in the vulnerability of the stock as affected by weather or age composition, the situation is more serious. Such variability makes for changes in the estimated statistics that are not easy to distinguish from true changes in the population parameters. Comprehensive treatments of the theory of variability in these respects have been given by Widrig (1954a, b) and by Gulland (1955).

Most of Widrig's discussion is in terms of effect No. 2, the availability, r, of the stock in different years. However, his treatment seems equally applicable to other kinds of variation in the vulnerability. Consider a statistic r'_i, representing the ratio of the catchability of the whole stock in year i to an arbitrarily chosen standard catchability c_s; so that:

$$r'_i = c_i/c_s$$

Then r' can be substituted for r in Widrig's computations, and the latter become applicable to a wider class of phenomena—some of which, in practice, are very difficult to distinguish from availability anyway.

CATCH PER UNIT EFFORT AS AN INDEX OF ABUNDANCE. When a single homogeneous population is being fished, and when effort is proportional to rate of fishing, it is well established that catch per unit effort is proportional to the stock present *during the time fishing takes place* (Ricker, 1940)—whether or not recruitment from younger sizes takes place during that time. If the stock is not homogeneous—not all equally vulnerable to fishing—total catch divided by total effort is proportional to stock size only in special circumstances: when the *relative* quantities of fishing effort attacking different subsections of the stock do not change from year to year, or when the relative size of the stock in the different subsections does not change (Widrig, 1954a).

Narrowing the discussion to *geographical* subdivisions of a population, for many kinds of fishing the vulnerability of a stock in different subareas will tend to vary approximately as stock density (fish present per unit area). If these are in direct proportion, then an overall C/f that is proportional to total stock size can be obtained by adding the C/f values for individual subareas, weighting each as the size of its subarea (Helland-Hansen, 1909, p. 8; Widrig, 1954b; Gulland, 1955, expression 2.4). However if vulnerability does not vary as density, then there is no completely satisfactory substitute for a determination of absolute stock size separately in each subarea in each year. This rather gloomy conclusion is indicated, in effect, by Gulland's expression (2.2). The least tractable populations are of those pelagic species which appear in varying proportions in different parts of their range in different years.

COMPETITION BETWEEN UNITS OF GEAR. The term "gear competition" has been used and discussed by a number of writers, but some confusion has resulted from inadequate definition. The sections above have dealt with the subject by implication, but a specific treatment may be useful. At least three kinds of effects have been included under the term:

1. A fish population is exploited by a fishery whose units of gear are scattered randomly over it, so that all fish are exposed to the possibility of capture at short intervals of time and there is no possibility of local depletion occurring. Further, the units of gear do not interfere with each other in respect to the mechanics of their operation. In such a situation, to-day's catch by any new unit of gear reduces to-morrow's catch by the others, and thus in a sense it may be said to "compete" with them. The competition takes the form of a faster reduction in the size of the population as a whole. As the fishing season progresses, each unit catches fewer and fewer fish (or at any rate fewer than it would have caught had there been no previous fishing that year); and the more gear present, the more rapid is this decrease in catch.

2. If fishing gear is dispersed unequally over the population, its action tends to produce local reductions in abundance greater than what the population as a whole is experiencing, leading to a different type of competition. Suppose that a population is vulnerable to fishing only in certain parts of its range (for example, only near the shore of a lake; or on only the smoother ocean bottoms). Then fishing in such areas produces a local depletion of the supply; additional nets

set in the same region increase the local depletion and catch per unit effort will fall off in proportion to the *local* abundance. The magnitude of this fall will be cushioned if some fish from the rest of the stock keep wandering into the fishing area and so keep the supply there from dropping as far as it otherwise would. However, competition between units of gear is intensified because catch per unit effort reflects the size of only the immediately available restricted portion of the stock, rather than the stock as a whole.

3. Finally, if the setting of an additional unit of gear interferes directly with other gear, there exists "physical" competition between them, which is independent of population abundance, even locally. For example, too many anglers at a pool may frighten the fish; setting a new gill net near one already in operation may scare fish away from the latter; or much fishing of a schooling fish may disperse the schools and so reduce fishing success more than proportionally to actual decrease in abundance. (There can also, of course, be physical *cooperation* between different units of gear.)

Competition of type 1 above can be considered normal and inevitable. It might be better not to call it competition at all, since the term is usually meant to suggest effects of types 2 or 3. Competition of types 2 and 3 may or may not be present in any given situation—it depends entirely on the nature of the fishery.

1H. MAXIMUM EQUILIBRIUM CATCH

Much of the work on vital statistics has devolved about or been stimulated by attempts to estimate the maximum equilibrium catch or maximum sustained yield for the stock. Some of this background is necessary for appreciation of the value or significance of some of the methods which will be described.

A simple approach is shown in Figure 1.2 (cf. Russell, 1931; Schaefer, 1955b). The *usable stock* of a species is defined as the weight of all fish larger than a minimum useful size. This stock loses members by *natural deaths* and, if there is a fishery, also by the *catch* which man takes. The usable stock is replenished by *recruitment* from smaller size categories, and by *growth* of the already-recruited members.

If a stock is not fished, all growth and recruitment is balanced by natural mortality. If fishing begins, it tips the balance toward greater removals, and occasionally fishing may steadily reduce the usable stock until it is commercially extinct. Much more often a new balance is established, because the decreased abundance of the stock results in (1) a greater rate of recruitment, or (2) a greater rate of growth, or (3) a reduced rate of natural mortality.

Ideally, the effects of concurrent variation of all three of these rates, with respect to size of the population, should be studied in order to define equilibrium yield and compute its maximum value. In actual practice to date, it has been necessary to abstract one or two variables for consideration, keeping the others constant, or else to consider only the net result of all three. The various proposals for estimating maximum sustained yield differ principally in respect to which of these three rates is permitted to vary with stock density, and in what way.

1. One group of methods assumes that rate of growth and rate of natural mortality are invariable. The *absolute number* of recruits is considered unvarying from year to year[3], a condition which means that *rate* of recruitment increases when the usable stock decreases, but only in a definite and narrowly-prescribed fashion. Such methods are treated in Chapter 10; their greatest usefulness has been for describing the short-term reactions of stocks to fishing, but they may have value in showing the direction in which rate of fishing should be adjusted in order to move toward maximum sustained yield.

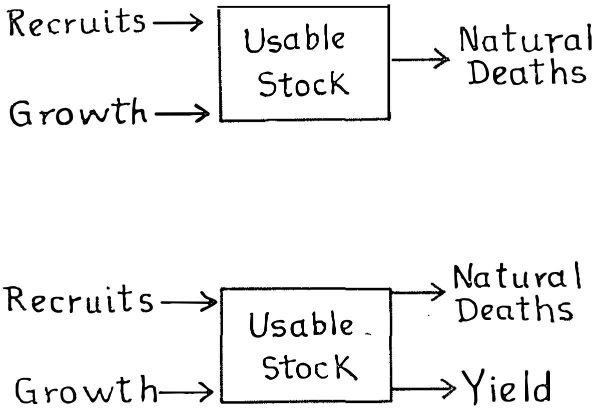

FIGURE 1.2. Diagram of the dynamics of a fish stock (fish of usable sizes), when there is no fishing (*above*) and when there is a fishery (*below*). (From Ricker, 1958, figure 1).

2. Variation in *recruitment* is approached empirically in Chapter 11. The results can be used directly to compute maximum sustained yield in situations where, as in the method above, the rates of growth and of natural mortality do not vary with size of stock.

3. At least one author has considered *rate of growth* as the primary variable in the adjustment of a stock to fishing pressure (Nikolsky, 1953), particularly for freshwater fishes having comparatively short life histories. While this does not lend itself very well to general regulation, Nikolsky suggests the determination of maximum rate of growth for each species, and regulation of abundance until something close to the maximum is achieved.

4. Finally, a few authors have attempted to relate surplus production (potential sustained yield) of a stock directly to its abundance, without any direct information on the rates of growth, recruitment, or natural mortality. Chapter 12 describes these computations.

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[3] More exactly, the assumption is that the absolute number of recruits does not vary with stock density, but it may fluctuate from year to year in response to environmental variability.

In addition to predicting the result of increasing or decreasing rate of fishing, most of the methods outlined can also be used to predict the effect of varying the minimum size of fish which is used by the fishery.

11. SAMPLING ERROR

In all of the methods of estimation to be discussed in subsequent chapters, the probable size of the sampling error is an important consideration. It must be evaluated, at least approximately, before any confidence can be placed in an estimate. When a computation of survival rate, for example, is calculated from recapture of only a few marked fish, or from an age-class with only a few representatives in a sample, it must be accepted with caution.

Available estimates of sampling variability or error are of two general sorts. One type depends on random distribution of the fish or random selection of all pertinent types of fish by the fishing apparatus, and is computed from the frequency distributions which are appropriate in the individual case (usually Gaussian, Poisson, binomial or hypergeometric). Examples of variances or standard deviations calculated on this basis are (3.2), (3.4), (3.6), (3.8), (3.11), (3.14), (5.3), (5.14), (5.15), (5.16). For small samples the positive and negative limits demarcating zones of equal confidence are not even approximately symmetrical about the observed value. In such cases it is frequently useful to use the asymmetrical confidence limits calculated for binomial distributions by Clopper and Pearson (1934), and for Poisson distributions by Garwood (1936) or Ricker (1937). Both types are conveniently available in graphical form in a paper by Adams (1951). The Poisson limits are especially simple to use, and can be employed as an approximation even when the binomial charts are more appropriate.

For larger samples a general idea of sampling variability can be had by regarding the observed ratio of (say) the marked fish to the total fish in a sample ($\hat{u} = R/C$) as though it were the true ratio u which exists in the population. The expectation of marked fish to be obtained is Cu, and its variance is given by the well-known formula:

$$V = Cu(1 - u) \tag{1.41}$$

With large R, this is approximated by:

$$\hat{V} = C\hat{u}(1 - \hat{u}) = R(1 - R/C) \tag{1.42}$$

and the standard deviation is the square root of this. In the (very frequent) event that R/C is small, this means that the standard deviation of the number of marked fish retaken is a little less than its own square root. Even when R/C is not especially small, this rule is good enough for preliminary orientation, so as to have in mind the order of size of the sampling variability to be expected. Similarly, the number of fish, n, of a given age in a sample can be regarded as having associated with it approximate limits of confidence set by the normal frequency distribution with $\sqrt{n}$ as standard deviation—provided it is not too small—less than 10, say. (For small numbers the binomial or Poisson limits should be used.)

The second general type of estimate of sampling variability is calculated from some form of replication in the data themselves. Such estimates will reflect part or all of the variation which arises from non-random distribution of the different categories of fish in the population being sampled: effects of grouping, for example. Expressions (3.19) and (3.20) are of this type. Objective estimates of variability are also involved in the methods of estimating confidence limits which are used in Examples 3F, 6A and 7D, and could be applied to 3G, 11A, etc. These estimates tend to be more realistic than those based directly on random sampling theory, though of course they are not necessarily exact; they are to be preferred when available.

Limits of confidence, of either type above, should preferably be calculated for statistics whose distribution is as nearly "normal" as possible. For example, in estimating population size, N, by most of the available methods, estimates of the *reciprocal* of N tend to be distributed nearly symmetrically about the mean. Confidence limits computed from the normal curve are likely to apply fairly well to 1/N, whereas they do not apply at all well to N (DeLury, 1958). Hence computations of confidence limits should be made in the first instance for 1/N, and then inverted to give the appropriate asymmetrical limits for N itself. Similar situations often occur where the logarithms of variates will have an approximately symmetrical or even nearly normal distribution, whereas the variates themselves do not.

No kind of estimate of sampling variability can reflect or adjust for all the systematic errors which may so easily arise from non-random fish distributions or behaviour. Systematic error tends to be larger than sampling error, and discussions of various kinds occupy much of the text to follow. Even if not larger, systematic effects are not removed by using more observations or making bigger experiments *of the same type*, so they deserve the closest attention.

CHAPTER 2.—ESTIMATION OF SURVIVAL RATE FROM AGE COMPOSITION

2A. SURVIVAL ESTIMATED FROM THE ABUNDANCE OF SUCCESSIVE AGE-GROUPS

The general method of estimating survival is by comparing the numbers of animals alive at successive ages. Long known in human demography, this procedure became available to students of fish populations as soon as age determinations began to be made on a large scale, from representative samples. This occurred about the turn of the century for North Sea species; the voluminous literature on the plaice contains early estimates of mortality and survival, as well as doubts concerning the representativeness of the samples available (Heincke, 1913a; Wallace, 1915).

If the initial number of fish of two broods, now age t and age $t + 1$, was the same, and if they have been subjected to similar mortality rates at corresponding ages, then an estimate of survival rate from age t to age $t + 1$ is obtained from the ratio:

$$\hat{s} = \frac{N_{t+1}}{N_t} \tag{2.1}$$

where N represents the number found, of each age, in a representative sample. If it can be assumed that survival is constant over a period of years, then a combined estimate can be made from a series of estimates of the form (2.1). *How* best to combine them presents a problem for which there is no universal answer[1].

In any sample of a population, the older ages will tend to be scarcer than the younger; hence, because of sampling variability, an s estimated from them is less reliable than one from younger ages. A formula which weights successive ages as their abundance is, from Jackson (1939):

$$\hat{s} = \frac{N_2 + N_3 + N_4 + \ldots . + N_r}{N_1 + N_2 + N_3 + \ldots . + N_{r-1}} \tag{2.2}$$

If the number of years involved is fairly large, it may be more accurate to separate two ages from the numerator and denominator, and compute $\hat{s}$ from the expression:

$$\hat{s}^2 = \frac{N_3 + N_4 + \ldots . + N_r}{N_1 + N_2 + \ldots . + N_{r-2}} \tag{2.3}$$

This makes the result less dependent upon the vagaries of representation of a single age-group.

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[1] Statistical aspects of this method are treated by Gulland (1955, Part III) and Jones (1956). They find that estimates of s made in this manner tend to have a small positive bias, although the estimate of instantaneous mortality rate from $i = \log_e N_t - \log_e N_{t+1}$ is not appreciably biased. Since it is usually desirable to use s and i estimates that conform exactly to $i = \log_e s$, unadjusted estimates of s are often used. In the examples of North Sea plaice which Gulland (p. 44) quotes, the individual estimates actually conform to this relation, and the means differ only because the s-values are averaged arithmetically instead of geometrically (as is usually appropriate for ratios generally). Gulland also discusses the effects of mistakes in age determination upon estimates of survival.

It usually happens, in fact, that the principal source of error in such survival estimates is the variable initial size of the broods involved; that is, the error in any single comparison of the type (2.1) is only to a minor degree the result of sampling variability—except among the very oldest ages. Since the oldest ages are likely to differ in survival rate anyway, a practical compromise estimate might seem to be to use the mean of separate estimates (2.1), excluding all which involve N values less than (say) 10. This again presents difficulties, however. Since it is ratios that are being averaged, their *geometric* mean is appropriate—the arithmetic mean has a systematic bias making it too great. But to estimate s from the geometric mean of a succession of ratios of the form:

$$\frac{N_2}{N_1}, \frac{N_3}{N_2}, \ldots \ldots \frac{N_r}{N_{r-1}}$$

is equivalent to putting:

$$s^{r-1} = \frac{N_r}{N_1}$$

Such an estimate, therefore, really uses data for only the oldest and the youngest age represented, and its sampling error will be correspondingly large. For these reasons the preferred method of obtaining a combined estimate of survival, under these circumstances, is to use the "catch curves" described in the next Section.

INCOMPLETE AGE CLASSIFICATION. Sometimes the older fish are not classifiable as to age, particularly when the distribution of length frequencies in the catch is the only criterion of age. In an extreme case the population may be divisible into only two usable groups—the youngest fully-vulnerable age and all older ages. In an ideal population with constant recruitment and constant survival rate, if the youngest usable age is represented by N fish, the older ones should be, successively, Ns, Ns^2, Ns^3, etc. The ratio of the youngest age to the whole can be represented as the sum of a geometric series (Heincke, 1913a):

$$\frac{N}{N + Ns + Ns^2 + \ldots} = \frac{1}{1 + s + s^2 + \ldots} = 1 - s$$

Hence an estimate of mortality rate, a, from an actual sample is:

$$\hat{a} = 1 - \hat{s} = \frac{N_1}{N_1 + N_2 + N_3 + \ldots} \tag{2.4}$$

To obtain an estimate of s in a situation like the above, Hylen *et al.* (1955) used:

$$\hat{s}^2 = \frac{N_3 + N_4 + N_5 + \ldots}{N_1 + N_2 + N_3 + \ldots}$$

This is very similar to the quadratic expression (2.3), but the fact that the two oldest age groups cannot be separated off the denominator makes the result slightly low.

EXAMPLE 2A. SURVIVAL RATE OF ANTARCTIC FIN WHALES, BY AGE COMPOSITION. (Data from Hylen *et al.*, 1955.)

The age frequencies of male fin whales in Norwegian catches sampled in the 1947/48 to 1952/53 seasons is given by the above authors as follows:

Age	0	I	II	III	IV	V	VI+
Frequency (%)	0.3	2.3	12.7	17.2	24.1	14.1	29.5

Ages IV and V are regarded as likely to be accurately determined, and they may possibly be representatively sampled, so that survival between these ages can be estimated from (2.1) as:

$$\hat{s} = \frac{14.1}{24.1} = 0.585$$

Alternatively, assuming a constant survival rate, ages V and older can be compared with age IV using (2.4):

$$\hat{a} = \frac{24.1}{24.1 + 14.1 + 29.5} = 0.357$$

$$1 - \hat{a} = \hat{s} = 0.643$$

This gives a larger figure than the simple comparison, and might suggest that older whales really survive better than the age IV-V group. However, strictly from these data, and without considering any accessory information that may be available about the whales, there is no way to be sure that age IV is as vulnerable to the whaling as age V, since the next younger age III is obviously much less vulnerable. It might be safer therefore to consider only the whales of age V and older; again using (2.4):

$$\hat{a} = \frac{14.1}{14.1 + 29.5} = 0.326; \qquad \hat{s} = 0.674$$

The effect of any increase in whaling effort over the time these stocks were being recruited would be to make this survival estimate greater than the average one prevailing at the time the samples were taken (Section 2F; see also Hylen *et al.*).

2B. SIMPLE CATCH CURVES

Edser (1908) was apparently the first to point out that when catches of North Sea plaice (*Pleuronectes platessa*) were grouped into size-classes of equal breadth, the logarithms of the frequency of occurrence of fish in each class form a curve which has a steeply ascending left limb, a dome-shaped upper portion, and long descending right limb which in his example was straight or nearly so through its entire length. This was soon recognized as a convenient method of representing catches graphically. Heincke (1913b) plotted a number of curves of this type and, combining them with information on rate of growth, computed mortality rates for a series of size intervals of the plaice, equating these approximately to age. Baranov (1918) later gave the name *catch curve* to the graph of log frequency against size, and elaborated the theory of estimating mortality and survival from it in the situation where the fish increase in size by a constant absolute amount from year to year.

The same kind of plotting is useful for the simpler situation where age rather than length is considered[2]. Most recent authors plot log frequency against age directly, and the name catch curve has been applied to this kind

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[2] The straightness of Edser's and Baranov's 1906 catch curve for North Sea plaice, plotted with length on the abscissa, was evidently a temporary phenomenon resulting from a recent increase in fishing effort. Plotted with age on the abscissa it would become the concave curve characteristic of such a situation (cf. Section 2F), since rate of increase in length drops off sharply among the older fish.

of graph as well (Ricker, 1948). The catch curve has a considerable advantage over the simple ratios of Section 2A, and over arithmetic plots of abundance at successive ages, when any kind of variation in survival rate has to be examined.

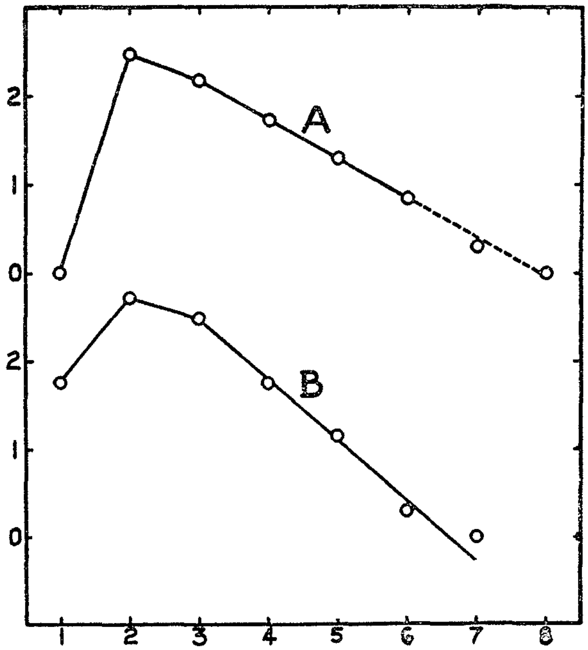

FIGURE 2.1. A. Logarithms of number of bluegills of successive ages, in a sample from Muskellunge Lake, Indiana, 1942. (From data of Ricker, 1945a.) B. Logarithms of the percentage representation of successive age-classes of pilchards in the catch from California waters, season 1941-42. (Redrawn from Silliman, 1943.)

The upper line of Figure 2.1 is an example of a straight catch curve, pertaining to the bluegills (*Lepomis macrochirus*) in a small Indiana lake (Ricker, 1945a). The rate of survival, s, from such a curve can be computed in two slightly different ways. The flatter the right limb, the greater is the survival rate. The difference in logarithm between age t and age $t - 1$ is of course negative; it can be written with a positive mantissa and then antilogged, giving s directly. Alternatively we could follow Baranov in keeping the difference of (base 10) logarithm at its negative numerical magnitude, changing the sign, and multiplying by 2.3026, which gives the instantaneous rate of mortality, i. A table of exponential functions will give the annual rate of survival, from the equation $s = e^{-i}$. Since we will almost always want to know i as well as s, one method of computation is as convenient as the other. The annual mortality rate, a, is equal to $1 - s$. If the survival rate *during* instead of *between* successive years is desired, it can be obtained by taking tangents on the curve at each age.

The ascending left limb and the dome of a catch curve represent age-classes which are incompletely captured by the gear used to take the sample: that is, they are taken less frequently, in relation to their abundance, than are older fish. This may come about either because the younger fish are more thickly distributed in another part of the body of water than that principally fished, or because they are less ready to take the baits or enter the nets. Other things being equal, the total mortality rate will be increasing during this period of recruitment. However, it is impossible to find out anything definite about the actual mortality rate during the years covered by the left limb and dome of the curve, simply because sampling of the population is not random[3].

We turn then to a more promising part of the curve, the descending right limb. Straightness of this right limb, or any part of it, is usually interpreted in the manner described by Baranov, which involves the following conditions:

1. The survival rate is uniform with age, over the range of age-groups in question.

2. Since survival rate is the complement of mortality rate, and the latter is compounded of fishing and natural mortality, this will usually mean that each of these, individually, is uniform.

3. There has been no change in mortality rate with time.

4. The sample is taken randomly from the age-groups involved. (If the sample is representative of the commercial catch, this condition is implied in 2 above.)

5. The age-groups in question were equal in numbers at the time each was being recruited to the fishery.

If these conditions are satisfied, the right limb is, in actuarial language, a curve of survivorship which is both age-specific and time-specific.

Deviations from the above conditions often result in nonlinear right limbs of the catch curve. Such nonlinear curves are quite common, and in the Sections to follow we attempt to set up standards for the interpretation of some of the more likely types. Equally important is the allied question: under what conditions can a linear or nearly linear catch curve result from postulates other than the above?

EXAMPLE 2B. TWO STRAIGHT CATCH CURVES: FOR BLUEGILLS AND CALIFORNIA SARDINES. (Data from Ricker, 1945a, and Silliman, 1943.)

Catch curves having a straight right limb have already been treated adequately, by Baranov and others, and need little comment. An interesting selection is presented by Jensen (1939). The bluegill example of Figure 2.1A was selected for its close adherence to theoretical requirements; much more often fluctuating recruitment makes it necessary to use averages over a period of years to obtain a reasonably representative survival rate. Silliman (1943, p. 4) has an example of a straight catch curve, reproduced here in Figure 2.1B. It

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[3] It is being assumed, of course, that the sample is taken from the commercial catch. If better means of sampling are available, they will push the representative part of the sample back to earlier years, and in this way it may be possible to detect and measure otherwise-inaccessible changes in total mortality and in natural mortality. Jensen (1939) interprets some experimental trawl catches in this manner.

pertains to the season 1941-42 of the fishery for California sardines (*Sardina caerulea*), and gives an estimated survival rate of about 0.20.

While straight catch curves will probably usually be interpretable in the manner proposed by Baranov and outlined in Section 2B, two principal possible exceptions should always be kept in mind: (1) a decrease in vulnerability to fishing with age, and the consequent tendency toward increase in survival rate, will not be reflected in the catch ratio, or will be very imperfectly reflected; and (2) long-term trends in recruitment deflect the slope of a catch curve without introducing much or any curvature. Obviously, information on these topics is not to be looked for in the catch curve, and must be obtained from other sources. To illustrate, Silliman (1943) tentatively concluded that an increase in recruitment of about 130% occurred between 1925-33 and 1937-42 in the pilchard stock. If any of this increase carried over into the years when the fish of Figure 2.1B were being recruited, the straight curve computed for those years would be too steep, i.e., would suggest a survival rate less than the true one. Some idea of the possible magnitude of this effect can be had from Silliman's data, assuming the recruitment increased at a constant exponential rate for ten years. If k represents this rate, we have $e^{10k} = 2.3$, $k = 0.083$, and the annual increase is 0.087. Hence the survival rate computed from the catch curve would be less than the true rate by only about 9% of the former, even assuming the increase in recruitment to have persisted through the entire formative period of Figure 2.1B.

Another danger in interpreting a straight catch curve lies in the possibility of a fortuitous balancing of opposed tendencies. For example, a straight curve like Figure 2.1A could conceivably result from the combination of a normally convex curve (natural mortality rate increasing with age) with the effect of a recent increase in rate of fishing. In view of the general increase in rate of fishing in the North Sea and North Atlantic during the period 1920-35, one wonders whether the approximate linearity of some of Jensen's (1939) curves for cod, haddock, and plaice in those waters has not been achieved in this manner. Such possibilities emphasize the desirability of continuous sampling of a stock, and also the value of having information on the level of fishing effort, etc., in successive years.

2C. NON-UNIFORM RECRUITMENT. USE OF CATCH PER UNIT EFFORT FOR ESTIMATING SURVIVAL

RANDOM VARIATION IN RECRUITMENT. Moderate fluctuations in recruitment from year-class to year-class, which are of an irregular character, make a catch curve bumpy, but do not destroy its general form, and hence do not greatly affect its value. Such irregularities are akin to those which result from random errors of sampling, but with this difference, that they do not tend to disappear as the size of the sample is increased. As a matter of fact, recruitment sufficiently uniform to make a really smooth catch curve appears to be rather rare. A good way to reduce irregularities from unstable recruitment is to combine the samples of successive years. If fishing has been fairly steady, and the population consequently is presumed to be in a state of equilibrium except for the variations in recruitment, then quite a number of years can be combined in this way. Even when secular changes in mortality rate have occurred it may still be useful to combine the samples of two successive years, as in this way a considerable increase in the regularity of the curve may often be obtained without too much sacrifice of information concerning the past history of the stock in question.

SUSTAINED CHANGE IN LEVEL OF RECRUITMENT. If recruitment changes suddenly from one steady level to a new one, and remains stabilized there, the effect on the catch curve can easily be distinguished and interpreted. As Baranov has shown, such a change shifts the position of a part of the right limb without changing its slope.

EXTREME VARIATION IN RECRUITMENT. Sometimes recruitment is exceedingly variable, adjacent year-classes differing by a factor of 5, 10, 25 or more; as shown, for example, by Hjort (1914) for cod and herring and by Merriman (1941) for striped bass. This makes it practically impossible to use the usual type of catch curve for estimating survival rate: comparisons must be made within individual year-classes, if at all.

TRENDS IN RECRUITMENT. More insidious than the above is the situation where recruitment has a distinct trend over a period of years. In actuarial language, the survivorship curve obtained by sampling in a single season will then be time-specific, and will not indicate actual mortality rates over the period concerned. Such trends in recruitment are likely to be reflected in trends in catch, after a suitable interval, but not all trends in catch are the result of variation in recruitment. The only direct way to check on the possibility of trends in recruitment is to continue the sampling over a considerable period of years, the assumption being that a trend cannot continue indefinitely in one direction. However, it will be useful to examine the exact nature of the shift in the catch curve which is produced by changing recruitment.

Examples of catch curves affected by a progressive change in recruitment are shown in Figure 2.2, Curves B and C. For comparison, Curve A is a curve of the Baranov type, based on uniform recruitment; its straight right limb has a slope corresponding to a survival rate of 0.670. Curve B is based on the same data, except that recruitment decreased by 5% per year over the period of years shown, i.e., it was 1.00, 0.95, 0.902, 0.857, etc., of its original value, in successive years. (The earlier years are to the right on the graph.) The right limb of Curve B is still straight, but it has a slope which corresponds to a catch ratio (apparent survival rate) of 0.705, which differs from 0.670 by 5% of the former. Similarly, when recruitment increases by 5% per year, as shown by Curve C, the line is straight with a slope corresponding to a catch ratio of 0.638, which differs from 0.670 by 5% (of 0.638). These and other examples show that the deviation of the true survival rate from the apparent survival rate, when expressed as a percentage of the latter, is numerically equal to the annual percentage change in recruitment, but of opposite sign; i.e., when recruitment increases, apparent survival rate decreases.

From the above it follows that in order to obtain a *curved* right limb of the catch curve by varying recruitment, the rate of change in recruitment must vary from year to year. Two examples are shown in Figure 2.2. Curve D shows the result of increasing the absolute decrease in the rate of recruitment by 0.05 each year; i.e., recruitment is 1.00, 0.95, 0.85, 0.70, etc., in successive years. A curved line is produced, but after only six years it terminates, because recruitment has been reduced past zero! Curve E shows the result of increasing recruitment in the same way. Here the annual rate of increase in recruitment (ratio of each year's increase to the preceding year's level) increases at first, and produces a short curved section, but soon the increase in the actual level of recruitment catches up to the increase in rate of increase, and the nearly straight section between age VII and age XIII results. During the tenth year shown (i.e., at age VII) recruitment is 3.2 times its original level; however, to produce a line which would have the original curvature throughout its entire length for that period, recruitment at age VII would have become many times greater.

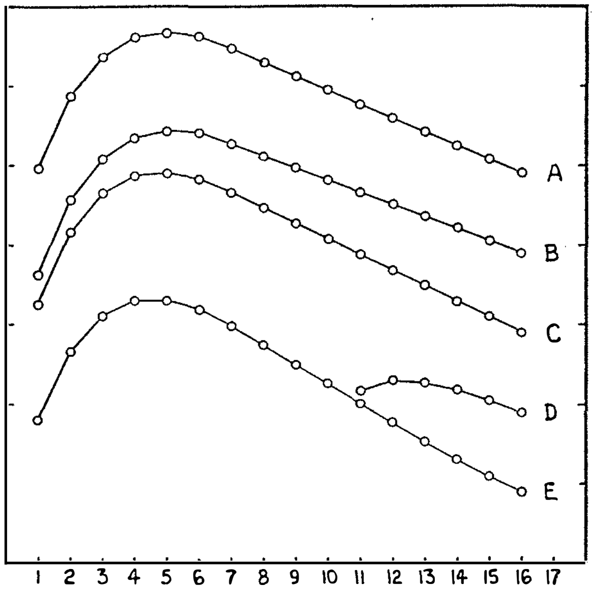

FIGURE 2.2. Effect of variation in recruitment on a catch curve when there is a constant survival rate of 0.67 from age VII onward. A. Steady recruitment. B. Curve based on the same data as A, but recruitment has decreased with time by 5 per cent per year, over the period of years shown. C. Similar to B, but recruitment has increased by 5 per cent per year. D. Recruitment has decreased at an accelerating rate. E. Recruitment has increased a rate which initially was accelerating, but later flattened off. Abscissa—age; ordinate—logarithmic units.

Such computations as these illustrate the fact that in order to obtain recognizably curved right limbs by varying recruitment, the changes in recruitment would soon become so great as to produce acute symptoms in other statistics of the fishery, e.g., in total catch, average size of fish caught, relative abundance of young fish in successive years, etc. Hence we can confidently expect that the effect of any reasonable trend in recruitment will be to change the slope of the catch curve, without appreciably changing its linearity. If any significant curvature does occur, its explanation should be sought elsewhere.

In interpreting a catch curve, it would be useful to have some independent estimate of recruitment from year to year, as it might then be possible to introduce a correction for any trend which has occurred. Such information may be available from other catch statistics, particularly the catch of the youngest age-groups, per unit fishing effort. Information on the number of spawners (potential egg deposition) in successive years might also seem to offer possibilities, but actually the relation between eggs deposited and the resulting recruitment will usually be unknown, even apart from fortuitous variations; it is about as likely to be inverse as direct (Chapter 11).

COMPARISON OF ABUNDANCE OF INDIVIDUAL YEAR-CLASSES AT SUCCESSIVE AGES. In order to reduce the error caused by variable recruitment, it is natural to try to follow separate year-classes throughout their life, comparing the number present at age t with the number at age $t - 1$, and so on. However, if this is attempted with ordinary age composition data, trial computations will readily show that the presence of an exceptionally numerous year-class depresses the estimated survival rates *at all ages* in the year of its first appearance; afterward it makes them all too great for as many more years as it remains in the fishery. The geometric mean of the survival rates estimated over a period of years tend toward the true value for each age (assuming the latter does not vary with time), but in practice there is usually little if any gain in accuracy over what would be provided by taking the mean of the slopes of the appropriate segments of the corresponding series of catch curves.

COMPARISON OF INDIVIDUAL YEAR-CLASSES ON THE BASIS OF CATCH PER UNIT OF EFFORT. A means of avoiding some of the difficulties caused by variable recruitment, of whatever type, is to compare the *catch per unit effort* of individual year-classes, in successive years of their existence. The principal reason this method is not used more often is the frequently great labour necessary to obtain a reasonably representative measure of effective fishing effort. Furthermore, its advantages are to some extent offset by possibilities of systematic bias that are not present in the ordinary catch curve. For example, there may be distortion resulting from changes in catchability of the fish from year to year, either from differences in distribution or behaviour of the fish themselves, or from variations in the seasonal deployment of the fishing apparatus, or from its variable effectiveness because of weather conditions. Apart from this, if quantity of effort changes much from year to year the mean C/f is attained at a different time in each fishing season (earlier in the season, the greater the effort); and the comparison then gives a survival rate which does not apply exactly to one year's time. An adjustment for this latter effect could presumably be made by using an iterative procedure analogous to that of Section 7D; or, more simply, the *C*/*f* values can be compared for restricted periods, such as corresponding months of the fishing season.

Survival rates estimated from catch per unit of effort differ from those obtained from catch curves in respect to the times involved. Survival rates from *C*/*f* comparisons give information about the current situation: they apply to the interval between the middle (approximately) of the two fishing seasons sampled. Ordinary catch-curve methods, by contrast, give estimates which tend to lag several years behind the time the data are collected and which represent average conditions during the years of recruitment (Section 2F).

The method of comparisons of catch per unit effort has been used principally with certain trawl fisheries whose effort is well standardized, and where the species is available over a wide area (Graham, 1938b; Jensen, 1939; Gulland, 1955).

Example 2c. Survival of Plaice of the Southern North Sea, Estimated from Catch per Unit of Effort of Individual Year-classes. (After Gulland, 1955, p. 43.)

Gulland's data for catch of plaice (*Pleuronectes platessa*) per 100 hours of fishing by standard trawlers, at successive ages in 3 years, is given in our Table 2.1. The ratio of *C*/*f* in successive seasons is an estimate of the survival rate for that year for the year-class in question. For example, the year-class of 1945, age V during the 1950-51 season, decreased in abundance from 1722 per 100 hours in 1950-51 to 982 in 1951-52; its estimated survival over that period was therefore $s = 982/1722 = 0.570$. For ages above XI, where the data are lumped, an approximate s is obtained from, for example, $87/(57 + 94) = 0.576$.

Gulland notes that there are no consistent trends in the s-values with age, and little difference between the two years shown: unweighted geometric means are 0.665 and 0.642[4].

2D. Effect of Recruitment Occurring over More than One Age.

General relationships. At the risk of spending time on what may be an obvious proposition, we can consider first the effect on a catch curve of having recruitment spread over several ages. Table 2.2 shows such a population, in which the total mortality rate increases from 0.3 to 0.6, and hence survival rate decreases from 0.7 to 0.4, during a period of recruitment which is completed three years after the fish first enter the fishery. If the population at the end of 1906 be *randomly* sampled (the sample taken by the fishery will not be representative), the ratios of the older age-groups will represent the definitive survival rate 0.4, and the greater survival rates characteristic of the years of recruitment appear only among the age-groups which are as yet incompletely recruited.

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[4] If the logarithms of the three catch samples of Table 2.1 are plotted as ordinary catch curves, they prove to be of the "concave" type (Section 2F), each with a break in slope whose timing corresponds fairly well with the resumption of large-scale fishing following World War II. The slopes of the steeper left-hand (more recent) portions of the right limbs indicate a survival rate of about 0.41 (which applies to the period 1946-50, approximately). Beverton (1954, p. 97) quotes age composition data for plaice from which he derives a similar figure, 0.437. The discrepancy between these estimates and Gulland's 0.64-0.66 is rather serious, and I have not seen an explanation of it.

Table 2.1. Catch per 100 hours of trawling (C/*f*) for plaice in the southern North Sea in three seasons, and the survival rates (*s*) estimated from this. (From Gulland, 1955, tables 3.1 and 3.2.)

Age	C/*f* 1950–51	*s*	C/*f* 1951–52	*s*	C/*f* 1952–53
II	39		91		142
		....		....	
III	929		559		999
		....		....	
IV	2320		2576		1424
		....		....	
V	1722		2055		2828
		0.570		0.637	
VI	389		982		1309
		0.671		0.529	
VII	198		261		519
		0.768		0.471	
VIII	93		152		123
		0.763		0.697	
IX	95		71		106
		0.600		0.859	
X	81		57		61
		0.741		0.702	
XI	57		60		40
		(0.576)		(0.673)	
XII+	94		87		99
Geometric mean		0.665		0.642	

This proposition becomes a little less obvious when the definitive survival rate itself changes over a period of years, as shown later in Figure 2.7. In that event the ratio of two of the older age-groups in a catch may represent a survival rate which they themselves have never actually experienced, but which is the definitive rate which used to prevail among mature fish (now long dead) at the time when the given age-groups were being recruited.

Age of effectively complete recruitment. Without a little study it will often be difficult to decide at what age recruitment is effectively complete, particularly with convex catch curves. It is advisable to try to duplicate any observed curve using trial values of the instantaneous rates of fishing and natural mortality, in order to get some idea of the actual situation. Since the length distribution of the fish in any age-group, of most fishes, tends to be fairly close to normal, it can readily be assumed that the curve of recruitment will usually have a fairly symmetrical shape: for example, the magnitude of p might be 0.01, 0.1, 0.5, 0.9 and 0.99 of its definitive value, in successive years of recruitment of a given year-class. (Asymmetry resulting from the median magnitude of p being something more or less than 0.5 will not affect our argument.) Now

TABLE 2.2. Decrease of different year-classes of a population in successive years of their life, when the total mortality rate is 0.3 at age III, 0.4 at age IV, 0.5 at age V, and 0.6 at all later ages. Each year-class starts to become vulnerable to fishing during the year following its third birthday, and is fully vulnerable by the time it reaches its sixth birthday. The last line of the table shows the ratios between the figures in the line immediately above it.

	Year-class (year in which fry were hatched)							
Year	1898	1899	1900	1901	1902	1903	1904	LM
	10,000							
1901								
	7,000	10,000						
1902								
	4,200	7,000	10,000					
1903								
	2,100	4,200	7,000	10,000				
1904								
	840	2,100	4,200	7,000	10,000			
1905								
	336	840	2,100	4,200	7,000	10,000		
1906								
	134	336	840	2,100	4,200	7,000	10,000	
Ratio..........	0.4	0.4	0.4	0.5	0.6	0.7		

a facile assumption would be that the number of years from the first age to the modal age of the catch curve would represent the ascending limb of a symmetrical curve of recruitment, and that hence an equal number of years to the right of the mode would be affected by recruitment and should be discarded in estimating survival rate.

Such an assumption would be misleading, for two reasons. In the first place, the number of fish in the first age taken (except sometimes when it is age 0 or age I) tends to be quite small, often of the same order of size as the number in the oldest age taken (cf. Fig. 2.1, 2.6, 2.8, 2.12, 2.13). That is, the identity of the first age to be taken is partly determined by the size of the whole sample. When the latter is of moderate size (several hundred fish), the fish from an age-class for which rate of fishing (*p*) is of the order of 0.01 of its definitive magnitude will probably be the first to appear; if the sample is increased eight- or ten-fold, an age-group may be represented for which *p* is in the neighbourhood of 0.001 of its definitive value. Now at the other end of the symmetrical curve of recruitment, an age-group which is either 99.9% vulnerable or merely 99% vulnerable is for practical purposes completely vulnerable, when it comes to estimating survival rate. Even 95% would be fairly satisfactory in most cases. Consequently the distance in years from the first age to the median age of recruitment is practically always a year or two too great to be used as an estimate of the distance to which recruitment will have a distorting effect beyond the median.

A second source of error is the fact that the modal age in the catch does not necessarily coincide with the median age of recruitment. Examples show that it may be at an age either younger or older than the median, its exact position depending principally on the magnitude of the total mortality rate. When annual mortality rate is moderate or small (0.5 or less) at the beginning of recruitment at least, there are usually two adjacent ages having much the same number of fish, with the mode falling sometimes in the median age of recruitment, sometimes in the next older age. In the latter event the distance from the first age present to the modal age would be more than ever misleading, if it were considered as an estimate of the distance to which the effects of recruitment extend beyond the mode.

Considering both of the effects just described, it appears that the modal age in the catch will commonly lie quite close to the first year in which recruitment can be considered effectively complete. In the examples used here there is at most one unusable age-group intervening between the first usable age and the modal age (or the second of two nearly-equal ages), as shown by Figures 2.8 and 2.12. When recruitment is abrupt, the first year beyond the modal age seems usable, as illustrated in Figure 2.1, and in Figure 2.9 the point for age VI comes close to being usable.

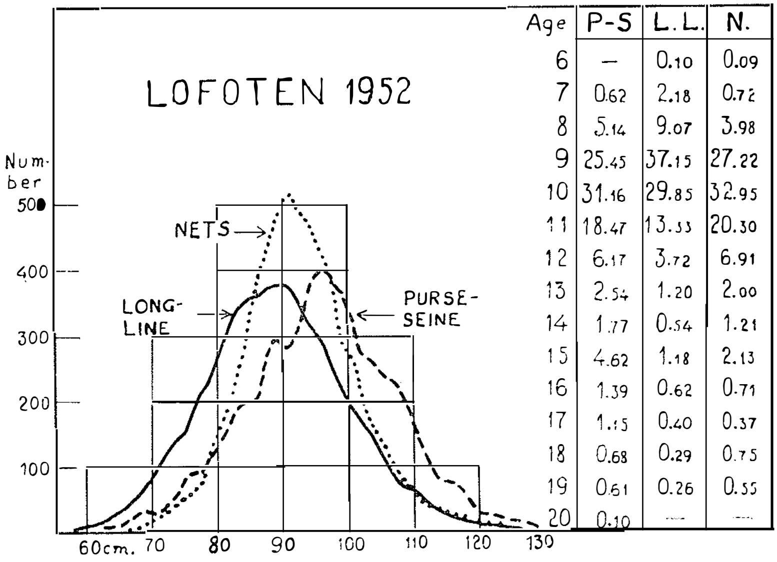
VULNERABILITY VARYING CONTINUOUSLY WITH AGE. The question arises whether a stable or "definitive" rate of fishing, beyond a certain age, is commonly achieved at all in fish populations. Perhaps p usually continues to increase throughout life, or it might conceivably rise to a maximum and then decrease if the older fish become too large to be captured or held by the hooks or nets in use. Obviously no universal answer is possible to such a question, and to obtain information concerning it usually requires more than a catch curve.

A rate of fishing independent of age, above some minimum, would be rather likely in trawl fisheries, and Hickling (1938) in fact found that rate of return of tags from North Sea plaice (*Pleuronectes platessa*) tended to level off above a tagging length of about 25 cm. In some freshwater gill-net catches, whitefish (*Coregonus clupeaformis*) did not change appreciably in vulnerability above 30 cm. fork length (Ricker, 1949a). In a line fishery for lingcod (*Ophiodon elongatus*), which begin to be caught at about 40 cm., there was no great change in rate of recapture of tagged fish in the principal size range, 66-90 cm.; but among the few fish taken from that size up to 120 cm. there was some decrease in rate of return—possibly the result of an increase in natural mortality at great ages (Chatwin, 1958). Using the virtual-population method, Fry (1949) and Fraser (1955) found that vulnerability increased in sport fisheries for lake trout (*Cristivomer namaycush*) and smallmouth bass (*Micropterus dolomieui*), over a rather broad range of ages. For the trout there was a suggestion of subsequent decline in vulnerability among the oldest fish, ages X-XIII (cf. Example 8B).

Evidently the question of relative vulnerability needs continual examination. The kinds of distortion introduced by different types of trend in p are discussed in the next Section.

Age or size of arrival on the fishing grounds. A distinction can sometimes be made between the vulnerability of the whole of the stock at a given size, and the vulnerability of that portion of it which is on the fishing grounds. In fact, the term recruitment has been used (by Beverton, etc.) in the sense of physical movement onto the fishing grounds, instead of its more common meaning of overall increase in vulnerability to capture by the gear in use. For production computations a minimum reference age is necessary, but it need not necessarily be the age at which the fish move onto the grounds (this being often difficult to discover), nor even the age at which they become vulnerable to a particular gear.

Occasionally it is possible to classify the reduced vulnerability of smaller fish into a portion that results from their relative scarcity in places where most fishing is carried on, and a portion due to their "habit" of avoiding capture by nets, hooks, etc. For example, Rollefsen (1953) compared the sizes of Lofoten cod caught by long-lining and by purse seines (Fig. 2.3). Considering the latter to be representative of the sizes of cod present (something which probably needs confirmation), it would appear that vulnerability to hooks actually *decreases* with increase in length from the smallest fish up to quite large sizes (60-110 cm. or so). At the same time, the vulnerability of the stock as a whole (as distinct from that part of it which assembles on the Lofoten spawning grounds) to long-line fishing increases at least up to a size of 90 cm. Another type of information on this point is described in Section 5G.



Age	P-S	L.L.	N.
6	—	0.10	0.09
7	0.62	2.18	0.72
8	5.14	9.07	3.98
9	25.45	37.15	27.22
10	31.16	29.85	32.95
11	18.47	13.33	20.30
12	6.17	3.72	6.91
13	2.54	1.20	2.00
14	1.77	0.54	1.21
15	4.62	1.18	2.13
16	1.39	0.62	0.71
17	1.15	0.40	0.37
18	0.68	0.29	0.75
19	0.61	0.26	0.55
20	0.10	—	—

Figure 2.3. Length and age distribution of Lofoten cod taken by three kinds of gear. (From Rollefsen, 1953, figure 1).

2E. CHANGE IN MORTALITY RATE WITH AGE.

In addition to increase in fishing mortality rate by progressive recruitment, there can be other types of change in mortality. In Table 2.3 are shown two balanced populations, constructed on the basis that the survival rate, s, changes by the absolute figure 0.1 in each year of the life of the fish, and that all mortality is the result of fishing.

TABLE 2.3. Effects of a change in survival rate with age, upon catch and upon catch ratio, when all mortality is the result of fishing. In the left hand side of the table mortality is 0.1 initially and increases to 0.9, hence survival decreases with age, from 0.9 to 0.1; in the right side survival increases with age from 0.1 to 0.9. The "catch ratio" columns are to be compared with the adjacent survival rates.

Age	Survival rate	Survivors	Catch	Catch ratio	Survival rate	Survivors	Catch	Catch ratio
		100,000				100,000		
I	0.9		10,000		0.1		90,000	
		90,000		1.80		10,000		0.09
II	0.8		18,000		0.2		8,000	
		72,000		1.20		2,000		0.18
III	0.7		21,600		0.3		1,400	
		50,400		0.93		600		0.26
IV	0.6		20,160		0.4		360	
		30,240		0.75		240		0.30
V	0.5		15,120		0.5		120	
		15,120		0.60		120		0.40
VI	0.4		9,072		0.6		48	
		6,048		0.47		72		0.45
VII	0.3		4,234		0.7		22	
		1,814		0.36		50		0.47
VIII	0.2		1,451		0.8		10	
		363		0.22		40		0.40
IX	0.1		327		0.9		4	
		36				36		

The left half of the Table is a recruitment situation. Catch ratios are consistently higher than the true survival rate, the discrepancy being 35% to 50% over most of the range covered.

In the right half of Table 2.3, where mortality decreases, catch ratio is always less than the adjacent survival rates. Noteworthy is the fact that over the range of survival rates from 0.5 to 0.9 there is not much change in catch ratio. If encountered in practice, such a segment of a catch curve would probably be interpreted as substantially meeting the uniform conditions mentioned earlier, the irregularities being ascribed to small fluctuations in recruitment.

An example modelled after situations more likely to be encountered in actual investigations is shown in Figure 2.4. The population described by these curves has an instantaneous natural mortality rate of 0.2 during ages I through X. This is combined with a rate of fishing that increases from 0.1 at age I to 0.7 at age VII, then remains steady for three more years. This latter is shown by the straight portion of the catch curve from age VII to age X, and, if continued, would be represented by the dotted projected line.

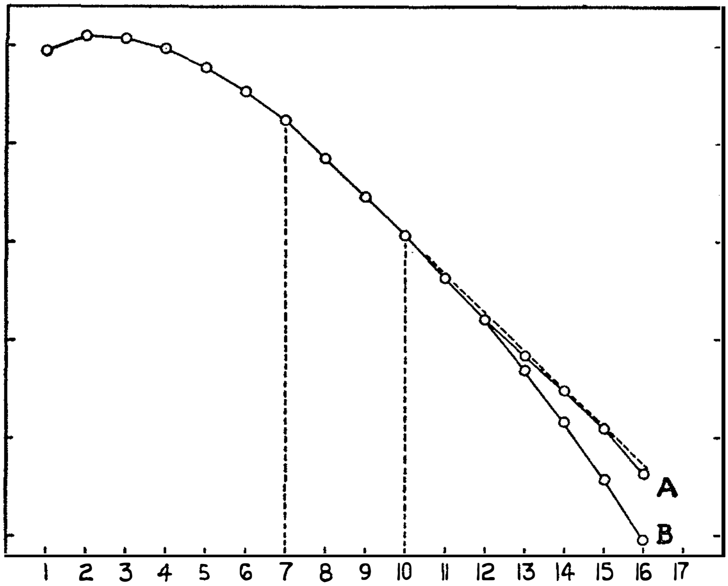


FIGURE 2.4. Catch curve for a population which has a constant fishing and natural mortality rate from age VII to age X, followed by a decrease in rate of fishing (Curve A), or by an increase in natural mortality (Curve B). Abscissa—age; ordinate—logarithmic units.

Three variations, after age X, are examined. First, the rate of fishing is made to decrease by 0.1 unit during each year of age, for six years, the result being shown by Curve A. There are some fluctuations, but the net result differs very little from the dotted line, and would scarcely be distinguishable in an actual investigation. This means that this section of the curve gives a fair estimate of the survival rate during the previous state of balance (ages VII to X), but does not reflect the actual survival rate, which is rising. This is illustrated more graphically in Figure 2.5A, in which the catch ratio, R, is compared with the actual survival rate, S.

Secondly, the rate of natural mortality is made to increase from 0.2 to 0.9, as shown by Curve B of Figures 2.4 and 2.5. The decrease in survival is faithfully reflected by the catch ratio, the latter being only inappreciably greater (Fig. 2.5B).

Finally, rate of fishing is made to decrease while natural mortality increases, so that total mortality remains steady. The catch curve for this situation has not been drawn in Figure 2.4, since it almost coincides with Curve B. This means that the curve obtained does not represent the actual survival rate, which (since survival rate is constant) is the sloping dotted line of Figure 2.4. Curve C of Figure 2.5 shows the discrepancy between catch ratio and survival rate.

Additional examples of the effects of continuous change in rate of fishing with age have been computed by Beverton and Holt (1956). Panels (a)-(e) of their figure 2 illustrate cases where *p* (their F) decreases, while in panels (f)-(h) it increases. In panel (i), *p* increases to a maximum and then decreases; this proves to be a particularly misleading situation, since the right limb of the catch curve is nearly straight, but indicates an apparent survival rate not much more than half the actual.

From the above and similar examples, the following conclusions can be drawn:

1. An increase (or decrease) in *natural* mortality rate, among the older fish of a population, is correctly represented by the catch curve, when rate of fishing is the same for all the ages involved.

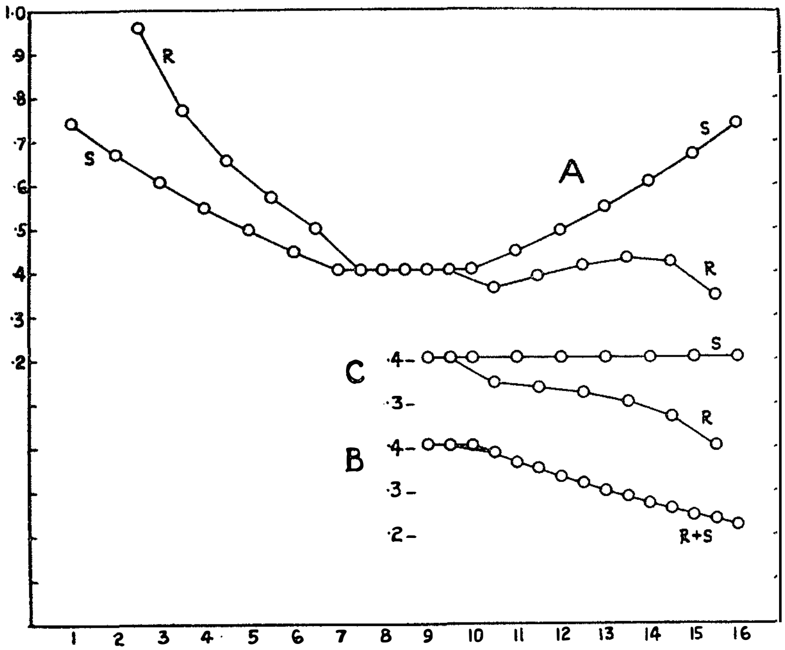


FIGURE 2.5. Comparison of survival rates (*s*) and catch ratios (R) for the populations of Figure 2.4. A. Decrease in rate of fishing. B. Increase in natural mortality. C. Decrease in rate of fishing compensated by an equivalent increase in natural mortality. Abscissa—age; ordinate—survival rate and catch ratio.

2. A decrease in rate of *fishing*, among the older fish in a population, is not correctly reflected in the catch curve, and in many situations the resulting curve approximates closely to the survival rate obtaining at ages prior to the decrease in rate of fishing.

3. When rate of fishing increases with age throughout life, the catch curve is useless for estimating survival rate: in effect, the curve consists only of the portions which we have called the ascending limb and dome, and the catch ratio between successive years is always greater than the true survival rate, often very much greater.

4. When natural mortality increases with age, and rate of fishing decreases, the catch curve tends to represent the survival rate characterized by the *observed* natural mortality plus the *original* rate of fishing.

5. Hence, altering the wording of 1. a little, an increase in natural mortality rate, among the older fish of a population, is at least reasonably well represented by the catch curve, whether rate of fishing is steady or whether it decreases.

In so far as these conclusions involve the rate of fishing, they apply only when the latter has been stabilized for enough years that all the fish involved have been subjected to the appropriate rates for each age, throughout their life. If this is not so, there is no restriction on the type of curve which may be obtained when rate of fishing varies with age. For example, if a new fishery begins to attack a previously unexploited population, the number of fish taken at each age will be the product of the abundance at that age and the rate of fishing at that age. Thus the ratio of the number of fish taken at age t to the number at age $t - 1$ will be the product of the natural survival rate times p_t/p_{t-1}, the ratio of the rates of fishing at the two ages.

The considerations above are of particular importance in dealing with catch curves which have the right limb convex upward. Theoretically, such could result from a steady increase in rate of fishing with age; but this situation seems likely to be uncommon, except possibly in sport fisheries where there is very great interest in large specimens (Section 2C). On the basis of what has been found up to this point, a curve which is convex to the very end will ordinarily indicate an increase in natural mortality rate with age, among the older ages at least, since a decrease in rate of fishing with age does not cause much or any deflection of the catch curve in either direction. On the same basis, a concave curve could only mean that natural mortality in the population decreases with age. However, alternative explanations of curvature are available when there has been a change in mortality rate with time (Section 2F).

Example 2D. SURVIVAL RATE IN AN UNEXPLOITED HERRING POPULATION: A CONVEX CATCH CURVE

Dr. A. L. Tester has courteously brought to our attention some convex catch curves of exceptional interest. During the fishing season of 1938-39 a population of herring (*Clupea pallasi*) on the east coast of the Queen Charlotte Islands, British Columbia, was exploited commercially for the first time. Five samples totalling 580 fish were taken and their ages determined. The points of Curve A of Figure 2.6 are the logarithms of the percentage representation of each age-group. The unsmoothed curve appears generally convex, but is quite bumpy, because of the moderate fluctuations in recruitment which are encountered among herring from this general region.

To smooth out the curve and get a representative picture of the age distribution of natural mortality, there are several possible procedures. A simple freehand curve fitted to the data for 1938-39 is shown in Figure 2.6A. As a check on the investigator's judgment the curve can be smoothed by a running average of 3, as shown in Figure 2.6B. This procedure of course tends to flatten the dome of the curve, so that the modal point should not be considered at all in drawing a new freehand curve, and even the point to either side of it will be a little depressed. Also the curve is extended one year at either end by the process. The left-hand end does not concern us, but at the right-hand end it may "improve" the picture because the point for age XII, represented by no fish in the sample, would be $-\infty$ on Curve 2.6A. Actually, of course, there are very likely a few fish of this age or even older in the population, so that the delay in the asymptotic fall of the curve suggested in Figure 2.6B is according to expectation.

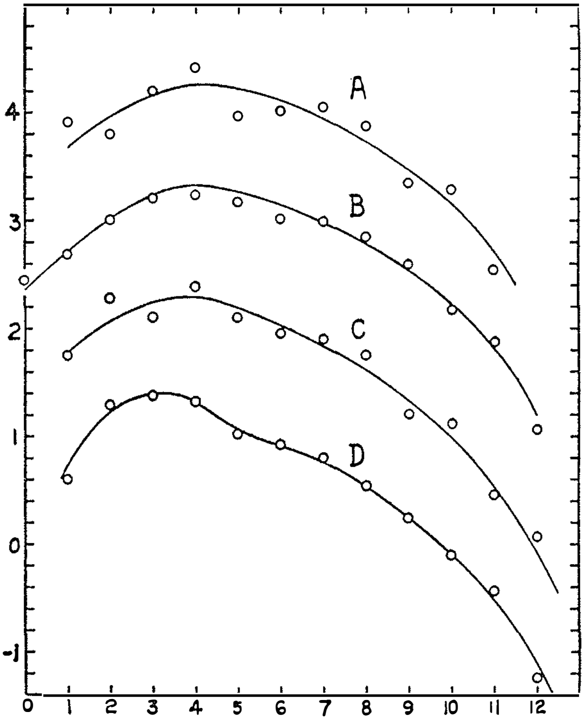


FIGURE 2.6. Catch curves for a population of herring from the Queen Charlotte Islands, British Columbia. A. Age composition during the first year of exploitation, 1938–39. B. The same, smoothed by a running average of 3. C. The combined samples of 1938–39 and 1939–40. D. The combined samples for the first 4 years of exploitation. All curves are in terms of the logarithms of the percentage frequency at each age, set one log-unit apart on the figure, with the ordinate scale applying to Curve D. (From unpublished data of Dr. A. L. Tester.)

To get a better idea of the primitive distribution of natural mortality it is also possible to use data for later years, to help smooth out the curve. They have this disadvantage, that each additional year used brings the influence of the fishery farther into the catch, and accordingly fewer ages can be considered representative of the original natural mortality rate. Curve 2.6C shows the combined data for 1938-39 and 1939-40, giving each year equal weight, while Curve 2.6D is based on the combined data for the first four years of the fishery.

The percentage annual survival rates found by taking tangents at successive ages, on the four curves of Figure 2.6, are shown below for ages whose relative numbers are not affected by the new fishery (or very little so):

Age	VI	VII	VIII	IX	X	XI	XII
Curve							
A.	72	63	58	52	42	28	. .
B.	69	66	60	52	47	31	. .
C.	. .	. .	59	48	41	29	21
D.	. .	. .	. .	48	43	32	19

The figures for age VI are slightly less than what was determined from the actual slope, because of the proximity of age V, for which recruitment is presumed to be somewhat incomplete. The determination of the age distribution of mortality in unexploited populations such as this is of especial interest, because often it may be the only clue to the natural mortality rate under conditions of exploitation.

Under conditions of a developed fishery, the original convexity of the catch curves for British Columbia herring stocks tends to be diminished, but is still quite recognizable (Tester, 1955). In the southern part of the North Sea, Jensen (1939) also shows strongly convex curves for herring in two areas. Jensen suggests increased natural mortality or emigration among older fish, and net selectivity making younger fish more vulnerable, as possible causes of the convexity of the North Sea curves. In regard to the last, the analysis of this Section shows that net selectivity of this sort would not in fact produce any appreciable curvature, so this possibility can be ruled out. The reason is that while such nets sample the older stock less completely than the younger, they also permit more fish to survive to the older ages, and the combination of these two opposed tendencies results in a fairly straight catch curve (cf. Fig. 2.4A).

Catch curves for a number of other species under unexploited conditions have now been obtained, and all indicate an increase in natural mortality among the older fish. From northern lakes there is information for sauger (*Stizostedion canadense*), rock bass (*Ambloplites rupestris*), whitefish and lake trout (Ricker, 1949a; Kennedy, 1953, 1954b). A similar increase in natural mortality was observed in fished lakes, among perch (*Perca flavescens*), black crappies (*Pomoxis sparoides*), yellow bullheads (*Ameiurus natalis*) and several other species in Indiana (Ricker, 1945a), the survival rates in these instances being estimated from recoveries of marks. Although the more heavily fished bluegills in the same waters had a nearly straight catch curve (Fig. 2.1A) it is probable that originally they survived less well at the older ages then present: we must assume that no individual of any species is capable of living forever. Also, a sample of older plaice than those available to Gulland (Example 2C) would probably behave similarly.

2F. CHANGE IN MORTALITY RATE WITH TIME

All of the conclusions obtained in the last Section presuppose that, however they may vary with age, the rate of fishing and rate of natural mortality for any given age are constant from year to year. But the effort used in a fishery can vary from year to year for a variety of reasons. Some fisheries are of recent origin, and the gear in use has been expanded since their beginning. Others have passed through a profitable phase, and now their decreased return per unit effort tends to drive off boats which formerly fished them. Economic conditions play a large part in determining what constitutes profitability and thus affect total fishing effort. Hence a consideration of secular change in rate of fishing cannot be avoided. Similar changes in natural mortality rate may possibly occur at times; their effects can readily be examined, but they are not considered here.

INSTANTANEOUS RECRUITMENT. Table 2.4 shows a population in which the survival rate for fish of all catchable ages is 0.7, 0.6, and 0.5 in three successive calendar years, then remains steady at 0.4 for four years. In this situation

TABLE 2.4. Decrease of successive year-classes in a population acted on by a survival rate (s) which decreases for three years and then remains steady, but is always the same for fish of all recruited ages during any given year. Recruitment takes place abruptly when the fish become age III. The figures tabulated show the number of survivors of 10,000 recruits, at the beginning and end of each year.

		Year-class							
		1898	1899	1900	1901	1902	1903	1904	1905
Year	s								
		10,000							
1901	0.7								
		7,000	10,000						
1902	0.6								
		4,200	6,000	10,000					
1903	0.5								
		2,100	3,000	5,000	10,000				
1904	0.4								
		840	1,200	2,000	4,000	10,000			
1905	0.4								
		336	480	800	1,600	4,000	10,000		
1906	0.4								
		134	192	320	640	1,600	4,000	10,000	
1907	0.4								
		54	77	128	256	640	1,600	4,000	10,000
Catch ratio		0.7	0.6	0.5	0.4	0.4	0.4	0.4	

(unlike Table 2.2) the commercial catch will sample the population representatively, since recruitment to the fishery occurs abruptly. Such a random sample of the population, taken at the start of any given year, would have the successive age-groups represented in proportion to the figures in the horizontal rows of the table, beginning with the youngest at the right. Each of the catch ratios shown in the last row represents the ratio of *all* of the pairs of figures in the two adjacent columns above it. Obviously then, no matter at what time year-classes t and $t - 1$ are sampled, the ratio of their abundance is a measure of the survival rate which existed during the first year that year-class $t - 1$ became vulnerable to fishing. *Thus the survival rates which we estimate from age-frequencies in a catch are ancient history.* They pertain to past years, to the time when the year-classes involved were being recruited to the catchable size range, and are independent of what survival rates have prevailed since that time. In terms of the catch curve, this means that the slope of any given part of the curve will represent the survival rate which prevailed at the time the fish in question were being recruited to the fishery.

GRADUAL RECRUITMENT. In the example just given recruitment takes place suddenly, one age being completely vulnerable, the next younger one completely invulnerable. In practice recruitment usually takes place less abruptly, and is often very gradual. A model of that sort has been constructed in the following manner: a stock of fish which gains a uniform number of recruits each year is considered to have an unchanging instantaneous natural mortality rate of 0.2. To this is added a rate of fishing which increases for the first six years after the fish enter the fishery, as follows:

Year	*Percentage of the definitive rate of fishing*
1st	0.5
2nd	5
3rd	20
4th	45
5th	70
6th	90
7th and later	100

These values are approximately those estimated from an actual fishery.

The definitive rate of fishing varies in successive calendar years as follows:

Year	*Definitive rate of fishing*	*Natural mortality rate*	*Total mortality rate*	*Annual mortality rate*	*Survival rate*
	p	q	i	a	s
Up to 1	0.2	0.2	0.4	0.330	0.670
2	0.3	0.2	0.5	0.394	0.606
3	0.4	0.2	0.6	0.451	0.549
4	0.5	0.2	0.7	0.503	0.497
5	0.6	0.2	0.8	0.551	0.449
6	0.7	0.2	0.9	0.593	0.407
7 and later	0.8	0.2	1.0	0.632	0.368

Adding 0.2 to the rate of fishing gives the definitive instantaneous mortality rate for each year, and from Appendix II the annual mortality rate and survival rate were found in the usual manner. The same statistics were estimated for each year of recruitment, at each level of (definitive) total mortality. Armed with these survival rates, a comprehensive table was prepared, analogous to Table 2.4, showing the number of surviving fish in each successive brood, for a series of years sufficient to give the complete history of the period of change. Annual deaths in each age category were found by subtraction, for four different years—the 1st, 7th, 12th and 24th—and by dividing these between fishing and natural mortality in the ratio of p to q, the number of each age-class in the catch was computed. The logarithms of these values are shown in Figure 2.7, curves A to D.

Curve A, showing the catch after an indefinite number of years of steady survival rate 0.670, is a simple catch curve with six years involved in the left limb and dome (corresponding to the six years of recruitment) and a long straight right limb.

Curve B, based on the catch in year 7, when the survival rate of 36.8% was first achieved, shows by its partially concave right limb that survival rate has been decreasing. However, the curve is not representative anywhere of the *current* survival rate. Its steepest part, between age VII and age VIII, corresponds to a survival rate of 51%; that is, approximately the survival rate of three years previously (year 4 in the schedule above). For a series of years near its outer end the curve is still straight, and here represents the original survival rate of 0.67.

Curve C is based on the catch in year 12, after the 36.8% survival rate has been stabilized for six years. Here, for the first time, there appears a portion of the curve (age VII to age VIII) which is steep enough to represent the current rate of survival. The slope of the curve at older ages gradually decreases, and between ages XVII and XVIII it still has the original slope. Between ages VII and XI, and also XV to XVIII, there is not much change in slope; consequently, even if there were considerable fluctuation in recruitment, a fairly good estimate of both the old and the new survival rate could be made from a curve such as this, simply by measuring its greatest and its least slope, on the right limb. The region between ages XI and XV shows the maximum curvature. (A catch curve which would have no such variation in rate of change in curvature would result if mortality rate were to change gradually over the whole series of years involved.)

Curve D is the new balanced population, which only appears after 18 years of the new mortality rate of 0.632. It is similar to A, but of course has a much steeper slope of the right limb.

The types of curve obtained during a period of transition from a larger to a smaller rate of fishing, and hence of total mortality, are shown by Curves E and F of Figure 2.7. The change is quantitatively the same as shown by B and C, but in reverse. Starting from the balanced situation of Curve D, after six years' progressive decrease in mortality rate Curve E is obtained. Such a curve, if found in an actual investigation, would scarcely be interpreted as indicating a recent decrease in mortality, since the whole region up to age XI could well be in the range of recruitment. Hence the survival rate estimated would be that indicated by the straight outer limb, and would of course be wide of the current value, but representative of the former value.

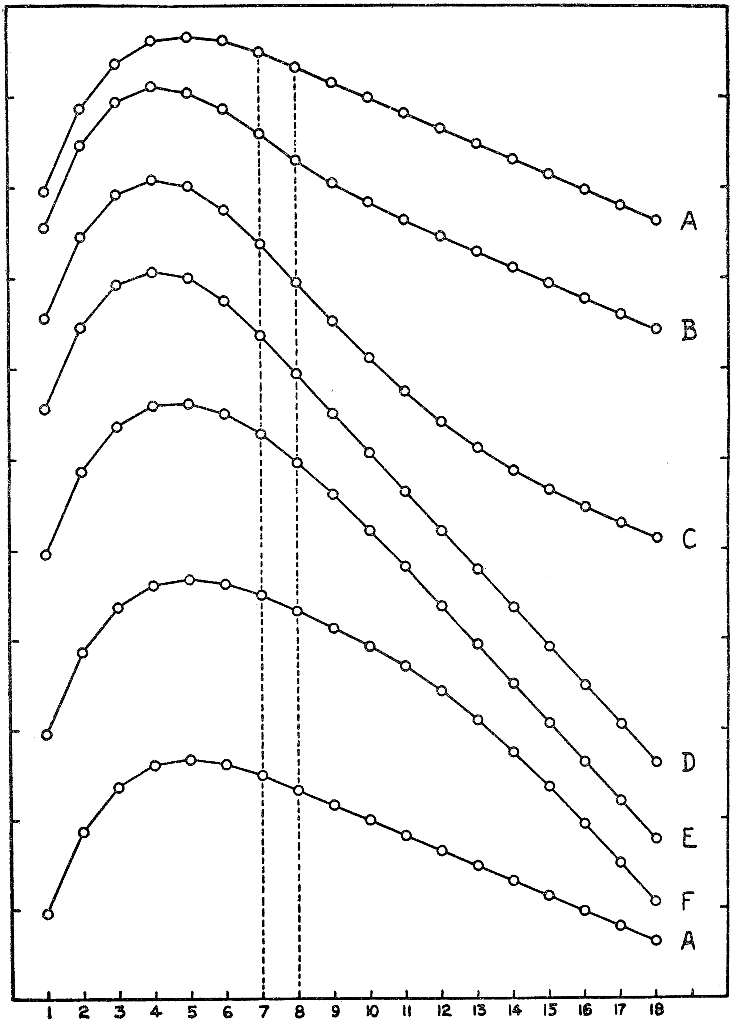


FIGURE 2.7. Catch curves illustrating changes in rate of fishing with time. In every instance recruitment is complete following the first 6 ages shown, and the instantaneous rate of natural mortality is the same, 0.2, for all ages and years. A. Constant rate of fishing of 0.2. B. Rate of fishing has increased from 0.2 to 0.8 during the preceding 6 years. C. Five years after B, with rate of fishing stabilized at 0.8. D. Balanced curve for rate of fishing 0.8. E. Rate of fishing has decreased from 0.8 to 0.2 during the preceding 6 years. F. Five years after E, with rate of fishing stabilized at 0.2. Abscissa—age; ordinate—logarithmic units.

Curve F, representing conditions 11 years after the mortality rate began to decrease, and 5 years after it was stabilized at 0.670, is a convex curve entirely analogous to concave Curve C. There is the same region of maximum curvature between ages XI and XV, with rather flat portions to either side of it. In practice, the outer end of such a curve might be interpreted as representing a state of near balance, but the region from age VII to age XI would again present difficulty, because of the possibility of incomplete recruitment. Even if this were ruled out, it would be harder to estimate current survival rate here than on the same part of Curve C, because there is no point of inflexion.

In general then, secular changes in rate of fishing result in curved right limbs of the catch curve, these being concave if fishing has increased, and convex if fishing has decreased. The latter type will usually be much harder to interpret in terms of the survival rate in past years, for two principal reasons: (1) there is danger of confusion with the type of convex curve which results from a natural mortality rate which increases with age; and (2) it is difficult or impossible to delimit the part of the curve affected by incomplete recruitment. The concave type of curve, on the other hand, is not likely to occur except as a result of increased fishing, and the point of maximum slope on the right limb will always give the most recent available estimate of survival rate.

It is difficult to express the relationships of this section in quantitative terms, but for the examples worked out to date the following statements seem to be true:

1. If the peak of recruitment is at age m, the survival rate estimated at age n on the catch curve pertains to a period approximately $n - m$ years prior to the date the sample was taken, except as noted below.

2. When the bulk of recruitment occupies a period of say $2x$ years (x years from the first *important* age to the modal age in the catch), the most recent representative survival rate observable on the catch curve will pertain to a period x years prior to the date the sample was taken.

3. If mortality becomes stabilized following a period of change it will, strictly speaking, require $2x$ years for the new stable survival rate to begin to appear in the catch curve, though for practical purposes a somewhat shorter period will usually suffice.

Obviously it will be desirable to have as much information as possible about fishing effort in past years when interpreting a catch curve. The simple fact that effort has decreased, or increased, or remained fairly steady will be of considerable value. If good quantitative estimates of effort are available, then it may be possible to interpret different segments of the curve in relation to fluctuations in the rate of fishing, or perhaps even to compute the actual rate of fishing and of natural mortality by Silliman's method (Section 7C).

EXAMPLE 2E. SURVIVAL IN THE LOFOTEN COD STOCK: CONCAVE CATCH CURVES. (Data from Rollefsen, 1953.)

Rollefsen presents the length frequencies of cod (*Gadus callarias*) caught by three kinds of gear in the 1952 Lofoten cod fishery: purse seines, longlines and gill nets. He also tabulates the distribution of ages in the three kinds of samples (Fig. 2.3). The three gears differ considerably in the range of sizes they select, and the stock itself is a selection of the *mature* fish from the great shoals which roam the Barents Sea. Consequently the chances of obtaining a representative survival rate from these data might appear particularly unfavorable.

Logarithmic plots of the three age distributions are shown in Figure 2.8. There is moderate, but not excessive, variation in recruitment from year to year; the year-class of 1937, age 15 in 1952, was a particularly good one. The right limbs of the three distributions are all markedly concave upward. From the analysis of Sections 2E and 2F, this could either be a result of a decrease in rate of natural mortality (*not* fishing mortality) with age, or a result of a recent increase in rate of exploitation of the stock as a whole. Data over a period of years would reveal the relative importance of these two alternatives.

Examples of annual survival rates computed from the slopes of the freehand lines are as follows:

Age interval	Purse seines	Longlines	Gill nets
XI-XII	$s = 0.33$	$s = 0.29$	$s = 0.30$
XII-XIII	$s = 0.50$	$s = 0.40$	$s = 0.37$
XIII-XIV	$s = 0.63$	$s = 0.56$	$s = 0.60$
XIV-XVI (av.)	$s = 0.75$	$s = 0.76$	$s = 0.75$

The seines suggest a somewhat greater survival rate than the other gears, up to age XIV, but the other curves would be useful to a first approximation. From age XIV onward there is little difference between the three, though of course the seine curve should be more reliable because it is based on a larger sample of the old fish. We may conclude that even knowledge of the existence of considerable net selectivity should not discourage attempts to obtain some kind of information about survival rate from age distribution.

Rollefsen points out that purse seining has been only recently introduced at Lofoten, and that it takes larger fish than the two historic methods. Insofar as the purse seine has increased the overall rate of fishing it would contribute to a (temporary) concavity of the catch curves; however the greater vulnerability of *large* fish to the seines would tend to have the opposite effect.

Another example of increase in rate of fishing is seen in Figure 2.6D, which is the average age distribution for the first four years of a fishery. The short concave section immediately to the right of the dome reflects the greater mortality rate caused by the start of the fishery.

EXAMPLE 2F. SURVIVAL OF LAKE WINNIPEGOSIS WHITEFISH: A SINUOUS CATCH CURVE.

(Data from Bajkov, 1933.)

A very interesting curve, for the whitefish (*Coregonus clupeaformis*) of Lake Winnipegosis, is shown in Figure 2.9. The data are taken from Bajkov (1933, p. 311), who used them to compute the whitefish population of the lake by Derzhavin's method (Section 8A); hence he presumably considered them

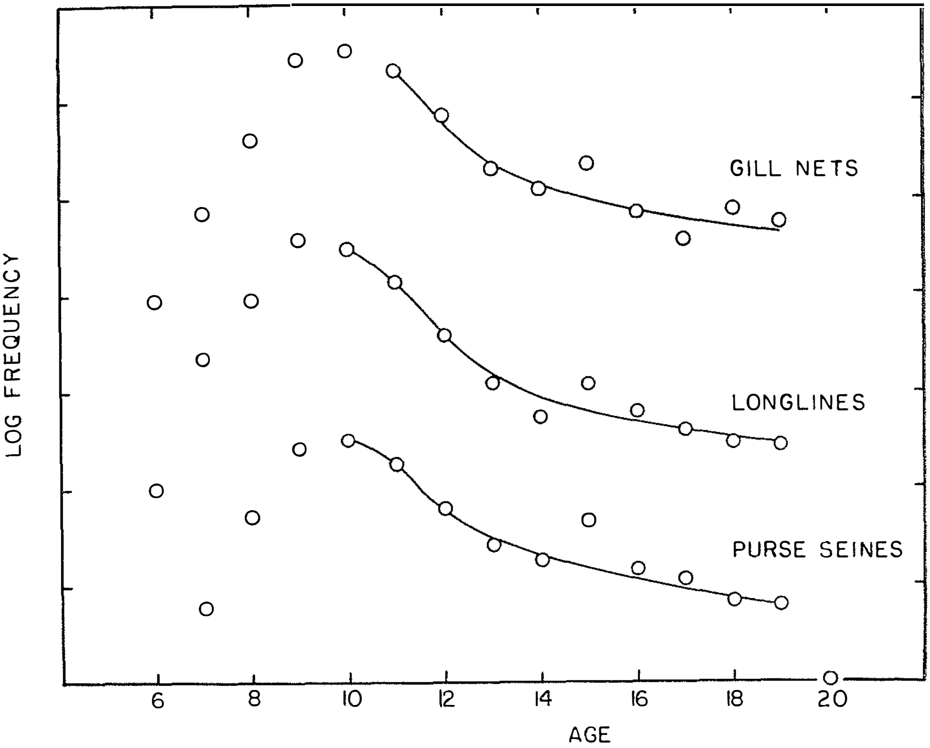


FIGURE 2.8. Catch curves for Lofoten cod taken by three kinds of gear. The ordinate divisions are 1 log unit. (Data from Rollefsen, 1953).

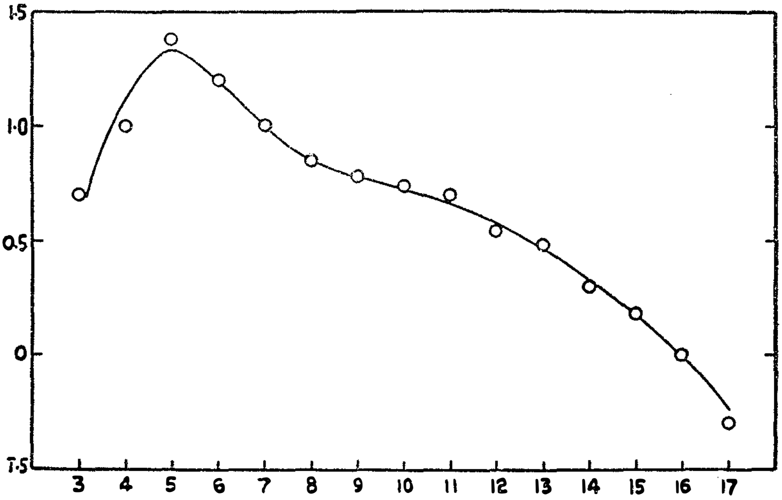


FIGURE 2.9. Catch curve for the whitefish of Lake Winnipegosis, 1928. Abscissa—age; ordinate—logarithm of the percentage of the catch which occurs at each age. (From data of Bajkov, 1933).

representative. The right limb has two steep portions, separated by a period of four years in which it is considerably flatter. More than one kind of irregularity might produce such a curve. In terms of possible variations in fishing, the concave part of the curve would suggest an increase, and the convex part a decrease, in fishing effort over the corresponding times in past years. A second possibility is that there may have been a pronounced cyclical trend in recruitment: an increase for several years, followed by four years of decrease, then two or more years of increase. Finally, the two steeper parts of the curve might indicate a younger and an older age range in which natural mortality is relatively heavy, separated by a period of less severe natural mortality from age VIII to age XII.

Dr. K. H. Doan courteously compiled data on the number of gill nets used on Lake Winnipegosis, shown in Table 2.5, and has also obtained the information that Dr. Bajkov's samples were taken during the winter fishing season early in 1928. From the catch curve it appears that recruitment is spread over ages III through V, or perhaps even VI; age IV will be taken as the mode. Hence the slope at age t on the curve reflects the survival rate $t - 4$ years previous to 1928. Taking tangents on the curve at successive ages gives the series of survival rates (s) shown in Table 2.5, and after 1916 a suggestive inverse relationship between them and the gear in use is evident. The direct relation between number of nets and the instantaneous rate of total mortality (i) is about as good; theoretically it should be somewhat better. The relationship could be "improved" by drawing the catch curve in the light of the net data; as actually drawn, sudden changes are obscured by rounding of the curve. On any system, the points for ages XVI and XVII (1915 and 1916) are wide of the expected value, which suggests a sharp increase in natural mortality rate among the oldest fish, such as is found among whitefish elsewhere. Aside from the last-mentioned effect, it would seem that fluctuations in fishing effort alone *may* be sufficient to account for the sinuous shape of this catch curve.

TABLE 2.5. Number of gill-nets licensed on Lake Winnipegosis, Manitoba, compared with the rate of survival, s, and the instantaneous rate of mortality, i, of the whitefish, as deduced from the catch curve.

YEAR	NETS	s	i	YEAR	NETS	s	i
1915...........	*No data*	0.55	0.60	1921.........	3,304	0.84	0.18
1916...........	2,745	0.63	0.46	1922.........	4,112	0.87	0.14
1917...........	9,535	0.68	0.39	1923.........	5,560	0.87	0.14
1918...........	8,580	0.72	0.33	1924.........	5,765	0.76	0.27
1919...........	*No data*	0.75	0.29	1925.........	6,722	0.66	0.42
1920...........	7,730	0.80	0.22	1926.........	7,422	0.63−	0.45+

It would be pressing the data too far to attempt any more exact analysis. Number of nets licensed has obvious limitations as a measure of fishing effort. We should, for example, expect them to be more efficiently utilized as time goes on, since motors were introduced among the fishing fleet during the period shown, and doubtless other improvements in efficiency of utilization occurred. We should also expect more intensive utilization of nets when prices were good (1917-20, 1925-29) than when markets were slacker. Some such considerations are necessary to explain why the instantaneous rate of mortality more than doubled between 1921-23 and 1925-26, whereas the number of nets was scarcely doubled. Considering that there is some natural mortality, an increase in fishing effort should be followed by a somewhat *less* than proportional increase in instantaneous mortality rate. Another factor which should be considered is the possibility of a decrease in recruitment, since in the later history of this lake the whitefish disappeared as a commercial fish.

Notice that the curve of Figure 2.9 is one of the type which does not show the current (1928) survival rate, since fishing effort was increasing right up to the time the sample was taken. The steepest slope of the curve, corresponding to $s = 0.63$, represents the survival rate about two years earlier.

EXAMPLE 2G. A SERIES OF CATCH CURVES FOR LAKE OPEONGO LAKE TROUT. (Data from Fry, 1949.)

Fry tabulated the catch of lake trout (*Cristivomer namaycush*) in Lake Opeongo by ages, based on a nearly-complete creel census and a scale sample usually of about a third of the catch (Table 2.6). Three considerations make interpretations of catch curves difficult here. 1. The lake became accessible to motorists first in 1935, so that in that year fishing effort increased sharply from a previous lower level. 2. The catch is taken almost wholly by trolling, with which kind of fishing there may be not only the slow recruitment to maximum vulnerability indicated by the table, but afterward a gradual decrease in vulnerability—perhaps because the larger fish are harder to handle and not easily boated by unskilful fishermen (but see Example 8B, below). 3. Fry (p. 31) notes that the scale census was partly voluntary, and hence was not completely random because of a tendency for possessors of *big* fish to bring their catch in for appraisal and approval.

Point 2 would tend to make estimates of mortality rate too great among the older fish, whereas point 3 would make them too small. As far as the latter is concerned, fish less than 8 lb. would scarcely be exhibition pieces in a lake where 12-pounders are fairly common, and fish of age XI or less rarely exceeded 9 lb., so there need be little uneasiness about selective sampling of ages through XI.

Several catch curves from Table 2.6 are plotted in Figure 2.10. All are concave, decreasing in slope at about age XII; this decrease is probably mainly the result of selection of large fish in scale sampling, but it is more pronounced during or just after periods of increasing fishing effort, as would be expected. The most useful slopes of these graphs are for ages IX-XI, as indicated below:

Period	Av. effort *hours*	Rate of survival s	Instantaneous mortality rate i
1936	2030	0.50	0.70
1937-39	1780	0.30	1.21
1940-42	960	0.35	1.06
1943-45	1010	0.43	0.85
1946-47	1480	0.42	0.87

TABLE 2.6. Fishing effort (hours of trolling), catch, and age of the catch of Opeongo lake trout. Age is based upon a direct sample in all years except 1936, when it is computed from the length distribution of the fish caught. (Data from Fry, 1949.)

Year	Fishing effort	Catch	Catch by ages														
			III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII
	hours																
1936.......	2,030	2,600	30	95	128	233	474	665	478	260	118	57	19	25	10	15	11
1937.......	2,240	2,700	0	4	34	198	650	1025	555	176	38	4	8	8	0	0	0
1938.......	1,630	1,650	12	74	127	275	420	439	195	90	3	9	3	0	3	0	0
1939.......	1,380	1,550	39	36	116	221	321	393	223	90	47	24	13	15	4	4	4
1940.......	1,170	1,400	20	84	82	224	434	364	120	46	14	6	0	6	0	0	0
1941.......	1,130	1,100	8	79	144	275	235	200	104	22	11	11	11	0	0	0	0
1942.......	570	630	7	18	46	117	217	121	53	28	8	9	2	2	0	0	0
1943.......	710	900	6	42	42	121	272	211	133	42	0	24	6	0	0	0	0
1944.......	920	1,050	8	26	84	114	197	202	198	93	44	31	9	22	9	4	4
1945.......	1,400	1,420	0	11	32	69	170	352	373	159	84	37	21	43	16	37	16
1946.......	1,740	1,220	19	30	78	116	240	325	217	93	47	26	11	7	0	7	4
1947.......	1,230	885	3	30	55	85	217	221	153	76	18	12	3	0	6	3	3
Mean percentage................			0.8	3.0	5.8	12.5	23.2	26.6	16.1	6.3	2.2	1.3	0.6	0.7	0.3	0.4	0.2

The 1936 estimated mortality rate of 0.70 reflected, in part, the pre-1935 period of lighter fishing. The increase to 1.21 in 1937-39 is presumably the result of the increased exploitation, but the full effect of 2000 hours per year does not have a chance to be manifested. A residual effect of the 1936-39 years of heavy fishing remains in the samples of 1940-42, shown by the moderately large $i = 1.06$, though the actual fishing was least in the latter period. Considering that important recruitment extends over about 5 years, the only period where age IX-XI survival rate is approximately in balance with the observed fishing effort is 1943-45. The value $i = 0.85$, or 43% survival per year, must be

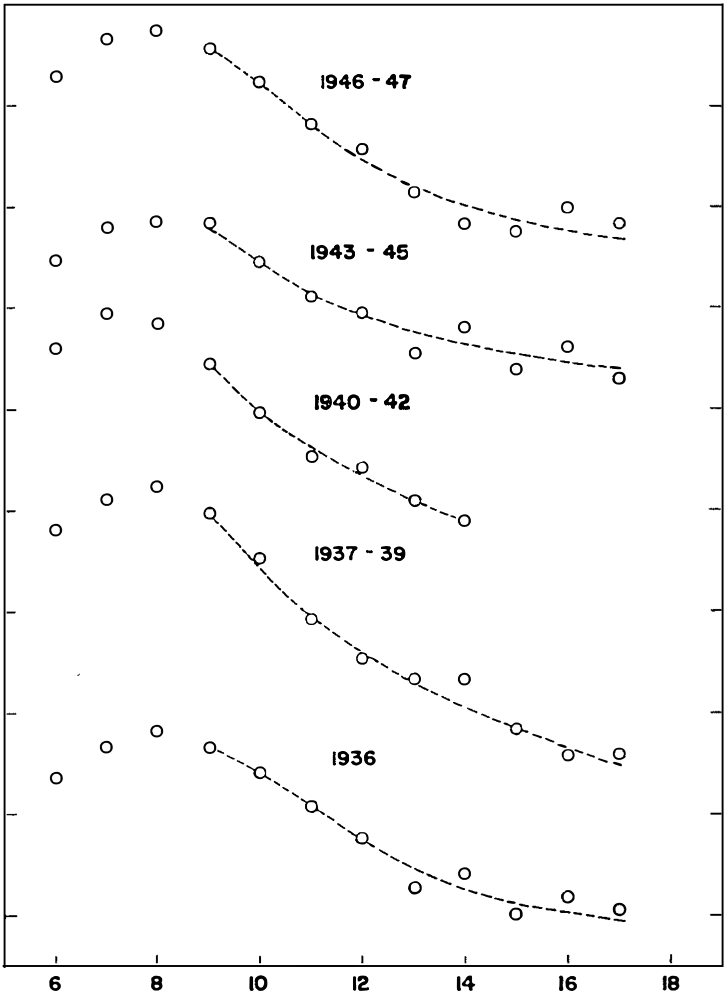


FIGURE 2.10. Catch curves for Opeongo trout. Abscissa—age; ordinate—log frequency. (Data from Fry, 1947).

appropriate to a mean fishing effort of about 980 hours per year (mean of 960 and 1010). The two later years of greater effort, 1946-47, were sufficient to raise this only slightly.

2G. CATCH CURVES BASED ON LENGTH FREQUENCIES

It was mentioned earlier that in Baranov's original catch curve the logarithm of frequency per unit length interval was plotted against length, and that the relation of length to age was estimated separately. There are situations in which this method appears very attractive. For example, when it is a question of assembling a representative sample of the catch from a widely scattered fishery, it may be necessary to sample so many fish that determination of the age of all of them becomes very tedious, or the scales needed for age determination may not always be forthcoming. In such a situation there would be two curves available: (A) a curve of mean length against age, based on a relatively limited body of data, and (B) a representative curve of the logarithm of frequency against length, based on all the samples available, suitably weighted. The two curves can be combined by taking the slope on each at corresponding points, i.e., at a given age on Curve A, and at that age's corresponding mean length on Curve B. The former would be represented by $\mathrm{d}l/\mathrm{d}t = k$ (say), and the latter by $\mathrm{dF}/\mathrm{d}l = -i'$, where l represents length in centimeters; t, age; and F, the logarithm of frequency per centimeter length interval. Hence $\mathrm{dF}/\mathrm{d}l = -i'k$, and $i = 2.30\ i'k$, according to the second method of estimation described in Section 2B.

Unfortunately, this method of computation suffers from a serious limitation: it is useful only on curves, or parts of them, where the increase in length of the fish is a constant number of centimeters per year. For this information we are again indebted to Baranov (1918), who in his figure 12, reproduced here as Figure 2.11, shows an artificial catch curve (A_1B_1) based on length, which was formed by adding up the contributions, to each length-interval, of a succession of overlapping age-classes which decrease in numbers by 50% per year ($i = 0.69$). Up to age VII, the mean length of the fish is made to increase twice as fast as from age VII onward. The result is that while the first slope of the catch curve (i'_1) obtained from ages through mean age VI, multiplied by the first rate of growth (k_1), will yield the true instantaneous mortality rate 0.69; and the increased slope (i'_2) from age IX onward, multiplied by the slower rate of growth (k_2) for older fish, also gives the value 0.69; yet there is an interval from mean age $6\frac{1}{2}$ to mean age $8\frac{1}{2}$, approximately, in which the slope of the catch curve bears no simple relation to the survival rate.

I have myself constructed a similar population model in which rate of growth decreased continuously instead of changing suddenly. Without presenting the details, the annual mortality rate put into the model was $a = 0.4$, while the rates "recovered" from it at different ages by the method of the last paragraph were 0.20-0.22. As a matter of fact, when mortality rate is small and fairly steady, and rate of increase in length is decreasing at a moderate rate, the number of fish at certain intermediate sizes exceeds the number at smaller sizes nearby, as is shown by Curve CD of Figure 2.11, and has been demonstrated for an actual fish population by Hart (1932, fig. 4). In that event dF/d*l* becomes a positive coefficient in places, and could not possibly be used to estimate mortality rate in the manner described above.

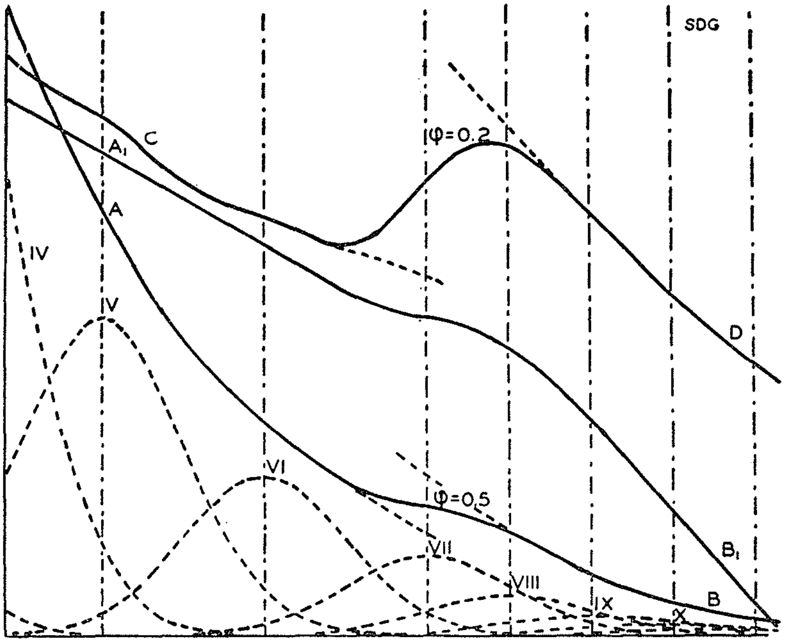


FIGURE 2.11. Synthetic population curves made by summing the contributions, to successive length-classes, of several overlapping age-groups, each normally distributed as to length. The dotted bell-shaped curves are the length distributions of successive age-groups, each half as numerous as the preceding; the rate of increase in length decreases between ages VII and VIII to half of its previous magnitude. Curve AB is the sum of the dotted curves, and shows the length frequencies of the total population. Curve A_1B_1 shows the logarithms of length frequencies of the populations, and is equivalent to a catch curve. Curve CD is a synthetic curve similar to AB, based on fish which have the same rate of growth but which decrease in numbers by only 20% per year. Abscissa—length; ordinate—frequency (log frequency for A_1B_1). (Redrawn from Baranov, 1918, by Dr. S. D. Gerking.)

Mortality rates estimated as above from rate of growth and length frequencies always tend to be too small, if absolute rate of increase in length is decreasing with age. Elster (1944, p. 294), for example, used a combination of length frequency distribution and rate of growth to compute a total mortality rate of 88% per year for Blaufelchen (*Coregonus wartmanni*) of commercial size in the Bodensee. Although this is a rather high rate, the method of estimation tends to make it somewhat too small, rather than too large.

At present, then, catch curves based on length frequencies are much less useful than those based on age, even when the successive ages overlap thoroughly and make a smooth curve. Their slope can be used for an unbiased estimate of survival rate only if the absolute increase in mean length of the fish between successive ages is uniform over a range of ages which, in terms of corresponding mean lengths, is somewhat greater than the range of lengths over which the slope of the graph is to be measured. However this will certainly not be the last word on this subject. Length frequencies are always much easier to obtain than age, and sometimes age is not available at all. Furthermore length is of particular interest when gear selection is being studied, because fishing gear commonly selects fish on the basis of size, not age, and there would be much advantage in dealing with a length frequency curve directly. New developments in the interpretation of length frequency curves may confidently be expected.

EXAMPLE 2H. SURVIVAL OF PACIFIC HALIBUT: A CONCAVE CATCH CURVE BASED ON LENGTH FREQUENCY DISTRIBUTION. (Data from Thompson and Herrington, 1930, p. 72.)

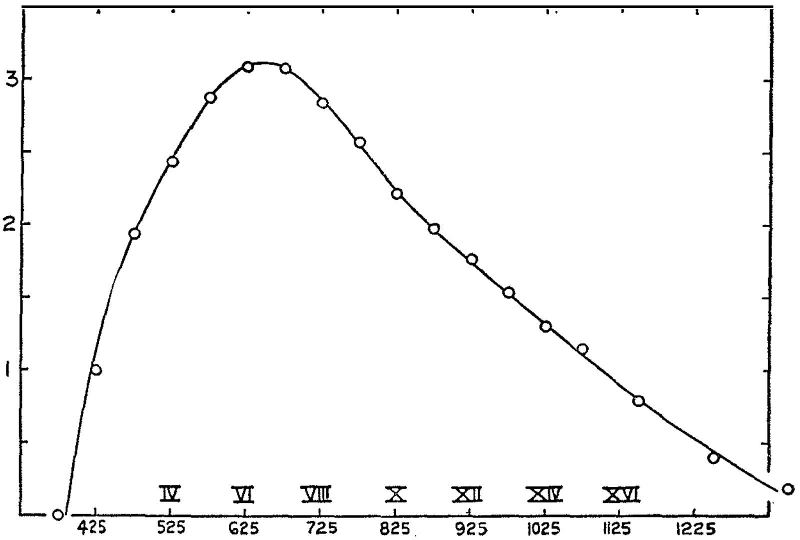


FIGURE 2.12. Catch curve for the Pacific halibut population (southern grounds), from samples taken for tagging in 1925 and 1926. Abscissa—mean length of successive 5-centimeter length groups, in millimeters. (The ages indicated are only approximate, and at ages below IX are typical of the sample only, not of the population.) Ordinate—logarithm of the number of fish taken at each length interval. (From data of Thompson and Herrington, 1930.)

Catches of Pacific halibut (*Hippoglossus hippoglossus*) taken for tagging, south of Cape Spencer, have been used to construct a catch curve based on length frequencies. The catches of 1925 and 1926 are combined in order to smooth out some of the irregularities in recruitment[5]. The catch curve (Fig. 2.12) is plotted in terms of frequency per 5-cm. length interval (near the end the average

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[5] The two years also differ in that there are relatively more small fish in 1926 and more large ones in 1925. However, between ages IX and XIII their curves have much the same slope. Since considerably more fish were handled in 1926, it would be somewhat better to give each year equal weight, but this has not been done here.

for a 10-cm. range has been used.) Dunlop has shown that the mean length of commercially caught Goose Island halibut tended to increase by a little less than 5 cm. for each year's increase in age, from age IV to age XIV; between age IX and age XIV it is exactly 5 cm. per year (Thompson and Bell, 1934, p. 25). This is indicated on Figure 2.12 by roman numerals above the approximate mean length of each age-group. Beyond age XIV there is little direct information on rate of growth; from the situation in other fishes, a decrease in rate of increase in length might be anticipated among old individuals. For estimating survival rate, the curve of Figure 2.12 will be useful only from age IX, which is probably the first fully-recruited age, to age XIV, where linearity of growth may cease. Within these limits, the curve is noticeably concave, and this suggests a recent decrease in survival rate. Accordingly, the slope of the steepest part of the curve, between ages IX and X, will come closest to being an estimate of its current magnitude.

Thompson and Bell (p. 12) give estimates of the fishing effort in southern halibut waters, which are shown below in terms of thousands of units ("skates") of gear set:

Year	Effort	Year	Effort	Year	Effort
1911	240	1917	386	1923	504
1912	343	1918	309	1924	483
1913	436	1919	333	1925	462
1914	365	1920	394	1926	494
1915	381	1921	487	1927	499
1916	264	1922	500	1928	569

If there had been a continuous increase in fishing effort and hence in total mortality rate, right up to 1925-26, then the curve of Figure 2.12 would not, anywhere, be steep enough to represent the current rate of survival. As a matter of fact, however, there were two periods of more or less stable effort: 1921-26, when the gear averaged 490,000 skates; and 1916-20, when it averaged 337,000 skates—though in this case with considerable fluctuation between years. The more recent rather stable period lasted six years, or nearly the same length of time as it takes the halibut to become completely vulnerable to fishing. Consequently by analogy with Curve C of Figure 2.7 we can expect that the steepest part of the catch curve will in fact represent the survival rate which actually prevailed at the time the samples were taken. This steepest slope occurs between ages IX and X, and is -0.066 log units per centimeter, which corresponds to -0.33 log units per year. Hence $i = 2.303 \times 0.33 = 0.76$, $a = 0.53$ and $s = 0.47$[6].

We can also make an estimate of the survival rate which obtained among fully-vulnerable fish in 1916-20. This will be given by the slope of the line

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[6] There is fairly good agreement between this figure and the survival rate of 0.416 estimated by Thompson and Herrington (1930, p. 70) from the recaptures of the halibut tagged in 1925, over a period of four years. The agreement, however, is partly accidental, since halibut of all sizes tagged were used in their estimate, and those which, for at least a year after marking, were in the incompletely-vulnerable size range, were retaken relatively less frequently during the year after tagging than during later years. Since the majority of the fish used were of this sort, this effect is quite important, and makes their estimate of apparent survival rate too *high*. Using completely-vulnerable fish only, the tagging data yield an apparent survival rate of 0.33. Possible explanations of the discrepancy between this figure and the 0.47 obtained here are given in Example 4D, below.

from ages X to XIV inclusive, and corresponds to $s = 0.61$. However, since this is getting into the region where the catch curves for the separate years do not agree too well, it would be better to say that this is the survival rate which would be indicated, if we could be sure that the sample were reasonably representative.

2H. CATCH CURVES FOR ANADROMOUS FISHES

Anadromous fishes may conveniently be divided into three categories: (1) those which reproduce only once and then die; (2) those which may reproduce in each of two or more successive years; (3) those which may reproduce more than once, but at intervals longer than one year. All three types usually have one feature in common, that fishing tends to be concentrated on the migrating fish which are about to mature and reproduce.

The best-known examples of the first type above are found among the Pacific salmons (*Oncorhynchus* spp.). A catch curve from a sample of the migrating run of such fish is obviously of no value for estimating mortality rate, though the information may occasionally be used to estimate survival rate in another manner (Section 8G).

Anadromous fishes of group 2, of which the Atlantic salmon (*Salmo salar*) and shad (*Alosa sapidissima*) may be taken as examples, present a somewhat different picture. Here catches taken from the spawning run can be made to give information about mortality rate, provided the maiden fish can be distinguished from those which have already spawned at least once. Beginning with the first[7] age-group in which practically no maiden fish occur, the abundance of successive ages from there on will reflect the population survival rate between them, subject to the usual provisos regarding random sampling, uniformity of recruitment, and so on. However, it may be found, and this is usual among salmon, that recidivists are so rare as to constitute only a minor part of the total catch, apparently because of a very heavy sea mortality which is not the result of fishing. Shad, on the other hand, seem to survive in larger numbers and to greater ages (Fredin, 1948).

Finally, the very interesting situation where more than one year elapses, between spawnings, has most of the characteristics of the one just discussed. If fish are caught only in the spawning migration, the survival rate obtained from the catch curve is the (geometric) mean annual rate for all the years between one spawning migration and the next (not the overall survival for the total time elapsed between one migration and the next.) Among anadromous fishes, this behaviour is best known for sturgeons (*Acipenser*); non-anadromous salmonoid fishes in some northern lakes appear to spawn only in alternate years.

EXAMPLE 2I. CATCH CURVE FOR KURA RIVER STELLATE STURGEON. (Data from Derzhavin, 1922.)

Derzhavin's comprehensive study of the sevriuga or stellate sturgeon (*Acipenser stellatus*) of the Kura River contains information on a wide variety of topics. From his table (p. 67) of the age and sex composition of this sturgeon

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[7] If both the age and the number of spawnings of each fish can be determined, such comparisons can be made for all age-groups.

as caught in the Caspian Sea near the mouth of the river, the catch curves of Figure 2.13 are plotted. When the sexes are segregated, the males are seen to occur at a much younger average age than the females. Since the fish are taken on their spawning run, this indicates that the males mature earlier, on the average. Derzhavin gives 12 to 15 years for males and 14 to 18 years for females as the principal range of ages at first maturity, though some of either sex were taken as early as 8 years. Sevriuga of both sexes spawn "at intervals of several years, possibly five", but it is not known that the two sexes have the same average interval between spawnings. If the elapsed time were longer for the younger females, as is suggested by Roussow's (1957) work with *Acipenser fulvescens*, it would explain the longer ascending limb of their catch curve.

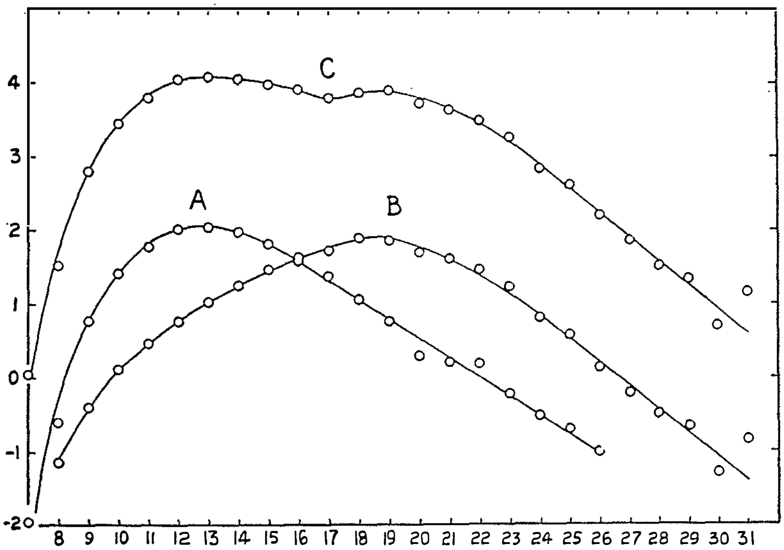

FIGURE 2.13. Catch curves for the stellate sturgeon of the Kura River. A. males; B. females; C. sexes combined. Abscissa—age; ordinate—logarithm of the number of fish occurring at each age, per thousand of the total sample, for curves A and B; curve C is drawn two units higher. (From data of Derzhavin, 1922.)

A point of general interest is that when vulnerability to fishing depends on maturity, differences in age at maturity of the two sexes tend to broaden the left limb and flatten the dome of the catch curve, when the sexes are not separated. In ordinary fisheries, a difference in rate of growth of the sexes will have a similar effect. However, it will probably rarely happen that the dome will actually have a dint in it, as was found for the Kura sevriuga.

2I. STRATIFIED SAMPLING FOR AGE COMPOSITION

When an overall random sample is used to plot the catch curve and estimate survival rate in a stock, there is commonly a series of older ages which are represented by only a few individuals if the sample is of any ordinary size—say 100 to 1000 fish. The same is usually true of one or a few of the youngest ages, which ages may be of interest in examining net selectivity, etc. If good information concerning these terminal ages is desired, special effort must be expended on them.

1. A very simple plan is to take a special sample of the catch for fish above a certain size. For example, 1/1000 of the catch might be used for the general sample, and 1/100 of the large fish for the special one. Growth or survival rates computed from the special sample are used for the older ages (Ricker, 1955a). However, this procedure is not particularly efficient, since a part of the fish whose scales or otoliths are read in the special sample must be discarded because they belong to ages incompletely represented in the size range of that sample. Also, this consideration makes it rather unlikely that it would be profitable to use more than two different sampling fractions.

2. Ketchen (1950) suggested a different plan, which works well when a really large representative *length* sample can be obtained for the whole catch. Dividing the catches into length groups one centimeter broad, otoliths are collected for age determination from fish in the large sample, up to some fixed number in each length group or (in the terminal groups) to such smaller numbers as are available. From the percentage representation of each age in its otolith sample, an age composition for each length group of the representative length sample was determined, and the whole added by ages to build up an estimate of the age composition of that sample, hence of the catch[8].

Obviously methods 1. and 2. above might advantageously be combined, when the time or facilities for taking a really large length sample are not available. In fact, by grafting Ketchen's procedure onto it, the method of using different sampling ratios is considerably improved: no age-determined fish need be discarded, a complete (computed) catch curve is obtained, and more than two different sampling fractions might sometimes be employed to advantage.

Both of the methods above imply that it is desirable to have more accurate information on the sparsely-represented ages than what a moderate-sized single sample will supply—which is not necessarily true for all purposes, although generally so.

3. When catches from a stock are landed by many boats, at many ports, and over a considerable period of time, the assembling of a single representative length or age distribution becomes very complex indeed—involving numerous individual samples which are eventually combined into one representative picture using a series of weighting factors. Details for particular situations have been published, but no general description would be profitable. Subsampling by length for the age determinations may be of great assistance, but sometimes age at a given length will differ significantly as between different catches. Several papers describing problems and methods in use are included

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[8] From a large length sample of cod, Fridriksson (1934) took a subsample for age determination and applied this computational procedure, thus decreasing the influence of sampling error and of any possible systematic bias in the subsample. However the advantage gained in this way is ordinarily small compared to what is afforded by Ketchen's procedure.

TABLE 2.7. Age distribution in a sample (Y) of male Strait of Georgia lemon soles as determined from a stratified subsample (X).

Size class (*cm.*)	Subsample (X)	Age groups in X						Sample (Y)	Calculated age representation in Y					
		IV	V	VI	VII	VIII	IX		IV	V	VI	VII	VIII	IX
27	6	5	1	..	..	..	..	6	5.0	1.0				
28	9	3	4	2	..	..	..	9	3.0	4.0	2.0			
29	10	4	4	1	1	..	..	30	12.0	12.0	3.0	3.0		
30	10	1	5	4	..	..	..	51	5.1	25.5	20.4			
31	10	..	8	2	..	..	..	54	..	43.2	10.8			
32	10	1	7	1	1	..	..	48	4.8	33.6	4.8	4.8		
33	10	1	3	3	2	1	..	41	4.1	12.3	12.3	8.2	4.1	
34	10	..	2	6	1	1	..	27	..	5.4	16.2	2.7	2.7	
35	10	..	1	4	3	..	2	13	..	1.3	5.2	3.9	..	2.6
36	6	..	..	1	3	2	..	6	..	..	1.0	3.0	2.0	..
37	3	..	..	1	1	1	..	3	..	..	1.0	1.0	1.0	..
38	1	..	..	..	..	1	..	1	..	..	..	..	1.0	..
Totals...	95							289	34.0	138.3	76.7	26.6	10.8	2.6
Percentage									11.8	47.9	26.5	9.2	3.7	0.9

in Volume 140, Part I, of the Rapports et Procès-Verbaux of the International Council for the Exploration of the Sea; see especially Pope (1956) for a discussion of stratified sampling.

EXAMPLE 2J. AGE COMPOSITION OF A LEMON SOLE CATCH OBTAINED BY THE STRATIFIED SUBSAMPLING METHOD OF KETCHEN (1950).

Table 2.7, provided by Dr. K. S. Ketchen, is a computation of age composition of a random catch sample (Y) using a subsample (X) stratified by length, for lemon sole (*Parophrys vetulus*). Up to 10 otoliths were read in each subsample, the age frequencies being in the left half of the Table. These are applied *pro rata* to the actual numbers in the Y-sample, in the right-hand side of the Table. Totals of these columns represent the estimate of age composition of the catch. This would be used to estimate survival rate, recruitment, etc., subject to the various considerations outlined earlier in this Chapter.

Selection of the best maximum number of fish to be included in each length class is a matter of some importance (cf. Gulland, 1955). It depends upon the breadth of the length classes used and hence the total size of the sample to be "aged", on the number of samples actually or potentially available to represent the fishery under consideration, on the degree of difference between intra-sample and inter-sample variability, and on the labour involved in taking additional samples.

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

3A. GENERAL PRINCIPLES OF POPULATION ESTIMATION BY MARKING METHODS

The attaching of tags to fish, or marking them by mutilating some part of the body, was first done in order 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, the rate of exploitation, and, secondly, the total population, of the 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" or the "Lincoln index".

Schaefer (1951a, b) has traced the principle of the method back to Laplace in 1783. and sketches its subsequent history to about 1945. Laplace used it to estimate the population of France from a register of births for the whole country (the "marked" individuals) and a ratio of births to population obtained from a relatively restricted area. About 10 years after Petersen's first work, Knut Dahl employed the same procedure to estimate trout populations in Norwegian tarns, and applications to ocean fishes also started during 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. the rate of exploitation of the population
2. the size of the population
3. the survival rate of the population from one time interval to the next; most usefully, between times one year apart
4. the rate of recruitment to the population

Of course not all mark-and-recapture experiments can provide all this information; often only the population size is involved. During the past 10 years 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) and Chapman (1952, 1954).

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. Note that whereas the *marking* should ideally be restricted to a short space of time, the subsequent sample may be taken over quite a long period.

(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* the fish taken in the samples, but it is not essential.

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

(4) *"Point" censuses.* Samples for marking and for obtaining recoveries are made at three or more[1] periods or "points" in time, these periods being preferably short as compared with the intervening periods. More specifically, the first sample is for marking only, the last is for recoveries only, and the intermediate one or ones are 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.

In experiments using tags, the 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: and they often require rather involved tabulations and solving complex expressions.

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

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

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 has the advantage that it 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 be applied to multiple censusing also (Chapman, 1952).

In practice, sampling can be and probably usually is somewhat intermediate between direct and inverse. An experimenter may have time for up to two

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

weeks of census sampling (let us say) but would be glad to stop earlier if a reasonable number of recaptures has been taken. However if his decision is made 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.

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.

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).

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.

3B. PETERSEN METHOD (SINGLE CENSUS)

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. We have:

M number of fish marked

C the catch or sample taken for census

R the number of recaptured marks in the sample

We wish to know:

u the rate of exploitation of the population

N the size of the population at time of marking

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

$$\hat{u} = \frac{R}{M} \tag{3.1}$$

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:

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

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

$$V(\hat{u}) = \frac{R(C - R)}{M^2C} \tag{3.2}$$

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

$$\widehat{(1/N)} = \frac{\hat{u}}{C} = \frac{R}{MC} \tag{3.3}$$

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

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

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

$$\hat{N} = \frac{MC}{R} \tag{3.5}$$

with a sampling variance of:

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

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

Confidence limits can be obtained more simply, however, by treating R as a binomial or Poisson variable (whichever is appropriate), obtaining limits for it directly from a table or chart (cf. Section 1I), and substituting these in (3.5).

Although expression (3.5) is a consistent estimate of N, in the sense that it tends to the correct value as sample size is increased, it is not quite the best estimate[2]. This is true whether sampling is direct or whether it is inverse. Bailey (1951) and Chapman (1951) have shown that with ordinary "direct" sampling (3.5) tends to overestimate the true population. They propose modified formulae which give an almost unbiased estimate, of which Bailey's is as follows:

$$\hat{N} = \frac{M(C + 1)}{R + 1} \tag{3.7}$$

It is usually worth while to use (3.7) in place of (3.5), in direct sampling, even though with large values of R there is little difference.

The large-sample sampling variance for $\hat{N}$ in (3.7) is given by Bailey (1951, expression 2.15) as approximately equal to:

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

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 3A).

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[2] That a best estimate does not remain a best estimate when it is inverted is one of the uncomfortable facts of statistical life. The same is true as between a statistic and *any* function of it, other than a linear one. For analogous examples see Sections 2A and 11B (Table 11.1).

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).

Chapman's expression corresponding to (3.7) differs slightly:

$$\hat{N} = \frac{(M + 1)(C + 1)}{R + 1} \tag{3.9}$$

and his expression for the variance is similarly adjusted, but practically these are indistinguishable from Bailey'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):

$$\hat{N} = \frac{C(M + 1)}{R} - 1 \tag{3.10}$$

Using $\hat{N}$ for N, the approximate asymptotic variance of (3.10) is:

$$V(\hat{N}) = \frac{(M - R + 1)(\hat{N} + 1)(\hat{N} - M)}{R(M + 2)} \tag{3.11}$$

EXAMPLE 3A. TROUT IN UPPER RÖDLI TARN: A SIMPLE PETERSEN EXPERIMENT. (Data from Dahl, 1919.)

An early application of Petersen's method was made by Knut Dahl, beginning in 1912. He wished to estimate the trout (*Salmo fario*) population of some small Norwegian tarns, as a guide to what amount of fishing they should have. From 100 to 200 trout were caught by seining, marked by removing a fin, and distributed in systematic fashion around the tarn so that they would quickly become randomly mixed with the unmarked trout. Shortly afterward, more seining was done, and the fraction of marked fish in the catch determined. In the account which I have (Dahl, 1919), the actual numbers of fish marked and recaptured are not given, but from the resulting estimates for the 1912 experiment in Upper Rödli tarn, the following table is prepared, in which these figures are of the right general magnitude:

	Total number of trout	Number of marked trout	Ratio
In the sample—			
Actual number	177(C)	57(R)	0.322
Limits of 95% confidence	......	46-71	0.26-0.40
In the tarn—			
Actual number	334($\hat{N}$)	109(M)	
Limits of 95% confidence	413-269	......	
Ratio of catch to population	......	0.52	
Limits of 95% confidence	......	0.42-0.65	

The steps in preparing this schedule are as follows: The ratio of marked to total trout in the sample is first estimated as 57/177 = 0.322, and by reference to Clopper and Pearson's (1934) chart the 95% limits of confidence of the ratio are 0.26—0.40. Multiplying these by 177, the limits of confidence for the actual number of recaptures are 46-71. The best estimate of the number of fish in the population is now calculated from (3.7) as:

$$\hat{N} = \frac{M(C + 1)}{(R + 1)} = \frac{109 \times 178}{58} = 334$$

By substituting 46 and 71 for R + 1 in the above, the confidence limits for $\hat{N}$ are 422 and 273.

Finally, the rate of exploitation is $\hat{u} = R/M = 57/109 = 0.52$; its range for 95% confidence is $46/109 = 0.42$ to $71/109 = 0.65$. As a matter of fact, in Dahl's experiment the rate of exploitation played an important part, for he undertook to fish the tarn until about half of its fish were removed, as estimated from recovery of marked ones.

3C. EFFECT OF RECRUITMENT

A straightforward application of formulae 3.1—3.7 is justified only if a number of conditions are met, chief among which are the following:

(1) that the marked fish suffer the same natural mortality as the unmarked;

(2) that the marked fish are as vulnerable to the fishing being carried on as are the unmarked ones;

(3) that the marked fish do not lose their mark;

(4) that the marked fish become randomly mixed with the unmarked; *or* that the distribution of fishing effort (in subsequent sampling) is proportional to the number of fish present in different parts of the body of water;

(5) that all marks are recognized and reported on recovery;

(6) that there is only a negligible amount of recruitment to the catchable population during the time the recoveries are being made.

All of these conditions are of general applicability to experiments of this type, and are discussed in more detail below. Number 6 is essential to the estimate of population, but not to estimating rate of exploitation. Notice that natural mortality will not interfere with the accuracy of the results, as long as it is the same for both marked and unmarked groups. The population estimate obtained applies to the time at which the marked fish were released.

Of the requirements above, the condition that recruitment be negligible is one that often will not be met. Where it is not, the estimate of population is too great. A correction for this effect can be applied by one of several methods.

1. If the population being estimated is divided into age-groups which overlap only a little in length, then by choosing the lower limit of size of fish to be marked at the trough between two age-groups, a boundary can be established whose position will advance as the season progresses and the fish grow larger. In this way there will be little or no recruitment into the marked size range, and C and R should remain in strict proportion throughout the time recoveries are

obtained; always provided that the marked fish grow as much as the unmarked, and that they suffer the same mortality.

2. If the age-groups in the fishery overlap so thoroughly that no such point of demarkation can be found, the rate of growth of the fish throughout the season can sometimes still be estimated, by scale-reading. Suppose, for example, that we wish an estimate of the fish 200 mm. long or longer as of July 1st. Assume for the moment that a sufficient number of fish can be marked immediately prior to July 1 to give adequate recoveries later. Take the scales from a sample of fish caught near July 1 and ascertain the mean growth increment, from the time of the last annulus, of fish of the two age-classes whose mean length lies nearest to 200 mm. From time to time throughout the fishing season take additional samples and determine the increment of these same age-classes. By applying these increments proportionately, the average seasonal growth of fish which on July 1 were 200 mm. long can be determined with fair accuracy. Now by including only fish greater than this size in the daily catches (C), the effect of recruitment is avoided, and the population estimate consequently will be a true one.

3. When information on rate of growth is not obtainable in the detail necessary for the method just outlined, an approximate correction, which is far better than none at all, can often be made. First calculate the per annum rate of growth of fish of the appropriate size—a thing that can be done using scales from a single group of fish, taken at any time (though consideration must be given to possible effects of selective sampling, cf. Section 9A). Then divide by the fraction of the growing season that is concerned, i.e., from July 1 to the successive days of the fishing season on which fishing is done. Add these successive values to 200 mm. and proceed as above.

The fact that recoveries are being made over a considerable period of time, rather than on a single day or other short interval, is in itself no obstacle to the accurate estimation of population, after the effects of recruitment have been excluded.

If it were necessary to mark fish for a considerable period prior to July 1 in order to get a sufficient number, the same procedure as described above could be extended backward. That is, fish less than 200 mm. could be marked in May and June, the exact minimum size in successive weeks to be determined by an examination of rate of growth prior to July 1. It is not *essential* that such smaller fish be used, provided the total mortality rate remains substantially the same over the length range in question, but it will provide more fish for marking than would otherwise be available. In either event there is a disadvantage in extending the marking period too far backward, for natural mortality will remove some of the marked fish before July 1 and make subsequent population estimates too great. If necessary, approximate corrections can be made for this by deducting the estimated mortality for the fraction of the growing season concerned.

4. A method that does not involve age or growth estimates has been described by Parker (1955). After a marking, addition of new fish to the catchable population "dilutes" the marks, and the ratio of recaptures to total sample, R_t/C_t, tends to fall off with time, t. If this fraction is plotted against time and a line fitted, the intercept at $t = 0$ is an estimate of R_t/C_t at time of marking, which can be divided into the number marked, M, to get an estimate of initial population. It may be preferable to use some transformation of R_t/C_t in the graph: the logarithm may be convenient, or the arcsin of its square root as used by Parker.

This method is most useful when the experiment extends over a sufficient period of time for recruitment to be quite pronounced. An estimate of error in the transformed R_t/C_t can be made by calculating the standard deviation from the regression line and then the standard error of the intercept at $t = 0$ (see Snedecor, 1946, section 6.9). Transformed back to original units and converted to population by dividing into M, these limits will in general be wider than those based on Poisson or hypergeometric theory. They will also be more realistic, since the variation about the regression line may be greater than expected, because of non-random distribution and sampling.

Example 3b. Bluegills in Muskellunge Lake: A Petersen Experiment with Recruitment Eliminated by means of Length Analysis

In Figure 3.1 is shown the length distribution of the bluegills (*Lepomis macrochirus*) handled in a marking experiment on Muskellunge Lake, Indiana (Ricker, 1945a). The population was sampled by means of two kinds of traps, which took small fish and larger fish respectively, though unfortunately the intermediate length range, 60 to 90 mm., was poorly sampled. From length frequencies and scale-reading the stock could be divided into age-groups fairly well, as shown by the arrows in Figure 3.1. Fish of 123 mm. and longer were marked. Recaptures were obtained in the traps and from fishermen's catches during the period from June 16 to September 7. From the figure, the legal-sized population (125 mm. group and up) at the beginning of this period contained a majority of III-year-old and older fish, but by the end of summer the II-year-old group had almost completely grown into the fishery, and the older ones contributed only a minor share of the catch. The point of division moves from between the 135- and 140-mm. groups in May to between the 165- and 170-mm. groups in the latter part of August, advancing 5 mm. each half-month. The fact that the marked fish grow as rapidly as the unmarked was shown by the fact that the minimum size of marked fish recaptured increased by about 5 mm. each half-month following June 15. (In a later experiment different marks were used for fish greater and less than 142.5 mm. in early June, with the same result.)

The data of the experiment are summarized in Table 3.1. Considering first the fish of age III and older, the ratio of marked to unmarked is about the same in traps and in fishermen's catches, so the combined estimate of $28/727 = 0.0385$ gives the mean fraction of marked ones in the population. The estimated population as of the first half of June is therefore 140/0.0385 = 3,640; or better, from (3.7), $\hat{N} = 140 \times 728/29 = 3{,}520$. This estimate is doubtless slightly high, because no account is taken of natural mortality during the short period marking was in progress. An approximate correction for this could be made, but it evidently would be unlikely to exceed, say, 5 per cent.

The rate of exploitation by fishermen is estimated very simply from Table 3.1 as $\hat{u} = 23/140 = 16\%$. The correction just mentioned would slightly

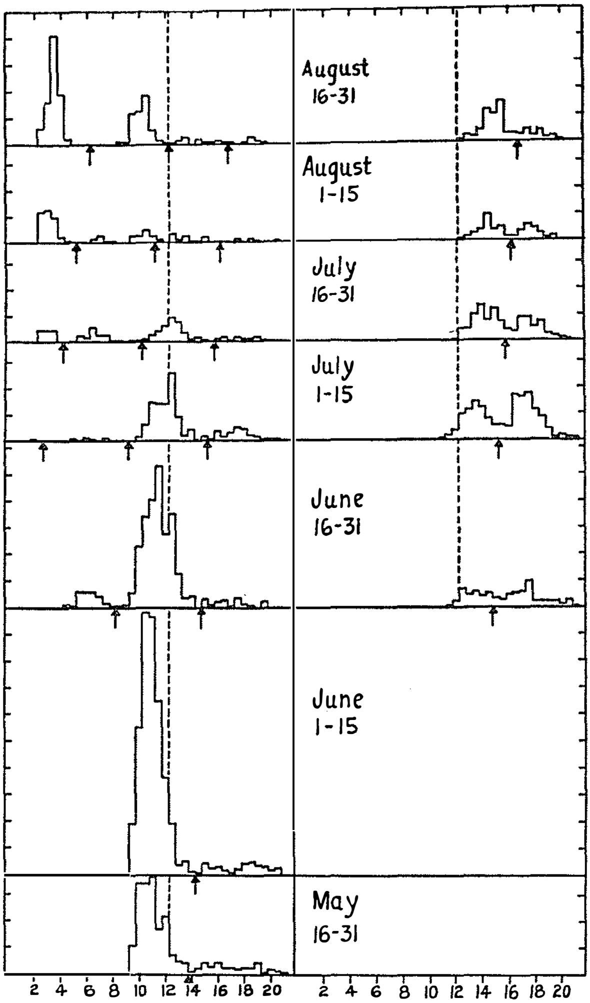

FIGURE 3.1. Length frequency distribution of bluegills caught in traps (left side) and by fishermen (right side), Muskellunge Lake, Indiana, 1942, by semi-monthly periods. Each ordinate division represents 20 fish. The vertical broken line represents the minimum size of fish marked, and the minimum size which could legally be taken by fishermen. Ordinate—frequency; abscissa—length in centimeters.

TABLE 3.1. Bluegills marked (M) prior to June 16, 1942, in Muskellunge Lake, number of recaptures (R), and the catch from which recaptures were taken (C).

Half-month period	6-II	7-I	7-II	8-I	8-II	9-I	Total
A. Age III and older fish: 140 marked							
Traps							
Recaptures	3	0	1	0	1	...	5
Total catch	35	50	21	10	12	...	128
Fishermen							
Recaptures	3	9	8	2	1	0	23
Total catch	120	230	165	39	36	9	599
B. Age II fish: 90 marked, of legal size in early June							
Traps							
Recaptures	2	0	0	0	0	...	2
Total catch (legal in early June)	77	25	10	5	8	...	125
Total catch (whole age-group)	487	187	80	21	20	...	795
Fishermen							
Recaptures	1	5	6	1	4	0	17
Total catch (legal in early June)	44	96	92	44	80	19	375

increase this estimate, as would an allowance for fish caught by the few boats whose catches were not checked.

Turning now to the age II fish of Table 3.1, we observe that the ratio of marked to unmarked "legal" fish is smaller in trap recaptures than in fishermen's but not significantly so. Combining the two, the best estimate of population in early June, from (3.7), is $\hat{N} = 90 \times 501/20 = 2{,}250$. The rate of exploitation by fishermen is $\hat{u} = 17/90 = 19\%$, not significantly different from that for the larger fish.

We can also try to estimate the size of the whole of the age II group of fish from the trap records, by assuming the marked and unmarked portions to be equally vulnerable to trapping. From the table, the whole age-group should be $795/125 = 6.36$ times as numerous as is the part of it which was of legal size in early June (compare the relative sizes of the parts of the age-group in June 1-15 on either side of the dotted line in Figure 3.1). The whole age II brood is therefore estimated as $6.36 \times 2{,}250 = 14{,}300$ fish.

3D. EFFECTS OF MARKING AND TAGGING

DIFFERENTIAL MORTALITY. A frequent effect of marking is extra mortality among marked fish, either as a direct result of the mark or tag, or indirectly from the exertion and handling incidental to marking operations. In either event recoveries will be too few to be representative; hence population estimates made from them will be too great and rates of exploitation will be too small. For example, Foerster (1936) found that yearling sockeye salmon (*Oncorhynchus nerka*) marked by removal of the ventral fins survived to maturity only about 38% as often as did unmarked ones. Foerster's method of estimating and correcting for this error depended on special circumstances of the migratory behaviour of the salmon, so it is usually necessary to look to other methods. One approach is to compare returns from different kinds of tags or marks. If one method of marking obviously involves more mutilation of the fish than another, yet both marks are recaptured with equal frequency, then neither is likely to be producing any significant mortality. The opposite result, however, while suggesting that mortality is caused by the more severe procedure, would not necessarily exonerate the milder one. Neither result would shed light on effects of capture and handling, as distinct from the marking proper. When fish are being tagged, and are more or less obviously bruised or abraded in the process of capture, it is possible and useful to keep a record of the degree of injury and apparent vigor for each fish separately. When recaptures come in, these can be checked against the record to see if the less vigorous fish are less frequently retaken.

Both of the above checks were made in an experiment on Shoe Lake, Indiana (Ricker, 1942b). Half of the bluegill and other sunfishes (*Lepomis* spp.) were marked by removing the two pelvic fins; the other half were given a jaw tag in addition to the mark. The result proved very interesting. Tagged fish were retaken as frequently as untagged, in traps, but in anglers' catches they were much less numerous than untagged ones; and this situation lasted through the second summer of the experiment. Among tagged fish, there was no association between rate of recapture and an estimate of trap damage based chiefly on the extent to which the tail was split. Because the tag produced a rather serious and prolonged lesion, while the fin scars and tail membranes healed quickly, it was concluded that trapping, handling, removing the fins, and even the presence of the tag all resulted in very little or no mortality; but that the tag, presumably by interfering with feeding, vitiated estimates of population made from recoveries of line-caught fish. On large-mouthed fishes however the jaw tag interferes much less with normal feeding.

Another disadvantage of the jaw tags, doubtless related to the above, was that they reduced the rate of growth very markedly in all species of fish on which they were used. This is not too important, perhaps, since the number on the tag makes it possible to identify the size class to which the fish belonged when tagged. Fortunately, when medium-sized fish are marked by removing a fin or fins, no such retardation of growth occurs (Example 3b; Ricker, 1949b).

DIFFERENCES IN VULNERABILITY OF MARKED AND UNMARKED FISH. A more insidious source of error is a tendency for marked or tagged fish to be either more, or less, vulnerable to fishing than are native wild fish. This may result from several causes.

1. If the fish used were not originally a part of the population being estimated, they may obviously behave differently, whether or not they are marked or tagged. This consideration usually makes hatchery-reared fish, or wild fish from strange waters, useless for estimating native populations.

2. When tags are used, the tag itself may make a fish more, or less, vulnerable to fishing. The jaw-tagged bluegills mentioned above are a case in point: the tagged ones were much less vulnerable to angling. Another example is of salmon tagged with two disks joined by a wire passing through the body. Though excellent from several standpoints, these "Petersen disks" have the disadvantage that they make the fish more vulnerable to gill nets than are untagged fish, by reason of the twine catching under the disk.

3. Probably of more general applicability are differences in behaviour as a result of tagging or marking. The process of capturing and marking a fish may often impose a certain physical or (for all we know) psychological hardship upon it[3]. It would not be surprising, therefore, to find it behaving differently after the handling, for a longer or shorter period. For example, marked centrarchids, when first released, usually swim down and burrow into the weeds. The same tendency, if it persists, might make them more apt to enter a trap funnel than an untouched fish. Any fish, after marking, may be "off its feed", and hence less likely to be caught by methods involving baited hooks. If marking makes a fish less inclined to move about, it will be less apt to be caught in fixed gear like traps or gill nets, but it may be more likely to be caught in moving gear like seines or otter trawls. With other fish a tag may be a stimulus resulting in increased or more erratic movement for some days or weeks. For example, Dannevig (1953, figure 3) found that tagged cod were retaken by gill nets with rapidly decreasing frequency over the first 15 to 20 days after tagging, but during the same period recaptures from hook gear remained steady (1948) or actually increased (1949).

Effects of these sorts will in general be hard to detect, and hard to distinguish from actual mortality due to tagging. The rate of recapture in successive weeks, or months, after tagging may provide suggestive information. So may comparisons of recaptures by different methods of fishing, for vulnerability to one kind of gear may be affected, but not to another, as in the case of the jaw-tagged sunfish or the cod mentioned above. What makes the use of these criteria difficult is that ordinarily recaptures are none too numerous, and their limits of sampling error may be so wide that significant systematic errors are hard to demonstrate.

EXAMPLE 3C. CORRECTION FOR EFFECTS OF TAGGING ON VULNERABILITY OF CHUM SALMON IN JOHNSTONE STRAIT, B.C. (From Chatwin, 1953.)

Chum salmon (*Oncorhynchus keta*) were tagged at two sites along their migration route from Queen Charlotte Sound through narrow 100-mile-long Johnstone Strait into the Strait of Georgia (Table 3.2). The fish moved from

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[3] Black (1957) and others have demonstrated some of the physiological aspects of this type of stress.

TABLE 3.2. Chum salmon tagged and recovered in Upper Johnstone Strait (Area 12) and Lower Johnstone Strait (Area 13), with estimated percentage returns for fish *entering* the Strait. (From Chatwin, 1953.)

Tagging locality	No. tagged	Percentage recovery by localities				
		Area 12	Area 13	Other	Unknown	Total
Area 12	1733	15.98	10.09	11.74	1.73	39.54
Area 13	1952	0.15	14.65	14.81	1.33	30.94
Entrance of 12 (computed)	..	13.10	10.44	12.81	1.45	37.80

Area 12 (upper Johnstone Strait) through Area 13 (lower Johnstone Strait), and were tagged about midway along each Area.

Recaptures of Area 12 fish were expected to be about twice as great in Area 13 as in 12, since they were exposed to only half of the Area 12 fishery and there was about the same amount of fishing in each Area. In fact, however, more were caught in 12 than in 13 (15.98% and 10.09%, respectively). This fact, plus a consideration of times of tag recoveries, indicated that the tag or the tagging procedure delayed the fish's movement by a few days. (Similar effects have been observed in river tagging; see Killick, 1954.)

For estimating rate of exploitation, the data of the chum experiment have two defects: (1) there is the extra vulnerability due to the tagged salmon's delay in resuming migration; and (2) it would be desirable to refer the results to a (hypothetical) tagging point for fish *as they first enter the fishery* at the upper end of Area 12. Chatwin made both these adjustments in a single operation, using the assumption that the fish tagged in Area 13 were delayed to the same degree as those in Area 12. The rate of recovery of tagged fish *entering* Area 13 is, from Table 3.2, $10.09/(1 - 0.1598) = 12.01\%$; as compared with 14.65% recovery of those tagged *in* Area 13. If the same relation applies in Area 12, where 15.98% of local tags were retaken, the corrected rate of exploitation in Area 12, applicable to untagged fish entering the Area, is:

$$12.01 \times 15.98/14.65 = 13.10\%$$

Of the 86.90% which remain after traversing Area 12, 12.01% are taken in Area 13, or 10.44% of the original arrivals to the fishery. In a similar way the recaptures below Area 13, of fish entering Area 12, were estimated as 12.81%. These three percentages are then added, and increased by the small percentage of "unknown" recaptures, to obtain a final representative rate of exploitation of 37.8%. However, there were a few other complications in the situation, one of them being the possibility of incomplete reporting of tags recaptured.

In this experiment only the rate of exploitation could be estimated, and not the total population, because in the lower Strait of Georgia the Johnstone Strait chums became mixed with others, and the catch statistics cannot distinguish them by origin.

3E. LOSS OF MARKS OR TAGS

Another source of error in population estimates concerns the tags or marks themselves. Tags have been placed, at one time or another, on many different parts of a fish. The conventional strap tag is usually attached either at the base of the tail fin, or on the gill cover, or around the lower or upper jaw. Tags attached with wires are usually run through the flesh near or beneath the dorsal fin. Visceral tags are inserted into the body cavity. Whatever tag or tagging site is used, it is most important that the attachment be reasonably permanent, if the results of the experiment are to be used to estimate population abundance. Evidence of nonpermanent attachment can sometimes be had by examining a sample of the catch closely, in which case the scars left by shed tags can often be detected.

When fish are marked, rather than tagged, a similar loss of the mark may occur. An early method of marking, used by Petersen on plaice, was to punch holes in the dorsal fin. For more normally-shaped fish the usual method, in fresh water at least, is to remove one or more fins. Many fishes possess considerable power of regeneration of fins, especially when they are not cut too close to the base. I have seen regenerated pectoral fins of large crappies (*Pomoxis annularis*) which were perfect except for a certain waviness of the rays; these had been clipped about one-fifth way from the base a year earlier. Experience in Indiana with post-fingerling largemouth bass (*Huro salmoides*), black crappies (*Pomoxis nigromaculatus*), and a variety of sunfishes (*Lepomis*), catfishes (*Ameiurus*), and perch (*Perca flavescens*) showed that the pectoral fins did not regenerate at all, and the pelvic fins usually did not, when cut as closely as possible to the base. At most, the pelvic fins regenerated imperfectly, so they could be distinguished by even a quick inspection, and it was very rarely that both fins of a pair regenerated significantly.

For really young fish, results have been more variable. Young Indiana bass, 50 to 75 mm. long when clipped, exhibited at most a very imperfect regeneration of pectoral or pelvic fins over a period of two or three months in ponds, or up to eight months in aquaria (Ricker, 1949b). On the other hand, Meehan (1940) reported that young largemouth bass marked in Florida usually regenerated closely-clipped pectoral and ventral fins perfectly within a few weeks. Possibly this is associated with more rapid growth in southern waters. The anal and soft dorsal fins of even large centrarchids, however, regenerated quickly and often practically perfectly, no matter how closely cut.

In salmonid fishes regeneration is apparently less easy, and the dorsal, anal, and adipose fins have all been used with good results, as well as the paired fins. Some regeneration may occur, particularly of the adipose, but it is practically always imperfect, unless the cutting is done when the fish are very small. It is comparatively easy to check on the extent of fin regeneration by keeping a number in captivity, or by sampling wild marked stock at frequent intervals, or by using two unassociated fins for the mark.

A source of error similar to regeneration is the natural absence of fins in wild fish. The incidence of such can, however, readily be discovered by examining fish of a wholly unmarked population. I have observed them on salmon (cf. Foerster, 1935), but they seem to be very rare in fresh water.

3F. NON-RANDOM DISTRIBUTION OF MARKS AND OF FISHING EFFORT

To make a marking experiment representative, it is necessary that either the marked fish, or the total fishing effort, be randomly distributed over the population being sampled. As an illustration, consider a population consisting of 10,000 fish in each of two halves of a lake, 20,000 in all. Twice as many traps are set in one half as in the other, so that, both for marking and for recoveries, one end is sampled twice as efficiently as the other. In an experiment of the Petersen type, 1/5 of the fish at one end are marked, and 1/10 of those at the other. Similarly, after mixing of the marked fish into the unmarked, 1/5 and 1/10, respectively, are taken and the marked fish among them recorded. Eliminating sampling error, the result is as follows:

	First half	Second half	Total
Actual population (N).......	10,000	10,000	20,000
Number marked (M)........	2,000	1,000	3,000
Sample taken (C)...........	2,000	1,000	3,000
Recoveries (R)..............	400	100	500

If the data of the experiment are treated as a whole, the estimated population is 3000×3000/500 = 18,000, which is 10% low. This error can be avoided, however, by considering the two halves of the lake separately and calculating the population of each. When there is any reason to suspect unequal fishing effort in two or more parts of a lake, it will be valuable to divide the experiment into parts in this way, as was done, for example, by Lagler and Ricker (1942). This type of error always tends to make the result of a common calculation less than the sum of the separate calculations.

C. H. N. Jackson seems to have been the first to point out that if either the marking *or* the subsequent sampling is done randomly,[4] the estimate obtained is not biased. For example, if after the non-random marking in the illustration above, a random sample were taken, say of one-fourth, the total number of fish in it would be 5,000, and the number of marked fish 750, giving a population estimate of 3000×5000/750 = 20,000, the correct figure.

To play safe, it is well to try to make both the marking and the subsequent sampling random, even though either one singly would suffice. Proceeding in this way, it was not difficult to obtain a representative picture of the populations of most of the spiny-rayed fishes of small Indiana lakes (Ricker, 1942b, 1945a, 1955a; Gerking, 1953a). Other information concerning the randomness of the procedure can be obtained by comparing the ratio of marked to unmarked fish caught by different types of gear, or gear set in different situations, provided of course the gear does not tend to select marked from unmarked fish, or vice

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[4] The randomness is relative to the population structure; it need not necessarily exist in any geographical sense.

versa. Schumacher and Eschmeyer (1943) were able to make a test of the randomness of distribution of their marked fish in a pond of 68 acres, by draining it and recovering a large part of the total fish present. They found the ratio of marked to unmarked fish, of several species, to be little different from what they had previously computed from their trap samples, but bullheads (*Ameiurus*), carp (*Cyprinus*), and bigmouth buffalofish (*Megastomatobus*) showed significant or near-significant differences. This they attribute to the fact that a large part of the pond was too shallow for their nets, the fish in question being presumably insufficiently active to attain a random distribution during the two weeks of their experiment. Similarly Lagler and Ricker (1942) found little mixture of the fish populations of the two ends of a long narrow pond, over a two-months' period. Additional tests have been reported by Carlander and Lewis (1948), Fredin (1950) and others.

A salutary measure, when it is feasible, is to take the sample in which recaptures are sought by using an entirely different kind of gear from that used to catch fish for marking. For example, if fish for marking are taken in traps, and recoveries are obtained by angling, there is little likelihood of *similar* bias being present in both gears.

Large lakes, river systems and ocean banks present even more difficult problems. Many ocean fisheries cover so wide an area that representative tagging of the whole population is impossible, while fishing effort may vary greatly from bank to bank. This makes it necessary to select smaller units for examination, in which event the problem of wandering may be troublesome.

River fish are also amenable to enumeration by Petersen's method, if they are not of a roving disposition, and as a matter of fact their populations often prove to be surprisingly stable (Scott, 1949; Gerking, 1953b). Adjustments for a small amount of movement were made by the authors just mentioned, this being determined by sampling at sites above and below the section under consideration.

The first report of an application of the Petersen method to a migrating fish was apparently by Pritchard and Neave (1942). Tagging of coho salmon (*Oncorhynchus kisutch*) was done at Skutz Falls on the Cowichan River, British Columbia, and recoveries were made in tributaries of Cowichan Lake, many miles upstream. Close agreement of the tagged:untagged ratio in widely-separated tributaries provided evidence that tagging had been random with respect to the destination of the fish and to their expectation of recovery. Howard (1948) described a much more extensive study with sockeye salmon (*O. nerka*) at Cultus Lake, British Columbia, noting various kinds of heterogeneity in the data, and the procedure necessary for a reasonably reliable result.

3G. UNEQUAL VULNERABILITY OF FISH OF DIFFERENT SIZES

Unequal vulnerability of different sizes of fish to the fishing gear being used is a source of systematic error in population estimates very similar to that just discussed. It can be illustrated by the same numerical data as used in

Section 3F above, putting, in place of the two halves of the lake, two size groups of fish, one twice as vulnerable to fishing as the other. Detection of possible unequal vulnerability can be accomplished by comparing the rate of recapture of marked fish of different sizes, when enough recaptures are made to minimize the effects of sampling error. However, differential mortality, or different behaviour of marked fish as compared with unmarked, might give a similar picture if it affected, say, small fish more than large ones.

In general, it seems likely that variation in vulnerability with size, though a common enough phenomenon, will not usually be a serious problem. For one thing, its effects can be minimized by excluding from consideration fish which are near the limits of vulnerability to any given type of fishing gear, or by using the less selective types of gear for experiments of this sort, or by dividing the fish into two or more size groups. Even in the example of Section 3F, which would probably represent a rather extreme situation, the bias in the population estimate was only 10%. Cooper and Lagler (1956) found that the efficiency of an electric shocker varied from about 7% for 3-inch trout up to 40% for 11-inch ones; even so, a Petersen estimate made for the whole population was only 30% low.

What should always be avoided is the combining of data concerning two or more *species* to make a common estimate. There may sometimes be a temptation to do this, when data are available for two or more species of similar kind and size, with only a few recaptures for each. But, obviously, different species may differ greatly in vulnerability over the whole size range of both, and consequently such a combined estimate can be much too low. Thus in small lakes of Indiana the redear sunfish (*Lepomis microlophus*) is about 10 times as vulnerable to trapping as is the very similar bluegill (*L. macrochirus*), while its abundance is usually about a fifth of that of the bluegill. In an experiment based wholly on trap data, the number of redears marked would be twice the number of bluegills, and the number of marked redears recaptured would be 20 times the number of marked bluegills. A calculation similar to that of the last section will show that if the two species were to be treated as a unit, the resulting population estimate would be less than the combined population of the two species by 64%. An actual example is provided by Krumholz (1944), who found that the sum of the estimates of the population of bass (*Micropterus*), bluegills and pumpkinseeds (*Lepomis gibbosus*) in a small lake, when calculated separately, was 19,080, whereas the figure obtained from an estimate made by lumping all species together was 9,700.

EXAMPLE 3D. PLAICE PLANTED IN THISTED-BREDNING: A PETERSEN EXPERIMENT WITH UNEQUAL VULNERABILITY BY SIZE. (Data from Petersen, 1896, p. 12.)

Petersen marked 10,900 out of 82,580 plaice transported into Thisted-Bredning, one of the expansions of the Limfjord, by punching a hole in the dorsal fin. These fish were of nearly commercial size and were available to fishermen the same year. Two samples of plaice from the fishery were examined, 1,000 in all, of which 193 had the mark. Now this is a curious result, for the fraction of marked fish in the sample (0.193) is greater than in the original number transported (0.132); whereas, if any native fish at all were present in Thisted-Bredning, we should expect the fraction of marked ones in the sample to be smaller.

To see if the difference is greater than could be ascribed to sampling error, we proceed as follows:

	Transported	In the sample	Limits of 95% confidence
Total number	82,580	1,000	
Number of marked ones	10,900	193	168–222
Ratio	0.132	0.193	0.168–0.222

It appears that only once in about 40 times, on the average, would a similar sample have a fraction of marked ones as low as 0.168, whereas the actual fraction put in was 0.132. We may accordingly conclude, as did Petersen, that the experiment does not wholly meet the requirements of random sampling. A possible disturbing factor would be, for example, a tendency for the markers to select larger fish for marking, combined with a tendency for larger fish to be more quickly caught by fishermen than smaller ones. Though there is thus an element of uncertainty in the actual determination, there is no reason to question Petersen's conclusion that the Thisted-Bredning plaice were almost all of imported origin.

Notice that the rate of commercial exploitation cannot be calculated in this example without knowing either the total number of fish, or the total number of marked fish, which were removed from the broad. Petersen did make estimates of rate of exploitation, but for this he used tagged fish.

EXAMPLE 3E. A PETERSEN ESTIMATE OF THE LEMON SOLES OF HECATE STRAIT: ADJUSTMENTS FOR SIZE DIFFERENCE IN VULNERABILITY, AND FOR MIGRATION. (From Ketchen, 1953.)

Ketchen (p. 468) tagged and released 3,003 lemon soles (*Parophrys vetulus*) into a population being actively fished in Hecate Strait, British Columbia. Recaptures were made by the commercial boats. However, the average length of the commercial catch was somewhat greater than that of the group tagged. To obtain an estimate of the stock of commercial sizes, the number of tags released was reduced by an approximate factor obtained by superimposing the two frequency distributions (Fig. 3.2). The lined area of the graph includes 23.9 "per cent units", so the number of tags put out was reduced by this percentage, to 2,285. (Of these, 30 had been retaken before the start of the period shown in Table 3.3.)

Two factors affected the representativeness of the recoveries. On the one hand, the stock was moving gradually northward, so that new fish were entering the fishing area and old ones (including tagged ones) were moving out. On the other hand, tagging was done from a single boat and the tagged fish, whether from their position or their behaviour, were temporarily less catchable than the untagged ones. The latter effect was indicated by disproportionately few recaptures made in the first few days after tagging. Both of these two effects tend to make for too large an estimate (of the population on hand at the time of tagging), but the first increases in importance with time, whereas the second decreases. Consequently, from a computation of population at two-day inter-

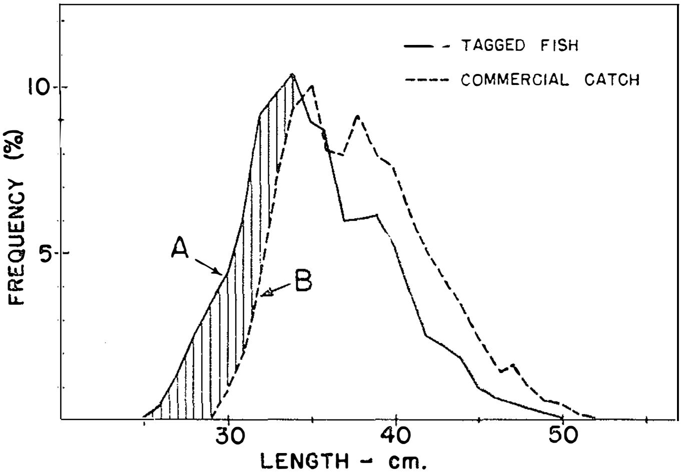

Figure 3.2. Length frequency distributions of lemon soles taken by the commercial fishery, and of those tagged and released, as percentage. The lined region of overlap comprises 23.9% of the area of either polygon, and represents the percentage by which the number of tags must be reduced to obtain the number "effectively" tagged for this fishery. (From Ketchen, 1953, figure 3).

Table 3.3. Petersen estimates of a lemon sole population, from recaptures made at 2-day intervals. (Data from Ketchen, 1953.)

Interval	Tags recaptured	Total fish caught	"Effective" no. of tags at large	Population estimate (from expression 3.7)
	R	C	M	N
	pieces	*pieces*	*pieces*	*millions*
1	19	81,000	2255	9.1
2	19	46,400	2236	5.2
3	27	67,900	2217	5.4
4	41	132,100	2190	6.9
5	74	173,600	2149	5.0
6	45	102,500	2075	4.6
7	50	118,800	2030	4.7
8	60	146,300	1980	4.7
9	47	127,600	1920	5.1

vals (Table 3.3), it is possible to select the low point as the best available estimate of the stock on the grounds when tagged. This can be taken as 4.7 million fish of commercial size (average, 0.937 lb.), or 4.4 million pounds—an estimate which is still probably somewhat high. For a different estimate of this population, see Example 6C.

3H. INCOMPLETE CHECKING OF MARKS

It need hardly be added that incomplete discovery or return of tags or marks can lead to serious error. When fish are examined by observers employed especially for the purpose, or by efficient mechanical devices for detecting metal tags, this danger is minimized. Very often, however, reliance must be placed on commercial or sport fishermen to turn in records. Experience shows that this is almost certain to give incomplete returns—varying a great deal, of course, with local interest, publicity given to the experiment, the amount of handling which the fish get, the type of tag or mark used, and the size of the reward offered, if any. Cash rewards are undoubtedly a great help but tend to be expensive, and have been utilized chiefly in commercial fisheries. The same principle could be applied to sport fisheries, rather inexpensively, by using returned tags as tickets in a sweepstakes, with the prizes donated by local merchants or sportsmen's organizations. Whatever type of inducement is used to encourage non-professional reporting, it will always be desirable to have a substantial part of the catch examined by trained observers, if this is at all practical.

3I. SCHNABEL METHOD (MULTIPLE CENSUS)

During the middle 1930's David H. Thompson in Illinois and Chancey Juday in Wisconsin began making population estimates from experiments in which marking and recapture was done concurrently. Neither published his results, but Dr. Juday interested Miss Zoe Schnabel (1938) in a study of the theory of the method, which has since been known by her name. The term "multiple census" is also applied, and refers to the fact that each day's catch can be regarded as a separate census.

Strictly speaking, the method requires that population be constant, with no recruitment and no mortality during the time the experiment is carried out; but it is often useful even if these conditions are only approximately satisfied.

The following information is available:

M_t the total marked fish at large at the start of the tth day (or other interval), i.e., the number previously marked less any accidentally killed at previous recaptures.

M ΣM_t, the total number marked.

C_t the total sample taken on day t.

R_t the number of recaptures in the sample C_t.

R ΣR_t, the total recaptures during the experiment.

We wish to estimate:

N the population present throughout the experiment.

The theory of this method has been discussed by DeLury, Chapman and others. The simplest estimate is the short formula of Schnabel (1938):

$$\hat{N} = \frac{\Sigma(C_t M_t)}{\Sigma R_t} = \frac{\Sigma(C_t M_t)}{R} \qquad (3.12)$$

This estimate, like (3.5), is asymmetrically distributed, and its limits of confidence are most easily computed by treating R as a Poisson variable. However, similarly to (3.3), the estimate of the reciprocal of N has a more nearly normal distribution; this estimate and its approximate large-sample variance are:

$$(1\hat{/}N) = \frac{\Sigma R_t}{\Sigma(C_t M_t)} = \frac{R}{\Sigma(C_t M_t)} \qquad (3.13)$$

$$V(1\hat{/}N) = \frac{R}{(\Sigma C_t M_t)^2} \qquad (3.14)$$

From the estimated standard error (the square root of 3.14) limits of confidence can be calculated for $(1\hat{/}N)$ using *t*-values for the normal curve. These limits are then inverted to give a confidence range for $\hat{N}$.

Expressions (3.12) and (3.13) are both only approximations to the maximum likelihood estimate of N. DeLury (1951) proposed an iterative solution of the true maximum likelihood equation (his expression 1.3), which consisted of adjusting (3.12) by a series of weights of the form:

$$W_t = \frac{1}{1 - M_t/N} \qquad (3.15)$$

and inserting them in the equation to give:

$$\hat{N} = \frac{\Sigma W_t C_t M_t}{\Sigma W_t R_t} \qquad (3.16)$$

$\hat{N}$ from (3.12) is used first in (3.15), and later trials (if required) use successive estimates of N obtained from the weighted computation (3.16).

More recently DeLury (1958) points out that the maximum likelihood solution depends heavily on the assumption of random mixing and sampling; in effect it weights each point on a graph of R_t/C_t against M_t (fitted with the restriction that the line go through the origin) as:

$$\frac{C_t}{\frac{M_t}{\hat{N}}\left(1 - \frac{M_t}{\hat{N}}\right)} \qquad (3.17)$$

Because of the likelihood of non-random mixing of marked and unmarked fish, Dr. DeLury now considers it more useful to weight such points simply as C_t, omitting the denominator terms in (3.17). This leads to the explicit solution proposed originally by Schumacher and Eschmeyer (1943). In inverted form it is:

$$(1\hat{/}N) = \frac{\Sigma(M_t R_t)}{\Sigma(C_t M_t^2)} \qquad (3.18)$$

For the variance of (3.18), the basic datum is the mean square of deviations from the line of R_t/C_t against M_t (whose slope is the estimate $1/\hat{N}$), given by Schumacher and Eschmeyer[4] as:

$$s^2 = \frac{\Sigma(R_t^2/C_t) - (\Sigma R_t M_t)^2/\Sigma C_t M_t^2}{m - 1} \tag{3.19}$$

where m is the number of samples included in the summations. However, instead of computing confidence limits directly for $\hat{N}$, as Schumacher and Eschmeyer do, it is better to compute them for the more symmetrically distributed $1/\hat{N}$ (DeLury, 1958). From the formula for the standard error of a regression coefficient, the standard error of $1/\hat{N}$ is:

$$\frac{s}{\sqrt{\Sigma C_t M_t^2}} \tag{3.20}$$

For computing limits of confidence for $1/\hat{N}$ from (3.20), t-values are used corresponding to $m - 1$ degrees of freedom. Limits of confidence for $\hat{N}$ are found by inverting those obtained for $1/\hat{N}$.

As with Petersen estimates, the reciprocals of the above estimates of $1/\hat{N}$ are not quite the best estimates of N itself; instead, they are somewhat too great. For (3.12) a simple adjustment is available which gives a better result (Chapman, 1952, 1954):

$$\hat{N} = \frac{\Sigma(C_t M_t)}{R + 1} \tag{3.21}$$

Limits of confidence for (3.21) can be obtained by considering R as a Poisson variable.

EXAMPLE 3F. SCHNABEL AND SCHUMACHER ESTIMATES OF REDEAR SUNFISH IN GORDY LAKE, INDIANA. (Data from Gerking, 1953a.)

Gerking compared different estimates of populations of various sunfishes in a small lake. Our Table 3.4 reproduces part of his table 3, for part of the stock of redear sunfish (*Lepomis microlophus*). As often happens, a few marked fish died from effects of trapping or from other causes, and these are deducted from the number marked on the day in question, hence from the number at large next day (M_t).

Columns 2 and 5 of Table 3.4 provide the Schnabel-type estimates. The original short Schnabel formula (3.12) gives $\hat{N} = 10740/24 = 448$; the modified Schnabel (3.21) is $\hat{N} = 10740/25 = 430$.

Columns 6-8 contain the products needed for the Schumacher estimate and its standard error. The estimate of 1/N is 2294/970296 = 0.0023642. The variance from the regression line is, from (3.19):

$$s^2 = \frac{7.7452 - (2294)^2/970296}{14 - 1} = 0.17851$$

$$s = 0.42250$$

From (3.20):

$$s_{1/\hat{N}} = \frac{0.42250}{\sqrt{970296}} = 0.00042892$$

---

[4] Schumacher and Eschmeyer's formula (3) contains a misplaced square bracket, but they use it in the correct orm; Fredin (1950) has published the accurate expression, as have Crossman (1956) and DeLury (1958).

TABLE 3.4. Computations for Schnabel and Schumacher estimates for age III redear sunfish in Gordy Lake, Indiana, from trap recaptures. (Data from Gerking, 1953a, table 3, using only the June 2-15 data.)

1 Number caught C_t	2 Recaptures R_t	3 Number marked (less removals)	4 Marked fish at large M_t	5 C_tM_t	6 M_tR_t	7 $C_tM_t^2$	8 R_t^2/C_t
10	0	10	0	0	0	0	0
27	0	27	10	270	0	2700	0
17	0	17	37	629	0	23273	0
7	0	7	54	378	0	20412	0
1	0	1	61	61	0	3721	0
5	0	5	62	310	0	19220	0
6	2	4	67	402	134	26934	0.6667
15	1	14	71	1065	71	75615	0.0667
9	5	4	85	765	425	65025	2.7778
18	5	13	89	1602	445	142578	1.3889
16	4	10	102	1632	408	166464	1.0000
5	2	3	112	560	224	62720	0.8000
7	2	4	115	805	230	92575	0.5714
19	3	...	119	2261	357	269059	0.4737
162	24	119	984	10740	2294	970296	7.7452

Since $t = 2.160$ for 13 degrees of freedom (Snedecor, 1946, table 3.8), the 95% confidence range for $1/\hat{N}$ is 2.16 times the above, or ± 0.0009265. Confidence limits for $1/\hat{N}$ are 0.0023642 ± 0.0009265 or 0.0014377 and 0.0032907, and the reciprocals give limits for $\hat{N}$.

These estimates and their estimated confidence ranges are summarized below:

Kind of estimate	$\hat{N}$	95% range
Original Schnabel (from 3.12)	448	320-746 (from 3.14)
Modified Schnabel (3.21)	430	302-697 (Poisson)
Schumacher (from 3.18)	423	304-696 (from 3.20)
Weighting formula (from 3.16)	440	

Gerking (1953) computed an estimate using the weighting formula (3.16); using only the data of Table 3.4, it is shown as the last item above. In this and other similar comparisons, the differences among the estimates are small compared to the confidence limits.

3J. SYSTEMATIC ERRORS IN SCHNABEL CENSUSES. ESTIMATION OF LOSSES AND ADDITIONS TO THE STOCK

In population estimates of Schnabel's type, systematic errors can assume complex forms, and to examine their effects theoretically would be a protracted task. In general, all the sources of error discussed earlier in the chapter must be considered here too. Special mention may be made of three which are of greater importance in this method.

1. *Error due to recruitment.* This can sometimes be avoided by the method discussed earlier, of making allowance for growth of the fish and confining the marking (or the calculation) to a single age-class or some otherwise-restricted segment of the population. For examples see Wohlschlag and Woodhull (1953). Another method is to plot the trend of successive population estimates, and extrapolate back to time zero (Example 3G).

2. *Error due to natural mortality.* In the absence of recruitment, the effect of natural mortality, affecting marked and unmarked fish equally, is to make a Schnabel estimate less than the initial population size, though greater than the final population size. If natural mortality is exactly balanced by recruitment, the Schnabel estimate becomes greater than the population size since the replacements will not have marked fish among them.

3. *Error due to fishing mortality.* This differs from the last in that it is usually possible to obtain a record or estimate of the marked fish removed in this way, and if so this number can be subtracted from the number of marked fish at large in the lake. The fisherman's records are also an additional source of data for the population estimate. However, unless recruitment exactly balances the loss to fishermen, the population estimate will not be equal to the initial population present, nor even exactly equal to the average population present.

The probable effects of these and other errors should be examined in each experiment separately. Other things being equal, the shorter the time in which recoveries are made, the better the estimates obtained by Schnabel's method; and this provides an incentive to more intensive work. (If the experiment does extend over a long period, it can be broken up for analysis by the "point-census" method if numbered tags are used, or if the marks used are changed at intervals.) However *too* short a period makes it difficult to attain a random distribution of the marked fish.

ESTIMATION OF NATURAL LOSSES AND ADDITIONS TO THE STOCK. If natural mortality or emigration from a stock occurs during a multiple census experiment, but additions are excluded, a Schnabel estimate tends to be less than a Petersen estimate; the former being affected by the losses whereas the latter is not. DeLury (1951) points out that the difference between these two estimates can be used to estimate the magnitude of the rate of loss during the course of the experiment. Expression 1.19 on page 292 of his paper can be used for an approximate direct estimate.

Alternatively, trial values of the rate of loss could be introduced into the Schnabel computation until one is obtained which makes the final estimate equal to a previously-obtained Petersen (or other unbiased) estimate of initial population.

Schnabel estimates of 1/N made on successive days during an experiment tend to increase with time when there are losses from the population but no additions to it. Hence another possible criterion for the best trial estimate of natural mortality rate would be that which eliminates this trend from the successive *daily* estimates of 1/N (*not* the cumulative estimates).

If both mortality and recruitment (or emigration and immigration) can occur, DeLury (1958) shows that estimates of rates of mortality and recruitment can be obtained by a multiple regression procedure.

Unfortunately, the sampling errors of all these estimates tend to be large, and DeLury's bead-drawing trials suggest that it would rarely be possible to obtain useful values for rate of accession or loss from the Schnabel situation.

EXAMPLE 3G. SCHNABEL ESTIMATE OF CRAPPIES OF FOOTS POND, INDIANA. (Data from Lagler and Ricker, 1942.)

Lagler and Ricker give estimates of the numbers of various species of fishes of Foots Pond, Indiana, using Schnabel's method of estimation. The recoveries extended over a period of 7 weeks during the summer. All recoveries were from the same traps as used to catch fish for marking, since fishing was negligible during this time. Table 3.5 gives the data for the white crappies (*Pomoxis annularis*) of the northern part of the pond, accumulated by 5-day periods. The direct unweighted Schnabel estimate, from (3.12), is 3090 fish; using (3.21) it is 67,900/23 = 2950 fish.

TABLE 3.5. A Schnabel estimate of crappies from the north half of Foot's Pond, Indiana. (Data from Lagler and Ricker, 1942.)

Period	C_tM_t	Recaptures R_t	Individual estimate C_tM_t/R_t	$\frac{10^4 \times R_t}{C_tM_t}$
1..............	2,850	1	2,850	3.51
2..............	2,860	2	1,430	6.99
3..............	2,700	1	2,700	3.70
4..............	4,060	1	4,060	2.46
5..............	9,190	4	2,300	4.35
6..............	14,880	6	2,480	4.03
7..............	0	0	.....	....
8..............	9,440	2	4,720	2.12
9..............	15,080	2	7,540	1.33
10..............	6,840	3	2,280	4.39
Total...........	67,900	22	3,090	

Observe that the estimates tend to increase somewhat throughout the experiment. This may be the result either of recruitment to the population or of differential mortality of marked fish. There is no good way of deciding between these alternatives, which of course do not exclude each other. An adjustment for either effect can be made in a manner similar to Parker's correction for recruitment in Petersen experiments (Section 3C). A linear relationship is obtained between the successive (not the cumulative) estimates of 1/N (from expression 3.13), and the mid-times of the successive units of the experiment; by producing this back to zero time, a population estimate unaffected by natural mortality is obtained. Using least squares without weighting, the reciprocal of population during experimental period 1 is 4.58×10^{-4}; at the start of this period ($2\frac{1}{2}$ days earlier) it would be a little higher, 4.72×10^{-4}. The estimate of the stock at the latter time is therefore 2120 fish, or 970 less than the comparable direct Schnabel estimate.

3K. SCHAEFER METHOD FOR STRATIFIED POPULATIONS

In work with migratory or diadromous fishes, it often happens that the fish can be sampled and marked at one point along their migration route, and then recovered later at a different place. In effect, the population is divided into a series of units, each partially distinct from adjacent units. This is an example of *stratification*, which has been considered at length by Chapman and Junge (1954). Stratification may also exist in respect to space, for non-migratory fishes.

We noticed earlier that if *either* the marking sample or the recovery sample is random, then an unbiased (consistent) estimate of the total population can be obtained by the Petersen method. But if both the original marking and the sampling for recoveries are selective, the Petersen estimate may be biased. If both marking and recovery favor the same portion of the population, the Petersen estimate tends to be too small. For the estimate proposed by Schaefer (1951a, b), the time of marking is divided into periods here designated by i, and the time of recovery into periods designated by j. We have:

M_i the number of fish marked in the ith period of marking (T_α of Schaefer)

M ΣM_i, the total number marked

C_j the number of fish caught and examined in the jth period of recovery (C_i or c_i of Schaefer)

C ΣC_j, the total number examined

R_{ij} the number of the fish marked in the ith marking period which are recaptured in the jth recovery period ($m_{\alpha i}$ of Schaefer)

R_i total recaptures of fish tagged in the ith period ($m_{\alpha .}$ of Schaefer)

R_j total recaptures during the jth period ($m_{.i}$ of Schaefer)

These data are arranged in a table of double entry, shown in Table 3.6 of example 3H. For each cell of the table, an estimate is made of the portion of the population available for marking in period i *and* available for recovery in period j; and the sum of these for all cells is the total population:

$$\hat{N} = \Sigma \hat{N}_{ij} = \Sigma \left(R_{ij} \cdot \frac{M_i}{R_i} \cdot \frac{C_j}{R_j} \right) \tag{3.22}$$

This is expression (32) of Schaefer (1951a, b).

Chapman and Junge's analysis indicates that (3.22) gives a maximum likelihood estimate only under the same conditions that the Petersen estimate does: that is, when either tagging or subsequent sampling for recoveries is done without bias. However it is fairly easy to see that (3.22) will frequently give a better estimate than (3.5). This is because (3.22) is consistent, and (3.5) is not, in the limiting situation where the successive "strata" tagged maintain their separate identity and can be treated as separate populations. In that event only the diagonal cells of a table like Table 3.6 would be occupied, and the formula (3.22) becomes the sum of a number of independent Petersen estimates (since $R_{ij} = R_i = R_j$ in that event).

In many practical situations there will be a considerable degree of distinctness maintained among successive groups of fish tagged, along with some intermingling between groups (for examples, see Killick, 1955). This intermediate situation is less favorable for estimation of the population than is either complete separation, or completely random mixing at tagging or recovery; nevertheless (3.22) performs rather well in such circumstances. Another advantage of the Schaefer treatment is that it can provide estimates of the population present in successive time intervals, both at the point of tagging and at the point of recovery.

Chapman and Junge (1954) proposed another possible estimate of N for stratified populations (their estimate $\hat{N}_3$), but it is rather cumbersome and, to be consistent, it needs the same assumptions as (3.22). In fact, Chapman and Junge demonstrate that no consistent estimate of N is possible in the situation where neither the tagging nor the subsequent sampling takes a constant fraction of the successive strata.

EXAMPLE 3H. ESTIMATION OF A RUN OF SOCKEYE SALMON, USING STRATIFIED TAGGING AND RECOVERY. (From Schaefer, 1951a.)

The Birkenhead sockeye (*Oncorhynchus nerka*) run was tagged near Harrison Mills, British Columbia, and recoveries of tags were made on the spawning grounds, about 200 miles upriver. The distribution of tagging and recoveries is shown in Table 3.6. Stock estimates from formula (3.22) are given in Table 3.7. In the latter, the last row shows the approximate abundance of fish going past the tagging point in successive weeks, while the last column shows the approximate number reaching the spawning stream in successive weeks.

Schaefer notes that since the values of M_i/R_i in the last row of Table 3.6 do not vary greatly, a simple Petersen estimate should approximate closely to the result in Table 3.7. The sum of the C_j column is $\Sigma C_j = 10{,}472$, while the sum of the M_i row is $\Sigma M_i = 2{,}351$. The Petersen estimate is therefore (from expression 3.5):

$$\hat{N} = 10{,}472 \times 2351/520 = 47{,}340$$

as compared with 47,860 from Table 3.7. Such close agreement would of course not often be encountered.

3L. CONTRIBUTIONS OF SEPARATE STOCKS TO A COMMON FISHERY

The marking technique can be used, if various conditions are satisfied, to estimate the contribution of each of a number of river races of salmon to a common oceanic fishery. Marking is done on young fish before they leave the river.

TABLE 3.6. Recoveries from sockeye salmon tagged in successive weeks at Harrison Mills, divided according to week of recovery upstream; together with the total number tagged each week (M_i), and the number recovered and examined for tags (C_j). (Data from Schaefer, 1951a, table 3.)

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

TABLE 3.7. Computed estimates of sockeye salmon passing Harrison Mills, using Schaefer's method. (From Schaefer, 1951a, table 4.)

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

Subsequently the ratio of marked to unmarked is observed (a) in the fishery concerned, (b) in the various rivers where the migrants were tagged. Junge and Bayliff (1955) have outlined the conditions necessary for an unbiased estimate, and these are sufficiently formidable that the authors have no example of an experiment satisfactory from this point of view. However their studies and experiments are still in an early stage.

CHAPTER 4.—POPULATION AND SURVIVAL FROM MARKING EXPERIMENTS EXTENDING THROUGH TWO OR MORE TIME INTERVALS. RATE OF SURVIVAL CONSTANT

4A. MARKING DONE PRIOR TO THE FIRST FISHING SEASON

When marking experiments are done in two or more successive years, or when a single year's experiment is divided into two or more parts, it becomes possible to estimate the rate of survival in the population, in addition to population size and rate of exploitation. This is easiest if the survival rate does not vary between the periods being examined (though it may exhibit parallel seasonal fluctuations *within* each period). This chapter describes procedures when s is constant, while the next deals with estimates when survival changes.

Suppose that fish are marked during a short period of time at the start of a certain year. During that year and also in later years they are susceptible to the same fishing and natural mortality rate as are unmarked fish, which rates do not vary appreciably over a period of years. We are given:

M the number of fish marked

R_1 the recaptures in year of marking

R_2, R_3, etc. recaptures in later years

We want to know:

s the survival rate between years

N_1 the population at the start of year 1

u the rate of exploitation

The situation is similar to that for estimating survival from age composition, but it is much more favourable in one respect: there is no variability of recruitment to worry about, since we are dealing with a single group of fish of known initial abundance. The statistics involved in such an experiment are shown in Table 4.1. The survival rate s is estimated as the ratio of one year's recaptures to the preceding year's:

$$\hat{s} = \frac{R_2}{R_1} = \frac{R_3}{R_2} = \ldots\ldots = \frac{R_n}{R_{n-1}} \qquad (4.1)$$

In so far as these ratios are uniform, within acceptable limits of sampling error, a combined estimate of s can be made in one of several ways. A *weighted* estimate of s can be obtained most simply by using one of the formulae (2.2) and (2.3), which in the recapture symbols are:

$$\hat{s} = \frac{R_2 + R_3 + \ldots\ldots + R_n}{R_1 + R_2 + \ldots\ldots + R_{n-1}} \qquad (4.2)$$

$$\hat{s}^2 = \frac{R_3 + R_4 + \ldots\ldots + R_n}{R_1 + R_2 + \ldots\ldots + R_{n-2}} \qquad (4.3)$$

TABLE 4.1. Mortality and survival in a stock of M fish marked at the beginning of year 1, in which rate of exploitation (u), expectation of natural death (v), and consequently total mortality rate (a) and survival rate (s) are all constant over a period of five years The successive entries in the "Recoveries" row are equivalent to R_1, R_2, etc. of the text.

Year	1	2	3	4	5
Initial stock of marked fish...........	M	Ms	Ms^2	Ms^3	Ms^4
Recoveries..........................	Mu	Mus	Mus^2	Mus^3	Mus^4
Natural deaths......................	Mv	Mvs	Mvs^2	Mvs^3	Mvs^4
Total mortality.....................	Ma	Mas	Mas^2	Mas^3	Mas^4

An *unweighted* estimate of s, which may be preferable in some situations, can be obtained from a graph of the logarithms of successive R values, whose slope is an estimate of the logarithm of the survival rate. It is a good plan to plot this graph anyway, in order to check on curvature (change in survival with time).

Given an estimate of s from one of these sources, the stock of marked fish at the beginning of successive years is quickly estimated as M, Ms, Ms^2, etc. and can be summed over the whole of the experiment. Divided into the total recoveries of marked fish, this yields a weighted estimate of mean rate of exploitation, $\hat{u}$, for the duration of the experiment, i.e.:

$$\hat{u} = \frac{R_1 + R_2 + \ldots + R_n}{M(1 + s + s^2 + \ldots + s^{n-1})} \tag{4.4}$$

If for any reason the data concerning recoveries in the year of marking are lacking or imperfect, it is still possible to estimate s and u by extrapolating back. In that event R_1 and the corresponding numerator term can be dropped from formulae (4.2) and (4.3), while (4.4) becomes:

$$\hat{u} = \frac{R_2 + R_3 + \ldots + R_n}{sM(1 + s + s^2 + \ldots + s^{n-2})} \tag{4.5}$$

In using (4.5), it is important to make sure that whatever influences have made the first year's data unusable have not affected the total mortality rate of the marked fish in that year. Such effects, however, would not affect the estimate of s, except to increase its sampling error by decreasing the number of recaptures on which it is based.

Because it is difficult to mark any large number of fish within a short space of time, the device has sometimes been used of computing, for each recaptured fish, its exact "time out" in days, and dividing up recaptures by weeks, months or years on that basis (e.g., Hickling, 1938). This procedure works especially well with fisheries which are prosecuted on a year-round basis, so that there is no serious seasonal variation in expectation of recovery of tags. It also works better if the spread of tagging dates is not *too* protracted. With a seasonal fishery, however, the expectation of recapture of a tagged fish varies with the time of year at which it is released, and any broad mixture of tagging dates introduces an additional effect into the interpretation of recoveries.

EXAMPLE 4A. SURVIVAL ESTIMATE WHEN FISH ARE MARKED PRIOR TO THE FISHING SEASON IN SUCCESSIVE YEARS

Data pertaining to an hypothetical marking experiment are as follows. A group of 5,000 fish was marked just before the first fishing season, well scattered over the area being fished. Recoveries were: 1st year, 2,583; 2nd year, 594; 3rd year, 175; 4th year, 40; 5th year, 7; these representing a complete canvas of the fishery.

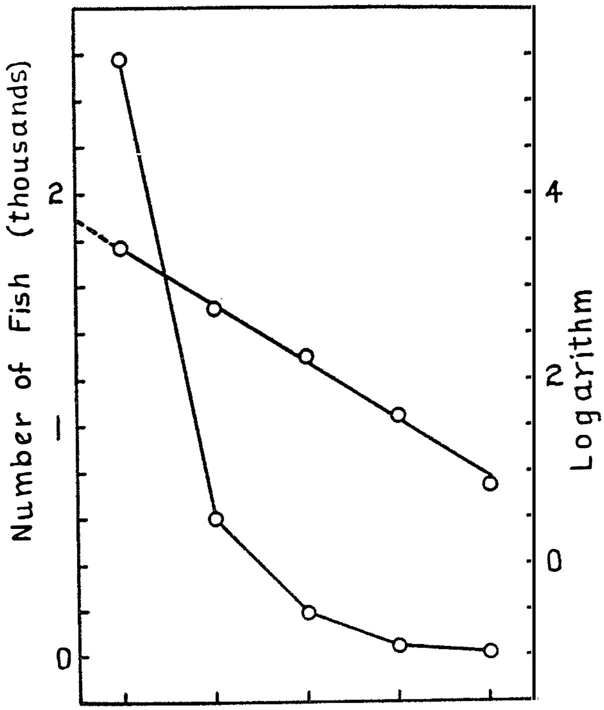

FIGURE 4.1. Number of recoveries (curved line) and their logarithms (straight line), in successive years of the experiment of Example 4A.

The most obvious piece of information from these data is that the rate of exploitation, from the data of the first year, is $\hat{u} = 2583/5000 = 0.517$. To obtain the survival rate, the logarithms of the recoveries are plotted (Fig. 4.1). The line has a slope of -0.608 log-units per year, corresponding to a survival rate of antilog $\bar{1}.392 = 24.7\%$ per year. Jackson's methods give, from (4.2), $s = 0.241$; and from (4.3), $s = 0.256$.

Having obtained s in one of these ways, a schedule can be constructed (Table 4.2), similar to Table 4.1, on the basis of 5,000 fish marked. The mean rate of exploitation, from (4.4), is $\hat{u} = 3399/6634 = 0.512$. Since the total

TABLE 4.2. Mortality and survival in a population, based on the indicated recoveries from an initial stock of 5,000 fish, and the assumption of a constant rate of exploitation and total mortality rate.

Year	1	2	3	4	5	Total
Initial stock of marked fish	5,000	1,235	305	76	18	6,634
Recoveries	2,583	594	175	40	7	3,399
Natural deaths	1,182	336	54	18	6	1,596

mortality is $a = 1 - 0.247 = 0.753$, it follows that the annual expectation of natural death is $v = 0.753 - 0.512 = 0.241$. From Appendix II, $i = 1.398$, and $p = ui/a = 0.95$.

All of the above estimates apply most reliably to conditions during the years soon after tagging, for two reasons: (1) the mean survival rate, on which they depend, was calculated principally from recoveries in the first two years; (2) if the 5,000 fish marked had originally the same age composition as the commercial catch, then later the marked population becomes older than the catch, year by year, and, consequently, is more likely to differ from the catchable population in respect to natural or fishing mortality, or both.

EXAMPLE 4B. SURVIVAL OF NORTH SEA PLAICE ESTIMATED FROM TAGGING EXPERIMENTS. (Data from Hickling, 1938.)

Hickling reviews the extensive English plaice-tagging experiments of 1929-32. The individual experiments were done over periods no longer than a month, as a rule, and in any event returns are tabulated according to actual number of days elapsed from the day of tagging, grouped in sequences of 365 days. In the published data, recaptures are separated into 2 groups: those of the first year and those of all subsequent years.

Data for the plaice marked off Heligoland in May, 1951, are shown in Table 4.3. We notice first that the rate of first-year recovery increases with increase in size of the fish, from 4% to 45% or 50%. According to Hickling's figure 27, showing recaptures for all experiments, the first-year rate of recapture of plaice commonly reaches a plateau at 25-26 cm. Plaice of this size and larger can reasonably be considered fully recruited to the fishery, even though it may be possible that a part of the poorer returns from smaller fish is a result of greater tagging mortality or loss of tags among them. The figures 45-50% are, however, called here the "apparent" rate of exploitation of the fully-vulnerable fish, because it would be desirable to examine possible systematic errors before accepting them wholeheartedly (see below).

On the assumption that the survival rate of *fully-vulnerable* tagged fish[1] is constant from one year to the next, its numerical value is estimated in column 6,

---

[1] Hickling, following Thompson and Herrington (1930), estimated survival from the returns of all tagged fish regardless of size, and consequently obtained a composite figure which does not apply to any particular part of the stock, nor yet to the stock as a whole.

TABLE 4.3. Plaice marked off Heligoland in May, 1931, and recaptures made, arranged by 5-cm. length classes. (Data from Hickling, 1938, table 16.)

1 Length-class	2 No. marked	3 1st-year recaptures	4 Apparent rate of exploitation	5 Later recaptures	6 Apparent survival rate	7 Apparent survival rate (interpolated)	8 Apparent total mortality rate	9 Apparent expectation of natural death
cm.	M	R_1	u'	$R_2+..$	s'	s'	a'	v'
15–19	249	9	0.036	10	....	....	....	....
					0.527			
20–24	300	66	0.220	21		....	....	....
					0.241			
25–29	342	154	0.450	43		0.230	0.770	0.320
					0.218			
30–39	112	56	0.500	11		0.189	0.811	0.311
					0.164			

using expression (2.4). Survival figures are estimated principally from the ratio of first-year to second-year recoveries: hence they pertain to a period of time when the fish in question are, on the average, at least half a year older than when the corresponding rate of exploitation was estimated (from recoveries in the 12 months immediately after marking). This is indicated in Table 4.3 by setting the primary survival estimates in the spaces between the exploitation estimates (column 6). The ratio of later recaptures to first-year recaptures of course decreases with size at marking; however it should be completely stabilized for the *marking* size which is less than 25 cm. by half a year's growth (about 2 cm.), and it should be *nearly* stable for sizes 2 or 3 cm. less. Consequently the estimated apparent survival rate of 0.241 from the 20-24 cm. tagging class is probably very little biased, while estimates from the two larger classes should not be biased at all (by incomplete vulnerability). The 15-19 cm. group, however, yields an erroneous (too high) estimate of survival—although, since exploitation is less, we could reasonably expect the survival rate for the small fish to be appreciably greater than for larger fish. In the last two columns of Table 4.3 values of v' (apparent expectation of natural death) are obtained by subtraction ($= a' - u'$). The corresponding apparent instantaneous rates of natural mortality, q', are, from (1.8), 0.61 and 0.64. These estimates are somewhat higher than natural mortality figures obtained by other methods, and suggest that in these experiments there may be systematic error of one or more of the types described in Sections 4C and 4D below. Some of the possibilities could be examined using month-by-month and year-by-year recoveries (cf. Example 4c), but the plaice data have not been published in sufficient detail for this.

4B. Marking Done Throughout the First Fishing Season, with Recoveries in at Least Two Seasons

With large-scale fisheries in big bodies of water it is difficult or impossible to capture and mark a large number of fish in a short space of time, distributing them more or less evenly over the population under review, and the seasonal character of the fishing may make it undesirable to divide up recaptures according to the number of "days out". It is necessary therefore to see whether estimates of survival, etc., can be made when, for practical reasons, marking is carried on *during* instead of *before* a fishing season.

If the experiment is to be used to estimate rate of fishing, it is very important that the marking be done in some rather definite manner, in relation to the incidence of mortality in the population. In an ideal situation, the natural and fishing mortality rate in the population would both be distributed evenly over the whole year, in which case it is best that marking be done at a uniform absolute rate throughout the year. Such a group of marked fish would be analogous to a year-class of recruits entering a fishery at a uniform absolute rate over a year's time. If the fishery is more seasonal, it will be best, and often easiest, to mark fish at a rate more or less proportional to the industry's weekly landings, which would correspond exactly to the situation above if natural mortality were negligible, or were similarly distributed. In general little or nothing will be known of the seasonal distribution of natural mortality, so that our ideal situation will often be as good an assumption as any. However, if the fishery is really sharply limited as to season, corrections could be introduced on the basis of natural mortality occurring throughout the year, or throughout the growing season.

SEVERAL YEARS' RECAPTURES. The discussion here will concern only the simpler situation postulated above. In Section 1E it was shown that if i and a represent respectively the instantaneous and yearly rates of total mortality, the mortality among a group of fish recruited or marked at a uniform absolute rate would be $(i - a)/i$. Of these the fraction p/i or u/a would be killed by capture, and q/i or v/a would die from natural causes. From this a schedule can be constructed (Table 4.4) showing catch and total mortality in all years.

TABLE 4.4. Mortality and survival in a stock of fish marked throughout year 1. In all years, the annual mortality rate = a; survival rate = s. In year 1, the actual mortality is $(i - a)/i$, and survival is a/i (see the text). All entries are fractions of the number of fish marked during year 1.

Year	1	2	3	4	5
Marked fish at large at start of year...............	—	$\frac{a}{i}$	$\frac{sa}{i}$	$\frac{s^2a}{i}$	$\frac{s^3a}{i}$
Recoveries................	$\frac{u(i-a)}{ai}$ $\frac{p(i-a)}{i^2}$	$\frac{ua}{i}$ $\frac{pa^2}{i^2}$	$\frac{usa}{i}$ $\frac{pa^2s}{i^2}$	$\frac{us^2a}{i}$ $\frac{pa^2s^2}{i^2}$	$\frac{us^3a}{i}$ $\frac{pa^2s^3}{i^2}$
Natural deaths............	$\frac{v(i-a)}{ai}$	$\frac{va}{i}$	$\frac{vsa}{i}$	$\frac{vs^2a}{i}$	$\frac{vs^3a}{i}$
Total deaths..............	$\frac{i-a}{i}$	$\frac{a^2}{i}$	$\frac{sa^2}{i}$	$\frac{s^2a^2}{i}$	$\frac{s^3a^2}{i}$

An interesting and somewhat unexpected feature of this tabulation concerns the recoveries. In order to plot a catch curve, involving the year of marking, to show survival rate directly, it will be necessary to adjust the number of first-year recoveries. A first impulse would be to double their number, since if the fish are marked at a uniform rate through a season, it might seem that on the average they would be subject to only half the mortality of those present from the start of the season. However, for the number of recoveries in the first year (R_1) to be a member of the geometric series of later years (R_2, R_3, etc.), it should equal Mua/si. As R_1 actually equals $Mu(i-a)/ai$, the factor by which R_1 must be multiplied to get a value that fits into the series is:

$$\frac{ai}{Mu(i - a)} \cdot \frac{Mua}{si} = \frac{a^2}{s(i - a)} \tag{4.6}$$

Accordingly, before plotting the catch curve, the recoveries of the first year must be multiplied by $a^2/s(i - a)$.

We are then comparing the two quantities:

$$\frac{R_1 a^2}{s(i - a)} \tag{4.7}$$

$$\frac{R_2 + R_3 + \ldots.}{s + s^2 + \ldots.} \tag{4.8}$$

Both of these represent the number of first-year recoveries that would be expected *if* the tagging had been done at the start of the first year instead of throughout it. Expression (4.7) is computed from the actual number of first-year recoveries, whereas (4.8) is computed from the recoveries of later years—using a uniform instantaneous mortality rate in both cases.

If the comparison above shows that first-year recoveries do not agree with those for later years, it suggests the presence of error of "type C", to be described later. If however the adjusted point for year 1 lies close to the line established by the later years, we are faced with the problem of getting the best combined estimate of rate of exploitation. The simplest procedure is perhaps to combine two separate estimates. From Table 4.4, we have for year 1:

$$\hat{u} = \frac{R_1 a i}{M(i - a)} \tag{4.9}$$

And hence:

$$\hat{p} = \frac{R_1 i^2}{M(i - a)} \tag{4.10}$$

For the recaptures of later years, we can use a modification of formula (4.5) which can readily be deduced by comparing Table 4.4 with Table 4.1:

$$\hat{u} = \frac{i(R_2 + R_3 + \ldots. + R_n)}{aM(1 + s + s^2 + \ldots. + s^{n-2})} \tag{4.11}$$

$$\hat{p} = \frac{ui}{a} = \frac{i^2(R_2 + R_3 + \ldots + R_n)}{a^2M(1 + s + s^2 + \ldots + s^{n-2})} \tag{4.12}$$

The two estimates of p, (4.10) and (4.12), can be averaged arithmetically, weighting each as the total number of recaptures involved: viz., R_1 and $(R_2 + R_3 + \ldots + R_n)$, respectively.

TWO YEARS' RECAPTURES. When marking is done throughout a year, and recaptures for only two years are obtained (the year of marking and the following one), the computation of a survival rate becomes hazardous, because there is no check on its constancy. However, if the latter be assumed, letting M be the number of fish marked in year 1, and R_1 and R_2 be the number of these recaptured during year 1 and year 2, respectively, the data available are, from Table 4.4:

$$\frac{R_1}{M} = \frac{u(i - a)}{ai} = \frac{p(i - a)}{i^2} \tag{4.13}$$

$$\frac{R_2}{M} = \frac{ua}{i} = \frac{pa^2}{i^2} \tag{4.14}$$

Dividing (4.13) into (4.14):

$$\frac{R_2}{R_1} = \frac{a^2}{i - a} \qquad (4.15)$$

The right-hand member of this equation is a simple function of s or i, which can be taken directly from Appendix II.

Because of the uncertainty of this method, it is very desirable to do a marking experiment in two successive years, whenever only one year following the year of marking can be expected to yield a substantial number of recoveries.

4C. SYSTEMATIC ERRORS: TYPES A AND B

The general discussion of various kinds of systematic errors in Chapter 3 is of course applicable also to experiments in which survival rate is being estimated. Some types of error are of special interest and importance when recoveries extend over a long period. They can be classified according to their effects on the various statistics being estimated:

TYPE A. There are sources of error which affect the estimate of rate of fishing, but not the estimate of total mortality and survival. In this category can be placed (1) the death of any considerable number of fish, or the loss of their tags, shortly after marking or tagging; and (2) incomplete reporting of marks or tags actually taken by fishermen (assuming the reporting to be equally efficient or inefficient during all the years of the experiment). Errors of this sort scarcely require further comment. If fish die just after tagging, the apparent rate of exploitation obtained will be less than the true rate; the true rate is equal to the apparent rate divided by the ratio of the number of fish which survive the effects of tagging to the total number put out. Or if reporting is incomplete, the true rate of exploitation will be equal to the apparent rate divided by the fraction reported. That the estimates of total mortality and survival will remain unaffected by either of these is obvious from the fact that, in estimating survival rate by formula (4.1), (4.2) or (4.3), no use was made of the number of fish marked. Special efforts must be made to discover possible errors of these two kinds, since the data of the experiment give no clue to them. For example, to check on marking mortality or immediate loss of tags, fish of different degrees of apparent vigor, or fish tagged in different ways, can be used, or the fish can be held under observation. To check on efficiency of reporting of tags by fishermen, or of their recovery by mechanical devices, a part of the catch can be examined by special observers; this is always a desirable procedure anyway. An elaborate series of corrections of this kind has been made for sardine tagging experiments (see Clark and Janssen, 1945a, b; Janssen and Aplin, 1945).

TYPE B. A second group of errors includes those which affect the estimate of total mortality, but not the estimate of rate of fishing. Here belong (1) any loss of tags from the fish which occurs at a steady instantaneous rate throughout the whole period of the experiment; (2) extra mortality among the tagged or marked fish, similarly distributed in time; (3) emigration of fish from the fishing area, similarly distributed in time. The effects of any of these three are in most ways comparable to ordinary natural mortality. Suppose the loss takes place at instantaneous rate k, making the apparent total instantaneous mortality rate $p + q + k = i'$, as compared with the true rate $p + q = i$. The apparent annual mortality rate corresponding to i' will be a', a larger quantity than the true mortality rate a. The apparent rate of exploitation (i.e., rate of recovery of tagged fish with tags still attached) is, say, $u' = pa'/i'$. Obviously the rate of fishing p is equal to $u' i'/a'$, just as much as to ui/a; and since u', i' and a' are all available from the data of the experiment, an unbiased estimate of p can be had.

It will often happen that for the population being studied an independent estimate of i and a will be available, made from an analysis of the ages of the fish in the catch. Given a satisfactory estimate of i from this source, and of p from a marking experiment, a complete and reliable description of mortality in the population becomes possible.

Another variant of Type B error occurs when the tags or marks are continuously lost or disappear, but the rate of loss is variable. For example, the rate of loss of tags might accelerate with time as the tags worked loose from the fish, so that very few fish with tags would remain after two or three years, even though many of the fish actually lived (without their tags) much longer. Such a situation would be reflected in a nonlinear recapture curve; that is, the graph of the logarithm of recaptures against time would be convex upward. Alternatively, the more loosely applied tags might come off rapidly at first, so that there would be a deceleration of the rate of loss of tags in general, resulting in an upwardly concave recapture curve. If in such cases the rate of acceleration or deceleration be constant, the differences between successive logarithms of recaptures should be in a linear sequence when plotted against time, and this second derivative line could be used as a basis for an unbiased estimate of rate of fishing. The latter could be computed along lines analogous to those just described, or, more simply but less accurately, by using one of the graphical methods described in Section 4E. Similarly, any empirical relationship derived from the observed trend of the recaptures might be used, though perhaps with less assurance than when the formula describes an easily-grasped theoretical position. For example, Graham (1938a) fitted a straight line to the logarithms of the logarithms of number of recaptures, and extrapolated back along it.

A comparison of the apparent total mortality rate obtained from a fin-clipping or tagging experiment with the value obtained from a catch curve is probably the best method of discovering any variety of type B error. If this is impossible, it will be useful to compare survival rates estimated from different types of marks or tags, to see if any differences appear. It may also be helpful to examine a large number of fish to see if holes left by lost tags can be found, though since such scars often heal up quickly, no quantitative estimate of the loss will usually be obtained in this way.

EXAMPLE 4C. FISH MARKED PRIOR TO THE FISHING SEASON, WITH INCOMPLETE TAG RECOVERY

The tag recovery data of Example 4A can also be used to illustrate a situation where the search for tags among the fish caught is incomplete. Suppose, for example, that the tags in question are internal iron tags, and are recovered with something less than complete efficiency by magnets installed in processing plants. Trial runs with these magnets showed their efficiency to have been, in successive years, 0.88, 0.70, 0.92, 0.90, and 0.82. A similar situation would arise if the recoveries were made not from the commercial catch, but from experimental catches in which the fish were not killed; the series of figures just given would then represent the relative sizes of these catches in successive years. In either event a correction must be made for variations in the size of the catch effectively examined; that is, each year's recoveries must be reduced to the basis of 100% efficiency, or to the basis of some standard size of catch (cf. Jackson, 1939).

In the present example, the adjusted number of recoveries for the first year is 2583/0.88 = 2,930; later years yield, in the same manner, 848, 190, 44, and 8, respectively. These adjusted figures can now be applied in (4.2), giving $s = 0.272$, though the method of fitting a straight line to the logarithms of the adjusted values, weighting each point as the *unadjusted* number of recaptures on which it is based, is here the preferable one. The rate of exploitation is found as in Example 4A, but using the adjusted figures.

EXAMPLE 4D. TYPE B ERROR IN HALIBUT TAGGING EXPERIMENTS. (Data from Thompson and Herrington, 1930.)

Estimates of total apparent mortality and of rate of fishing for fully-vulnerable halibut on grounds south of Cape Spencer are obtained in Examples 5E and 5F of the next Chapter, from recaptures of tagged fish. In Example 2H, survival was estimated from the catch curve of the fish taken for tagging. These estimates are compared as below:

Year	Method	Survival s	Instantaneous mortality	Rate of fishing p	Apparent natural mortality q'
1926	tagging........	0.331	$i' = 1.11$	0.57	0.54
1927	tagging........	0.320	$i' = 1.14$	0.51	0.63
..	catch curve.....	0.47	$i = 0.76$	..	..

The survival figure 47% was obtained from the size distribution of fish used for tagging in 1925 and 1926, and almost the same value can be computed from the relative numbers of halibut used by Dunlop for age determination (Thompson and Bell, 1934, p. 25). As shown in Example 2H, total fishing effort was remarkably steady during the period 1921-27, so the 47% survival obtained from the age-distribution should be entirely comparable to the 32% or 33% obtained from tag recoveries.

Even if there were not this cross-check, the q'-values shown above, which are impossibly high for the true q of a long-lived fish, would indicate that something besides natural mortality contributes to the disappearance of the tagged fish. The only obvious possibility is that there has been "Type B" error throughout the time of the experiment, resulting from a continuous loss of tags from the fish or from a movement of tagged fish out of the fishery. On the assumption that the 0.76 mortality rate from age-frequencies is the true one, the necessary instantaneous rates of loss can be computed by difference: they are 1.11 – 0.76 = 0.35 for 1926, and 1.14 – 0.76 = 0.38 for 1927. Shedding of tags is believed to be infrequent in these experiments, so that movement of tagged fish away from the fishing grounds probably accounts for most of this. The latter is a likely-enough possibility, because halibut move a lot and are found, sparsely, over a much greater area of the sea bottom than the grounds customarily fished. In nature, wandering away from the fishing grounds is presumably balanced by return movements back onto the grounds, but in the first year or two after tagging the outward movement of tagged fish would exceed their return, and it is these years which mainly determine the survival rates of Examples 5E and 5F.

4D. Systematic Errors: Type C

A third group of errors includes those which make the first year's recoveries not directly usable in estimating either total mortality or rate of fishing, but which do not prejudice the estimation of either of these from the data of later years. Here may be mentioned (1) abnormal behaviour of the marked or tagged fish during the season of their marking; (2) non-random distribution of marked fish in the general population during the year of marking, combined with (possibly only temporary) non-random distribution of fishing effort. In either event the marked fish may be either more or less vulnerable to capture during the year of marking than during later years; but they are assumed to have regained their usual behaviour by the beginning of the year following marking, and in the latter year either fishing effort or the fish marked must be randomly distributed.

Table 4.5. Mortality and survival in a population of marked fish where rate of exploitation (u_1), natural deaths (v_1), and total mortality (a_1) are different in the first year from later years (u_2, v_2, a_2), but are identical among those later years. A unit number of fish was marked just prior to year 1.

Year	1	2	3	4
Initial population	1	s_1	s_1s_2	$s_1s_2^2$
Recoveries	u_1 $\frac{p_1a_1}{i_1}$	u_2s_1 $\frac{p_2a_2s_1}{i_2}$	$u_2s_1s_2$ $\frac{p_2a_2s_1s_2}{i_2}$	$u_2s_1s_2^2$ $\frac{p_2a_2s_1s_2^2}{i_2}$
Natural deaths	v_1	v_2s_1	$v_2s_1s_2$	$v_2s_1s_2^2$
Total deaths	a_1	a_2s_1	$a_2s_1s_2$	$a_2s_1s_2^2$

Type C errors can be very serious when few recoveries are made beyond the year of marking. If, however, fair numbers of marked fish are obtained for at least two years after marking, type C error is merely troublesome: that is, it complicates estimation of the rate of fishing but does not distort the result. A model is shown in Table 4.5. The first year's rate of fishing for marked fish (p_1) is either greater or less than that for later years (p_2). Consequently, rate of exploitation (u_1), expectation of natural death (v_1), and total mortality rate (a_1) for the first year all differ from the corresponding statistics for later years. The estimate of mortality rate (a_2) made from recaptures of marked fish after the first year should reflect the real mortality rate of the population. To calculate rate of fishing we proceed from the assumption that the instantaneous rate of natural mortality (q) is the same in the first year as in later years. However, no direct equation can be set up because of the exponential relation between a and i, and it is necessary to proceed by successive trials.

In Table 4.5, the fraction of recoveries in year 2, which is represented by $u_2 s_1$, is available in the data of the experiment as R_2/M; hence:

$$u_2 = \frac{R_2}{s_1 M}$$

If all the later years' data are used, this expression becomes, by analogy with (4.5):

$$u_2 = \frac{R_2 + R_3 + R_4 + \ldots + R_n}{s_1 M(1 + s_2 + s_2^2 + \ldots + s_2^{n-2})} \tag{4.16}$$

In these expressions everything is known except s_1.

Another estimate can be made somewhat less directly. The necessary data are available to evaluate:

$$u_1 = \frac{R_1}{M}$$

From (1.8):

$$p_1 = \frac{u_1 i_1}{a_1} = \frac{R_1 i_1}{M a_1}$$

Now the natural mortality rate q is equal to $i_1 - p_1$, and q being the same in the second as in the first year, we have also $p_2 = i_2 - q$. From (1.8), and substituting:

$$\begin{aligned} u_2 &= \frac{p_2 a_2}{i_2} = \frac{a_2}{i_2}\left(i_2 - q\right) \\ &= \frac{a_2}{i_2}\left(i_2 - i_1 + p_1\right) \\ &= \frac{a_2}{i_2}\left(i_2 - i_1 + \frac{R_1 i_1}{M a_1}\right) \end{aligned} \tag{4.17}$$

In this expression a_2 and i_2, R_1 and M, are all available directly from the experiment, while i_1 and a_1 are directly related to the unknown s_1 of equation (4.16). Thus for any trial value of i_1 (or a_1 or s_1), u_2 can be calculated from both (4.16) and (4.17), and successive trials will yield a best value which makes the two estimates equal.

When marking is done *throughout* the first year, as in Table 4.4, some modification of the above procedure will be necessary. Here p_1 will be the first year's instantaneous rate of fishing mortality, but it will be directly applicable only to fish marked at the very beginning of the season. The total instantaneous mortality rate, applicable to such fish, is $p_1 + q = i_1$. From Table 4.4, the total first-year mortality among the marked group as a whole is $(i_1 - a_1)/i_1$, and the survivors are a_1/i_1. A possible estimate of u_2 is therefore:

$$u_2 = \frac{R_2 i_1}{M a_1}$$

or, if all recoveries beyond year 1 be used, then by analogy with (4.11):

$$u_2 = \frac{i_1(R_2 + R_3 + R_4 + \ldots + R_n)}{a_1 M(1 + s_2 + s_2^2 + \ldots + s_2^{n-2})} \tag{4.18}$$

The first-year recoveries, as a fraction of the total fish marked, will be:

$$\frac{R_1}{M} = \frac{p_1}{i_1}\left(\frac{i_1 - a_1}{i_1}\right)$$

Evaluating p_1 from this, and proceeding as in the development of (4.17):

$$u_2 = \frac{a_2}{i_2}\left(i_2 - i_1 + \frac{R_1 i_1^2}{M(i_1 - a_1)}\right) \tag{4.19}$$

The rate of exploitation u_2 can now be evaluated as before. (It saves a little time to know that if (4.18) turns out greater than (4.19), the trial value of i_1 is too *great.*)

Type C errors are easy to detect. If marking is done just before the fishing season, it will show up at once on a graph of the logarithms of recoveries in successive years, as a displacement of the point for the first year above or below the straight line drawn through the points for later years. If marking is done during the fishing season, then the recaptures of year 1 should first be multiplied by $a^2_2/s_2(i_2 - a_2)$ before taking the logarithm and plotting (Section 4B).

If type B error (continuous loss of tags, etc.) is present as well as type C, then it is the *apparent* survival and mortality rates which should be used throughout the calculations above, rather than the true rates, in order to obtain an unbiased estimate of p_2.

EXAMPLE 4E. FISH MARKED THROUGHOUT THE FISHING SEASON, WITH UNREPRESENTATIVE FIRST-SEASON MORTALITY

In an hypothetical population 1,500 fish were marked, throughout a fishing season. Recoveries were: same year, 450; 2nd year, 312; 3rd year, 125; 4th year, 50; 5th year, 20. From (4.2), the survival rate after the first year is $s_2 = 195/487 = 0.400$, $a_2 = 0.600$, and $i_2 = 0.916$. The fish were tagged from and returned to schools which were being actively fished, so there is reason to suspect the first year's mortality may be too great to be representative of the population as a whole. To test this, we evaluate $450a_2^2/s_2(i_2 - a_2) = 1{,}282$, and finding it greater than $312/s_2 = 780$, conclude that our suspicions are justified (cf. Fig. 4.2). Consequently, it is necessary to depend on recaptures in the second and later years to obtain an estimate of rate of fishing.

Using equations (4.18) and (4.19), we select trial values of i_1, and obtain the following:

Trial value of i_1..........	1.00	1.20	1.22	1.24
u_2, from (4.18)...........	0.329	0.357	0.360	0.363
u_2, from (4.19)...........	0.479	0.379	0.369	0.358

Graphical interpolation between the last two gives 1.233 as the best estimate of i_1, and 0.362 as the best estimate of u_2. From the latter, the rate of fishing is $p_2 = 0.362 \times 0.916/0.600 = 0.553$; and $q_2 = 0.916 - 0.553 = 0.363$.

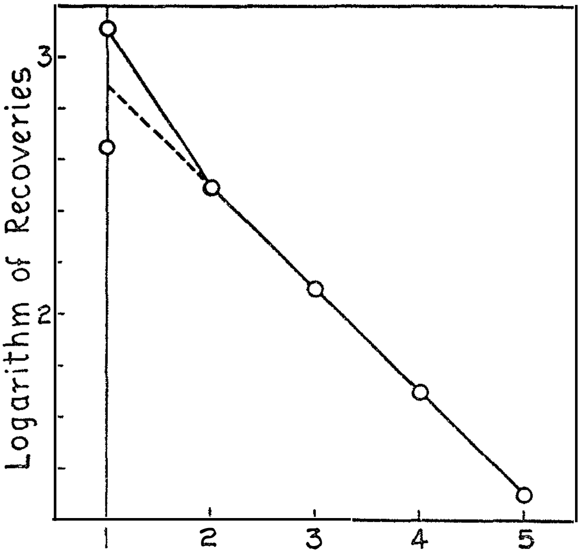

FIGURE 4.2. Logarithms of recoveries of marked fish, in successive years of the experiment of Example 4E. The lower point for year 1 represents the actual logarithm of the number of recoveries; the higher point is the logarithm of $a^2/s(i - a)$ times the recoveries. The latter should lie on the line established by recoveries in later years, if there were no type C error.

It is possible to check the value of u_2 obtained above by an approximate calculation. If there were no natural mortality at all in the first year, the survivors at the start of the second year would number $1{,}500 - 450 = 1{,}050$; hence a minimal estimate of u_2 is $312/1050 = 0.297$, and a maximal value of v_2 is $0.600 - 0.297 = 0.303$. But the fraction of the fish marked in the first year, which die naturally in the same year, should be about half this, since they enter the population in uniform numbers throughout the season. Hence a fairly good estimate of the first year's expectation of natural death among all fish marked will be $0.303/2 = 0.152$, and the actual deaths will be $0.152 \times 1500 = 228$. A better estimate of u_2 will therefore be $312/(1500-450-228) = 0.38$, which is close to the 0.362 obtained in the last paragraph. This approximate computation should be fairly good as long as v_2 is, say, less than 0.4.

If desired, a schedule similar to Table 4.5 can now be constructed, showing population and natural mortality among the 1,500 fish tagged, in successive years:

Year	1	2	3	4	5
Initial population	...	862	345	138	55
Catch	450	312	125	50	20
Natural mortality	188	205	82	33	13
Total mortality	638	517	207	83	33

Another cause of increased (or decreased) returns in the first year would be a failure to get the fish marked at a rate proportional to that at which the fishery is making landings. For example, if relatively more marking were done near the beginning of the fishing season, then the rate of exploitation of the marked fish during the year of marking would be greater than $p(i - a)/i^2$. In its effect upon recoveries, this state of affairs would resemble the situation just considered, and could be treated in the same fashion, except that the first year's natural mortality could be increased somewhat to compensate for the longer average time the marked fish are at large.

4E. Graphical Methods of Estimating Effectiveness of Fishing

Various graphical methods of estimating the effectiveness of fishing from marking experiments have been proposed, and at this point in the earlier review (Ricker, 1948, Section 26) several were discussed. There would be little value now in repeating these comments, but it is impossible to overestimate the influence of the work of Thompson and Herrington (1930), Graham (1938a) and Clark and Janssen (1954a), in stimulating the investigation of appropriate methods of analysis in America and in Europe.

The principles and limitations of graphical extrapolation to estimate effectiveness of fishing from tag returns are illustrated for the two situations below.

1. Figure 4.1 (page 113) illustrates a possible procedure. The straight line fitted to the logarithms of successive catches can be produced back to the begining of year 1, the time of marking. It could be argued that this intercept represents the logarithm of the number of fish which would be retaken if recaptures were to be continuously made at the rate established immediately after tagging (before natural mortality had a chance to reduce their number), and that hence the antilogarithm of the intercept, divided by N, should be the rate of fishing, p.

Closer consideration shows that such an estimate of p will be approximate only. Turning to Table 4.1, if the "recoveries" of each year be considered as pertaining to the middle point of the year[2], we have the series:

$$\mathrm{M}u,\ \mathrm{M}us,\ \mathrm{M}us^2,\ \mathrm{M}us^3,\ \text{etc.}$$

separated by unit time intervals. These constitute a geometric series with common ratio s. The point we are interested in (the beginning of the first year) lies one-half of a unit time interval to the left of $\mathrm{M}u$, and must therefore be $\mathrm{M}us^{-\frac{1}{2}}$ or $\mathrm{M}u/\sqrt{s}$. Dividing by the number of fish marked, M, gives the expression:

$$\frac{u}{\sqrt{s}} \qquad (4.20)$$

---

[2] It is obvious that it is this assumption which is incorrect, in both this argument and that of method 2 below. The mean date of recapture of tags is in advance of the middle of the fishing of each year, and when mortality rate is moderate to large the difference is important.

which we originally proposed to identify as the rate of fishing, p. Comparing with the true formula $p = ui/a$, we find that (4.20) differs in so far as $1/\sqrt{s}$ differs from i/a. From Appendix II it is evident that as $i \rightarrow 0$, these two expressions become the same; for larger values of i we have:

i	i/a	$1/\sqrt{s}$
0.5	1.27	1.28
1.0	1.58	1.65
1.5	1.93	2.12
2.0	2.31	2.72

Thus over a considerable part of the range of i values likely to be encountered, (4.20) could be used for p without serious error, but when i exceeds 1.0 the error becomes considerable (i.e., $u/\sqrt{s}$ is greater than p). In that event it will be worth while to calculate p from the u obtained by expression (4.5) or, what amounts to the same thing, to interpret the intercept obtained by graphical extrapolation in terms of (4.20).

2. When marking is done throughout the first year a similar possibility of extrapolating exists, which can be illustrated from Figure 4.2 (p. 125). We might argue that the marking, which actually was spread evenly through the first year, could fairly be considered as having been concentrated at its middle. Similarly the recaptures, which are spread through the succeeding years, could be considered as concentrated at the middle of each. Then, in Figure 4.2, the intercept of the straight line (logarithms of recoveries) with the ordinate for the middle of year 1 should represent the logarithm of the number of fish which would be recaptured in year 1 if the fishery were compressed into a short space of time immediately following the marking at the middle of the year, without allowing time for natural mortality to take effect. Such an intercept, divided by the number of fish marked, would seem to be an estimate of the rate of fishing, p.

Considering the "Recoveries" row of Table 4.4, from year 2 onward, it is evident that it constitutes a geometric series with common ratio s, and that the point at year 1 which fits into the series will be ua/is. Substituting $R_2/M = ua/i$, the true year 1 intercept becomes R_2/Ms; or, if all the data for later years be included, this intercept is:

$$\frac{R_2 + R_3 + \ldots + R_n}{sM(1 + s + s^2 + \ldots + s^{n-2})} \tag{4.21}$$

Comparing this with the true p which can be estimated from recoveries after the first year, shown in (4.12), it is evident that they differ in that (4.12) has i^2/a^2 where (4.21) has $1/s$. As may be seen by comparing a^2/i^2 and s in Appendix II, the two latter expressions do not differ a great deal over a part of the range of i values likely to be encountered in work of this sort; but when i becomes larger than, say, 0.8, the error is considerable, making (4.21) greater than p.

CHAPTER 5.—POPULATION AND SURVIVAL FROM MARKING EXPERIMENTS EXTENDING THROUGH TWO OR MORE TIME INTERVALS. RATE OF SURVIVAL VARIABLE

5A. SURVIVAL RATE WHEN MARKING IS DONE AT THE START OF FISHING IN TWO CONSECUTIVE YEARS

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:

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

We wish to know:

N_1	the population at the start of year 1
s_1	the survival rate during year 1 (from the time of marking in year 1 to the time of marking in year 2)

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; hence 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:

$$\hat{s}_1 = \frac{R_{12}M_2}{M_1R_{22}} \tag{5.1}$$

This is the large-sample formula of Ricker (1945a, 1948). It can now be modified for the more usual small-sample situation, by analogy with (3.7) above and (5.12) below:

$$\hat{s}_1 = \frac{R_{12}M_2}{M_1(R_{22} + 1)} \tag{5.2}$$

The analogy with (5.12) also provides an estimate of the variance of (5.2):

$$V(\hat{s}_1) = \hat{s}_1^2 - \frac{M_2^2R_{12}(R_{12} - 1)}{M_1^2(R_{22} + 1)(R_{22} + 2)} \tag{5.3}$$

The estimate of s_1 from (5.1) or (5.2) can be transformed directly to a_1 and i_1, hence p_1 and q can be computed, using (5.18). The value of p_2 is also available, if acceptable data of the type shown by equation (5.17) are at hand.

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 which is greater than that of the fish marked in the first year, M_1, by one year's growth (cf. 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 3B above.

EXAMPLE 5A. SURVIVAL RATE OF BLUEGILLS IN MUSKELLUNGE LAKE, FROM MARKINGS DONE AT THE START OF TWO CONSECUTIVE YEARS. (Data from Ricker, 1945a, pp. 383-384.)

The procedure of Section 5A was the principal one used during the 1940's to estimate vital statistics of populations of fishes in small Indiana lakes. An example concerning bluegills (*Lepomis macrochirus*) of Muskellunge Lake will be described.

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 (5.2):

$$\hat{s}_1 = \frac{13 \times 93}{230 \times 14} = 0.37546$$

From (5.3), the variance of $\hat{s}_1$ is:

$$V(\hat{s}_1) = 0.37546^2 - \frac{93^2 \times 13 \times 12}{230^2 \times 14 \times 15}$$

$$= 0.140970 - 0.121455 = 0.01952$$

The standard error is the square root of this, or 0.1397.

The attractive simplicity of this procedure is unfortunately often marred by the doubts occasioned by a possible lack of homogeneity among the group of fish being handled, or from within-season variations in mortality rate which are not the same for all age-groups. A discussion of some of these considerations can be found in the paper cited above, particularly the section on pumpkinseeds, pp. 385-386.

5B. SURVIVAL RATE WHEN MARKING IS DONE THROUGHOUT THE YEAR, AND THERE IS A DIFFERENCE IN RATE OF FISHING BETWEEN THE YEARS

Some progress has been made in the analysis of data from experiments in which marking is done throughout the year and survival rate is not constant. In the situation where the change in survival, *s*, is the result of a change in rate of fishing, *p*, we can proceed as below.

Suppose M_1 fish are marked during year 1, of which R_{11} are retaken that year and R_{12} in year 2; also M_2 fish are marked during year 2, of which R_{22} are retaken the same year. From Table 4.4, suitably modified, three equations can be taken:

$$\frac{R_{11}}{M_1} = \frac{p_1(i_1 - a_1)}{i_1^2} \tag{5.4}$$

$$\frac{R_{12}}{M_1} = \frac{p_2 a_2 a_1}{i_2 i_1} \tag{5.5}$$

$$\frac{R_{22}}{M_2} = \frac{p_2(i_2 - a_2)}{i_2^2} \tag{5.6}$$

Dividing (5.6) into (5.5) gives:

$$\frac{R_{12}M_2}{R_{22}M_1} = \frac{a_1 a_2 i_2}{i_1(i_2 - a_2)} = \frac{a_2^2}{(i_2 - a_2)} \cdot \frac{a_1 i_2}{a_2 i_1} \tag{5.7}$$

Now the expression $a_1 i_2/a_2 i_1$ is close to unity when i_2 differs only a little from i_1, particularly when neither i_1 nor i_2 exceeds, say, 0.9. Under such circumstances we may write:

$$\frac{R_{12}M_2}{R_{22}M_1} = \frac{a_2^2}{i_2 - a_2} \text{ (approximately)} \tag{5.8}$$

and s_2 or i_2 can be taken directly from the corresponding entry in Appendix II.

If the number of recaptures warrants it, and especially if observations on fishing gear in use suggest that p_1 and i_1 are likely to differ considerably from p_2 and i_2, it is desirable to evaluate the term $a_1 i_2/a_2 i_1$ in (5.7). This can be done by two-stage iteration, as follows: (1) Take the approximate values of i_2, p_2 and q obtained above as first estimates. (2) Select a reasonable trial value of p_1, add q to get a trial i_1, and calculate the right-hand side (RHS) of (5.4); repeat until the i_1 is obtained which makes the RHS equal the LHS. (3) Using this i_1, calculate the correction term $a_1 i_2/a_2 i_1$ in (5.7) and compute $a_2^2/(i_2 - a_2)$; the latter will correspond to a new estimate of i_2 which can conveniently be obtained from Appendix II. (4) Using this new i_2, calculate p_2 from (5.6) and get q by subtraction. These improved estimates of i_2, p_2 and q are used to start again at stage (2) above, and the process continues until there is no further improvement.

EXAMPLE 5B. SURVIVAL RATE OF MUSKELLUNGE LAKE BLUEGILLS, FROM MARKING DONE THROUGHOUT TWO CONSECUTIVE YEARS. (Data from Ricker, 1945a.)

The marking of bluegills during the fishing season of 1942 included 100 fully-vulnerable age III individuals, of which 7 were recaptured that year, so that $R_{11}/M_1 = 0.07$. The total number of legal fish marked that year was 400, of which 41 were retaken by fishermen in 1943, so that $R_{12}/M_1 = 0.1025$. Finally, 131 age III individuals were marked during the fishing season of 1943, with 14 recaptures the same year, giving $R_{22}/M_2 = 0.1068$.

From the approximate relationship (5.8):

$$\frac{a_2^2}{i_2 - a_2} = \frac{R_{12}M_2}{M_1R_{22}} = \frac{0.1025}{0.1068} = 0.958$$

From Appendix II, $i_2 = 1.23$; and from (5.6), $p_2 = 0.1068\times1.5129/0.5223 = 0.309$, and $q = 1.23 - 0.31 = 0.92$.

The above is as good a result as these data are apt to provide, considering the small number of recaptures in the categories R_{11} and R_{22}. However, to illustrate the complete method we will proceed. Take a trial $i_1 = i_2 = 1.23$; $p_1 = p_2 = 0.31$. Using the tabulated values of $i^2/(i - a)$ in Appendix II, the RHS of (5.4) becomes $0.31/2.897 = 0.1068$, as compared with the actual 0.07. Varying p_1, with q constant at 0.92, gives the additional values below:

p_1	q	i_1	$i_1^2/(i_1-a_1)$	RHS of (5.4)
0.31	0.92	1.23	2.897	0.1068
0.25	0.92	1.17	2.850	0.0877
0.20	0.92	1.12	2.811	0.0715
0.19	0.92	1.11	2.803	0.0677

Interpolation between the last two gives $p_1 = 0.194$ as the best value, hence $i_1 = 0.194 + 0.92 = 1.114$. Again using Appendix II, the correction term in (5.7) is evaluated as:

$$a_1i_2/a_2i_1 = 0.6031/0.5754 = 1.048$$

and the adjusted $a_2^2/(i_2 - a_2)$ will be $R_{12}M_2/R_2M_1$ divided by this, that is, $0.958/1.048 = 0.914$. This corresponds to $i_2 = 1.32$; hence from (5.6), $p_2 = 0.1068 \times 1.742/0.587 = 0.314$. Thus the estimate of p_2 is not much changed, but $q = 1.32 - 0.31 = 1.01$, which is appreciably greater than 0.92.

Again solving (5.4) by iteration, with trial p_1 values:

p_1	q	i_1	$i_1^2/(i_1-a_1)$	RHS of (5.4)
0.19	1.01	1.20	2.873	0.0662
0.20	1.01	1.21	2.881	0.0692
0.21	1.01	1.22	2.889	0.0726

The interpolated value of p_1 is now 0.202, and $i_1 = 1.01 + 0.20 = 1.21$. A second estimate of the correction term in (5.7) is:

$$a_1i_2/a_2i_1 = 0.5800/0.5552 = 1.045$$

This is practically the same as the 1.048 obtained on the previous trial, so the definitive estimates can be taken to be $i_2 = 1.32$, $i_1 = 1.21$, $q = 1.01$, $p_2 = 0.31$, $p_1 = 0.20$.

Corresponding to $i_1 = 1.21$ is $s_1 = 0.30$, and this may be compared with the estimate $s_1 = 0.375$ obtained for the same population in Example 5A. The difference is less than the standard error of the latter (0.140).

5C. "Triple-catch Trellis" Method for Estimating Population, Survival and Recruitment.

Work done on estimating insect populations by marking, begun by Jackson in 1933, has led to an extensive literature of statistical estimation based on "point" samples. In point sampling, catches are ideally made in short periods of time (each one day long, for example), and these points are separated by periods of several days or weeks during which no collections are made. A variety of methods of grouping recaptures have been examined, and the merits of stochastic as compared with deterministic models are beginning to be explored (Hamersley, 1953). Both approaches lead to iterative solutions with heavy algebra whenever recoveries are made on more than two occasions. With only two sets of recoveries, however, simple explicit solutions are available for several deterministic models. Of these it seems necessary to consider only one, the variety of triple-catch or "3-point" trellis[1] in which recaptures are grouped according to the time at which they were marked. Bailey (1951) has the clearest account of the procedure, having developed it from the more general solutions of Dowdeswell *et al.* (1940) and subsequent writers.

Most investigators who deal with insect material favour distinctive remarking of recaptured animals so that their complete capture history can be traced. Using the kind of grouping discussed below, an animal would be counted as two recaptures the second time it was recovered and as three recaptures on any third occasion, etc. However, remarking and giving double weight to an already-recaptured animal magnifies the bias resulting from any capture-proneness that may characterize certain individuals of the population; and when working with vertebrates it is usually well to avoid it for that reason (this applies when the animals are originally captured for marking by the same method as used for subsequent recaptures).

If capture-proneness is not a worry, remarking will permit an analysis on the basis of grouping recaptures according to the length of time elapsed *since last recapture.* This procedure makes slightly better use of the data (Leslie, 1952; Moran, 1952), but only at the expense of much more involved tabulations and calculations; these will not be described here.

In the procedure outlined by Bailey, three catches or samples are taken. On the first occasion (here called time 1) the fish are marked; at time 2, recaptures are noted and returned to the water, and unmarked fish are given a different mark; at time 3, the previous marks, of both categories, are listed (as well as the unmarked individuals, of course). Loss of some fish by accidental death due to the fishing procedure affects the result only by reducing the population to that extent. However if a previously-marked fish is accidentally killed at the second sampling, it should be replaced by a new one similarly marked.

The categories of individuals in the 3 samplings are as shown in Table 5.1. We wish to know:

N_1, N_2, N_3 the population present at each sampling (N_2 = Bailey's x)

s_{12}, s_{23} the survival rates between times 1 and 2, and 2 and 3, respectively ($s \leq 1$). (s_{12} = Bailey's λ)

r_{12}, r_{23} the "rates of accretion" of new recruits between the same times: these rates are strictly analogous to survival rates; they represent initial stock plus *all* new recruits during the period, divided by the initial abundance at the start of the period ($r \geq 1$). (r_{23} = Bailey's μ)

Values of s and r can be used to calculate instantaneous rates of mortality (i) and recruitment (z), respectively:

$$i = -\log_e s \tag{5.9}$$

$$z = +\log_e r \tag{5.10}$$

(i/t_{12} = Bailey's γ; z/t_{23} = Bailey's β)

---

[1] This name refers to the triangular lattice in which numbers marked and recaptured can be arranged; see Dowdeswell *et al.* (1940).

TABLE 5.1. Categories of fish newly marked, examined, and recaptured, in Bailey's triple-catch trellis method. Shown in brackets below our symbols are those used by Bailey, 1951 (at left), and by Wohlschlag, 1954 (at right).

Period No.	Fish newly marked	Fish examined for marks	Recaptures from 1st marking	Recaptures from 2nd marking
1 (1,0)	M_1 (s_1,R_0)	......	......	......
2 (2,1)	M_2 (s_2,R_1)	C_2 (n_2,F_1)	R_{12} (n_{21},m_{01})	......
3 (3,2)	......	C_3 (n_3,F_2)	R_{13} (n_{31},m_{02})	R_{23} (n_{32},m_{12})

Bailey's small-sample formulae for direct estimates of N_2, s_{12} and r_{23}, are:

$$\hat{N}_2 = \frac{M_2(C_2 + 1)(R_{13})}{(R_{12} + 1)(R_{23} + 1)} \tag{5.11}$$

$$\hat{s}_{12} = \frac{M_2 R_{13}}{M_1(R_{23} + 1)} \tag{5.12}$$

$$\hat{r}_{23} = \frac{R_{12}(C_3 + 1)}{C_2(R_{13} + 1)} \tag{5.13}$$

Approximate variances for these are also given by Bailey:

$$V(\hat{N}_2) = \hat{N}_2^2 - \frac{M_2^2(C_2 + 1)\,(C_2 + 2)R_{13}(R_{13} - 1)}{(R_{12} + 1)\,(R_{12} + 2)\,(R_{23} + 1)\,(R_{23} + 2)} \tag{5.14}$$

$$V(\hat{s}_{12}) = \hat{s}^2_{12} - \frac{M_2^2 R_{13}(R_{13} - 1)}{M_1^2(R_{23} + 1)\,(R_{23} + 2)} \tag{5.15}$$

$$V(\hat{r}_{23}) = \hat{r}^2_{23} - \frac{R_{12}(R_{12} - 1)C_3(C_3 + 2)}{C_2(C_2 - 1)\,(R_{13} + 1)\,(R_{13} + 2)} \tag{5.16}$$

From the above, the corresponding statistics for other times and intervals can be calculated, if instantaneous mortality and recruitment rates are considered uniform.

It is not necessary that the time intervals between the three samplings be equal, but it is often convenient to make them so. If the two intervals are unequal, the derived instantaneous rates i_{12} and z_{23} should be reduced to a per-day basis for calculating the other N's, *r*'s and *s*'s.

Although ideally the three samples above should be taken at "points" or really short intervals of time, Wohlschlag (1954) used the method in a continuous experiment, by dividing the experiment into 3 equal periods and considering all sampling and marking as though it had been concentrated at the middle of each period. This seems accurate enough for any experiment on the usual scale; with very large numbers of recaptures, and a high rate of recapture, a correction for the non-central expectation of average time of recapture might be introduced.

The survival formula (5.12) is identical with (5.2) of Section 5A, though the symbols are slightly different. The differences between the procedures involved may seem great at first, but they actually are trivial. In the present method, "point" samples (1, 2 and 3) are taken for both marking and recoveries. Section 5A presupposes a "point" release of marks followed by a long interval of sampling for recoveries, then another point marking and extended recovery period. From the point of view of Table 5.1, the first extended recovery period of Section 5A should be grouped with the *second* marking sample to form "Point 2". The identity of (5.2) and (5.12) is a consequence of the fact that, in making Petersen estimates, expectation of the recovery ratio R/C is unchanged by any natural mortality which affects marked and unmarked equally; hence recoveries can be made over a protracted period.

The rate of accretion, r, and the derived instantaneous rate of recruitment, z, have not usually been computed for fish populations because they do not have the same direct biological meaning that survival rates do. That is, recruits to a commercial fish population usually result from a reproductive season that occurred several years earlier—in contrast to game bird populations, for example, where the young usually become adult in the year following their hatching. However there is no objection to computing r and z for fishes for descriptive purposes and, especially in "point" sampling, the imagination has little difficulty in grasping the relationship implied.

Notice that the accuracy of a population estimate from (5.11) depends principally upon the magnitudes of the three R-items; of which R_{13}, in the numerator, will normally tend to be the smallest. Good design in such an experiment would aim at having R_{12}, R_{13} and R_{23} all about the same size, and this is likely to be accomplished if M_1 is made considerably larger than M_2 or (what may be easier) if a large number of fish are examined in the third sample. If R_{13} turns up small regardless, it will be a good idea to explore the applicability of (3.7) for estimates of N_1 and N_2, using one of the devices discussed in Section 3C to remove the effects of recruitment. In the notation used here, the accuracy of an estimate of N_1 from (3.7) would depend mainly on the magnitude of R_{12}, while the accuracy of an estimate of N_2 would depend on R_{23}.

EXAMPLE 5C. ABUNDANCE, SURVIVAL AND RECRUITMENT BY THE TRIPLE-CATCH TRELLIS METHOD

An hypothetical marking experiment on a limited population is shown in Table 5.2. Formulae (5.11)—(5.16) yield the estimates below. (Many significant figures are given because they are required in the variance computation.)

$$\text{Population at time 2} = \hat{N}_2 = \frac{400\times481\times163}{121\times175} = 1481.04841$$

$$V(\hat{N}_2) = 1481.04841^2 - \frac{400^2\times481\times482\times163\times162}{121\times122\times175\times176}$$

$$= 2{,}193{,}504.39 - 2{,}154{,}362.58 = 39{,}141.81$$

$$\text{standard error} = 197.84$$

Survival rate between times 1 and 2:

$$\hat{s}_{12} = \frac{400\times163}{500\times175} = 0.745143$$

$$V(\hat{s}_{12}) = 0.745143^2 - \frac{400^2\times163\times162}{500^2\times175\times176}$$

$$= 0.555238 - 0.548696 = 0.006542$$

$$\text{standard error} = 0.08088$$

TABLE 5.2. Marks put out and recaptures made in the triple-catch trellis experiment of Example 5c.

Period No.	Fish newly marked	Fish examined for marks	Recaptures marked at time 1	Recaptures marked at time 2
1	$M_1 = 500$	......	......	......
2	$M_2 = 400$	$C_2 = 480$	$R_{12} = 120$	......
3	......	$C_3 = 1000$	$R_{13} = 163$	$R_{23} = 174$

"Rate of accretion" of new recruits between times 2 and 3:

$$\hat{r}_{23} = \frac{120\times1001}{480\times164} = 1.52591463$$

$$V(\hat{r}_{23}) = 1.52591463^2 - \frac{120\times119\times1000\times1002}{480\times479\times164\times165}$$

$$= 2.32841545 - 2.29980697 = 0.0286084$$

$$\text{standard error} = 0.16915$$

Suppose that the first interval, t_{12}, was 10 days long, while t_{23} was 7 days long. The instantaneous rate of *mortality* for t_{12} is $i_{12} = -\log_e 0.74514 = 0.2942$, or 0.02942 per day. The instantaneous rate of *recruitment* for the second interval is $z_{23} = \log_e 1.5259 = 0.4226$, or 0.06037 per day. Hence if rates of recruitment and mortality have been uniform, the population has been increasing at an instantaneous rate of $0.06037 - 0.02942 = 0.03095$ per day.

From the above and the previously-obtained estimate of N_2, estimates of N_1 and N_3 can be computed. For example, the instantaneous rate of increase is $10 \times 0.03095 = 0.3095$ for the time interval t_{12}; from column 12 of Appendix II, this corresponds to an actual increase of 0.3632 from time 1 to time 2. Given $\hat{N}_2 = 1481$, $\hat{N}_1 = 1481/1.3632 = 1087$ fish.

5D. SURVIVAL ESTIMATED FROM MARKING IN ONE SEASON, IN CONJUNCTION WITH FISHING EFFORT DATA

Consider a change in rate of fishing which results from a change in fishing effort from one year to the next. Suppose that p_1, q, i_1, a_1, etc. are statistics describing the first year of an experiment, while p_2, q, i_2, a_2, etc. describe the second year, only q being common to both (cf. Table 4.5, Section 4D). Of M_1 fully-vulnerable fish marked at the start of the first year, R_{11} are recaptured that year, R_{12} the next year. To estimate survival rate (s_1), another piece of information is necessary. In default of a second year's marking, this may be provided by data on fishing effort (f) in the two years; which data, if they really represent effective effort as the fish encounter it, will be proportional to rate of fishing, p. We have:

$$\frac{f_1}{f_2} = \frac{p_1}{p_2} \tag{5.17}$$

Also, from Table 4.5:

$$\frac{R_{11}}{M_1} = u_1 = \frac{p_1 a_1}{i_1} \tag{5.18}$$

$$\frac{R_{12}}{M_1} = u_2 s_1 = \frac{p_2 a_2 s_1}{i_2} \tag{5.19}$$

Dividing (5.18) into (5.19) gives:

$$s_1 = \frac{R_{12}}{R_{11}} \cdot \frac{p_1}{p_2} \cdot \frac{a_1 i_2}{i_1 a_2} \tag{5.20}$$

In this expression, R_{12}/R_{11} and p_1/p_2 are known; the correction term $a_1 i_2/i_1 a_2$ is the same one already encountered in (5.7) above, and it can be handled in the same manner as there. A first estimate of s_1 is obtained by putting $a_1 i_2/i_1 a_2$ equal to unity, and i_1 is calculated. This makes it possible to estimate p_1 from (5.18), whence $q = i_1 - p_1$; then p_2 is calculated from (5.17), and $i_2 = p_2 + q$. We are now in a position to evaluate $a_1 i_2/i_1 a_2$, and get an improved estimate of s_1 from (5.20). Further iteration is usually not necessary.

EXAMPLE 5D. SURVIVAL RATE OF BLUEGILLS AT SHOE LAKE, INDIANA, COMPUTED WITH THE AID OF INFORMATION ON FISHING EFFORT. (Data from Ricker, 1945a, pp. 393, 413, 419.)

Because of the war, cane-pole fishing effort on Shoe Lake decreased from 163 pole-hours per acre in 1941 to 106 in 1942; i.e., $p_1/p_2 = 1.54$. A representative value for rate of exploitation of bluegills in 1941 was 0.32, while in 1942 there were retaken by fishermen 0.049 of bluegills which had been marked prior to the fishing season in 1941. Disregarding the a and i terms in (5.20), a first estimate of s_1 is $1.54 \times 0.049/0.32 = 0.236$; which gives $a_1 = 0.764$, $i_1 = 1.444$, $p_1 = 0.32 \times 1.444/0.764 = 0.605$, $q = 1.444 - 0.605 = 0.839$, $p_2 = 0.605/1.54 = 0.393$, $i_2 = 0.393 + 0.839 = 1.232$, $a_2 = 0.708$. Using the whole of formula (5.20) we get:

$$\hat{s}_1 = 0.236 \left(\frac{0.764 \times 1.232}{1.444 \times 0.708}\right) = 0.217$$

This value of s_1 can now be used to obtain better estimates of a_1, i_1, a_2, and i_2, but when these are used in (5.20) the same value for s_1 is obtained. Consequently, 0.22 is the best estimate of survival rate in the first year. For comparison, the value computed by the method of Section 5A was 0.24.

EXAMPLE 5E. SURVIVAL RATE AND RATE OF FISHING OF HALIBUT, COMPUTED WITH THE AID OF FISHING EFFORT. (Data from Thompson and Herrington, 1930.)

Widespread halibut tagging in the area south of Cape Spencer, Alaska, was done during 1925 and 1926, though not on exactly the same grounds in the two years. Data for the 1925 season are described in Example 5F below. Of 762 fish of approximately age VIII or older tagged throughout 1926, recaptures were made as follows: 106 in 1926, 147 in 1927, and 52 in 1928.

Neglecting for the moment any difference in fishing effort between 1927 and 1928, a first estimate of apparent survival rate (the complement of the rate of disappearance of tagged fish from the fishing grounds) is:

$$\hat{s}_1' = \frac{52}{147} = 0.354$$

However, from the data on gear used south of Cape Spencer, cited in Example 2H, we know there was an increase in fishing from 494,100 "skates" of line set in 1926 and 498,600 in 1927, to 569,200 skates in 1928. This is at least a clue concerning the relative magnitude of the rates of fishing in these years, so we may estimate the 1927:1928 ratio as $p_1/p_2 = 0.876$. Using (5.20) without the a and i terms:

$$\hat{s}_1' = 0.354 \times 0.876 = 0.310$$

which will be a second estimate of apparent survival rate.

A slight improvement can be made by using the whole of (5.20). A trial value of p_1 is required, but it need be only quite approximate; we will take trial $p_1 = 0.72$[2]. Hence trial $p_2 = 0.72/0.876 = 0.82$, or 0.10 more than p_1. Considering natural mortality rate constant, a trial i_2 is therefore equal to $i_1 + 0.10 = 1.17 + 0.10 = 1.27$. Consequently, using all of (5.20), and taking a/i values from Appendix II:

$$\hat{s}_1 = 0.310 \times 0.5894/0.5663 = 0.323$$

Turning now to a serious estimate of rate of fishing, we notice first that tagging was done throughout the fishing season, which is the situation discussed in Section 4B. The possible existence of Type C error is tested by the method of expressions (4.7) and (4.8); the test is fortunately not complicated by any significant difference in fishing effort, as between 1926 and 1927. Since we have already called 1928 year 2 and 1927 year 1 when applying (5.20), for consistency the years 1 and 2 of the formulae of Chapter 4 must here be designated 0 and 1, respectively. The two quantities to be compared are:

$$\mathrm{R}_0 a_1^2/s_1(i_1 - a_1) = 106 \times 1.012/0.323 = 332$$
$$\mathrm{R}_1/s_1 = 147/0.323 = 455$$

Since 332 is considerably less than 455, there is a deficiency of recaptures in the first year as compared with the two later years, which means Type C error is present. This means using repeated trials with (4.18) and (4.19). Because of the change in rate of fishing after 1927, only the first term of numerator and denominator should be used in (4.18). It is convenient to rewrite these expressions with this modification, and with the subscripts reduced by 1 to conform to the present numerical designation:

$$u_1 = \frac{i_0 \mathrm{R}_1}{a_0 \mathrm{M}}$$

$$u_1 = \frac{a_1}{i_1}\left(i_1 - i_0 + \frac{\mathrm{R}_0 i_0^2}{\mathrm{M}(i_0 - a_0)}\right)$$

---

[2] This was obtained by averaging two extreme limits for p_1. Rate of exploitation in 1927 obviously cannot be less than $u_1 = 147/(762 - 106) = 0.24$, hence a minimum p_1 is 0.27; a maximum value for p_1 is the instantaneous rate of total (apparent) mortality, calculated from $-\log_e 0.310 = 1.17$. The average of 0.27 and 1.17 is 0.72, the figure chosen; actually their geometric mean, 0.56, would be a better choice.

In selecting a trial i_0, notice that recaptures in 1926, when adjusted to a full year basis above, are 123 less than expected, so that the full-year u_1 would be approximately 332/762 = 0.436 instead of approximately 455/762 = 0.597. The difference between these, 0.16, will be a useful trial difference between i_1 and i_0 to use in the expressions above. Given $s_1 = 0.323$ and $i_1 = 1.13$, a trial $i_0 = 1.13 - 0.16 = 0.97$. Application of this and two other trial values is shown below:

Trial i_0	First u_1 value	Second u_1 value	Difference
0.97	0.302	0.321	−0.019
1.00	0.305	0.304	+0.001
1.01	0.307	0.299	+0.008

The best i_0 is evidently very close to 1.00. From it is calculated $\hat{u}_1 = 147/762 \times 0.632 = 0.305$. Using (1.8), $\hat{p}_1 = 0.305/0.599 = 0.51$, which is the instantaneous rate of fishing for 1927. It is a rather smaller figure than the $\hat{p} = 0.57$ for 1926, computed by the same method from the 1925 tagging experiment (Example 5F), though the fishing gear used was practically the same in 1926 and 1927. However tagging was not done on exactly the same grounds, and the agreement of the two experiments can be considered very satisfactory.

Although the estimate $\hat{s}_1 = 0.323$ above involved using a trial p_1 (0.72) that proves to be considerably too large, s_1 is changed very little by using the more accurate figure 0.51: it is reduced to $\hat{s}_1 = 0.320$, which means i_1 would go up to 1.14. This change, however, makes no difference to the estimate of p_1 which follows.

5E. MARKING DONE THROUGHOUT THE YEAR. NATURAL MORTALITY VARIES WITH AGE.

If the instantaneous natural mortality rate, q, of the fish changes with age, with or without change in p, the computation becomes even more complicated, and I have not succeeded in setting up equations in which all the unknowns would be determinable—by successive approximations or otherwise. Even so, some progress might be made by using an estimate of one of the unknowns derived by analogy with another species of fish, or with the same species in another body of water. If q varies with age, it is essential to break up the fish marked into two or more groups. If age-groups are easily recognizable, we could, for example, mark ages III and IV differently in year 1 of the experiment. In year 2, the same thing would be done, but of course the fish that were age III in year 1 are now age IV. (If age-groups are not convenient units, any other moveable dividing lines can be used, provided that they are made to move at the rate at which fish of corresponding size are growing.)

Using the same symbols as formerly, we have:

Recaptures, during year 1, of a unit number of age III fish marked during year 1:

$$\frac{p_{\mathrm{III}}(i_{\mathrm{III}} - a_{\mathrm{III}})}{i_{\mathrm{III}}^2} \qquad (5.21)$$

Recaptures during year 2 (i.e., at age IV), of the unit number of fish marked at age III during year 1:

$$\frac{p_{\mathrm{IV}}\, a_{\mathrm{IV}}\, a_{\mathrm{III}}}{i_{\mathrm{IV}}\, i_{\mathrm{III}}} \qquad (5.22)$$

Recaptures, during year 2, of a unit number of age IV fish marked during year 2:

$$\frac{p_{\mathrm{IV}}(i_{\mathrm{IV}} - a_{\mathrm{IV}})}{i^2_{\mathrm{IV}}} \qquad (5.23)$$

Without introducing a complicated set of symbols for the number marked and number recaptured in each category, it is obvious that the expressions above can all be evaluated from the data. The rates of fishing p_{III} and p_{IV} (which might be equal) can be evaluated, as described in Section 5B, from (5.21) and (5.23). However, it seems essential to put in trial values of both q_{III} and q_{IV} simultaneously, in order to check survival rate against expression (5.22). This means of course that no definite decision can be reached concerning the size of either, though a series of corresponding values can be set up; i.e., if q_{III} is so and so, q_{IV} must be such and such. This might have value, as showing, for example, whether or not q increases with age.

5F. RATE OF FISHING DURING YEARS OF RECRUITMENT

Most fisheries include in their catch representatives of one or more young age-groups which are not yet fully vulnerable to fishing. That is, even when rate of fishing and natural mortality are constant among several older ages, the youngest fish cannot be expected to fit into the same picture. The fact they are incompletely recruited is another way of saying that their fishing mortality rate is less than the maximum or definitive rate, because some of their members are too small to be consistently taken by the kind of fishing gear in use. This being true, their total mortality should also be less than the definitive rate, other things being equal.

When recruitment occurs abruptly, there is little need to worry about the incompletely-recruited groups, because they form only a small part of the catch. In that event, marking or tagging experiments should avoid such fish, or mark them distinctively so that they will not be confounded with fully-vulnerable fish in the analysis, or make an adjustment for their lesser size such as was used, for instance, in Example 3E. If, however, recruitment extends over a period of several years, it may happen that the incompletely-recruited groups are not merely important, but actually comprise the greater part of the catch. In that event, it seems essential to mark these young fish and try to obtain some kind of information concerning them.

Fish incompletely recruited are subjected to a smaller total mortality rate than are older fish, if natural mortality does not vary with age. However, because rate of fishing is increasing with age, the ratio of one year's recaptures to the previous year's does not represent the survival rate which actually exists between the two years, but will be somewhat too great. No complete evaluation of fishing and natural mortality is possible under these circumstances, but an analysis can be made on the assumption that the *natural* mortality rate of the fish of the incompletely-recruited age-groups is the same as that of those completely vulnerable. This is done by evaluating survival rate and rate of fishing first from the wholly-recruited age-groups, then working back, year by year, into those incompletely recruited.

Two kinds of data may be used for this, either recoveries of tags or the numerical frequencies of the incompletely-recruited age-groups in the catch, though the information which the two provide is not necessarily the same (Section 5G). The actual procedures are difficult to describe in general terms, but can readily be followed in the two examples below.

EXAMPLE 5F. SURVIVAL RATE AND RATE OF FISHING FOR INCOMPLETELY-RECRUITED AGE-GROUPS OF HALIBUT, FROM RECOVERIES OF TAGS. (Data from Thompson and Herrington, 1930.)

Data pertaining to the 1925 halibut tagging experiment off northern British Columbia and southern Alaska are shown in Table 5.3, taken from table 12 and the appendices of the work cited. The approximate age distribution indicated is from Dunlop's data in Thompson and Bell (1934). It is obvious,

TABLE 5.3. Number of halibut tagged in 1925 (excluding Cape Chacon), and the number recaptured, arranged by 5-cm. length intervals. (Data from Thompson and Herrington, 1930).

Approximate age when marked	Size group[a]	Number tagged	Number of Recaptures				
			1925	1926	1927	1928	Total
	375	1	..	..	..	..	0
	425	6	..	..	..	..	0
	475	28	..	..	..	3	3
IV	525	66	..	7	5	1	13
V	575	188	2	17	11	10	40
VI	625	293	8	55	26	10	99
VII	675	330	30	61	27	4	122
VIII	725	212	18	55	25	3	101
IX	775	142	10	35	5	2	52
X	825	63	9	11	8	1	29
XI	875	37	5	13	1	1	20
XII	925	25	1	4	2	3	10
XIII	975	21	1	7	1	1	10
XIV	1,025	15	1	3	0	1	5
XV	1,075	12	1	1	1	1	4
XVI	1,125	9	1	1	0	1	3
	1,175 up	14	0	1	1	0	2
	Total	1,462	87	271	113	42	513
VIII–XVI	725–1,125	536	47	130	43	14	234

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[a] The 375-millimeter group includes fish from 350 to 399 millimeters, etc. The "1175-up" group includes fish from the 1175 group through the 1625 group.

from the age distribution of the fish tagged (cf. Fig. 2.12, page 74), that recruitment to the fishery is not complete until about age IX. This is reflected also in the distribution of recaptured fish, for there is a relative scarcity of recaptures among the smaller fish during the year of tagging, also during the first year after tagging, and to some extent even during the second year after tagging.

Recaptures of all sizes of fish in 1925 are scarce, indicating "Type C" error. A first step is to estimate the apparent survival rate for completely vulnerable fish. Fish of age VIII when tagged will be age IX in 1926, so we can use recaptures from them and from all older fish to estimate apparent survival rate, here represented by s instead of s':

	1926		1927		1928
Recaptures....	131		44		14
Ratio (s_2)......		0.336		0.318	

There is good agreement between the two ratios. Taking $58/175 = 0.331$ as the best representative value, the apparent annual mortality rate is $a = 0.669$, and the apparent instantaneous mortality rate is $i = 1.106$. Whether or not this represents the true mortality rate of the population (that is, whether or not Type B error is present), these figures must be used to obtain the estimate of rate of fishing.

Since the fish were marked throughout the fishing season of 1925, the 47 recaptures in that year would not be expected to be a member of the geometric series of later years; instead $a^2/s(i - a)$ times 47, or 145, should be. However, this is much less than the $131/0.331 = 396$ which would be expected on the basis of later recoveries, so that "Type C" error is even more important than in the 1926 experiment discussed in Example 5E[3]. Using formulae (4.18) and (4.19) to obtain apparent rate of exploitation in 1926, the value $u = 0.345$ is obtained, from which $p = ui/a = 0.345 \times 1.106/0.669 = 0.570$.

Estimates of rate of fishing for the incompletely-recruited fish can now be found, approximately, by assuming that the apparent instantaneous natural mortality rate is the same prior to age IX as it is at older ages. This value is $1.106 - 0.570 = 0.536$, or say 0.54. The ratios of 1927 to 1926 recoveries, for successive age-intervals during the period of recruitment, are as follows:

Approximate age during survival period	Recaptures in 1926	1927	Ratio
V—VI	7	5	0.71
VI—VII	17	11	0.65
VII—VIII	55	26	0.47
VIII—IX	61	27	0.44

---

[3] A part of the apparent "Type C" error is the result of more tagging having been done in the second half of the fishing season than in the first half. The mean date of tagging in 1925 was July 14, whereas the middle point of the fishery appears to be about June 15 (Thompson and Herrington, p. 62). Another part of the Type C error might result from non-random local intraseasonal distribution of fishing effort, such as is described by the authors quoted on pages 64-65 of their paper. It might be, too, that the halibut are "off their feed" and incapable of taking baited hooks at a normal rate for a certain time after tagging because of some hardship involved in the catching and tagging procedure. The only bias which these effects will introduce into the rate of fishing, as estimated by the procedure below, will be what results from the mean date of tagging being different from the mean date of apparent natural mortality; a rough computation shows that the estimated rate of fishing, 0.57, would be reduced by no more than 0.01.

If p_5, p_6, etc. represents the rate of fishing in successive years, and A_5, A_6, etc. the average populations, then:

$$\frac{A_6 p_6}{A_5 p_5} = 0.71; \quad \frac{A_7 p_7}{A_6 p_6} = 0.65; \text{ etc.}$$

The use of this information to estimate successive values of p is shown in Table 5.4, which can readily be understood if the following things are kept in mind:

(1) N fish at the start of any year decrease to Ns at its close, and their average abundance during the year is Na/i (expression 1.10).

(2) M fish at the close of a year represent the survivors of M/s fish at its start, and during that year their average abundance was Ma/is.

TABLE 5.4. Approximate computation of rate of fishing for years of recruitment, on the assumption that the instantaneous rate of apparent natural mortality (natural mortality plus loss of tags) remains constant at 0.54.

Age	Apparent survival rate	Population	Mean population	Rate of fishing	$\frac{A_t p_t}{A_{t-1} p_{t-1}}$
V	0.492		$A_5 = 6,640$	$p_5 = 0.17$	
		4,560			0.71
VI	0.454		$A_6 = 3,150$	$p_6 = 0.25$	
		2,070			0.65
VII	0.398		$A_7 = 1,351$	$p_7 = 0.38$	
		823			0.47
VIII	0.368		$A_8 = 520$	$p_8 = 0.46$	
		303			0.44
IX	0.330		$A_9 = 183$	$p_9 = 0.57$	
		100			

We start with the arbitrary number of 100 fish at the end of the year in which they are age IX. During that year they are subject to the definitive mortality rate 0.67, hence at its start they numbered 100/0.33 = 303. Their average abundance was 100 × 0.67/1.11 × 0.33 = 183; the rate of fishing was of course the definitive rate 0.57, and the apparent natural mortality rate was 0.54. During the preceding year, the total apparent instantaneous mortality rate was $p_8 + 0.54$. Putting $p_8 = 0.4$ as a trial value, apparent $i_8 = 0.94$, apparent $a_8 = 0.609$, apparent $s_8 = 0.391$, and hence $A_8 = 303 \times 0.609/0.94 \times 0.391 = 502$. From this $A_9 p_9/A_8 p_8 = 183 \times 0.57/502 \times 0.4 = 0.519$. But the observed value of this ratio is 0.44, in the schedule on page 141, and hence the trial value $p_8 = 0.4$ is too small. One or two additional trials gives $p_8 = 0.46$ as the correct answer. This determines apparent $i_8 = 0.46 + 0.54 = 1.00$, hence apparent $a_8 = 0.632$ and apparent $s_8 = 0.368$; and the population at the start of age VIII is 303/0.368 = 823. All the necessary data are now available to repeat the computation for age VII, and so on as far as desired. The calculations are made easier by using Appendix II, where all the products involving i, a, and s can be found. Of the series of calculated p values shown in Table 5.4, those closest to age IX naturally have the greatest reliability. Three or four years away from age IX, both systematic and sampling error might well be excessive.

EXAMPLE 5G. SURVIVAL RATE AND RATE OF FISHING FOR INCOMPLETELY-RECRUITED AGE-GROUPS OF HALIBUT, FROM THE AGE COMPOSITION OF THE CATCH. (Data from Thompson and Herrington, 1930.)

The length frequency and approximate age frequency of halibut caught for tagging in 1925 and 1926 was plotted in Example 2H; of these, the fish less than approximately age X are shown in Table 5.5. For the purpose of this illustration these fish are considered to be representative of the ordinary commercial *catch* of that time (including those caught but not marketed, since the latter are said to probably die). Their frequency distribution by age permits a computation of rate of exploitation back into the years of recruitment, in much the same manner as in Example 5F, but it is the true rather than the apparent natural mortality rate which must be used. Using the estimate of i from age distribution (Example 2H), and the estimate of p from the 1925 tagging (Example 5F), the true instantaneous rate of natural mortality is estimated as $q = i - p = 0.76 - 0.57 = 0.19$.

TABLE 5.5. Computation of rate of fishing for the years of recruitment, from the approximate distribution of ages in the catch taken for tagging in 1925 and 1926, on the assumption that instantaneous natural mortality rate (q) remains constant at 0.19.

1 Approximate age	2 Length groups	3 Observed catch	4 Survival rate	5 Population	6 Average population	7 Rate of fishing	8 Calculated catch
			s		A	p	Ap
III	425+475	96	0.820		10,370	0.009	93
				9,370			
IV	525	270	0.800		8,400	0.032	269
				7,490			
V	575	740	0.737		6,460	0.115	742
				5,520			
VI	625	1,201	0.631		4,426	0.27	1,195
				3,485			
VII	675	1,175	0.522		2,563	0.46	1,179
				1,819			
VIII	725	681	0.492		1,302	0.52	677
				895			
IX	775	359	0.47			0.57	

In Table 5.5 the number and approximate age of the fish in question is shown in column 3. Taking the ages as accurate, the definitive rate of survival, $s = 0.47$, and the definitive rate of fishing, $p = 0.57$, are entered opposite age IX. Now the catch of 359 fish at age IX is equal to A_9p_9 where A_9 is the average population. The average population is equal to a/i times the initial population, hence that initial population is equal to i/ap times 359, or $359 \times 0.76/0.53 \times 0.57 = 895$. Following the procedure of Example 5F, a trial value of p_8 is now taken, $q = 0.19$ is added to give a trial i_8, and a trial A_8 is estimated as $895a/is$. Two or three attempts give $p_8 = 0.52$ as the figure which brings A_8p_8 closest to 681; s_8 can now be calculated as 0.492, the population at the start of age VIII is $895/0.492 = 1819$, and the whole procedure is ready to be repeated for age VII. Table 5.5 shows the complete computation.

5G. ESTIMATION OF PERCENTAGE OF THE YOUNGER AGE-GROUPS PRESENT ON THE FISHING GROUNDS

Comparisons of rates of fishing calculated by the methods of Examples 5F and 5G might be used to decide to what extent the reduced vulnerability of the various younger age-groups is due to their reaction to the fishing gear, and to what extent it results from their absence from the fishing grounds. If the two estimates of p agree at a given age during the recruitment period, it indicates that the fish are present on the grounds but are less vulnerable to the gear than the fully-recruited stock. If the estimate of p from tagging is greater than that from age composition, it indicates that the age-group in question was not yet completely present on the fishing grounds at the time tagging was done. The limiting situation, where all of the reduced vulnerability of recruitment years is due to absence from the fishing grounds, would be indicated by p-values from tagging which are the same for recruitment ages as for fully-vulnerable ages. For such comparisons it would of course be necessary to be sure that there was no extra tagging mortality among the younger fish.

In the actual example of Tables 5.4 and 5.5, since the p-values from tag recoveries tend to be even somewhat *less* than those from age composition for ages VI to VIII, it would be concluded that a lesser susceptibility to capture by longlining, rather than absence from the fishing grounds, accounts for the incomplete recruitment of those ages. Really young halibut are of course likely to be at least partly absent from grounds frequented by old fish, and the age V comparison is in that direction.

CHAPTER 6.—ESTIMATION OF SURVIVAL AND RATE OF FISHING FROM THE RELATION OF FISHING SUCCESS TO CATCH OR EFFORT

6A. GENERAL PRINCIPLES OF FISHING-SUCCESS METHODS

The methods of this Chapter are applicable when a population is fished until enough fish are removed to reduce significantly the catch per unit effort, the latter being considered proportional to stock present. For example, if removal of 10 tons of fish reduces C/f by a quarter, then the original stock is estimated as 10/0.25 or 40 tons. Instead of estimating C/f only at the start and finish of the experiment, usually a series of estimates is made; that is, a number of points are used to determine the rate of decrease of C/f and hence of the stock. The reason is of course that variables such as the weather, which affect vulnerability, tend to make single estimates of C/f unreliable for this purpose.

Obviously an important condition for application of these methods is that the vulnerability of the population should not exhibit significant seasonal trends within the time of the experiment. Equally important is the condition that the whole of the population shall be available to capture; or if it is not, adjustment for the differing vulnerabilities of different sections of the stock must somehow be applied (see Section 1G). Finally, there should be no significant excess of recruitment over natural mortality (or the reverse) during the experiment, except where these processes can be quantitatively evaluated.

The actual procedures and corresponding computations can be reduced to two main types. The first, introduced by Leslie and Davis (1939)[1], involves plotting the catch per unit effort against cumulative catch over a period of time; from the resulting straight line the initial population and the catchability can be estimated. In the second method, first described by DeLury in 1947[2], the logarithm of catch per unit effort is plotted against cumulative effort, and the fitted straight line yields the same statistics. Both methods came into common use in fishery investigations only after Dr. DeLury's exposition became available in 1947; see also Mottley (1949) and DeLury (1951).

The concepts and symbols employed are as follows:

N_0 original population size

N_t population surviving at the start of time interval t

C_t catch taken during time interval t

---

[1] The Leslie method was developed independently by DeLury (1947) and had also been under consideration by Mottley (1949). A method reminiscent of Leslie's was proposed by Shibata in 1941, but it was not as efficient, at least as it is described by Kawasaki and Hatanaka (1951). The latter plot on the ordinate arithmetic values of cumulative catch/cumulative effort, against cumulative effort on the abscissa.

[2] G. F. M. Smith (1940) was using a very similar procedure when he fitted an exponential curve to a graph of percentage recovery of marked starfish against cumulative fishing effort.

K_t	cumulative catch, to the start of time t
C	total catch (ΣC_t)
c	catchability—the fraction of the population taken by 1 unit of fishing effort (k of DeLury)
b	$1 - c$; the complement of catchability
f_t	fishing effort during time t
E_t	cumulative fishing effort, up to the start of time t
f	total fishing effort for the whole period of the experiment (E of DeLury)
C_t/f_t	catch per unit effort during time t (C_t of DeLury)

6B. POPULATION ESTIMATES FROM THE RELATION OF FISHING SUCCESS TO CATCH ALREADY TAKEN—METHOD OF LESLIE[3]

(a) GENERAL CASE. By definition, the catch per unit of effort during time t is approximately[4] equal to the catchability multiplied by the population present at the beginning of that time:

$$\frac{C_t}{f_t} = cN_t \tag{6.1}$$

The population at the start of time t is equal to the original population less the catch to date:

$$N_t = N_0 - K_t \tag{6.2}$$

From (6.1) and (6.2):

$$\frac{C_t}{f_t} = cN_0 - cK_t \tag{6.3}$$

Equation (6.3) indicates that catch per unit effort during time t, plotted against cumulative catch up to the start of time t, should give a straight line whose slope is the catchability, c. Also, the X-axis intercept is an estimate of the original population, N_0, since it represents the cumulative catch if C_t/f_t, and hence the population also, were to be reduced to zero by fishing. The Y axis intercept is the product of the original population, N_0, and the catchability, c.

(b) SPECIAL CASE. A special case of the Leslie method occurs when equal units of effort are used to make the successive catches, so the latter can be plotted directly against cumulative catch:

$$C_t = cN_0 - cK_t \tag{6.4}$$

This situation has been studied by Hayne (1949), Moran (1951) and Zippin (1956).

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[3] Leslie and Davis had also to deal with a complication not considered here, namely, that their unit of effort, a break-back trap, could catch only one rat at a time. For any given number of traps in use, this means that C/f increases less rapidly than population, because at higher densities encounters of rats with sprung traps are relatively more frequent than at lower densities.

[4] The approximation is very close if cf_t is never a very large fraction (more than 0.05 say). If cf_t were to vary so that a large fraction of the stock was taken in one or more of the time intervals, the decrease in catch per unit effort *within* that interval would interfere with the strict applicability of (6.1). For the special situation where successive values of f_t are equal, Bruce Taft has pointed out to me that the slope of (6.3) is equal to ca/i; the correction factor a/i being the actual mortality rate divided by the instantaneous rate, for the interval in which f_t units of effort operate. Similarly the intercept of (6.3) is then equal to N_0ca/i.

If the line (6.4) is fitted by least squares, Zippin shows that the statistical weighting for catches should be:

$$\frac{1}{\hat{N}_0 - K_t} \tag{6.5}$$

where $\hat{N}_0$ is a preliminary estimate obtained by eye.

A comparable weighting formula for the general situation (6.3) would be:

$$\frac{f_t}{\hat{N}_0 - K_t} \tag{6.6}$$

However, factors other than size of sample and number of marked fish at large usually play a big part in determining the scatter of the points about the regression line—for example, day to day variation in vulnerability of the fish. Hence it may often be more accurate, and it is always less trouble, to fit a line without weighting. The same considerations apply to Moran's (1951) maximum likelihood estimate of N_0, for which Zippin (1956, pp. 168-169) prepared charts to simplify the calculation when the number of successive catches is from 3 to 7.

EXAMPLE 6A. SMALLMOUTH BASS POPULATION OF LITTLE SILVER LAKE ESTIMATED BY THE LESLIE METHOD USING A LEAST-SQUARES LINE. (From Omand, 1951.)

Little Silver Lake in Lanark County, Ontario, is of 100-125 acres extent. It was trapped intensively for 10 days in September, 1949, and Leslie estimates of the fish populations were made. Since the same number of traps (7) were used on all 10 days of fishing, they can be considered collectively as a single unit of effort, so that the daily catch is also the catch per unit of effort—thus avoiding division of each catch by 7. The data for smallmouth bass (*Micropterus dolomieui*) are conveniently arranged as in Table 6.1, where the order of the columns keeps squares and products beside or between the primary data. The entries in Table 6.1 are given to one or two more figures than are really necessary: with a calculator it is customary to "play it safe".

Representing the K_t values by X and C_t values by Y, and representing the same quantities *measured from their means* by x and y, the formulae for the squares, products and primary regression statistics are as below, using the symbols of Snedecor (1946, Sections 6.5-6.9; n = number of observations):

$$\left.\begin{aligned} \Sigma xy &= \Sigma(\mathrm{XY}) - (\Sigma \mathrm{X})(\Sigma \mathrm{Y})/\mathrm{n} \\ \Sigma y^2 &= \Sigma(\mathrm{Y}^2) - (\Sigma \mathrm{Y})^2/\mathrm{n} \\ \Sigma x^2 &= \Sigma(\mathrm{X}^2) - (\Sigma \mathrm{X})^2/\mathrm{n} \end{aligned}\right\} \tag{6.7}$$

$$\text{slope} = \hat{b} = \frac{\Sigma xy}{\Sigma x^2} \tag{6.8}$$

$$\text{intercept} = \hat{a} = \frac{\Sigma \mathrm{Y} - \hat{b}\Sigma \mathrm{X}}{\mathrm{n}} \tag{6.9}$$

The numerical statistics are as follows:

$$\Sigma x^2 = 1{,}846{,}194 - 3770^2/10 = 424{,}904$$

$$\Sigma y^2 = 57{,}062 - 710^2/10 = 6652$$

$$\Sigma xy = 223{,}519 - 3770 \times 710/10 = -44{,}151$$

$$\text{slope} = \hat{b} = -44151/424904 = -0.103908$$

$$\text{intercept} = \hat{a} = \frac{710 - (-0.103908 \times 3770)}{10} = 110.173$$

TABLE 6.1. Computation of the regression line used in the estimation of the bass population of Little Silver Lake, Lanark Co., Ontario. (From Omand, 1951.) C_t/f_t = catch per unit effort; K_t = cumulative catch.

1 Catch no.	2 K_t^2	3 K_t	4 K_tC_t/f_t	5 C_t/f_t	6 $(C_t/f_t)^2$
	X^2	X	XY	Y	Y^2
1	0	0	0	131	17161
2	17161	131	9039	69	4761
3	40000	200	19800	99	9801
4	89401	299	23322	78	6084
5	142129	377	21112	56	3136
6	187489	433	32908	76	5776
7	259081	509	24941	49	2401
8	311364	558	23436	42	1764
9	360000	600	37800	63	3969
10	439569	663	31161	47	2209
Total	1846194	3770	223519	710	57062
Mean	....	377	....	71	....

These quantities determine the equation:

$$C_t/f_t = 110.173 - 0.103908K_t$$

Comparing with (6.3), we then write:

$$\text{catchability} = \hat{c} = -\hat{b} = +0.103908$$

$$\hat{N}_0 = \hat{a}/\hat{c} = 110.173/0.103908 = 1060.3$$

With an initial estimated population of 1,060, the 7 traps removed an average of 10.4% of the surviving population each day, or about 1.48% per trap.

Estimation of the sampling errors of $\hat{c}$ and $\hat{N}_0$ involves the Σy^2 of (6.7), which is not required otherwise. Variance and standard deviation from the regression line are:

$$s_{yx}^2 = \frac{\Sigma y^2 - \hat{b}\Sigma(xy)}{n - 2} \tag{6.10}$$

$$= \frac{6652 - (-0.103908)(-44151)}{10 - 2}$$

$$= 258.045$$

$$s_{yx} = 16.064$$

The standard error of the regression coefficient, $\hat{b}$, hence of the catchability, $\hat{c}$, is:

$$s_{\hat{b}} = \frac{s_{yx}}{\sqrt{\Sigma(x^2)}} \tag{6.11}$$

$$= \frac{16.064}{\sqrt{424{,}904}}$$

$$= 0.02464$$

The sampling error of $\hat{N}_0$ is given by DeLury (1951, formulae 2.6, 2.7). Upper and lower limits of confidence for any given level of probability (P) are the roots of the equation:

$$N^2(b^2 - t_P^2 s^2 c_{22}) - 2N(-ba - t_P^2 s^2 c_{12}) + (a^2 - t_P^2 s^2 c_{11}) = 0 \qquad (6.12)$$

Where:

$$c_{11} = \Sigma X^2 / n \Sigma x^2$$

$$c_{12} = \Sigma X / n \Sigma x^2$$

$$c_{22} = 1 / \Sigma x^2$$

t_P is the t value corresponding to a given probability P for $n - 2$ degrees of freedom, found from a t-table such as Snedecor's table 3.8

b, a, s and n are as above ($-b = \hat{k}$ of DeLury; $a = \widehat{kN}$ of DeLury)

For our example, adopting the probability level P = 0.05, t_P is 2.306 for 8 degrees of freedom; also:

$$c_{11} = 1846194/10 \times 424904 = 0.434497$$

$$c_{12} = 3770/10 \times 424904 = 0.000887259$$

$$c_{22} = 1/424904 = 0.00000235347$$

The roots of (6.12) are:

$$N = \frac{20.460 \pm \sqrt{418.603 - 349.372}}{0.015135}$$

$$= 802 \text{ and } 1901$$

These limits of confidence are of course quite asymmetrical with respect to the best estimate 1060 (see also examples BII(a) and (c)—p. 304 of DeLury, 1951).

6C. Population Estimates from the Relation of Fishing Success to Cumulative Fishing Effort—Method of DeLury

Equation (6.1) can be written in the form:

$$\frac{C_t}{f_t} = cN_0\left(\frac{N_t}{N_0}\right) \qquad (6.14)$$

or,

$$\log_e(C_t/f_t) = \log_e(cN_0) + \log_e(N_t/N_0) \qquad (6.15)$$

1. When the fraction of the stock taken by a unit of effort is small—say $c = 0.02$ or less—it can be used as an exponential index to show the fraction of the stock remaining after E_t units have been expended:

$$\frac{N_t}{N_0} = e^{-cE_t} \qquad (6.16)$$

Substituting (6.16) in (6.15):

$$\log_e(C_t/f_t) = \log_e(cN_0) - cE_t \qquad (6.17)$$

Changing to base-10 logarithms:

$$\log_{10}(C_t/f_t) = \log_{10}(cN_0) - 0.4343cE_t \qquad (6.18)$$

Thus a plot of the logarithm of catch per unit effort during time t, against cumulative effort up to the start of time t, yields a line whose slope is $0.4343c$, and whose Y-axis intercept is $\log_{10}(c\mathrm{N}_0)$. From these two both c and N_0 can readily be estimated.

2. When effort is measured in larger units, so that each unit takes some appreciable fraction of the stock, c cannot be used in the exponential formula (6.16). In that event the slope of the regression line of $\log(\mathrm{C}_t/f_t)$ against E_t can be antilogged to give the fractional survival of the stock, b, after the action of one unit of effort. Since f units of effort are used altogether, the estimate of survival to the end of the experiment is b^f, and the fraction of the stock removed is $1 - b^f$. This can be divided into the total removals, C, to give an estimate of initial population:

$$\hat{\mathrm{N}}_0 = \frac{\mathrm{C}}{1 - b^f} \tag{6.19}$$

Expression (6.19) is applicable with *all* values of b and c, but if c is really small the procedure given under 1. above is more convenient.

EXAMPLE 6B. ESTIMATING WHITEFISH IN SHAKESPEARE ISLAND LAKE BY THE DELURY METHOD. (From Ricker, 1949a.)

For 7 successive weeks a small lake on an island in Lake Nipigon, Ontario, was fished by gill nets in an identical manner—the same sizes of nets, positions and lengths of sets were repeated each week (Hart, 1932). Thus each week's catch is the catch of one unit of effort and its logarithm can be used in the left side of (6.18). For whitefish (*Coregonus clupeaformis*) of 13-14 inches fork length, the catches and their logarithms were as follows:

Week..........	1	2	3	4	5	6	7	Total
Catch.........	25	26	15	13	12	13	5	109
Logarithm.....	1.40	1.42	1.18	1.11	1.08	1.11	0.70	....

Plotting these figures against cumulative effort (0, 1, 2, etc., weeks of fishing), and fitting a straight line by least squares (unweighted) gives a slope of -0.1007 with standard error of 0.0211.

The antilogarithm of this slope is $b = 0.793$, so that each week an appreciable fraction of the stock was removed: 20.7%. After 7 weeks of fishing, net survival is estimated as:

$$0.793^7 = 0.197$$

In all 109 fish were caught; so, from (6.19), the initial population is estimated as:

$$\hat{\mathrm{N}}_0 = \frac{109}{1 - 0.197} = 136 \text{ fish}$$

Estimates for other length-classes of the Shakespeare Island whitefish were also obtained (Ricker, 1949a). There was probably some recruitment of smaller fish into the size-groups above, but it would be almost balanced by the number of fish which grew out of it into the next larger group.

6D. Systematic Errors in Fishing-success Methods

Inconstant catchability is perhaps the greatest potential source of error in applying methods of estimation based upon secular change in catch per unit of effort. Many populations have been found not to be amenable to this treatment, either because catchability varies with seasonal changes in environmental conditions or the fish's reactions, or because individual fish differ in vulnerability and those more vulnerable are more quickly removed. Either effect may produce changes in catch per unit effort which cannot be distinguished from those produced by changed abundance.

Less serious, but of widespread occurrence, is day-to-day or other short-term variation in catchability. Usually this merely increases the scatter of points along the line of graphs such as those in Figure 6.2, below. Occasionally it may be possible to relate it to other measurable factors and make appropriate adjustments. For example, in a sport fishery catchability may decrease on holidays when total effort is high, because of interference between fishermen or temporary fishing-out of the more accessible pools. On the other hand, effort may become greater whenever, and because, success is good. To adjust for the latter effect Mottley (1949) in one example used the square root of the catch, divided by effort, as the variable in the left-hand side of expression (6.3); however an adjustment of the fishing effort to some standard base would be more consistent with the theory of the method.

Obviously recruitment and natural mortality, or immigration and emigration, can introduce serious error into Leslie or DeLury calculations, unless opposed tendencies happen to be in balance. It is, of course, unlikely that the incidence of either recruitment or mortality would exactly coincide in time with the application of fishing effort, hence we should usually expect them to make lines such as those of Fgure 6.2 curved or irregular in shape. Experience shows, however, that points used to determine such lines seldom lie close to them, so that it is usually impossible to detect recruitment or natural mortality by any curvature which they may introduce. Evidently it is advantageous to concentrate the fishing effort into a rather short period of time, so that these disturbing effects will be minimized.

6E. Use of Fishing-success Methods with Marked Populations

Usually there is sufficient likelihood of significant departure from the conditions required for fishing-success estimates, that it is essential to check them. DeLury (1951) points out that such a check is provided by a concurrent analysis of a group of *marked* fish similar in other respects to the population being estimated. The estimated population of marked fish is then compared with the actual number marked. Quite a variety of causes may produce a discrepancy between the actual and the estimated number. Among these are:

1) Change in catchability, c, during the experiment, either (a) among the population as a whole because of seasonal change in habits or habitat; or (b) because of selective removal of the temperamentally more

vulnerable individuals; or (c) because catchability is itself a function of stock density, and decreases as the stock is thinned out.

2) Natural mortality during the experiment.
3) Mortality caused by the fishing gear during the experiment (e.g., fish held in a net may be removed by predators).
4) Mortality caused by the marking procedure or the tag or mark itself.
5) Emigration of fish from the population in the area of study.

All these causes tend to produce a deviation in the same direction—toward too small an estimate of population and too large an estimate of catchability—except that 1(a) *may* operate in the reverse manner. Thus unless there is reason to suspect a progressive increase in vulnerability, agreement of estimated and actual numbers of fish marked can be taken as fairly convincing evidence that errors (1b)-(5) above are inconsequential. On the other hand, if the estimated figure is too low, there are a number of possible reasons for it. However, usually one or more may be eliminated as very improbable, and quite often a single one stands out as the only likely cause of the observed discrepancy. In that event the difference between calculated and observed population provides a means of obtaining a numerical estimate of the effect in question.

Computations applicable to situations of this sort were developed by Ketchen (1953) for a population in which both immigration and emigration were possible. For a simple treatment it is necessary to postulate that immigration and emigration occur at constant instantaneous rates, proportional to the number of fish present in the fishing area. Let p, y and z be the instantaneous rates of fishing, emigration and immigration respectively, based upon the whole fishing season as a unit of time. (Note that immigration *adds to* the population and is given the opposite sign to p and y.) Based upon a unit of fishing effort, these instantaneous rates become p/f, y/f and z/f; p/f is the catchability, c, of the fish, while the other two are analogous quantities not easy to name.

Referring to Figure 6.1, the marked population, originally M in number, is affected by emigration and fishing, hence the slope of the line BC[5] is equal to:

$$p/f + y/f = (p+y)/f$$

from which $p + y$ can be calculated. The estimate of the apparent original number, M_a, is the X-axis intercept, OC. Had there been no emigration, C/f for the marked population would have decreased along line BD, having slope p/f, and the intercept OD would have been an unbiased estimate of the number marked, M. We note that:

$$\frac{p/f}{(p+y)/f} = \frac{\text{slope of BD}}{\text{slope of BC}} = \frac{\text{OB/OD}}{\text{OB/OC}} = \frac{\text{OC}}{\text{OD}} = \frac{M_a}{M} \qquad (6.21)$$

Hence p can be estimated from:

$$p = \frac{M_a}{M}(p+y) \qquad (6.22)$$

---

[5] Ketchen uses symbols for the slopes of the two observed regressions, as follows: for untagged fish (line AE), slope $=k=$ our $(p+y-z)/f$; for tagged fish (line BC), slope $=k'=$ our $(p+y)/f$; while k is used for catchability (our p/f).

The untagged population can now be treated in a similar manner. It is affected by fishing, emigration and immigration, so that the slope of the line AE is equal to:

$$p/f + y/f - z/f \tag{6.23}$$

from which z can be calculated since f is known and p and y were found above. If there had been no immigration or emigration, fishing success should have decreased along line AF, which is parallel to BD. The estimated apparent initial population, N_a (= OE), is to the true initial population, N(= OF), as the slope of AF is to the slope of AE, or as p/f is to $(p+y-z)/f$; hence an estimate of N is:

$$\hat{N} = N_a(p+y-z)/p \tag{6.24}$$

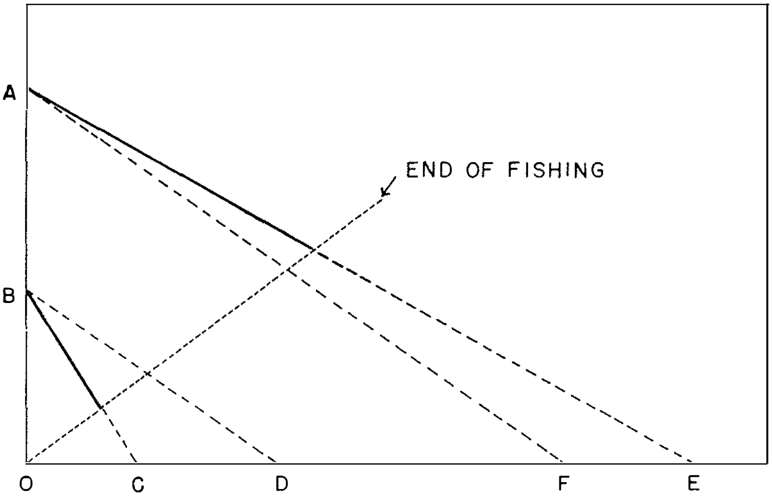

FIGURE 6.1. Diagram showing relationship between Leslie estimates of the whole population (above) and the marked population (below). (Modified from Ketchen, 1953.)

Using $\overline{N}$ for the actual average population, we may write, as in expression (1.11) and (1.12) of Chapter 1:

$$p\overline{N} = C = \text{catch} \tag{6.25}$$

$$y\overline{N} = \text{number of emigrants} \tag{6.26}$$

$$z\overline{N} = \text{number of immigrants} \tag{6.27}$$

From (6.25), $\overline{N}$ can be evaluated, and the number of emigrants and immigrants is then obtained from (6.26) and (6.27).

EXAMPLE 6C. RATE OF FISHING, IMMIGRATION AND EMIGRATION IN A MIGRATORY POPULATION OF LEMON SOLES. (Fom Ketchen, 1953.)

Ketchen worked with a population of lemon soles (*Parophrys vetulus*) which was in process of migration, so that individuals were entering and leaving the fishing area during the course of the fishery. Described in a somewhat simplified form, the experiment consisted of marking 2190 fish (= M) immediately prior to April 29, near the beginning of the fishery. Daily record was kept of fishing effort, number of fish caught, and number of tags caught. The plots of catch per unit effort against cumulative catch are shown in Figure 6.2, and least-square lines give the statistics below:

Slope of BC $= (p+y)/f = 0.000695$
$\hat{M}_a = 958$ pieces
Slope of AE $= (p+y-z)/f = 0.000246$
$\hat{N}_a = 5.83$ million lb.

We know also:

$f = 2{,}285$ boat-hours
$M = 2{,}190$ pieces
$C = 2.54$ million lb.

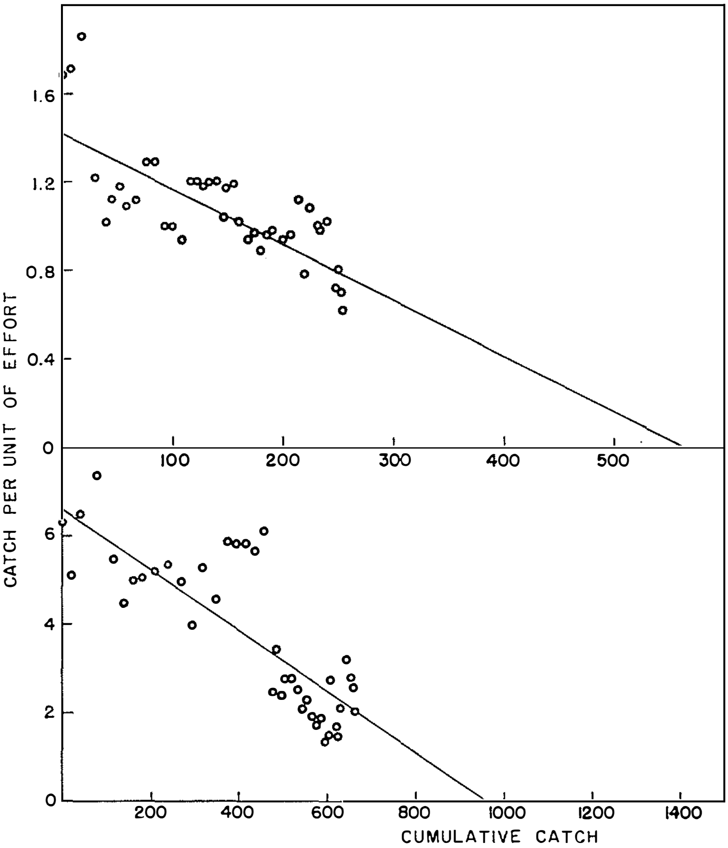

FIGURE 6.2. Leslie graphs of catches of unmarked lemon soles (in millions of pounds, above) and of tagged soles (in pieces, below) in Hecate Strait, B.C. (After Ketchen, 1953.)

The first entry above gives:

$p + y = 0.000695 \times 2285 = 1.588$

By (6.22), $p = 958 \times 1.588/2190 = 0.695$

Hence, $y = 1.588 - 0.695 = 0.893$

From (6.23), $p + y - z = 2285 \times 0.000246 = 0.562$

and $z = 1.588 - 0.562 = 1.026$

From (6.24), $\hat{N} = 5.83 \times 0.562/0.695 = 4.72$ million lb.

From (6.25), $\bar{N} = 2.54/0.695 = 3.65$ million lb.

From (6.26), quantity of emigrants $= 0.893 \times 3.65 = 3.26$ million lb.

From (6.27), quantity of immigrants $= 1.026 \times 3.65 = 3.74$ million lb.

The total quantity of fish involved during the experimental period is the initial number plus the immigrants, or $4.72 + 3.74 = 8.46$ million lb.

Dr. Ketchen's original account should be consulted for estimates of the total stock for the season, and for some of the consequences of possible variation in rate of immigration or emigration. In Example 3E an estimate of N was obtained from tag recaptures, as 4.4 million lb.; this is an independent estimate of the same quantity as the 4.72 million lb. obtained above.

6F. FISHING-SUCCESS METHODS WHEN MORE THAN ONE KIND OF FISHING EFFORT IS USED, OR WHEN THERE ARE DATA FOR ONLY A PART OF THE EFFORT

It often happens that catch/effort statistics are available for only a part of the fishing effort used on a population, or two different kinds of effort may be used which cannot be summed directly. The general formula for handling such data is given by DeLury (1951), and it was applied to this situation by Dickie (1955). Suppose:

f_t, f'_t, f''_t, etc. — the quantities of different kinds of effort applied each day (or other short interval)

c, c', c'', etc. — catchabilities of the stock by the above kinds of effort

Then for any selected kind of effort, f, the catch per unit effort, C_t/f_t, declines as:

$$C_t/f_t = cN_0 - \left(c + \frac{c'f'_t}{f_t} + \frac{c''f''_t}{f_t} + \ldots\right)K_t \qquad (6.28)$$

$$= cN_0 - \bar{c}K_t \qquad (6.29)$$

where $\bar{c}$ is the slope of the Leslie graph ($=\hat{k}$ of Dickie).

In general, we will be most interested in one particular type of gear, or will have catch per effort data concerning only one: let it be f, and let all others be f'. From the definition of $\bar{c}$ in (6.28) and (6.29) we have:

$$c = \frac{\bar{c}}{1 + \dfrac{c'f'_t}{cf_t}} \qquad (6.30)$$

Further, since $C_t/f_t = cN_t$, then $cf_t = C_t/N_t$; and similarly, $c'/f'_t = C'_t/N_t$. Hence the denominator term $c'f'_t/cf_t$ is equal simply to C'_t/C_t, the ratio of the catches taken by the two kinds of effort in successive fishing intervals. It follows that (6.30) becomes:

$$c = \frac{\bar{c}}{1 + C'_t/C_t}$$

If the ratio C'_t/C_t remains reasonably constant throughout the fishing season, it is also true that:

$$c = \frac{\bar{c}}{1 + C'/C} \tag{6.31}$$

Thus from the total catch of the two kinds of gear, plus the slope of the Leslie graph, the true catchability, c, can be obtained.

The condition that the two kinds of gear operate in at least approximately proportional quantities throughout the season can be checked by examining the seasonal distribution of the catch of each. In addition, if there is any serious deviation from this requirement, the Leslie line will not be straight, especially if C' is large relative to C.

If there is natural mortality in the population during the time of the experiment, it too will contribute to the value of c. An adjustment is possible if this can be estimated independently. Still following Dickie, let the instantaneous rate of natural mortality for the duration of the experiment be q; so that, in terms of a unit of effective fishing effort, it is q/f. Then:

$$c = \frac{\bar{c} - q/f}{1 + C'/C} \tag{6.32}$$

EXAMPLE 6D. ABUNDANCE AND MORTALITY OF BAY OF FUNDY SCALLOPS (*Placopecten magellanicus*) BY THE LESLIE METHOD, USING CATCH AND EFFORT DATA FOR PART OF THE FLEET. (From Dickie, 1955.)

To reduce the variability in catch per effort data, Dickie used the catch and fishing statistics of a part of the scallop dragger fleet which kept good records, and of these used only the part pertaining to calm days when dragging could be done with something approaching a standard or maximum efficiency. Of his eleven years' data (Dickie's figure 6 and tables III and IV), we select for illustration those for 1944-45.

Catch of sampled fleet	C	= 130,447 lb.
Catch of remainder of fleet	C'	= 563,783 lb.
Fishing effort of sampled fleet	f	= 320 boat-days
Slope of Leslie graph	$\bar{c}$	= 0.001399
Y-axis intercept (initial fishing success)	cN_0	= 589.6 lb. per boat-day
Instantaneous rate of natural mortality for the season	q	= 0.06
Instantaneous natural mortality per unit of sampled fishing effort	q/f	= 0.0001875

From (6.32):

$$c = \frac{0.001399 - 0.0001875}{1 + 563783/130447}$$

$$= 0.0002276$$

The initial population is estimated as:

$$\hat{N}_0 = \frac{589.6}{0.0002276} = 2{,}591{,}000 \text{ lb.}$$

CHAPTER 7.—ESTIMATION OF SURVIVAL AND RATE OF FISHING FROM CATCH AND EFFECTIVE FISHING EFFORT IN SUCCESSIVE YEARS

7A. Direct Comparison of Catch and Fishing Effort

If fishing effort is sufficiently great to remove at least a moderately large fraction of the stock in a year, and if it varies considerably between years, accompanying changes in mortality and survival of the stock can provide a basis for estimating rate of fishing.

In almost any situation a first step will be to plot catch, C, against effective effort, *f*, for successive years, and see what indication there is of regression or correlation between the two. Catch can increase with increasing effort only so long as there are reserves of stock to draw from. Hence if a fairly large significant correlation is found between C and *f*, it suggests that rate of exploitation has not been really severe—has been less than say 70-75% over most or all of the range of efforts represented.

If a correlation is indicated, favourable circumstances may permit an estimate of the rate of fishing from the curvature of the line relating catch to effort (Ricker, 1940). This method is applicable primarily to Type IA fisheries—those in which the combined action of recruitment and natural mortality has a negligible effect on the stock while fishing is in progress, so that the whole population change is due to fishing (Section 1E). It can be used in two somewhat different situations:

A. There is available catch, C, and effort, *f*, for the whole fishing season of at least two years; and also an index of relative initial abundance of the stock, N, in the same years, such as might sometimes be available from a measurement of C/*f* made early in each fishing season, for example.

B. There is available catch, C, and effort, *f*, for a moderately long series of years during which there have been no trends in abundance having a duration comparable to the length of the available series.

In either situation the effort data available are assumed to measure *effective* effort: that is, the instantaneous rate of fishing mortality, *p*, is taken as proportional to fishing effort, *f*.

Since all mortality is from fishing, catch is equal to population times the seasonal fishing mortality rate ($C = Nu$). In any two years, not necessarily consecutive, we have:

$$\frac{u_2}{u_1} = \frac{C_2/N_2}{C_1/N_1} = \frac{C_2N_1}{C_1N_2} \tag{7.1}$$

Since p varies as f, and $p = -\log_e(1-u)$ in the absence of natural mortality:

$$\frac{\log(1-u_2)}{\log(1-u_1)} = \frac{p_2}{p_1} = \frac{f_2}{f_1} \qquad (7.2)$$

In situation A, above, the ratio of N_1 to N_2 is known, as is C_1, C_2, f_1 and f_2; thus the right hand sides of (7.1) and (7.2) are both known, and the two equations can be solved simultaneously for u_1 and u_2, by trial. A graph from which a two-place solution can usually be obtained is given in Figure 7.1.

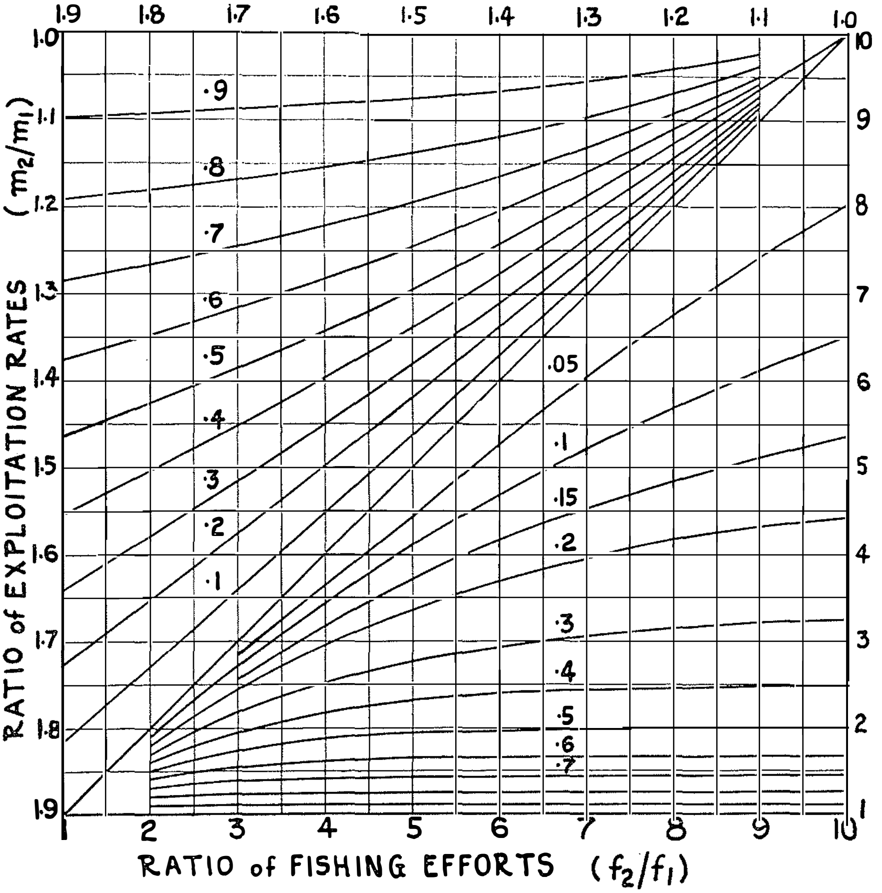

FIGURE 7.1. Relation between the ratio of fishing efforts (f_2/f_1) and the ratio of rates of exploitation (m_2/m_1), for Type I populations (in which $m = u$). The curved lines indicate even values of m_1, the rate of exploitation in the year having the smaller effort. (From Ricker, 1940, figure 3).

In situation B, the best procedure is to fit a line to a graph of catch against effort. The fact that the line must pass through the origin serves as a guide to the amount of curvature to be expected (Fig. 7.2, below). Using the adjusted catches, C′, corresponding to the maximum and minimum efforts, f, in the series, values are obtained appropriate to equations (7.1) and (7.2):

$$\frac{u_2}{u_1} = \frac{C'_2}{C'_1}; \text{ and } \frac{f_2}{f_1}$$

The equations can then be solved by trial, or by using Figure 7.1.

If it were desired to fit the relationship between C and f using a straight line, note that we are postulating a steady *average* level of stock, $\bar{N}$, for which:

$$C' = u\bar{N}$$

From the relations $1 - u = e^{-p}$, and $p = cf$, this can be developed to:

$$-\log_e\left(\frac{\bar{N} - C'}{\bar{N}}\right) = cf$$

Thus, using a trial value of $\bar{N}$, and observed C for C′, a straight line through the origin can be fitted, and successive fittings would provide the "best" $\bar{N}$. This procedure would give trouble, however, if any observed C happened to exceed $\bar{N}$.

EXAMPLE 7A. RATE OF EXPLOITATION USING FIGURE 7.1. (From Ricker, 1940, p. 56.)

Figure 7.2 shows catches and efforts modelled after data for a chinook salmon (*Oncorhynchus tshawytscha*) troll fishery, described to the writer by Dr. A. L. Tester. Catch tends to increase with gear, but not proportionally:

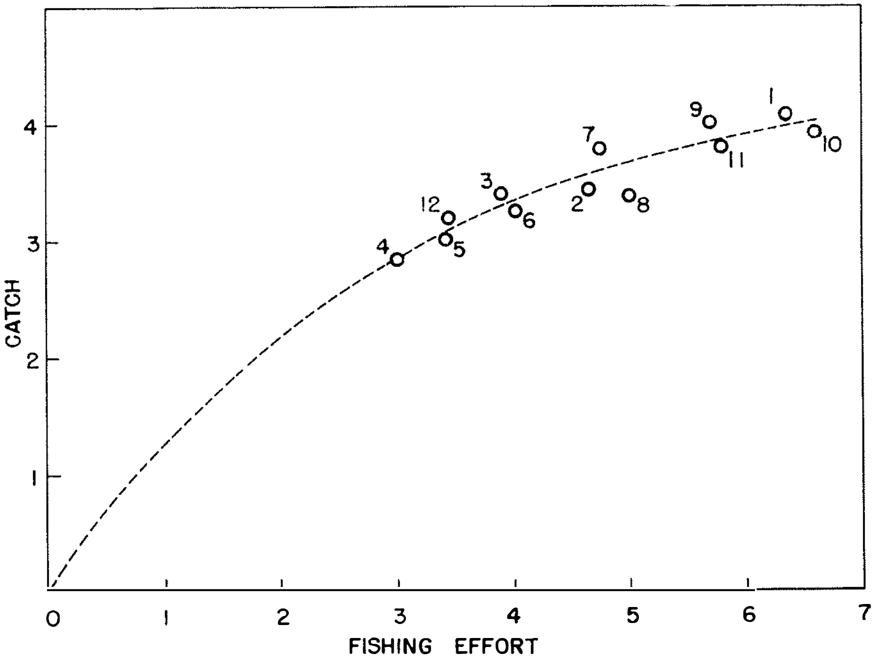

FIGURE 7.2. Graph of catch against fishing effort for the salmon fishery of Example 7A.

that is, catch per unit effort is less at the greater efforts. Comparison of years in which effort was approximately the same provides no indication of progressive change in C/f with time; hence the stock too cannot have had any sustained trend in abundance, though there is evidently year-to-year variation. A line was fitted freehand to the points on Figure 7.2 and the mean catches for the maximum and minimum effort were read as 4000 and 2830 fish, respectively. Their ratio is 1.41, as compared with an effort ratio of 660 to 300, or 2.20. From Figure 7.1 a preliminary value of $u_1 = 0.6$ can be read, and this can be improved to 0.63 by successive approximations in expressions (7.1) and (7.2). The other u-values are then calculated from (7.2), as shown in column 4 of Table 7.1.

TABLE 7.1 Effort and catch in a troll fishery, and computed rates of exploitation and initial populations (Example 7A).

Year	Effort	Catch	Exploitation	Population
	lines	*pieces*	u	*pieces*
1	636	4080	0.88	4600
2	465	3430	0.79	4300
3	390	3390	0.72	4700
4	300	2830	0.63	4500
5	342	3000	0.68	4400
6	402	3240	0.74	4400
7	474	3780	0.79	4800
8	501	3370	0.81	4200
9	570	4000	0.85	4700
10	660	3919	0.89	4400
11	579	3780	0.85	4400
12	345	3190	0.68	4700

7B. RATE OF EXPLOITATION ESTIMATED BY EQUALIZATION OF FISHING EFFORT—METHOD OF SETTE

Still considering Type IA fisheries (Section 1E), when a breakdown of catch and fishing by days or weeks is available, it is possible to total up, for each of two or more years, the catches which are taken during the time some standard amount of effort was used (O. E. Sette, in Ricker, 1940, p. 53). The most efficient amount to use is that which was actually expended in the year of least fishing. Assuming this constant effort is proportional to rate of fishing while it operates, the rates of fishing *for the indicated periods of time* must be the same. In the absence of natural mortality, equal rates of fishing mean equal rates of exploitation; and since $C = uN$, the catches of those periods are proportional to the initial populations. This gives the ratio $N_1:N_2$ needed in (7.1), and the actual population size can be obtained as in Section 7A.

EXAMPLE 7B. RATE OF FISHING AND SIZE OF STOCK COMPUTED BY SETTE'S METHOD

In three years overall statistics of a fishery attacking a circumscribed population (recruitment being absent during the fishing season) were as follows:

Year	Effort	Catch *(tons)*	Reduced catch
1923	2268	248	186
1924	1549	200	200
1925	1684	283	265

The column "reduced catch" is the catch taken up to the time that 1549 units of effort were expended in each year, some minor interpolation being made within a statistical catch period in order to obtain a catch corresponding to exactly 1549 effort units. The initial populations in the three years were in the ratio of the reduced catches, 186:200:265.

Applying (7.1) to the first two years above, with 1923 = year 2 because it had the greater fishing effort:

$$\frac{u_2}{u_1} = \frac{248}{200} \times \frac{200}{186} = 1.333$$

$$\frac{f_2}{f_1} = \frac{2268}{1549} = 1.464$$

Entering the upper half of Figure 7.1 with 1.464 on the abscissa and 1.333 on the ordinate, the value $m_1 = u_1 = 0.36$ is obtained; from which $p_1 = 0.446$ (Appendix II), $p_2 = 1.464 \times 0.446 = 0.653$, and $u_2 = 0.48$. Also the 1924 original population is estimated as $200/0.36 = 560$ tons, and that for 1923 as $248/0.48 = 520$ tons.

The years 1924 and 1925 differ so little in effort that a similar calculation is not likely to be useful; however 1925 can be compared with 1923. Better, all three years could be included in one analysis, as described for "situation B" in Section 7A.

7C. RATE OF FISHING AND NATURAL MORTALITY FROM COMPARISON OF SURVIVAL RATES AT TWO LEVELS OF FISHING EFFORT—METHOD OF SILLIMAN

A method proposed by Silliman (1943) is applicable to fisheries of either Type I or Type II—that is, natural mortality and recruitment may occur either during or outside of the fishing season. What is needed is that in the history of the fishery there shall have been two different levels of fairly uniform fishing effort, each persisting for long enough to give a reliable estimate of the prevailing survival rate, s. The assumptions required are that the instantaneous rate of natural mortality, q, be the same under both regimes; and, as usual, that rate of fishing, p, be proportional to the available physical measure of fishing effort, f.

The computations can be simplified (Ricker, 1945c) by using instantaneous rates, as follows:

$$p_1 + q = i_1 = -\log_e s_1 \tag{7.3}$$

$$p_2 + q = i_2 = -\log_e s_2 \tag{7.4}$$

$$p_1/p_2 = f_1/f_2 \tag{7.5}$$

The right-hand sides are known, so the equations can be solved directly for p_1, p_2 and q.

In Silliman's use of this method, fishing effort had been stabilized for long enough at each of two levels that the survival rate for each could be read from a catch curve. However the method can be applied also when there are only two adjacent years at each stable level of effort. In that event, unless recruitment is extremely even, it will usually be necessary to compare catches *of the same year-class* or group of year-classes in the two consecutive years, using only fully-recruited ages. This can be represented by the expression:

$$s = \frac{(C_b + C_c + \ldots . + C_j)_2}{(C_a + C_b + \ldots . + C_i)_1} \tag{7.6}$$

The subscripts a, b, etc., refer to age, while 1 and 2 refer to the two successive years compared.

Conceivably, more than two pairs (or short sequences) of years might be available for estimates of survival rate—each pair being characterized by constant effort. In that event the estimates of survival (s_1, s_2, s_3, etc.) and the levels of effort (f_1, f_2, f_3, etc.) can be combined to give a single best estimate of natural mortality rate, q, by using a regression line of i against f. A simple example is worked out by Widrig (1954b, p. 143). The same procedure is used in the Beverton-Holt method of Section 7D, but there the estimation of survival has to be less direct.

EXAMPLE 7C. RATE OF FISHING AND NATURAL MORTALITY RATE FOR CALIFORNIA SARDINES (*Sardina caerulea*), FROM COMPARISON OF TWO LEVELS OF FISHING EFFORT AND THE CORRESPONDING SURVIVAL RATES. (From Silliman, 1943.)

Survival rates were calculated from catch curves for two periods of the sardine fishery, as follows:

Period	Relative fishing effort	Survival rate	Instantaneous mortality rate ($= -\log_e s$)
1925-33	$f_1 = 1$	$s_1 = 0.60$	$i_1 = 0.511$
1937-42	$f_2 = 4$	$s_2 = 0.20$	$i_2 = 1.609$

The equations (7.3)-(7.5) are:

$$p_1 + q = 0.511$$

$$p_2 + q = 1.609$$

$$p_1/p_2 = 1/4$$

Solving these, $p_1 = 0.366$, $p_2 = 1.464$; and $q = 0.145$.

More recent work suggests that these preliminary results gave figures which are too low for the natural mortality and too high for the fishing mortality (Clark and Marr, 1956). There are various possible reasons for the discrepancy, among them (1) a temporary progressive increase in recruitment among the year-classes from which the 1937-42 survival rate was estimated, making s_2 too low; and (2) the possibility that the unit of gear used became more efficient over the time compared—perhaps because of better cooperation in locating the pilchard schools.

7D. RATE OF FISHING AND NATURAL MORTALITY FROM CATCH AND EFFORT STATISTICS, WHEN EFFORT VARIES CONTINUOUSLY—METHOD OF BEVERTON AND HOLT, 1956 (see also Beverton, 1954)

This method can be regarded as a combination of the methods of Silliman (Section 7C) and Ricker (Section 5D), generalized for the situation where fishing effort varies over a series of years. Survival rate is assumed identical for all ages considered, in any given year.

The basic information required is the catch per unit effort of fully-recruited year-classes in successive years. This can be written as:

$$\frac{(C_b + C_c + \ldots\ldots + C_j)_2/f_2}{(C_a + C_b + \ldots\ldots + C_i)_1/f_1} \tag{7.7}$$

where subscripts a, b, etc., refer to age, while 1 and 2 refer to successive years of the fishery as before. This fraction will be represented briefly by the symbol $(C/f)_2 \div (C/f)_1$; it is the ratio of the average populations *of these year-classes* in the two years. (The expression $(C_2/f_2) \div (C_1/f_1)$ would represent the ratio of availabilities based on all fully-recruited year-classes present each year; in some situations this would be a sufficiently good estimate of (7.7), and would be easier to obtain.)

Expression (7.7) would be an estimate of survival rate, s, if fishing effort were the same in the two years; but since effort changes, it is not any simple function of survival either in year 1 or in year 2. Since the average population of any fully-recruited age group in a season is equal to the initial population multiplied by a/i (expression 1.10), we can write:

$$\frac{(C/f)_2}{(C/f)_1} = \frac{\overline{N}_2}{\overline{N}_1} = \frac{N_2 a_2/i_2}{N_1 a_1/i_1}$$

$$s_1 = \frac{N_2}{N_1} = \frac{(C/f)_2}{(C/f)_1} \cdot \frac{a_1 i_2}{i_1 a_2} \tag{7.8}$$

The "correction term" $a_1 i_2/i_1 a_2$ is the same as appeared in the exactly comparable situations involving tag recaptures (expressions 5.7, 5.20). Taking logarithms:

$$\log_e s_1 = \log_e[(C/f)_2/(C/f)_1] + \log_e(a_1 i_2/i_1 a_2) \tag{7.9}$$

Since $-\log_e s_1 = i_1 = p_1 + q$, and $p_1 = cf_1$, this becomes, with some transposition:

$$-\log_e[(C/f)_2/(C/f)_1] - \log_e(a_1 i_2/i_1 a_2) = q + cf_1 \tag{7.10}$$

This is a linear equation in f_1, whose slope is the catchability, c, and whose Y-intercept is the instantaneous rate of natural mortality, q.

Because of the correction term, the line (7.10) must be fitted by successive trials. The log correction term is taken as zero for the first operation, or in other words $-\log_e[(C/f)_2/(C/f)_1]$ is taken as a first estimate of instantaneous mortality rate in year 1. These log values are plotted against f_1 for the series of years available, and a line is fitted by least squares. The slope of this line is a first estimate of c, and its Y-axis intercept is a first estimate of q. From these a value of i for each year is estimated from $i = q + cf$, from which are computed trial values for the log correction terms and hence improved values for the left hand side of (7.10). When the latter are plotted against f, a new line is fitted, and from the improved values of q and c a still better graph can be plotted. The third fitting is likely to be the last one which will be at all rewarding, but this can be gauged from the relative amount of change in c and q from fit 2 to fit 3, as compared with fit 1 to fit 2[1].

EXAMPLE 7D. SURVIVAL AND RATE OF FISHING FOR OPEONGO TROUT OF AGES IX-XI, FROM CATCH AND EFFORT DATA. (Adapted from Beverton, 1954, p. 119.)

Fry's (1949) account of the Opeongo lake trout (*Cristivomer namaycush*) provides some of the best data available to illustrate this method, and for our purpose it has the advantage that comparison can be made with treatments of the same data in other examples. Beverton's treatment is based on survival from age IX to age X; here, to illustrate the use of (7.7), we will use a combination of IX-X and X-XI. However since age XI fish are much less numerous than X, the result is mainly determined by the IX-X figures. The ratio (7.7), shown in row 8 of Table 7.2, is a first estimate of the survival rate in the years indicated; its natural logarithm (with sign changed) in row 9 is an estimate of instantaneous mortality rate. The latter is plotted against effort and a straight line fitted (Fig. 7.3). Its slope gives a first estimate of catchability as $c_1 = 0.000475$ and its Y-axis intercept estimates natural mortality as $q_1 = 0.454$. A series of rates of fishing in each year is estimated from c_1f (row 10), 0.454 is added to give i'_1 (row 11) and a'/i' is found from Appendix II (row 12). The correction term is then computed in row 13, being the ratio of the row 12 entries of successive years (year $t \div$ year $t+1$). The natural logarithm of this is taken in row 14, and it is added to row 9 in row 15, giving a second series of i values to be plotted against and fitted to the effort data. From this fitting, $c_2 = 0.000570$ and $q_2 = 0.350$. A new series of correction terms is calculated in rows 16-20, row 20 is added to row 9 to give the i_3 values of row 21, and from the regression of i_3 on f the third pair of estimates is $c_3 = 0.000592$ and $q_3 = 0.324$. A fourth iteration would change these very little. The final estimates of rates of fishing (p_3) are calculated as 0.000592 times effort (row 22); and these plus 0.324 give the i'_3 values of row 23.

Note that the estimates of catchability and natural mortality, c and q, are average values for the whole series of years. For total mortality, i, two kinds

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[1] Expressions describing the further complication of a rate of fishing which varies with size of the fish have been developed by Beverton and Holt (1956, p. 72); their utilization of course depends on having some objective measure of the relative magnitude of p at successive sizes.

Table 7.2. Computation of instantaneous mortality rate and rate of fishing by successive approximation for Opeongo trout of ages IX-XI.

1		1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947
2	Effort	2240	1630	1380	1170	1130	570	710	920	1400	1740	1230
	C/f at age:											
3	IX	24.8	11.9	15.9	10.3	9.2	9.3	18.5	23.9	25.5	12.4	12.4
4	X	7.9	5.5	6.4	3.9	2.0	5.1	5.9	11.1	10.9	5.4	6.2
5	XI	1.7	0.2	3.3	1.2	0.1	1.2	0.0	5.3	5.8	2.8	1.5
6	IX + X	32.7	17.4	22.3	14.2	11.2	14.4	24.4	35.0	36.4	17.8	....
7	X + XI	....	5.7	9.7	5.1	2.1	6.3	5.9	16.4	16.7	8.2	7.7
8	s_1	0.174	0.557	0.229	0.148	0.562	0.410	0.672	0.477	0.225	0.433	....
9	i_1	1.75	0.59	1.47	1.91	0.58	0.89	0.40	0.74	1.49	0.84	....
10	p_1	1.06	0.77	0.66	0.56	0.54	0.27	0.34	0.44	0.66	0.83	0.58
11	i'_1	1.51	1.22	1.11	1.01	0.99	0.72	0.79	0.89	1.11	1.28	1.03
12	a'_1/i'_1	0.516	0.578	0.604	0.630	0.635	0.713	0.691	0.662	0.604	0.564	0.624
13	$a'_t i'_{t+1}/i'_t a'_{t+1}$	0.893	0.957	0.959	0.992	0.891	1.032	1.044	1.096	1.071	0.904	....
14	$-\log_e[13]$	+0.11	+0.04	+0.04	+0.01	+0.12	−0.03	−0.04	−0.09	−0.07	+0.10	....
15	i_2	1.86	0.63	1.51	1.92	0.70	0.86	0.36	0.65	1.42	0.94	....
16	p_2	1.28	0.93	0.79	0.67	0.64	0.33	0.40	0.52	0.80	0.99	0.70
17	i'_2	1.63	1.28	1.14	1.02	0.99	0.68	0.75	0.87	1.15	1.34	1.05
18	a'_2/i'_2	0.493	0.564	0.597	0.627	0.635	0.726	0.704	0.668	0.594	0.551	0.619
19	$a'_t i'_{t+1}/i'_t a'_{t+1}$	0.874	0.945	0.952	0.987	0.875	1.031	1.054	1.125	1.078	0.890	....
20	$-\log_e[19]$	+0.13	+0.06	+0.05	+0.01	+0.13	−0.03	−0.05	−0.12	−0.08	+0.12	....
21	i_3	1.88	0.65	1.52	1.92	0.71	0.86	0.35	0.62	1.41	0.96	....
22	p_3	1.33	0.97	0.82	0.69	0.67	0.34	0.42	0.54	0.83	1.03	0.73
23	i_3	1.65	1.29	1.14	1.01	0.99	0.66	0.74	0.86	1.15	1.35	1.05

of estimate are available; those of rows 9, 15 and 21 are based more directly on observation, whereas those of rows 11, 17 and 23 depend more upon computation. Which of these is to be preferred depends upon the biological situation. If catchability is really the same from year to year, then estimate 23 is the preferable one, because it directly reflects each year's fishing effort; in that situation natural mortality rate must be variable (assuming errors of observation are negligible). If, on the other hand, catchability varies a lot between years and q is relatively unchanging, so that c as estimated is the mean of a fluctuating quantity, then row 21 is more likely to have the preferred estimates of actual mortality in successive years.

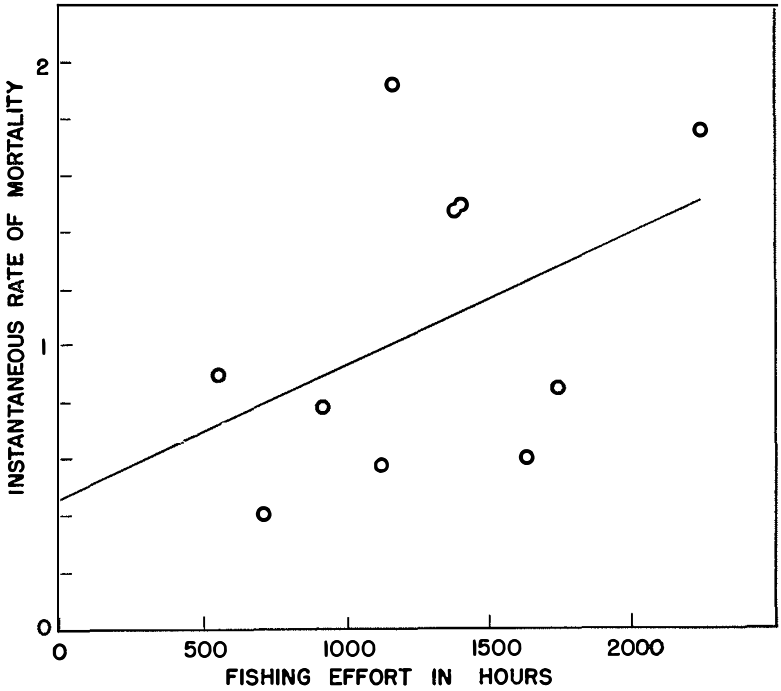

FIGURE 7.3. Fit of the first estimate of instantaneous mortality rate ($-\log_e s_1$) in Example 7D, to fishing effort. The Y-axis intercept is a first estimate of instantaneous rate of natural mortality, q_1, which is used to compute an improved survival estimate.

Standard errors for c (a linear regression coefficient) and for q (a Y-axis intercept) can be computed by standard procedures (cf. Snedecor, 1946, Sect. 6.9). The relative sampling error of q, of course, tends to be much greater than that of c, so that in general the catchability and fishing mortality rate are estimated with much greater precision than is the natural mortaliy rate. In this example the standard error of the catchability is 0.000330, compared with $c = 0.000592$. The standard error of the instantaneous natural mortality rate is 0.453, as compared with $q = 0.324$. Neither statistic is conventionally "significant", but the natural mortality estimate is much worse than the other.

TABLE 7.3. Comparison of estimates of population statistics, for fishing effort of 980 hours.

Example	Method	*c*	*p*	*q*	*i*
2G	Catch curve				
	age IX..........	....	....	..	0.85
8B	Virtual population				
	age IX..........	0.00056–0.00064	0.55–0.63	..	..
7D	Catch and effort				
	age IX..........	0.00058	0.57	0.25	0.82
	age IX+X......	0.00059	0.58	0.32	0.90

In conclusion, the results of this example can be compared with other methods (Table 7.3). From the catch curves (Example 2G) it was estimated that i was 0.85 when f averaged 980 hours. From the present example, for the same effort we can estimate $i = 0.32 + (980 \times 0.000592) = 0.90$, which is close to the same magnitude. Fry's method (Example 8B) yielded limits of catchability of 0.00056-0.00064 at age IX and 0.00037-0.00053 at age X. Example 7D gives $c = 0.000592$ for ages IX and X, and $c = 0.000583$ was obtained for age IX alone by Beverton (1954). The allround agreement is remarkably good.

Estimates of natural mortality are the least satisfactory ones by all methods. By the Beverton and Holt method the example above gave 0.32 ± 0.45 for ages IX-X; Beverton himself obtained 0.25 for age IX alone, with similar standard error. Although no limits of error can be assigned to it, I am inclined to favour the difference between the i of Example 2G and the p of the present example as the best available estimate of instantaneous natural mortality rate between ages IX and XI, viz. $0.85 - 0.58 = 0.27$.

CHAPTER 8.—ESTIMATION OF STOCK AND MORTALITY FROM STATISTICS OF THE CATCH AND ITS QUALITATIVE COMPOSITION

8A. Virtual Population and Maximum Rate of Exploitation When Age Composition is Steady—Method of Derzhavin

If fishing is the major cause of mortality, much information about the dynamics of a population can be obtained by making yearly age censuses of the catch and dividing the fish among their appropriate year-classes. The sum of the catch from a particular year-class, over all the years during which it contributes to the fishery, is a minimum estimate of its abundance at the time it was just entering the catchable size range. Similarly, partial sums will give the minimum number of fish in existence, of each year-class, in any given calendar year. The total of these sums in a particular year represents the minimum number of catchable fish present in that year, or what Fry has called the "virtual population". Thus it is possible, in retrospect, to make a minimum estimate of the number of fish present at a given date, as the sum of all fish of the appropriate ages which are actually caught in the future. Fish which die from natural causes are not included in this total.

The point of departure in developing this method was a paper by Tereshchenko (1917) concerning the Volga bream (*Abramis brama*), in which Baranov's assistance is acknowledged. The assumptions used there include: (1) representative sampling of the bream stock during the autumn-to-spring fishery; (2) complete recruitment of all bream of age II and older (i.e., those which had completed 3 growing seasons); (3) the same rate of exploitation for all ages; (4) negligible natural mortality at all ages greater than I; (5) constant recruitment at age II, from year to year. Under these conditions it is easy to see that the catch in a year must equal the number of age II recruits; consequently the total commercial stock is equal to the catch divided by the ratio of age II individuals to the total sample. In Tereshchenko's example, catch was taken as 20 million pieces, of which 66% were age II. Hence the total stock was calculated as 20/0.66 = 30 million pieces. (See also Baranov, 1918, p. 100, for this computation.)

Derzhavin (1922) freed this procedure of some of the very restricting conditions above and in effect developed a new approach. He did this (1) by using an age composition based on age and length data calculated over a period of years, so that possible short-term variability in year-class strength was smoothed out; (2) by using catch data for a long period of years and calculating the absolute abundance by ages for each year separately; and (3) by using a separate rate of exploitation for each age-class, calculated from the mean age composition. He perforce retained the assumption of no long-term trends in percentage age composition, while pointing out that this was not strictly in accord with the observed fact of moderate trends in the catch. Again fish dying from natural mortality were not considered, but natural deaths are of course likely to have been relatively fewer, among his potentially long-lived sturgeon, than among Tereshchenko's short-lived bream.

The total population considered by Derzhavin comprised all fish in the population at the start of a calendar year, including those of the previous year's hatch, since for these ". . . . . the large 'infant' mortality among the newly-hatched young no longer plays a role, and the surviving fry have grown . . . . . enough that they can become the prey of large fishes only." Let us designate fish as "age I" from January 1 of their first year of life, etc., and define:

x_1, x_2, etc. the fractional representation of each age, t, in the catch ($x_0 = 0$)

r the greatest age involved

Ignoring fish which die naturally from age I onward, the total stock at the start of a year will consist of: that year's catch, plus the next year's catch diminished by the number of age I fish in it (because these were not yet hatched at the beginning of the base year), plus the next year's catch not including the age I and age II fish, and so on.

Using average age composition for estimating the fraction of I's, II's, etc., the expression for population at the start of age I becomes (cf. Derzhavin, p. 15):

$$\begin{aligned} \mathrm{N} &= \mathrm{C}_1 + \mathrm{C}_2(1-x_1) + \mathrm{C}_3(1-x_1-x_2) \\ &\quad + \ldots + \mathrm{C}_r(1-x_1-x_2-\ldots\ldots -x_{r-1}) \\ &= \sum_{t=1}^{t=r} \mathrm{C}_t(1-x_1-x_2- \ldots\ldots -x_{t-1}) \qquad (8.1) \end{aligned}$$

If the fish do not appear in the fishery until after some years have elapsed—for example, at age V—then x_1, x_2, x_3 and x_4 are equal to zero, and the whole of the first four years' catch is included in the total stock. However, if only the stock *of commercial age* were needed, the first four terms of (8.1) would then be omitted from the total.

EXAMPLE 8A. VIRTUAL POPULATION OF KURA STURGEON. (From Derzhavin, 1922.)

From data on length composition and age determinations made in 1912-19, described in Example 2I, Derzhavin (p. 229) constructed a table of the probable absolute age structure of the sevriuga (*Acipenser stellatus*) catches taken in the Kura River for 1881 to 1915. The year-classes 1854-1906 were represented, at ages from IX to XXVII. Too extensive to be reproduced here, the columns of this table, when totalled vertically, provide estimates of the complete contribution, to the catch, of the year-classes 1872 through 1888; and also substantial portions of several adjacent broods.

Derzhavin, however, was most interested in estimating the total stock present in the sea in successive years. The percentage age composition was summed cumulatively from the oldest back to the youngest, a few very rare age groups being ignored at either end (Table 8.1, column 3). These sums comprise the terms $(1-x_1)$, $(1-x_1-x_2)$, etc., of expression (8.1). Each of them is then multiplied by the catch of the corresponding year. As an example, the stock for 1881 is computed in Table 8.1, column 5. The total is 9,383,000 sturgeon, 5,024,000 being age IX and older. The 1881 catch of 427,000 is 8.5% of the latter, which is an estimate of an upper limit for the overall rate of exploitation. The rate of exploitation of fully-vulnerable fish is of course greater than this: it can be computed for individual ages using Derzhavin's complete table. For example, 22,200 age XX fish were taken in 1881, and 50,400 of this year-class were captured in later years. The (maximum) rate of exploitation of age XX

TABLE 8.1. Computation of the 1881 stock of Kura River stellate sturgeon, after Derzhavin (1922). Catches are in thousands.

Age	Mean age composition of the catch	Cumulative age composition	Catches 1881–1907	Contribution to population at the beginning of 1881
1	0	1.000	427(1881)	427
2	0	1.000	405	405
3	0	1.000	437	437
4	0	1.000	539	539
5	0	1.000	591	591
6	0	1.000	589	589
7	0	1.000	720	720
8	0	1.000	651	651
9	0.006	1.000	699	699
10	0.027	0.994	738	734
11	0.061	0.967	814	787
12	0.107	0.906	694	629
13	0.118	0.799	544	435
14	0.110	0.681	540	368
15	0.093	0.571	451	258
16	0.080	0.478	573	274
17	0.076	0.398	702	279
18	0.090	0.322	621	200
19	0.076	0.232	564	131
20	0.052	0.156	583	91
21	0.042	0.104	745	77
22	0.030	0.062	548	34
23	0.018	0.032	517	17
24	0.007	0.014	503	7
25	0.004	0.007	490	3
26	0.002	0.003	403	1
27	0.001	0.001	292(1907)	0
Total				9383

fish in 1881 was therefore 22,200/(22,200 + 50,400) = 31%. In Section 8B it is shown that, under the equilibrium conditions which Derzhavin postulated, this 31% is really an estimate of the *total* annual mortality rate.

Outside of the USSR, Derzhavin's method was apparently first used by Bajkov (1933) in an application to the whitefish of Lake Winnipegosis, but that population was far from having a steady age composition (see Example 2F).

8B. VIRTUAL POPULATION AND MAXIMUM RATE OF EXPLOITATION WHEN AGE COMPOSITION VARIES—METHOD OF FRY

Considerable refinements of the Derzhavin method were made by Fry (1949), who apparently developed the procedure independently. For the Lake Opeongo stock of lake trout, continued sampling provided estimates of age compositions of the catch for each year individually, which were used to total up a more accurate series of virtual populations, V_t. Furthermore, Fry presented a much more extensive analysis and interpretation of the results obtained.

Apart from the minimum estimate of population size, the statistic which comes most readily from an analysis of this sort is a maximum estimate of rate of exploitation, $u(\text{max})$, which can be calculated for the whole stock or for individual ages separately. The latter is equal to the catch of a given age in a given year divided by the virtual population of that age in that year:

$$u(\text{max})_t = \frac{C_t}{V_t} \qquad (8.2)$$

From this a maximum estimate of rate of fishing is estimated as

$$p(\text{max})_t = -\log_e[1-u(\text{max})_t] \qquad (8.3)$$

A maximum estimate of catchability at age t (Fry's "maximum force of fishing mortality") is:

$$c(\text{max})_t = \frac{p(\text{max})_t}{f_t} \qquad (8.4)$$

Models can be used to compare the magnitude of $u(\text{max})$ with true u and with other population statistics. Three such are shown in Tables 8.2-8.4. From these and other models the conclusions below were obtained. These apply only to situations where neither p nor q vary with time (though they may be different at different ages):

1. The value of $u(\text{max})$ for the oldest age represented will always be unity, by definition, hence it will be larger than actual u. The next younger age will also have a considerable bias from the same source.

2. When neither the natural nor the fishing mortality rates vary with age, $u(\text{max})$ exceeds the true rate of exploitation, u, by a constant factor, apart from sampling fluctuation. The ratio $u(\text{max}):u$ equals $i:p$ or $a:u$; or in other words $u(\text{max})$ is equal to the true total annual mortality rate, a (Table 8.2, ages 8-13).

3. When natural mortality, q, increases with age, and rate of fishing is constant, $u(\text{max})$ tends to increase with age whereas true u decreases with age

TABLE 8.2. Comparison of virtual rate of removal and true rate of exploitation (*u*(max) and *u*) in a population in which rate of fishing (*p*) increases from age 3 to age 8 and remains constant thereafter; while the instantaneous rate of natural mortality, *q*, remains constant throughout. (The population, column 7, is rounded to the nearest integer, but fractions were retained in calculating it back from 1 fish surviving at age 16).

Age	*p*	*q*	*i*	*a*	*s*	Population	Total deaths	Catch	Virtual population	*u*(max)	*u*
						4210			1723		
3	.005	.2	.205	.185	.815		780	19		.011	.0045
						3430			1704		
4	.03	.2	.23	.206	.794		707	93		.055	.027
						2720			1611		
5	.1	.2	.3	.259	.741		706	235		.146	.086
						2020			1376		
6	.3	.2	.5	.394	.606		794	478		.35	.236
						1223			898		
7	.5	.2	.7	.503	.497		615	440		.49	.359
						608			458		
8	.6	.2	.8	.551	.449		335	252		.55	.413
						273			206		
9	.6	.2	.8	.551	.449		151	113		.55	.413
						123			93		
10	.6	.2	.8	.551	.449		68	51		.55	.413
						55			42		
11	.6	.2	.8	.551	.449		30	23		.55	.413
						25			19		
12	.6	.2	.8	.551	.449		14	10		.53	.413
						11			9		
13	.6	.2	.8	.551	.449		6	5		.56	.413
						5			4		
14	.6	.2	.8	.551	.449		3	2		.50	.413
						2			2		
15	.6	.2	.8	.551	.449		1	1		.50	.413
						1			1		
16	.6	.2	.8	.551	.449		1	1		1.00	.413
						0			0		

TABLE 8.3. Comparison of virtual rate of removal and true rate of exploitation (*u*(max) and *u*) in a population in which rate of fishing decreases after age 7. (The population is calculated back from 20 fish at age 18, in order to reduce error in rounding to nearest integers.)

Age	*p*	*q*	*i*	*a*	*s*	Population	Total deaths	Catch	Virtual population	*u*(max)	*u*
5	.6	.2	.8	.551	.449	42100	23200	17360	31360	.55	.413
6	.6	.2	.8	.551	.449	18860	10400	7800	14000	.56	.413
7	.6	.2	.8	.551	.449	8470	4670	3500	6200	.56	.413
8	.55	.2	.75	.528	.472	3810	2010	1473	2700	.54	.387
9	.50	.2	.70	.503	.497	1796	905	645	1227	.53	.359
10	.45	.2	.65	.478	.522	894	427	296	582	.51	.331
11	.40	.2	.60	.451	.549	467	210	141	286	.49	.301
12	.35	.2	.55	.423	.577	257	108	69	145	.48	.269
13	.30	.2	.50	.394	.606	148	58	35	76	.46	.236
14	.25	.2	.45	.362	.638	90	32	18	41	.44	.201
15	.20	.2	.40	.330	.670	57	19	9	23	.39	.165
16	.15	.2	.35	.295	.705	38	11	5	14	.36	.126
17	.10	.2	.30	.259	.741	27	7	2	9	.22	.086
18+	.10	.2	.30	.259	.741	20	13	7	7	....	....

TABLE 8.4. Comparison of virtual rate of removal and true rate of exploitation (u(max) and u) in a population in which natural mortality rate increases after age 7. (The population is calculated back from 10 fish at age 16, to reduce error in rounding off).

Age	p	q	i	a	s	Population	Total deaths	Catch	Virtual population	u(max)	u
						68380			31623		
3............	.03	.2	.23	.206	.794		14090	1838		.06	.027
						54290			29785		
4............	.1	.2	.3	.259	.741		14058	4686		.16	.086
						40232			25099		
5............	.3	.2	.5	.394	.606		15852	9511		.38	.236
						24380			15588		
6............	.4	.2	.6	.451	.549		10995	7330		.47	.301
						13385			8258		
7............	.4	.2	.6	.451	.549		6037	4025		.49	.301
						7348			4233		
8............	.4	.25	.65	.478	.522		3512	2162		.51	.294
						3836			2071		
9............	.4	.3	.7	.503	.497		1930	1103		.53	.287
						1906			968		
10............	.4	.35	.75	.528	.472		1006	537		.55	.282
						900			431		
11............	.4	.4	.8	.551	.449		496	248		.58	.276
						404			183		
12............	.4	.45	.85	.573	.427		232	109		.59	.270
						172			74		
13............	.4	.5	.9	.593	.407		102	45		.61	.264
						70			29		
14............	.4	.55	.95	.613	.387		43	18		.62	.258
						27			11		
15............	.4	.6	1.0	632	.368		17	7		.64	.253
						10			4		
16+..........	.4	.65	1.05	.650	.350		10	4			

(Table 8.4). The net result is an increasing discrepancy between *u*(max) and *u* so that the former can become 2 or 3 times the latter. However *u*(max) is close to *a* in such circumstances, being slightly greater than *a*.

4. Within the age-groups in which recruitment occurs, i.e., when *p* is increasing with age, *u*(max) exceeds true *u* by a much greater fraction of the latter than during a series of years when *p* does not vary with age. However, during such years *u*(max) is less than *a* (Table 8.2, ages 3-7).

5. If *u* decreases with age after reaching some maximum, and *q* is constant, *u*(max) decreases with age, but not as rapidly as *u*; hence *u*(max) considerably exceeds the total mortality rate, *a*, over the years concerned (Table 8.3, ages 8-17).

6. If the age sample which is taken from the catch (and which is applied proportionately to the whole catch to represent the age composition of the latter) is biased so that older fish tend to appear more frequently than their true abundance warrants, *u*(max) is somewhat less than it would otherwise be, but is not very seriously changed. However, if older fish appear disproportionately only in occasional years, important bias is introduced (Example 8B).

Space does not permit an evaluation of the effects of secular trends in *p* or *q* upon virtual population statistics, similar to what was done for catch curves in Chapter 2, but these effects should be examined in any experiment where they might be significant[1].

EXAMPLE 8B. VIRTUAL POPULATIONS AND MAXIMUM RATE OF EXPLOITATION OF OPEONGO TROUT. (From Fry, 1949.)

The estimated age composition of the catch of Opeongo trout for 1936-47 was tabulated in Table 2.6 of Example 2G. The minimum number of survivors of each brood at each age is obtained by summing the table diagonally from upper left to lower right, the result being shown in Table 8.5. (The italicized figures in the lower right corner are the average of the previous entries, since catches for years later than 1947 would be needed to supply actual data.)

For the year-classes 1934-37 the contributions of all ages to the fishery are available; these comprise the virtual population at age III, for those broods. (Fry points out that the average contribution of a year-class is less than one fish per 10 acres of water—indicating the sparseness of this population.)

The total virtual population of all ages is found by summing the entries of Table 8.5 diagonally from lower left to upper right; which procedure gives a result corresponding to the summing of column 5 of Table 8.1 above, in Derzhavin's method. Thus, at the start of the 1936 fishing season there were *at least* 10,129 fish of age III and older in the lake; there were at least 8640 in 1937, 7210 in 1938, 6959 in 1939, and 6599 in 1940.

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[1] In a paper published too late to be discussed here, Paloheimo (1958) has related virtual populations to fishing effort, using a procedure analogous to the iterative technique of Section 7D. This gives values of *p* and *q* which are somewhat superior to those obtained from either this Section or Section 7D separately. See also a forthcoming paper by Bishop (1959) for various aspects of the virtual population method.

TABLE 8.5. Virtual populations of Opeongo trout, arranged by age and brood. (Adapted from Fry, 1949.)

Year-class	Age III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	Total virtual population	Year
1919															11	10129	(1936)
1920														15	0	8640	(1937)
1921													10	0	0	7210	(1938)
1922												29	4	4	4	6959	(1939)
1923											34	15	7	4	0	6599	(1940)
1924										69	12	4	4	0	0		
1925									140	22	18	15	0	0	0		
1926								326	66	28	19	6	0	0	0		
1927							685	207	31	28	4	4	4	4	4		
1928						1396	731	176	86	39	33	22	20	20	16		
1929					1861	1387	362	167	77	63	52	50	50	41	4		
1930				1665	1432	782	343	120	74	63	54	48	26	10	3		
1931			1371	1243	1045	625	232	112	90	82	58	49	6	6	(3)		
1932		1294	1199	1165	890	569	205	101	73	73	42	21	14	(8)	(3)		
1933	1223	1193	1189	1062	841	407	207	154	112	68	31	20	(11)	(8)	(3)		
1934	1129	1122	1059	939	715	480	359	226	133	49	23	(20)	(11)	(8)	(3)		
1935	1277	1265	1229	1147	872	655	444	246	87	40	(28)	(20)	(11)	(8)	(3)		
1936	1388	1349	1265	1121	1004	732	530	157	64	(46)	(28)	(20)	(11)	(8)	(3)		
1937	1194	1174	1095	1049	928	731	379	162	(86)	(46)	(28)	(20)	(11)	(8)	(3)		

The maximum rate of exploitation at each age and in each year is now estimated as the ratio of catch to virtual population. As an example at random, 104 age IX trout were caught in 1941 out of at least 205 present; hence $u(\max) = 51\%$.

Average values of $u(\max)$ are plotted in Fry's figure 2. These suggest that, after the increase in vulnerability during the recruitment phase, there is a decrease in $u(\max)$ at the older ages, from 0.53 at age VIII to 0.26 at age XIII. According to Table 8.3 above, in an equilibrium fishery this would reflect an even greater decrease in true rate of exploitation, u, with age. However, the apparent decrease should be at least partly discounted, for two reasons. For one thing, it depends very heavily upon an exceptionally large estimated catch of fish older than age XIII in one year, 1945, which in turn seems to be based upon only 7 actual specimens. If only the first four years of the fishery are considered (1936-39), the apparent maximum vulnerability is at age X rather than age VIII; the $u(\max)$ series obtained is as follows: VII, 0.37; VIII, 0.60; IX, 0.66; X, 0.68; XI, 0.52; XII, 0.55; XIII, 0.52; XIV, 0.60; XV, 0.61. The smaller decrease in $u(\max)$ beyond age X indicated by this series may well reflect a real decrease in rate of exploitation, though for a complete analysis the possible effects of the changes in p should be examined.

8C. ESTIMATE OF ACTUAL POPULATION FROM VIRTUAL POPULATION AND RECOVERY OF MARKED FISH—METHOD OF FRASER

Fraser (1955, p. 172) shows how the virtual population estimate can be converted to an estimate of actual population when it is combined with results of a marking experiment. The virtual population, V, at the start of a given year, is the part of the then number of recruited fish which will subsequently be caught in all future years. The total recoveries from M fish marked at the start of year 1, in successive years of their appearance in the fishery, is $R_1 + R_2 + R_3 + \ldots.$ Hence the actual population of fish vulnerable to fishing at the start of year 1 can be estimated as:

$$\hat{N} = \frac{V\ M}{R_1 + R_2 + R_3 + \ldots} \tag{8.5}$$

This estimate is analogous to a Petersen estimate (expression 3.5), but it has some advantages over the latter. One advantage is that it is free from the bias which can occur in Petersen estimates because of differences in vulnerability of different sizes of fish (Section 3G). In addition, the Fraser estimate is less affected by systematic error arising from aberrant behaviour or aberrant vulnerability of fish immediately after marking. If marking makes a fish relatively invulnerable for some weeks or months, the reduced recoveries during that season will largely be compensated by increased recaptures the following season (unless natural mortality is large). Equally, if marking increases vulnerability temporarily, the excess recaptures in the first year are mostly compensated by fewer recaptures later. For a similar reason, with Fraser's method it is not so important to do the marking exactly at the start of year 1: the period of marking may be extended some days or weeks into the fishing season of year 1 without much effect upon the estimate $\hat{N}$.

On the debit side, a population estimate from (8.5) involves the delay and (usually) the sampling error inherent in any computation of virtual population. It also implies the use of a tag or mark which will not become progressively lost or indistinguishable *over the whole vulnerable life-span* of the fish, rather than for one or two years only.

8D. Rates of Natural and Fishing Mortality, Given Constant recruitment and Natural Mortality and Two or More Levels of Stable Catch—Method of Tester

When the history of a fishery shows two or more periods of (different) stable catch, C, which have in common the same natural mortality rate, q, and the same absolute level of recruitment, R, Tester (1955) shows that an estimate of q and R can be made. The type of calculation depends on the relative timing of natural and fishing mortality, and recruitment. The most likely situations are:

1. Instantaneous recruitment (as when the stock fished is that which comes in to spawn), with natural mortality restricted to the fishing season (Type IB of Section 1E).

2. Instantaneous recruitment, with natural mortality restricted to the time of year that fishing is *not* done (Type IA).

3. Continuous recruitment, with natural and fishing mortality occurring throughout the year (Type IIA).

Considering Type IB first, by arguments similar to those which lead to expressions (1.8) and (1.13) of Chapter 1, Tester develops the expression:

$$\mathrm{C} = \mathrm{N}u = \frac{\mathrm{N}ap}{i} = \frac{\mathrm{R}p}{i} = \frac{\mathrm{R}(i - q)}{i}$$

Hence:

$$i = q + \frac{i\mathrm{C}}{\mathrm{R}} \qquad (8.6)$$

The survival, s, and hence i can be obtained from the catch curve for each stable period; if i is plotted against iC, the slope of the line obtained is the reciprocal of the recruitment (1/R), and the Y-axis intercept is the natural mortality rate, q. If only two stable periods are available, an explicit expression for R is:

$$\mathrm{R} = \frac{i_1\mathrm{C}_1 - i_2\mathrm{C}_2}{i_1 - i_2} \qquad (8.7)$$

and q is obtained by substitution in (8.6).

Gulland (1957) points out that expression (8.6) can be rearranged so that i appears on one side only. If, as he suggests, $1/i$ is plotted on the ordinate against C on the abscissa, the least-squares slope of the line is an estimate of $-1/q\mathrm{R}$ and the Y-axis intercept is an estimate of $1/q$ (rather than the reciprocals of these quantities as given by Gulland). The corresponding equation is:

$$\frac{1}{i} = \frac{1}{q} - \frac{\mathrm{C}}{q\mathrm{R}}$$

It is also possible, of course, to plot C against $1/i$, in which event the least-squares slope is an estimate of $-q\mathrm{R}$ and the intercept is an estimate of R:

$$\mathrm{C} = \mathrm{R} - \frac{q\mathrm{R}}{i}$$

Since it is not a question of using the relationship for prediction, the more difficult intermediate or "functional" relation between C and $1/i$ might give the best available estimate of R and q; or an average of the q and R estimates obtained from the two expressions above might be used. This does not, of course, imply that the use of (8.6) is "wrong", and in fact there may be some advantage in having i rather than $1/i$ as one of the variables. When there are only two observed levels of C and i, the two expressions above, as well as (8.6), all reduce to the estimate for R shown in (8.7).

For Type IIA fisheries, in which recruitment is continuous and is balanced by mortality, we have, from (1.12) and (1.10):

$$\mathrm{C} = p\mathrm{N} = \mathrm{N}ap/i = \mathrm{R}p/i$$

so that the expression (8.7) and procedure developed for Type IB are applicable.

For Type IA fisheries different expressions are needed. Of N fish present at the start of the year, $\mathrm{N}u$ are caught; also $u = m$, since no natural mortality occurs during the time of fishing. The recruitment, R, is however still equal to $\mathrm{N}a$: the initial population times the total annual mortality rate. Hence:

$$\mathrm{C} = \mathrm{N}u = \mathrm{N}m = \mathrm{R}m/a;\ \text{or}\ m = \mathrm{C}a/\mathrm{R}$$

Combining (1.5) and (1.3) with the above, and taking logarithms:

$$i = q - \log_e(1-\mathrm{C}a/\mathrm{R}) \tag{8.8}$$

In order to fit the best straight line to (8.8) it is necessary to use trial values of R, and continue fitting until minimum residual variance is obtained. If only two levels of C and i are available, (8.8) can be rearranged into an expression explicit for R:

$$\mathrm{R} = \frac{\mathrm{C}_1a_1e^{i_1-i_2} - \mathrm{C}_2a_2}{e^{i_1-i_2} - 1} \tag{8.9}$$

In applications of this method the principal point at issue will be whether or not the average level of recruitment can be considered constant over the times involved. Tester's account should be consulted for this, and also for his method of computing catch-curve mortality rates so they refer to catches for the appropriate series of years.

8E. RATE OF FISHING ESTIMATED FROM RELATIVE INITIAL ABUNDANCE IN THREE YEARS, COMBINED WITH A BREAKDOWN OF CATCH INTO SEPARATE AGE-GROUPS, WHEN FISHING EFFORT VARIES BETWEEN YEARS—METHOD OF AASEN

A method proposed by Aasen (1954) makes use of statistics of catch, of age composition in successive years, and of the relative initial abundance of successive year-classes (a minimum of three are required). The assumptions required are (1) that instantaneous natural mortality rate be the same in all years, for any given age; (2) that rate of fishing be the same for at least three fully-recruited age-groups in any given year; (3) that natural mortality take place at a time of year other than the fishing (i.e., a Type IA population is considered) and that the statistical year be arranged so that natural mortality precedes fishing mortality. For the method to work well, it is also necessary that rate of fishing vary considerably between years, otherwise the numerator and denominator of (8.10) both tend to be close to zero and hence very susceptible to sampling error.

In designating catches, we let arabic numerals refer to successive year-classes and roman numerals refer to ages, so that, for example, C(2,I) is the catch of year-class 2 at the first age used in the analysis. Let the ratio of the initial sizes of these year-classes be represented by T: e.g., T(2/1) is the initial abundance of year-class 2 divided by the initial abundance of year-class 1. "Initial" in this sense means the start of the year in which full vulnerability is achieved. Aasen develops the expression below for the number of fish, belonging to the first of three successive year-classes, which survive at the start of the second year in which they are fully vulnerable to fishing but before the natural mortality of that year begins to operate:

$$N(1,II) = \frac{C(1,II) \times C(3,I) \times [C(2,I) - C(1,I) \times T(2/1)]}{C(1,II) \times C(3,I) \times T(2/1) - C(2,II) \times C(2,I) \times T(3/2)} \qquad (8.10)^2$$

Having this figure for a given year, other fully-recruited ages in the catch of the same year can be obtained from their relative abundance in the catch. The right-hand side of (8.10) can be calculated from catch and age-composition of any three successive years.

For the development of (8.10) and for its application to the Lofoten cod fishery, reference must be made to Aasen's paper. The biggest trouble comes, of course, in estimating the values of T. Special early sampling for determining initial abundance might sometimes be possible, as suggested in Section 7A. If year-class strength is estimated, in retrospect, from a consideration of the total contribution of successive broods to the fishery throughout their life, then this approach is fundamentally like that of Fry in Section 8B.

8F. POPULATION ESTIMATES BY "CHANGE OF COMPOSITION" OR "DICHOTOMY" METHODS

If a population is classifiable in two or more ways, and harvesting from it is selective with respect to this classification, then it is possible to make a population estimate from knowledge of the original composition, the final composition, and the composition of the harvested catch. The classification might be by age, size, colour, sex, etc. To date the procedure has been used mostly with game birds or mammals, for which classification by sex is often

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[2] This is Aasen's expression (10), corrected by substituting (his) β'_2 for α'_2 in the denominator. This mistake was evidently a slip in copying, since the correct expression is given in rearranged form immediately below.

easy and the kill is frequently very selective—whether by reason of legal restrictions or the habits of the animals. Chapman (1955) found it difficult to locate the origin of this method in space or time, but he has himself given it the most complete treatment to date.

Designating the two classifications of individuals by X and Y, the information available is:

n_1, n_2 the size of the samples taken at the beginning and end of the "harvest" period (times 1 and 2)

x_1, x_2 the number of X-items in samples n_1, n_2

y_1, y_2 the number of Y-items in samples n_1, n_2

$p_1 = x_1/n_1$; $p_2 = x_2/n_2$

C_x the number of X-individuals caught during the period of harvest (the period between times 1 and 2)

C_y the number of Y-individuals caught

$C = C_x + C_y$ the total catch

We wish to know:

N_x the number of X-items at time 1

N_y the number of Y-items at time 1

$N = N_x + N_y$

The maximum likelihood estimates of N_x and N are, after Chapman:

$$\hat{N}_x = \frac{p_1(C_x - p_2C)}{p_1 - p_2} \tag{8.11}$$

$$\hat{N} = \frac{C_x - p_2C}{p_1 - p_2} \tag{8.12}$$

N_y is obtained by difference. These formulae assume that there is no natural mortality, nor any other unaccounted mortality, during the time of the kill or harvest. During the harvest, of course, the two kinds of individuals in the population must be *un*equally vulnerable. On the other hand, during the sampling done at time 1 in order to determine p_1, the X-type and Y-type individuals should in general have the same vulnerability to the sampling apparatus; and similarly for the sampling at time 2.

An exception to this latter condition occurs in the case where the Y-type (say) is not caught at all during the harvest period ($C_y = 0$). If so, it is only necessary that the X-type and Y-type have the same *relative* vulnerability at times 1 and 2, in order to obtain from expression (8.11) an estimate of N_x (i.e., the ratio of the vulnerability of X to the vulnerability of Y at time 1 should be the same as this ratio at time 2). However (8.12) is not applicable in that event, so that no estimate of the Y-type population is then possible. In this situation it would be possible, as Chapman points out, to use a sport fish as the X-type and a trash fish as the Y-type, though if times 1 and 2 are very far apart the postulate of unchanged relative vulnerability of the two species may become risky.

Chapman's account can be consulted for estimates of the asymptotic variances of these estimates under different conditions, and other pertinent information. In practice, the size of C_x may have to be estimated by sampling the catch, thus increasing the variability, but this is not serious as long as a fair-sized and representative sample is taken.

Since a pre-harvest sample has to be taken for the dichotomy method, it will often be easy to mark the fish involved and try to obtain, concurrently with the dichotomy estimate, Petersen or Schnabel estimates (of the X- and Y-types of fish separately!). This would provide the check which is always so desirable in population estimation.

An advantage of the dichotomy method over marked-fish methods is that it avoids the potential mortality or distortion of vulnerability which are apt to be inherent in handling and marking fish. However, conditions appropriate for using the method do not seem to occur very frequently.

8G. ESTIMATE OF SURVIVAL FROM DIFFERENCES BETWEEN THE SEXES IN AGE AT MATURITY—METHOD OF MURPHY

Murphy (1952) used the age composition of individual year-classes of coho salmon (*Oncorhynchus kisutch*) returning to a fishway for an estimate of survival during the last year of sea life. In the southern part of their range cohoes mature at age II and age III; among mature age II fish males are in excess, whereas females are usually in excess at age III. Assume an equal number N of each sex approaching the end of their second year of life; let x be the fraction of age II males which matures; let y be the fraction of age II females which matures, and let s be the survival rate of non-maturing II's of both sexes up to the time they approach maturity as III's. Then the expected numbers in each category are as below, and can be equated to observed numbers A, B, C and D:

	Age II			Age III
	Total	Maturing	Not maturing	Maturing
Males.......	N	$Nx = A$	$N(1 - x)$	$Ns(1 - x) = C$
Females......	N	$Ny = B$	$N(1 - y)$	$Ns(1 - y) = D$

For age II matures, males exceed females and the difference is $A - B = N(x - y)$.

For age III matures, the females exceed males and the difference is $D - C = Ns(x - y)$.

These two differences thus provide an estimate of s, and hence of N:

$$\hat{s} = \frac{D - C}{A - B} \tag{8.13}$$

$$\hat{N} = \frac{1}{2}\left(A + B + \frac{C + D}{\hat{s}}\right) \tag{8.14}$$

The fishery attacks age III individuals, and its removals are included in the survival rate *s*.

Murphy's formula was somewhat simpler than the above: he could put B = 0, since mature age II females are almost unknown among cohoes and he observed none. On the other hand, the formulae become considerably more complex if an attempt is made to apply the same principle to other salmon. In British Columbia the sockeye (*O. nerka*), for example, have ages III, IV and V all represented by both sexes (although age III females are uncommon), and in addition a selective fishery can seriously distort the sex composition of the maturing IV's and V's. Hence, to apply the method, accurate information on the number and sex of the fish captured at each age would be needed, as well as of the escapement. Nor is it always possible to assume that there is an equal distribution of sexes just before the earliest year of maturity, because significant deviations from a 50:50 sex ratio have been observed among sockeye smolts in a few instances.

CHAPTER 9.—GROWTH IN LENGTH AND IN WEIGHT

9A. ESTIMATION OF RATE OF GROWTH

The techniques for determining the age of fish are diverse and have been amply reported. Few kinds of fish in temperate waters can hope to conceal their age from a persistent investigator: length frequency distributions, tagging experiments, scales, otoliths, opercular bones, vertebrae, fin rays, etc., can all be called on.

The early history of age determination in fishes has been reviewed by Maier (1906) and Damas (1909), among others. Evidently the method of length frequencies was introduced by Petersen (1892), the use of scales was initiated by Hoffbauer (1898), otoliths were first employed for age reading by Reibisch (1899), and various other bones by Heincke (1905). Much early work by D'Arcy Thompson and others, using Petersen's method, was later shown to be inaccurate because a succession of modes had been treated as belonging to successive year-classes, when in fact they represented only *dominant* year-classes which were separated by one or more scarce broods. However, length-frequency analysis has recently been given a wider applicability by the use of "probability paper" to help separate the age groups (Harding, 1949; Cassie, 1954; Partlo, 1955); while Tanaka (1956) describes a method of fitting parabolas to the logarithms of frequencies, which would be useful where probability paper is not available. Direct determination of rate of growth from successive measurements of tagged fish has sometimes been possible, but frequently the capture or tagging operation affects the rate of growth of the fish involved; and a net *decrease* in size of many tagged individuals, even after many months at large, has been observed both in freshwater and marine fishes (cf. Holland, 1957).

The various techniques of age determination have been reviewed by Rounsefell and Everhart (1953), and a number of comprehensive works justify their applicability in general or their application to particular species (e.g., Creaser, 1926; Graham, 1929a, b; Van Oosten, 1929). However no one claims that *all* his age determinations are infallibly accurate, and the older fish often present considerable difficulty.

In addition to telling the current age of the fish, markings on the hard parts (usually scales) are regularly used to compute the length of the fish at the end of previous growing seasons, as indicated by the spacing of the "annuli". Again an extensive literature exists concerning methods of making this computation, the most suitable method being different for different fishes. In anadromous fishes the scales also reveal the length of time spent in fresh water and in the ocean, respectively. Finally, in some species the scale, otolith or fin ray indicates at what age the fish first spawned (Rollefsen, 1935; Monastyrsky, 1940) and, in sturgeons, also the sequence of years between spawnings (Derzhavin, 1922; Roussow, 1957).

Suppose a sample of a fish population has been taken and the age of each fish in it has been determined. The average size of fish at each age is then computed. A plot of these average sizes can be used directly to estimate the rate of increase in size from year to year, provided (A) that there is no difference between year-classes in respect to rate of growth at any given age; (B) that the fish taken constitute a random sample of each of the age-classes involved (not necessarily a random sample of several age-classes simultaneously, as was desirable in estimating mortality rate); and (C) that there is no correlation between size of a fish *within* an age-group, and the mortality rate to which it is subject.

DIFFERENCES BETWEEN YEAR-CLASSES. Differences between successive broods in rate of growth can be tested very easily by taking samples in two or more successive years and comparing fish of the same age. If only one year's data are available, such differences will show up as irregularities in the line of plot of length against age, which can to some extent be adjusted by smoothing. Although differences in the rate of growth of successive broods in a population are fairly common, particularly when the broods vary greatly in abundance, they are not often a serious obstacle to obtaining a picture of the *average* growth pattern by this method.

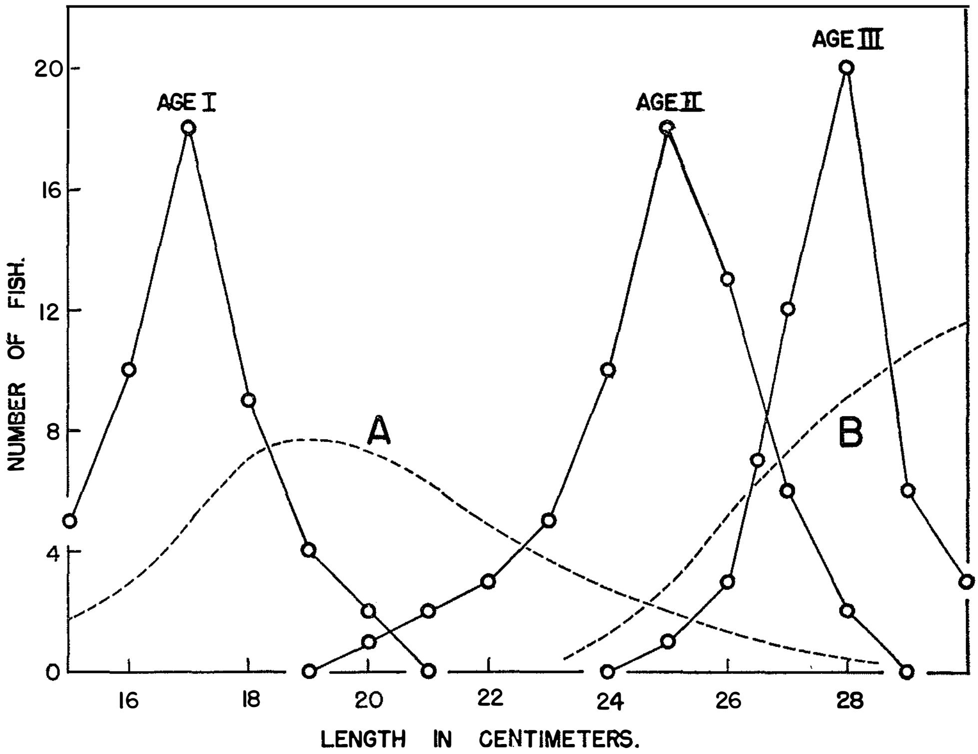

FIGURE 9.1. An illustration of the effect of selectivity of gear. Three age-frequency polygons (adapted from those for Clear Lake ciscoes; Hile, 1936, table 24) are fished by two hypothetical gears whose relative powers for taking different sizes of fish are as shown by curves A and B.

LIMITED REPRESENTATIVENESS OF SAMPLING. If only one sampling method is used, it will be very unlikely to be representative for all ages included. If it is most efficient for fish of intermediate size, it tends to select more of the larger members of the younger age-groups, and more of the smaller members of the older age groups (Fig. 9.1, Curve A). If this is not taken into consideration, and the sample is treated as though representative, the growth rate obtained will always be *smaller* than the actual. The same is true if the gear's maximum efficiency is for the smallest fish, or for the largest (Fig. 9.1, Curve B). The most direct way to avoid this trouble is to use several different kinds of sampling apparatus, all of which will probably be selective for size to some degree, but which select different size ranges. In sampling some lake fish, for example, shore seining might take age 0 and even age I representatively; minnow traps might cover ages I and II; fyke nets, ages IV-VII; and angling, ages V-X. This would leave age III in doubt, but from the specimens taken in the traps and nets a fairly accurate average value might be obtained, or that point could be interpolated.

SELECTIVE MORTALITY. Selective mortality might act to kill off either the smaller or the larger fish of a year-class more rapidly than the others. When man is the selective agent, it is usually the faster-growing fish which are removed in greatest proportion, or else those of intermediate but greater-than-average size. For example, in a heavily-fished trout stream most trout may be caught soon after reaching legal size. During the year that a brood becomes vulnerable to angling, its size distribution may be sharply skewed by the loss of most of the larger fish. Once all members of the brood are vulnerable, there should be little or no further selection of this sort, but the distortion of the distribution is not corrected. Only if the larger fish become harder to catch will the skewness diminish, disappear or (conceivably) be reversed. Selection for an intermediate size range is illustrated diagrammatically by Curve A in Figure 9.1.

TABLE 9.1. Calculated standard lengths in millimeters of ciscoes from Silver Lake, Wisconsin, taken during the summer of 1931. The fish of age I, only, are believed affected by net selectivity. (Data from Hile, 1936, tables 5 and 9.)

Age	No. of fish	Length at capture	Calculated lengths at successive annuli 1	2	3	4	5	6	7
VII......	1	201	77	111	135	158	172	186	196
VI......	21	194	78	119	142	158	177	189	
V......	108	188	80	126	150	168	182		
IV......	102	183	80	132	159	176			
III......	61	177	83	137	166				
II......	19	171	104	151					
I......	66	141	105						

Selection (by man or by nature) which removes a larger fraction of larger fish produces "Rosa Lee's phenomenon" (Lee, 1912): a slower estimated growth rate for young fish, when calculated from a representative sample of scales of older fish, than the true average growth at the age in question (Table 9.1).

Natural selection for size could conceivably bear more heavily on either the larger or the smaller fish. There is evidence that faster-growing fish may often mature earlier and also become senile earlier than slower-growing ones of the same brood. On the other hand, slow-growing fish should be more vulnerable to predation than fast-growing fish of the same age, because in general an animal has fewer enemies the larger it becomes. The actual situation in unexploited populations is little known, because relatively few have been sampled, and these not necessarily non-selectively. When both sexes are treated together, a combination of sex differences in rate of growth and in natural mortality rate might produce strong effects on calculated lengths. In many flatfishes, for example, females tend to grow faster and live longer than do the males, which would make calculated early growth increments increasingly great, in samples of mixed sexes, the older the age of the fish from which they were computed (Lee's phenomenon in reverse).

All the methods of detecting selective mortality of fish of different growth rates presuppose that representative samples are taken. This is a vital condition, because non-representative sampling which preferentially selects fish of intermediate size (Fig. 9.1A), can produce Lee's phenomenon to a marked degree. This is true whether the selection results from the physical characteristics of the net, or from the differing habits of fish of different sizes.

In addition, incorrect techniques of back calculation of size from annulus measurements can introduce an "artificial" Lee's phenomenon. For example, if scale annuli are taken as directly proportional to body length in a population where they are actually proportional to length less a constant quantity, the calculated first-year growth is always too small, and it becomes smaller, the greater the age of the fish from which it is calculated.

Some well-studied populations show little or no trace of Lee's phenomenon, however, the calculated growth at a given age being independent of the age of the fish whose scales are used for the calculation. For example, Hile (1936) found no significant evidence of it in ciscoes of Clear, Muskellunge and Trout Lakes, Wisconsin, after effects of net selection upon the youngest age were discounted.

In Lake Huron ciscoes, Lee's phenomenon is reversed at ages greater than III, so that calculated increments for ages IV and V tend to increase with the age of the fish from which they are computed (Van Oosten, 1929, p. 333). Van Oosten explains this as a result of "growth compensation" (see Section 9G).

In a typical example of Lee's phenomenon, the difference between calculated length and a true representative length at earlier annuli becomes greater at younger ages. However the reverse was observed by Hile (1936) among ciscoes of Silver Lake, Wisconsin (Table 9.1 here), and by Deason and Hile (1947) for *Leucichthys kiyi* of Lake Michigan. Scott (1949, table 17) observed an allied phenomenon in a rock bass population: there was no difference between the computed *first*-year growths of rock bass aged III-V years, and very little difference in their computed second-year growth; but at annuli III and IV the computed size of the older fish lagged behind the younger.

In all these examples the effect was not an accidental result of environmental variability, for it showed up even within individual year-classes. Formal explanations of these effects can usually be suggested by postulating appropriate combinations of selective mortality and selective sampling; but these have not always agreed with the apparent characteristics of the fishery in question.

EFFECT OF SELECTIVE MORTALITY UPON GROWTH CURVES. Deason and Hile (1947), among others, have discussed the distorting effect which selective mortality has upon growth curves. In Figure 9.2, based on the data of Table 9.1, several types of curve are illustrated. A. Curve A shows the sizes of the fish sampled, at the time of the last annulus on the scale. If Curve A is used to estimate growth from one year to the next, the figures obtained are too low because faster-growing fish are being selectively removed each year. B. Curve B of Figure 9.2 shows the average computed sizes, at successive earlier annuli, of fish sampled at age VI. These points of course indicate considerably more rapid growth rates, after age I, than does Curve A, yet even these rates are slightly too low to be representative of the population as a whole, since they are based on long-lived slow-growing fish. (Curve B estimates are also free of most of the effects of selective *sampling*, such as may be present in estimates of type A above and type D below.) C. In principle at least, a third growth curve (not shown in Figure 9.2) could be computed, based on a selection of fish of age VI whose average computed first year growth had been average—as shown by comparison with fish of a truly random sample of the same brood captured at the time of or shortly after their first annulus was formed. D. Finally, it is possible to adopt the plan of Scott (1949) and build up a growth picture of an hypothetical individual by adding successive yearly increments taken from the final complete year of each age sampled (Curve D of Figure 9.2). For example, starting with 105 mm. in the first year, a second-year growth of 47 mm. (= 151 − 104) is added; then 29 mm. (= 166 − 137) in the third year; and so on. This curve indicates more rapid increase in length during the first few years of life, and somewhat slower growth (on the average) in the penultimate years, than does Curve B[2]. It is also more regular than B, being based on much larger numbers of fish except in the last year.

If all these curves are available, which should be used? Evidently it is impossible to recognize any one of them as *the* growth curve of the population. Curve A is as close as it is possible to come to the actual size of the surviving fish at successive ages. Curve D best represents the average expected *increment* in length for fish which actually live through each year of life indicated, but the absolute levels of size (beyond age I) are fictitious. In production computations, if only Curve A is available, the apparent growth from year to year may seriously underestimate the true production potential of the stock. Using the method of Section 10C the best procedure is to base each year's rate of growth on the

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[2] The relatively steep slope of B from age 3 to 5, in comparison with the other curves, reflects the "growth com-compensation" discussed below.

initial size indicated by A and the increment indicated by D—changing both to terms of weight by means of the formula using the "between-ages-*b*" (see Section 9B). For the Beverton-Holt production computation (Section 10E) the most appropriate curve would perhaps be B, but no curve fully meets the

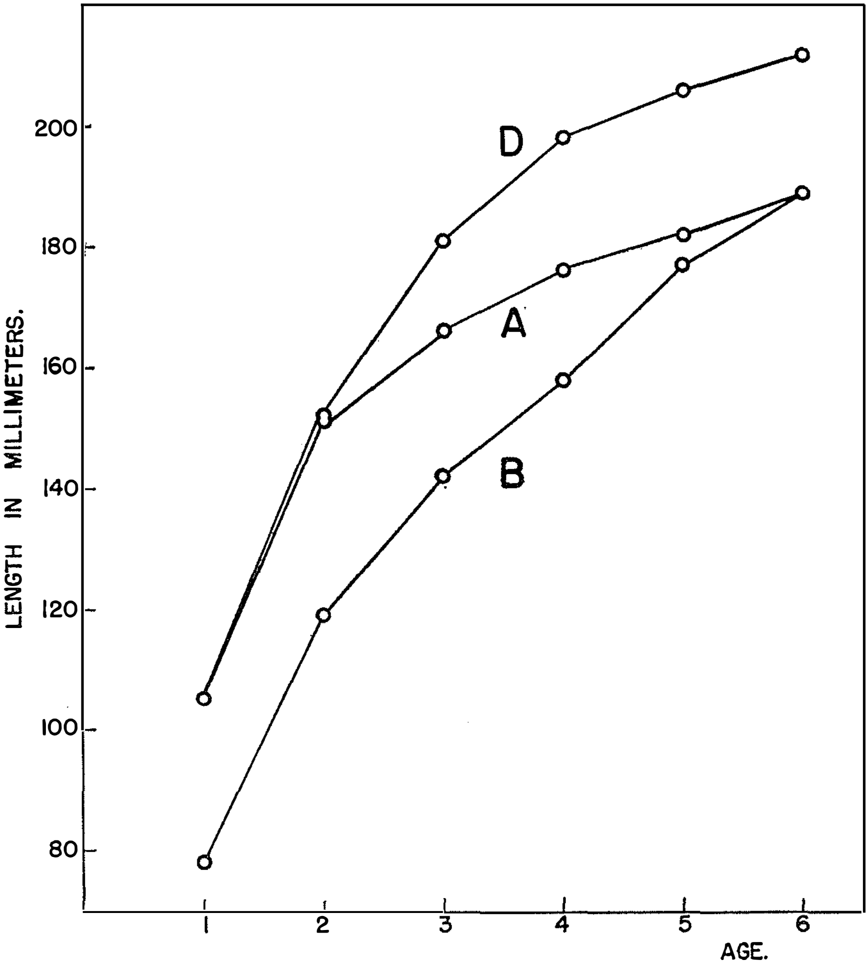

FIGURE 9.2. Increase in standard length of ciscoes of Silver Lake, Wisconsin. Curve A is the length corresponding to the last scale annulus on fish of the age shown. Curve B shows the computed length, at earlier annuli, of fish that were age VI when captured. Curve D is derived by successive addition of the last full year's increment computed from the scales of all fish sampled at each age. (Data from Hile, 1936; see also Table 9.1.)

requirements of this method: which is to say that the population itself does not, in situations where there is selective mortality. However this is not serious, since the rate of growth is likely to be more accurately measured than are the other parameters, in *any* production computation.

9B. LENGTH-WEIGHT RELATIONSHIPS

In fishes weight varies as some power of length:

$$w = al^b \tag{9.1}$$

This expression would apply best to an individual fish that was measured and weighed in successive years of its life. This of course is rarely possible. The value of b is usually determined by plotting the logarithm of weight against the logarithm of length for a large number of fish of various sizes, the slope of the line being an estimate of b. If the data are extensive, they can be grouped into *short* length-classes to speed up the computation, the average weight of the fish in each class being related to their average length.

Calculated in this manner, the value $b = 3$ describes "isometric" growth, such as would characterize a fish having an unchanging body form and unchanging specific gravity. A fair number of species seem to approach this "ideal", though weight is affected by time of year, stomach contents, spawning condition, etc. On the other hand, some species have b-values characteristically higher or lower than 3. There are sometimes marked differences between different populations of the same species, or between the same population in different years. An extreme example is the cisco in northern Wisconsin (Hile, 1936); neighbouring lakes had b-coefficients in different years as follows: Muskellunge Lake, 1.38-2.05; Trout Lake, 2.31-2.71; Silver Lake, 3.32-3.45; Clear Lake, 3.51-3.68. Though these of course did not apply to the whole length range of these fish, they did indicate marked differences in body form over the range in question.

The b-coefficient calculated as above may be called the "individual-b"[3]. It is sometimes useful also to calculate a "between-ages-b", for which the logarithm of the average weight of all fish *of a given age* is plotted against the logarithm of their average length. The between-ages-b is always a little greater than the individual-b because a rather wide range of sizes is included at each age: calculation from (9.1) will show that the weight of fish whose length is exactly l is less than the average weight of a series of fish of varying sizes whose average length is l. The difference between weights indicated by the two b's is commonly of the order of 5%; for example, Graham (1938b, p. 62) computes the average weight of age II gutted North Sea cod in March as 531 grams, whereas the average weight of age II cod of average length was 506 grams. The between-ages-b coefficient is useful mainly for converting, to weight terms, average lengths which have been calculated from scale annuli.

9C. INSTANTANEOUS GROWTH IN WEIGHT

From the point of view of fish production, increase in weight is a more fundamental aspect of growth than is increase in length, but it usually must be

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[3] In passing, notice that the "individual" type of b-coefficient, when calculated from a representative sample of all the fish *of a given age* ("within-age-b") may be consistently greater or less than the individual-b calculated for fish belonging to a mixture of ages; and this within-age-b may change significantly with age. Hence a computation of individual-b should preferably be from fish of mixed ages, if an overall picture is desired. The same effect crops up when two linear measurements of a fish are compared on logarithmic axes, as in studying body proportions.

arrived at indirectly. In a growth study, a frequent sequence of operations is as follows: 1. age determination from scales, and measurements to successive annuli; 2. establishment of the relation of scale size to fish size; 3. back calculation of a representative length increase for early ages; 4. extrapolation (if necessary) to obtain representative lengths at the oldest ages, possibly by the method described in Section 9E; 5. selection of the most appropriate representation of growth (page 189); 6. calculation of "between-ages-*b*" from the representatively-sampled ages; and 7. transformation of the computed average lengths for each age group to average weights for the same, using the "between-ages-*b*".

Of the kinds of growth described in Section 1F, the instantaneous growth rate is the one which can be directly compared with mortality—the latter also being expressed in instantaneous terms. A plot of the logarithm of weight shows the situation in this light (Fig. 9.3D). An estimate of the instantaneous rate of growth between two years is the difference of the two logarithms (divided by 0.4343 if base-10 logarithms have been used); this is shown in Figure 9.3C. If it is desired to have estimates of instantaneous growth centered on the end of the growth year (or centered on any other time), this can be obtained by taking tangents on the curve.

9D. MATHEMATICAL DESCRIPTION OF INCREASE IN LENGTH—FORMULA OF BRODY-BERTALANFFY

Fitting growth curves by mathematical expressions may be of value because (1) they assist in interpolation or extrapolation; (2) the expressions are useful in some production computations; and (3) they may shed light on the physiology of growth.

As far as they have been intensively studied, fishes all apparently exhibit an initial period of increasingly rapid absolute increase in length, followed by a decrease. The initial increasing phase is usually completed within the first two years of life, and if so, it may not appear at all in a graph of yearly increments. However it is frequently exhibited in centrarchids (Fig. 9.3A).

The changeover from increasing to decreasing length increments may be so slow and protracted as to make the age-length relationship effectively linear for almost the whole of the fish's life, or for as much of it as the available data pertain to. This approximation has been used successfully in some production computations (Example 10D). More commonly, a decrease in the yearly increment of length is quite evident as the fish grow older.

Two general approaches have been made toward describing growth curves mathematically. For S-shaped curves, attempts have been made to fit the logistic relationship (Yoshihara, 1951); the left-hand asymptote must be truncated somewhere near $t = 0$. The principal trouble with using the logistic curve is that it does not lend itself very readily to the mathematical manipulation necessary for calculating production, so it has had relatively little attention; however, see Yoshihara's application to a pilchard population.

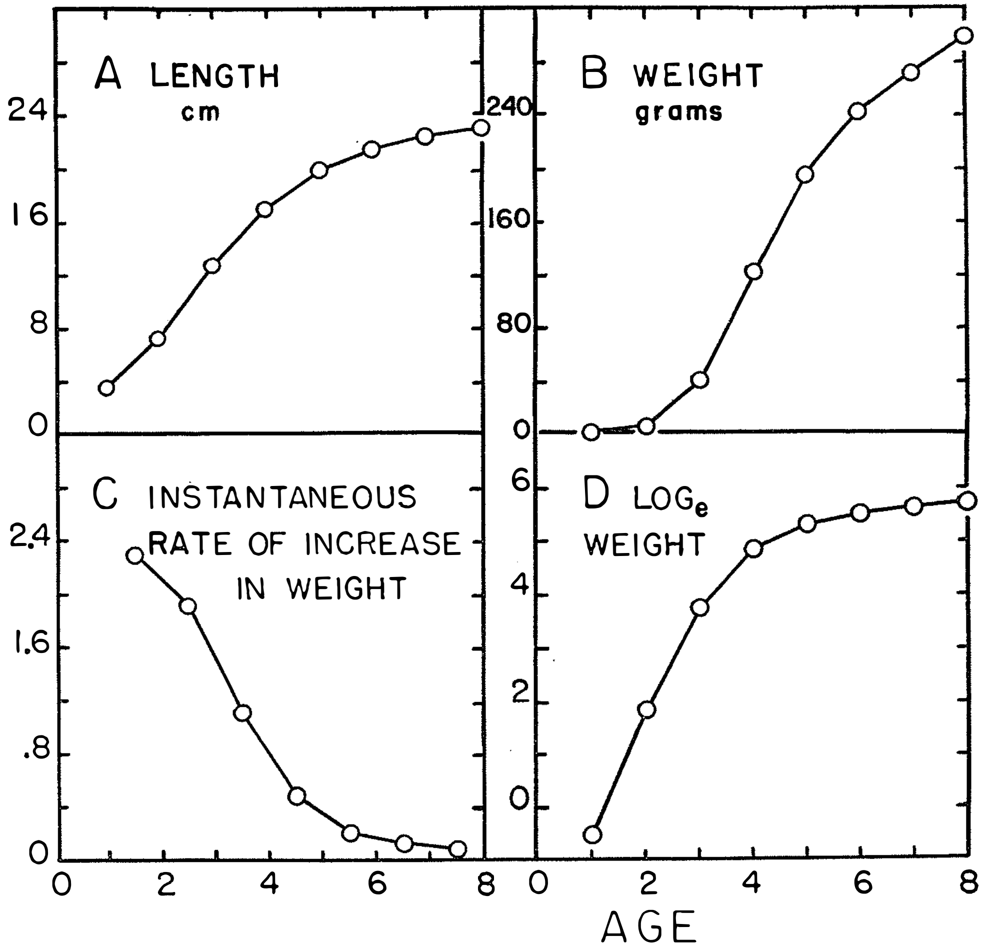

FIGURE 9.3. Example of different measures of growth (for *Lepomis macrochirus* in Spear Lake, Indiana). A. Fork length in centimeters. B. Weight in grams. C. Instantaneous rate of increase in weight. D. Natural logarithm of weight.

The second approach is to divide an S-shaped curve at the inflexion point and fit the two halves with separate curves. Thus, for the parts having increasing and decreasing slope, respectively, Brody (1927, 1945) uses:

$$l_t = Ae^{K't} \tag{9.2}$$

$$l_t = B - Ce^{-Kt} \tag{9.3}$$

where l is length and t is age; A, B and C are constants (parameters) having the dimensions of length; and K and K′ are constants determining the rate of change in length increment.

We are not concerned here with the first of these expressions, or with other expressions which have been used to describe embryonic, larval and early fingerling growth (cf. Hayes, 1949; Allen, 1950, 1951). Formula (9.3), however, has been found to be at least approximately applicable to many examples of growth of older fishes: sometimes from age I onward, but more commonly starting at a somewhat greater age.

Formula (9.3) contains 3 parameters, B, C and K. As t increases indefinitely, $l_t \rightarrow B$, which is the maximum or asymptotic length for the fish. Another form of (9.3) is:

$$l_t - (B - C) = C(1 - e^{-Kt}) \tag{9.4}$$

In this form, when $t = 0$, $l_t = (B - C)$; that is, the constant quantity $(B - C)$ is an adjustment which serves the purpose of shifting the time axis of the graph so that the adjusted length is zero when age is zero. The same effect can be achieved by shifting the length axis instead: that is, instead of using actual age, t, on the time scale, adjust it by some constant, t_0, which in effect gives a new time scale with origin at $t - t_0$. This changes Brody's relationship to the form used by von Bertalanffy (1934, 1938). Putting l_∞ for B, (9.3) becomes:

$$l_t = l_\infty\left(1 - e^{-K(t-t_0)}\right) \tag{9.5}$$

Obviously l_∞ is the value which l assumes as age increases indefinitely, and is called the average "maximum" or asymptotic length of the fish.

The change from (9.3) to (9.5) is a purely algebraic transformation, in which the parameter C is replaced by the new parameter t_0, the relation between them being:

$$t_0 = \frac{\log_e(C/B)}{K}$$

In (9.5), instead of using age as measured from time of hatching, we in effect start from the hypothetical time, t_0, at which the fish would have been zero length if it had always grown in the manner described by the equation.

Another form of (9.3) can be obtained by duplicating (9.5), using $t + 1$ for t, and subtracting the resulting equation from (9.5). Putting $k = e^{-K}$, this relationship is:

$$l_{t+1} = l_\infty(1 - k) + kl_t \tag{9.6}$$

This expression was developed empirically by Ford (1933) and by Walford (1946), and has been treated also by Lindner (1953) and by Rounsefell and Everhart (1953). It describes growth in which each year's increment is less than the previous year's by the fraction $(1 - k)$ of the latter, starting from an hypothetical initial size $l_\infty(1 - k)$ at true age zero. The relation between increments in successive years is clearer in the derived expression:

$$l_{t+2} - l_{t+1} = k(l_{t+1} - l_t) \tag{9.7}$$

A graphical presentation of (9.6) with l_{t+1} plotted against l_t is rather convenient (Fig. 9.4A). The slope of this "Walford line"[4] is equal to k, and the Y-axis intercept is l_∞ $(1 - k)$, from which l_∞ can be calculated. The asymptotic length, l_∞, is also the point at which the line (9.6) cuts the 45° diagonal from the origin.

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[4] A humorous but appropriate suggestion is that this should be written *Wal-Ford* line. However, although Ford developed the relationship involved, Walford first used this graphical presentation.

Calculating the equation (9.6) makes a convenient first stage in fitting (9.5) to a body of data. However fitting a line to the Walford graph directly is not very satisfactory, because both ordinate and abscissal values are subject to sampling error, and the points often lie erratically with respect to the line fitted; also, the two terminal values are used only once, and the remainder twice. For a better fit, the l_∞ obtained from a freehand Walford line can be used as a trial value in an expression (see Beverton, 1954, p. 157) derived from (9.5) by taking logarithms:

$$\log_e(l_\infty - l_t) = \log_e l_\infty + Kt_0 - Kt \tag{9.8}$$

Thus a graph of $\log_e(l_\infty - l_t)$ against t should be straight, and this straightness

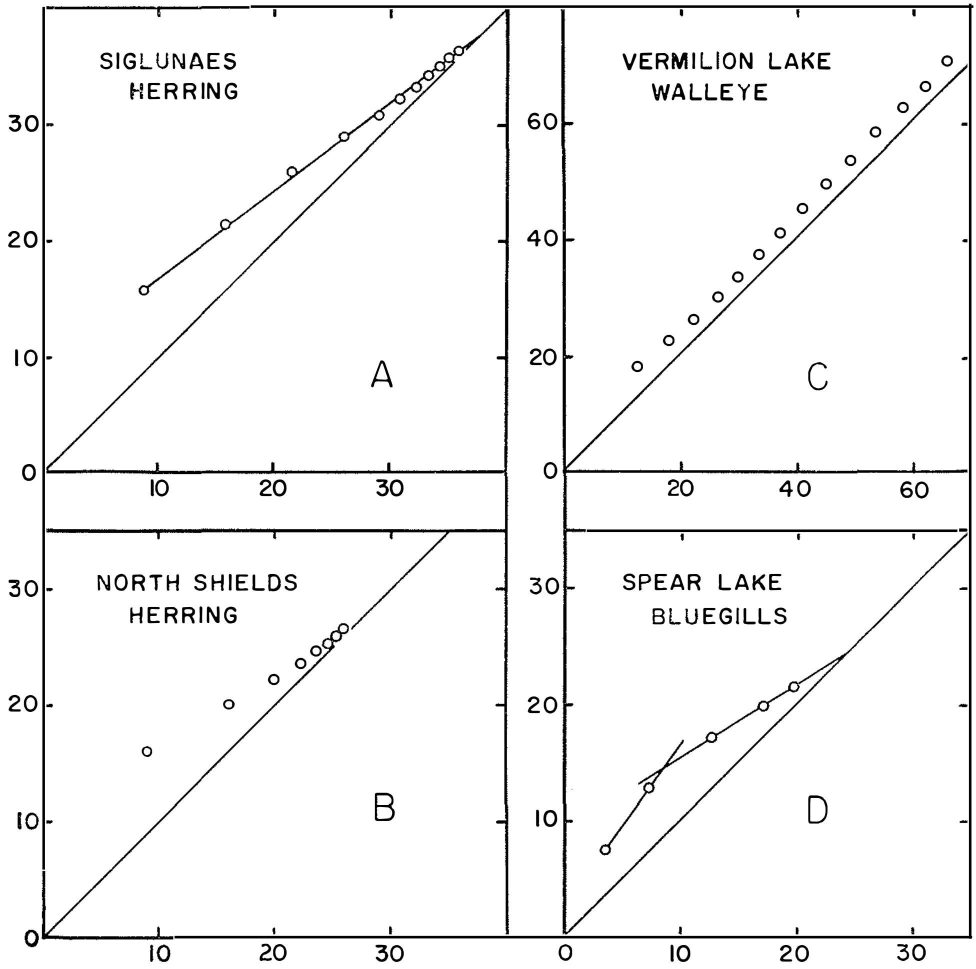

FIGURE 9.4. Walford graphs, of length in centimeters at age $t + 1$ against length at age t, for four fish populations. A and B, from Ford (1933), after data of Hjort. C, from Carlander and Hiner (1943). D, from Ricker (1955). In every instance the first point represents age II plotted against age I, and later points proceed in sequence.

is sensitive to changes in l_∞. A few trial plots will quickly yield the l_∞ which gives the best (straightest) line—which can usually be selected sufficiently well by eye. Finding the best l_∞ and corresponding line immediately determines K, which is the slope of the line; and also provides the value of t_0, since the Y-axis intercept of (9.8) can be equated to $\log_e l_\infty + Kt_0$. Of course, only those length observations should be used which actually conform to expression (9.5).

Von Bertalanffy has tried to provide the relationship (9.5) with a theoretical physiological basis, and he apparently considers it a generally-applicable growth law. However, one of the fundamental assumptions he uses is that anabolic processes in metabolism are proportional to the area of an organism's effective absorptive surfaces. This could seem reasonable if food were always available in excess, so that absorptive surface could actually be a factor limiting growth; and in the guppy experiments which are quoted in support of this relationship, food was actually provided in excess. In nature, fish are usually less fortunate; this is shown by the small average volume of food commonly found in their stomachs, and also by the great variability of their observed growth rates, both when we compare individual fish in the same environment and when we compare populations from different (but physically-similar) waters. Thus it seems unlikely that available absorptive surface is commonly a factor limiting the growth of wild fish. However, whatever may be the theoretical aspects of the expressions above, the formulae can be used on an empirical basis. The only caution necessary is to be sure that they do describe the pertinent ages of the fish under consideration.

The principal types of Walford graphs are shown in Figure 9.4. The Siglunaes herring (Curve A) are fitted with the line which Ford (1933) computed, with a Y-axis intercept of 9.57 cm. and a "maximum size" (l_∞) of 37.1 cm. The North Shields herring (Curve B) are a population for which Ford found that k changed considerably, increasing from 0.56 to 0.77 among the older fish. A similar trend can perhaps be observed even in Curve A, and it appears in certain other well-studied populations such as the Nebish Lake rock bass (Hile, 1941). A line practically parallel to the diagonal was obtained for Vermilion Lake walleye (Curve C). This form describes uniform absolute increase in length

TABLE 9.2. Average weight and average standard length of ciscoes from Vermilion Lake, Minnesota, and data for fitting a Walford line to length. (Data from Carlander, 1950.)

Age	No. of fish	Weight	Length	Using trial $l_\infty = 315$		Using final $l_\infty = 309$		Adjusted age
				$l_\infty - l_t$	$\log_e(l_\infty - l_t)$	$l_\infty - l_t$	$\log_e(l_\infty - l_t)$	
t		*oz.*	*mm.*	*mm.*		*mm.*		$t - t_0$
II	101	3.5	172	...	...	...	...	1.76
III	14	6.8	210	105	4.66	99	4.60	2.76
IV	136	10.5	241	74	4.30	68	4.22	3.76
V	52	13.5	265	50	3.91	44	3.78	4.76
VI	67	16.3	280	35	3.56	29	3.37	5.76
VII	81	16.8	289	26	3.26	20	3.00	6.76
VIII	54	17.8	294	21	3.04	15	2.71	7.76
IX	20	18.5	302	13	2.56	7	1.95	8.76
X	6	19.0	299	16	...	10	...	9.76
XI	2	19.0	306	9	...	3	...	10.76

with age, and it is approximated, up to a great age, by many long-lived freshwater and marine fishes in cool-temperate to subarctic waters. Finally, a graph which increases in slope, then later decreases, has been found among centrarchids in the warmer parts of eastern North America; Curve D is an example. The same has been observed in several bivalve mollusc populations: see Weymouth and McMillin's data for razor clams as plotted by Rounsefell and Everhart (1953), or Stevenson and Dickie's (1954) data on growth of scallops.

It is most important, of course, to use truly representative measurements for Walford graphs. One common danger is selection for large size among the younger fish, and this leads to depression of the left end of the line. A way to avoid this is to use lengths calculated from scale annuli of older fish to represent the younger ages (Section 9A). A lesser danger is reading scales of old fish consistently too low. This causes some depression of the right end of the line, but the error has to be gross in order to produce any considerable effect.

EXAMPLE 9A. FITTING A WALFORD GRAPH TO LENGTH DATA FOR CISCOES OF VERMILION LAKE, MINNESOTA. (Data from Carlander, 1950.)

The length column of Table 9.2 shows the mean length of ciscoes (*Leucichthys artedii*) of ages II to XI, in a sample of 533 fish; they can be used to plot a growth curve of the "A" type of Figure 9.2. Plotted on a Walford graph (Fig. 9.5A), the age II fish evidently do not conform to the linear series, possibly as a result of selection. Freehand fitting of a line to the Walford graph (discounting the last two points because based on so few fish) gave a slope of $k = 0.70$ (hence $K = -\log_e 0.70 = 0.37$) and an intercept on the diagonal of $l_\infty = 315$ mm. Using the last as a trial value of l_∞, values of $315 - l_t$ are computed (Table 9.2) and their natural logarithms are plotted against age for ages III-IX (Fig. 9.5B, open circles). This line is somewhat curved: additional trials show that $l_\infty =$ 309 mm. gives the straightest plot (Fig. 9.5B, solid dots). For this value of l_∞ the slope of the natural log line is $K = 0.41$ (hence $k = e^{-0.41} = 0.66$), and the Y-axis intercept is 5.84. Equating the latter to $\log_e l_\infty + Kt_0$ in (9.8), with $\log_e l_\infty = \log_e 309 = 5.74$:

$$t_0 = \frac{5.84 - 5.74}{0.41} = 0.24$$

The length equation of type (9.5) becomes:

$$l_t = 309 \left(1 - e^{-0.41(t-0.24)}\right)$$

The equation of type (9.6) is:

$$l_{t+1} = 105 + 0.66\, l_t$$

These expressions are computed for the data from fish of age III and older. To discover whether they are applicable to younger fish, lengths of age II and age I individuals warranted free from selection would be required—failing actual collections, such lengths might be computed from the scales of age III fish.

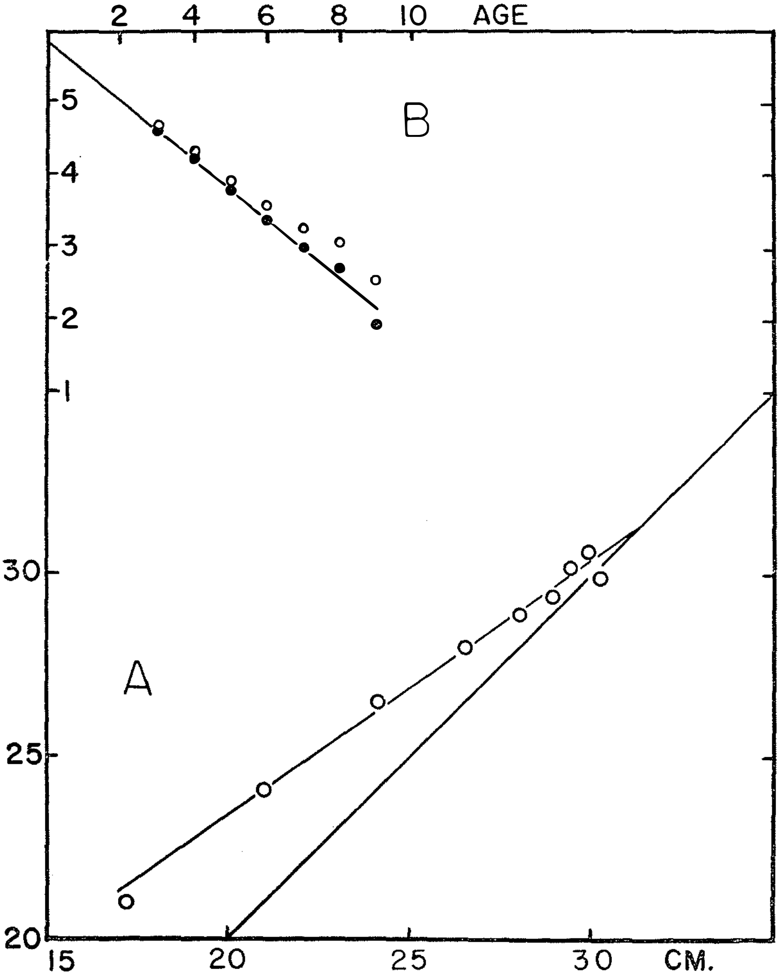

FIGURE 9.5. A. Walford graph for length of ciscoes of Vermilion Lake, Minnesota. The first point on the left is age III plotted against age II. B. $\text{Log}_e(l_\infty - l_t)$ plotted against age for trial values of $l_\infty = 309$ (open circles) and $l_\infty = 315$ (dots).

9E. USE OF A WALFORD LINE FOR ESTIMATING GROWTH OF OLDER FISH—METHOD OF MANZER AND TAYLOR

In general, the accuracy of age determinations tends to decrease among fish of the larger sizes, and for really old fish they may be practically useless. Attempts to fill in the gap by direct extrapolation along the curved line of an age-length or age-weight graph are usually unsatisfactory. However a better result can usually be obtained by plotting the Walford line. Provided available data extend into the region of decreasing increments, then, proceeding from the oldest reliable age available, lengths at older ages can be read off the graph as far as desired; or the formula (9.6) can be used.

A Walford graph can also be drawn by plotting length at recapture against length at marking of marked or tagged animals (Manzer and Taylor, 1947), though applicability to the wild population of course depends on the condition that the mark or tag does not retard growth. For fishes, the method will be useful chiefly when there are a number of recaptures made close to a year after marking, since the use of intervals shorter than a year would usually give trouble because of seasonal variations in growth rate. However Lindner (1953) has applied the method to recaptures of marked shrimps made during successive 10-day intervals of the season of tagging.

It is useful, when possible, to superimpose the Walford graph from age determination on that obtained from tag recoveries (Ketchen and Forrester, MS). Agreement of the two lines justifies moderate confidence in both as a representation of actual growth, because the most likely kinds of systematic error affect the two graphs differently. The position of the tag-recovery line is below the true position if the presence of a tag reduces the growth rate of the fish.

EXAMPLE 9B. GROWTH OF LEMON SOLES FROM TAG RECAPTURES, USING A WALFORD LINE. (From Manzer and Taylor, 1947.)

Manzer and Taylor plotted length at recapture against length at tagging for female lemon soles (*Parophrys vetulus*) which had been at large approximately a year. (Tagging and recaptures were both done during the winter spawning season, when no growth was in progress, so the *exact* time interval was not important.) For the stock off Boat Harbour, Strait of Georgia (Fig. 9.6), the points determine a typical Walford line, with the intercept with the diagonal indicating a "maximum" size of about 49 cm. Expected yearly increments at any initial length can easily be read from the line. If mean length for one age is obtained from other sources, growth throughout life can be extrapolated along the line. For example, if age III length is 29 cm., lengths at successive older ages are as shown in Figure 9.6. A growth curve obtained in this manner is analogous to the "D" type growth curve of Section 9A, because it is based on the surviving fish at successive lengths; hence it may overestimate the actual size achieved by average surviving fish at the older ages.

9F. INCREASE IN WEIGHT WITH AGE

Graphs of weight against age resemble those of length in being usually S-shaped. The point of inflexion is at an older age than on the corresponding length graph (Fig. 9.3B). Again a logistic curve can be fitted in some instances, but no examples will be attempted here. As with length, the two curves of Brody (9.2, 9.3, above) can be used for the age-weight relationship, but *both* are usually needed to describe the range of weights that are of interest in production calculations. Partial fits have been used, however: Thompson and Bell (1934) fitted (9.2) to the part of a halibut age-weight graph which they needed, and Allen (1950) has used (9.3) for the weight of trout older than a year.

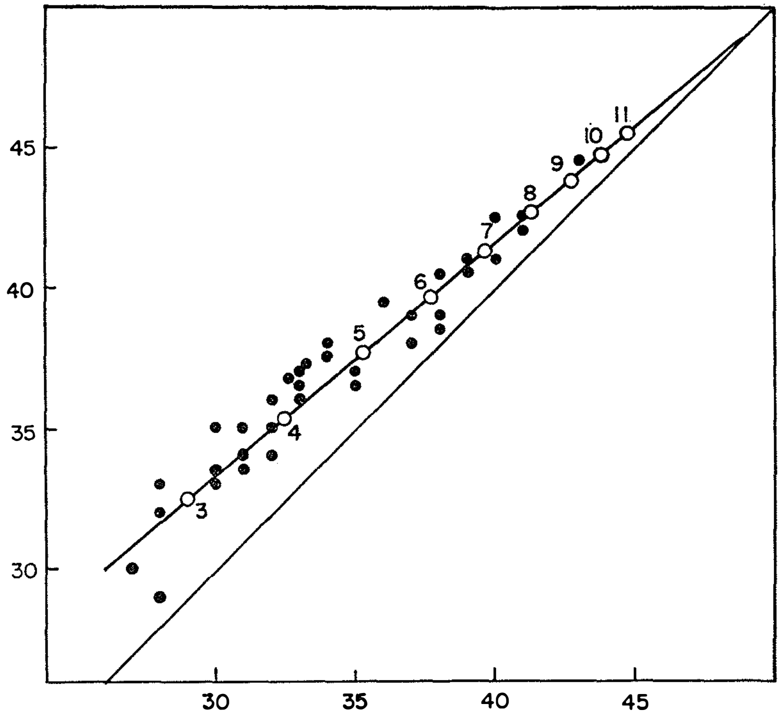

FIGURE 9.6. Walford graph of length of *Parophrys* at recovery (January-February, 1947) plotted against length at tagging (January-February, 1946). The open circles are estimates of average length at successive ages computed from the line, given that the average length at age III is 29 cm. (Data for tag recoveries from Manzer and Taylor, 1947.)

In terms of weight, (9.3) may be written in a form analogous to (9.5):

$$w_t = w_\infty \left(1 - e^{-K(t-t_0')}\right) \tag{9.9}$$

where t_0' is the hypothetical age at which weight would have been zero if growth had always conformed to this relationship. The fitting can be carried out in precisely the same way as the corresponding length equation (Section 9D). A Walford-type graph is plotted, w_{t+1} against w_t, and the value of w_∞ is obtained from the intersection with the 45-degree diagonal, or is calculated from the Y-intercept. As with t_0 for length, the value of t_0' can be obtained from trial graphs of $\log_e(w_\infty - w_t)$ against t, as indicated by the equation:

$$\log_e(w_\infty - w_t) = \log_e w_\infty + Kt_0' - Kt \tag{9.10}$$

In (9.9) and (9.10) the same symbol, K, has been used as in (9.5), *and it has the same numerical value.* This equivalence, which was used by Dickie and McCracken (1955), may be demonstrated as follows (from L. Dickie and J. Paloheimo, personal communication). Consider the weight-length relationship given in (9.1):

$$w = al^b \tag{9.11}$$

where b is the "year-class-b", a parameter which rarely lies outside the range 2.6-3.6. Now raise each side of (9.5) to the power b and multiply it by a:

$$al^b_t = al^b_\infty \, (1 - e^{-K(t-t_0)})^b \tag{9.12}$$

From (9.11) and (9.12):

$$w_t = w_\infty \left(1 - e^{-K(t-t_0)}\right)^b \tag{9.13}$$

This can be expanded as:

$$w_t = w_\infty \left[1 - be^{-K(t-t_0)} + \frac{b(b-1)}{2 \times 1}e^{-2K(t-t_0)} - \frac{b(b-1)\,(b-2)}{3 \times 2 \times 1}e^{-3K(t-t_0)} + \,.\,.\,.\,.\,.\right] \tag{9.14}$$

For values of $t - t_0$ greater than 2 to 4 or so (the exact limit depends on the magnitudes of K and b), terms of this expansion beyond the second can be neglected by comparison with the first two; hence for the corresponding ages:

$$w_\infty - w_t \rightarrow bw_\infty \, e^{-K(t-t_0)} \tag{9.15}$$

$$\log_e(w_\infty - w_t) \rightarrow \log_e b + \log_e w_\infty + Kt_0 - Kt \tag{9.16}$$

This expression differs from (9.10) in that $\log_e b + Kt_0$ replaces Kt_0 on the right side, but the slope of the line and hence the numerical magnitude of K is not changed.

From the above it follows that, among older ages, the Walford graphs of length and of weight should have the same slope, k. This is often true of all ages for which data are available, or of all ages for which the Walford length graph is linear. Because, among these older fish, weight increases more rapidly than length, there may sometimes be an advantage in estimating k and K from weight rather than from length: a better spacing of points is achieved.

EXAMPLE 9C. FITTING A GROWTH CURVE TO WEIGHT DATA FOR THE CISCO POPULATION OF VERMILION LAKE, MINNESOTA. (Data from Carlander, 1950.)

For most of the 533 ciscoes enumerated in Table 9.2, weight as well as length was recorded. Plotting these in a Walford graph (not shown here), neither age II nor age III falls on the trend established by the points for older years. Excluding these and the two oldest ages, free-hand fitting of a Walford line gave the values below:

$$k = 0.69; \quad K = 0.37; \quad w_\infty = 20.0 \text{ oz.}$$

Correcting this in the same manner as for the length plot, the best fit is close to $w_\infty = 19.8$ oz. and $K = 0.40$ (compare $K = 0.41$ from Example 9A). For this line the natural log intercept is 3.80. Hence:

$$t_0' = \frac{3.80 - 2.99}{0.40} = 2.02$$

and the weight equation, applicable to fish age IV and over, is:

$$w_t = 19.8\left(1 - e^{-0.40(t-2.02)}\right)$$

9G. GROWTH COMPENSATION

A by-product of the general type of growth in length and weight discussed above is the effect which has been called growth compensation. Though not necessary to the main theme of this Handbook, a brief description of its place in the growth picture seems desirable.

As it concerns length, growth compensation has been treated by a succession of authors, starting with Gilbert (1914); some of the more comprehensive papers are by Watkin (1927), Hodgson (1929), Van Oosten (1929), Ford (1933), Hubbs and Cooper (1935), and Hile (1941). Growth in weight was brought into the picture by Scott (1949). The phenomenon which these authors discuss is a correlation between the increments in size in successive years of life, among the fish of a given year-class. Negative correlations indicate growth compensation, because they show that the smaller fish tend to catch up with the larger. Positive correlations have been called "reverse growth compensation", but a shorter term might be "growth depensation"—adopting a word that was proposed in a different context by Neave (1954).

A typical brood of fish varies considerably in size at the end of its first growing season, partly because of differences in time of hatching, partly from congenital physiological differences, partly from differences in environment. Hodgson (1929) showed that growth compensation must occur among the fish of any brood whose members grow at the same rate at any given size, provided growth rate decreases with size and provided the fish differ in size to begin with. Somewhat more realistically, Scott (1949) pointed out that growth compensation is associated with a decrease in (absolute) yearly average increment, whereas depensation is associated with an increase in yearly increment, in the unit chosen (length or weight). As long as increases predominate in a year-class there is depensation; when decreases become more common, it shifts to compensation.

Considering weight first, the initially heavier fish of a brood usually tend to increase their advantage during the second year of life, and often continue to do so for one or more additional years. Eventually, however, the inflexion point of the weight-age curve is reached: the smaller fish start to catch up with the larger ones, and the correlation between increments in adjacent years shifts from positive to negative.

The course of length change is similar, but the change from growth depensation to growth compensation occurs earlier in life; often compensation begins as early as the second growing season, so that the phase of positive correlation is omitted. This difference, between length and weight, in the time of appearance of compensation and inflexion of the growth curve, is a necessary consequence of the fact that weight increases as a power of length. For example, if all fish of a brood were to increase in weight by the same absolute amount in a year, the smaller ones would be increasing more, in length, than the larger ones; hence growth in length would be compensatory.

These changes of course produce, or reflect, changes in the variability in size of the fish in a brood. Typically, standard deviation in weight or length of a brood increases early in life and later decreases, but the increasing phase lasts longer for weight than for length. However, selective mortality, when it occurs, can also affect size variability: it tends to decrease variability if the heavier mortality bears on either the large or the small fish of a year-class, and to increase it if intermediate sizes are most seriously affected.

9H. ESTIMATION OF SURVIVAL RATE FROM THE AVERAGE SIZE OF FISH CAUGHT

The average size of the fish in a catch (above some minimum) is obviously related to the annual mortality rate: the greater the mortality, the smaller the average size. Given some kind of expression for rate of increase in length or weight of the fish, a rough calculation of survival rate can be made from their average size. This can be useful when other methods are not available, or as a rough check on other methods. For this purpose average weight is usually easier to obtain from large numbers of fish than is average length: the fish can be counted and then weighed in bulk, or the information may be available from the industry's records. However, weight tends to vary more than length does, seasonally or from day to day.

All applications which I have seen presuppose that the survival rate is constant over the range of ages involved, that the population is in equilibrium with respect to the prevailing survival rate, that variations in year-class strength are not great enough to affect the result, and of course that the catch is representative of the population above the recruitment size. It is necessary to determine the rate of growth in length or weight of the fish in the population at successive ages, or to fit some kind of growth curve.

Baranov (1918, p. 94) computed survival rate from mean size, among other methods. As described in Section 10D below, he postulated a constant absolute increase in length of the fish in the recruited population, with weight varying as the cube of length. Subject to these limitations, by expression (10.8) the ratio of average weight of the fish caught ($\overline{w}$) to the weight at recruitment (w_R) is:

$$\frac{\overline{w}}{w_R} = 1 + \frac{3}{i'L} + \frac{6}{(i'L)^2} + \frac{6}{(i'L)^3} \tag{9.17}$$

where L is the length in centimeters at recruitment and i' is the instantaneous rate of mortality per centimeter of length increase. L being known, i' and hence i can be calculated.

Silliman (1945) fitted an empirical formula of the form $l = k_1 + k_2\ (t - k_3)^3$ to the mean length (l) of California sardines of commercial size in successive years (t is age; the k's are constants), and combined it with the exponential survival formula to obtain an expression for the instantaneous mortality rate, i. Parallel computations can be made with any other integrable mathematical expression that may be fitted to a graph of length or weight against age. For the Brody-Bertalanffy growth formula, Beverton and Holt (1956, Appendix B) derive the expression:

$$i = \frac{K(l_\infty - \bar{l})}{\bar{l} - l_R} \tag{9.18}$$

where $\bar{l}$ is the average length of fish in the catch that are as large as or larger than the first fully-recruited length l_R; K and l_∞ must first be determined, as described in Section 9D.

A more generally applicable procedure is to work with a succession of observed growth rates such as are used in Section 10C. Consider:

g_1, g_2, g_3, etc. the average instantaneous rate of increase in weight, determined empirically for successive years of the vulnerable life of the fish

i the instantaneous mortality rate, the same in all years

w_R the weight at which the fish first became fully vulnerable

$\overline{w}$ the average weight of the fish in the catch which weigh w_R or more. (With considerably less accuracy, commercial statistics may sometimes be used for average weight, putting w_R equal to the average or 50% recruitment size.)

Under equilibrium conditions, the bulk of a unit number of fish at time of recruitment, and at yearly intervals thereafter, is successively w_R, $w_Re^{g_1-i}$, $w_Re^{g_1+g_2-2i}$, etc. The sum of these is the *weight* of stock continuously on hand, per unit number of annual recruits, namely:

$$w_R\left(1 + e^{g_1-i} + e^{g_1+g_2-2i} + e^{g_1+g_2+g_3-3i} + \ldots.\right) \tag{9.19}$$

The number of fish in each year-class, surviving from a unit number of recruits, is successively 1, e^{-i}, e^{-2i}, etc. Adding up these to enough terms that the survivors are of negligible bulk in the population, the *number* of fish in the stock becomes (following 1.13) practically equal to $1/(1 - e^{-i})$:

$$1 + e^{-i} + e^{-2i} + \ldots. = \frac{1}{1 - e^{-i}} \tag{9.20}$$

The average weight of the fish in the stock is (9.19) divided by (9.20); and this divided by w_R is:

$$\frac{\overline{w}}{w_R} = \left(1 - e^{-i}\right)\left(1 + e^{g_1-i} + e^{g_1+g_2-2i} + \ldots.\right) \tag{9.21}$$

Like the analogous expression (9.17) above, (9.21) can readily be solved for i by successive approximations. If growth rate changes so rapidly, over some part of the life cycle, that a year is too coarse a division of time, g-values for any shorter interval can be used in (9.21), and the resulting i will of course apply to that shorter interval.

Estimates of mortality and survival based on average size of the fish must usually be regarded as inferior to those obtained from a catch curve (for example), but they may often prove suggestive by reason of their agreement or disagreement with other methods. Their greatest weakness is that they do not detect possible age variation in mortality rate.

CHAPTER 10.—COMPUTATION OF YIELD FROM A GIVEN RECRUITMENT

10A. General Conditions

The goal of most work on growth and mortality in fish populations has been an assessment of the yield of the stock at different levels of fishing effort, or with different size limits for recruitment. In the computations of this Chapter the yield calculated is that which will be obtained from whatever number of recruits are coming into the fishery. The regulation of recruitment is considered in Chapter 11; the calculations in this Chapter are usually made in terms of yield *per recruit*, or per unit weight of recruits. Except in Section 10F, equilibrium situations are postulated: that is, the conditions which exist after the specified conditions have been in effect long enough to affect all ages for the whole of their exploited life.

An important condition for these calculations is that the instantaneous rates of natural mortality and of growth, at any given age, be constant over the range of conditions examined. The very limited information available concerning *mortality* suggests that this may often be close to the truth over a fairly wide range of population densities, but the question needs constant re-examination. On the other hand, *growth* has sometimes been found to vary markedly with change in population density—so much so that Nikolsky (1953) has suggested that rate of growth could be used, by itself, as an index of the degree to which a stock approaches its maximum productivity. Whether or not this is ever practical, variation in growth rate, when it occurs, sets strict limits to the range of stock densities over which useful predictions of yield can be made using the methods of this Chapter, as Miller (1952) has emphasized. Fortunately, not all stocks react to exploitation by increasing growth rate: those which do seem usually to be the dominant species in the habitat from which they obtain the bulk of their food (cf. Ricker, 1958a).

When the effect of a change in selectivity of gear or in minimum size limit *along with* a change in rate of fishing is being examined, the accompanying shifts in overall stock density need not be especially great, though the age distribution will change drastically. In such circumstances the methods of this Chapter perform fairly well, provided the recruitment effect can be properly taken into consideration.

Subject to these conditions, computations of equilibrium yield per unit recruitment have been attempted by a number of authors. In general, the rate of growth in weight of a fish varies with age, and rate of fishing may also be different at different ages or sizes, particularly during the phase of recruitment. The most direct approach breaks the population up into age-, size- or time-intervals sufficiently small that rates of growth and mortality can be considered constant within each, without important error; and yield statistics for whole populations are obtained by summing the results for all the intervals represented. Alternatively, we may attempt to obtain a single expression for yield by fitting mathematical expressions to growth and mortality, and combining the two.

For the most part we will confine the discussion here to yield in weight of fish taken, with some reference to yield per unit of effort and the market value of the yield, per pound. Particularly in sport fisheries, other characteristics of the take may sometimes be more important—the size of the fish caught, for example. Allen (1954, 1955) has dealt extensively with the effects of size limits and bag limits upon various characteristics of the catch and yield in sport fisheries.

Computations of the kinds described in the sections to follow can be quite time-consuming, particularly if charts are being prepared to show a number of complete surfaces of possible conditions—each of one of the general types presented by Baranov (1918, fig. 10), Thompson and Bell (1934, fig. 9) or Beverton (1953, fig. 2). For a large-scale operation it would pay to use electronic computing apparatus, which can handle any of the expressions involved with dispatch once the "program" had been set up. However, usually it is only values in regions of special interest that are required, and these can be obtained quite rapidly with a desk calculator.

10B. ESTIMATION OF EQUILIBRIUM YIELD—METHOD OF THOMPSON AND BELL (1934)

In the second paragraph of Section 1F the technique was described of computing the weight of a population by combining an age frequency distribution with the empirically determined average weight of fish of successive age groups. Abundance at successive ages can be computed from appropriate series, for example those of expressions (1.13), (1.27) or (1.28), and each such frequency is multiplied by the average weight of the fish at this age.

The weight of fish dying at each age is then i times the average weight of the stock at that age, and this is divided between fishing and natural causes in the ratio of their respective instantaneous mortality rates, $p:q$. This is essentially the procedure adopted by Thompson and Bell (1934, p. 29) to compute yield under equilibrium conditions, for different combinations of fishing and natural mortality[1]. It can be used to compute, by successive trials, either or both of two pieces of information:

(1) the value of p which produces maximum yield (in weight) for a given value of q.

(2) the value of p which produces maximum yield for a given value of i.

This procedure ignores a probable direct effect of fishing upon the average weight of the fish in a stock: if growth and fishing are concurrent but recruitment is not, then the greater the rate of fishing, the smaller is the average size (during

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[1] However, Thompson and Bell divide the total mortality in the ratio of m to n, instead of p to q, when computing separate shares for catch and natural mortality. In situations where neither p nor q is really large, $m:n$ is a fair approximation to $p:q$, but it is just as easy to use the correct ratio.

the fishing season) of a fish of a given age, because more are taken early in the season before much growth is made. However the method is often useful for orientation.

Among computations of this type, the curves of Tester (1953) are of considerable interest: they show the variation in equilibrium yield per unit weight of recruits that occurs with change in rate of fishing and change in natural mortality rate, for three different types of weight-age relationship.

Example 10a. Computation of Equilibrium Yields at Different Levels of Fishing Effort by Thompson and Bell's Method

A population is characterized by an instantaneous natural mortality rate of $q = 0.35$, and by the distribution of average individual weights at successive ages shown in column 2 of Table 10.1. If fishing occurs concurrently with natural mortality, what rate of fishing gives maximum yield?

Table 10.1. Computation of survivors and annual yield from an annual recruitment of 1000 fish at the start of age 3, under equilibrium conditions. The instantaneous rate of natural mortality is 0.35, and of fishing is 0.50. Individual weights at each age are as shown in column 2.

1 Age	2 Average weight	3 Initial population	4 Deaths	5 Catch	6 Yield
	lb.	*pieces*	*pieces*	*pieces*	*lb.*
3	4.1	1000	573	337	1380
4	12.2	427	245	144	1760
5	19.4	182	104	61	1180
6	24.2	78	45	26	630
7	27.1	33	19	11	300
8	30.0	14	8	5	150
9+	(32)	6	6	4	130
Totals			1000	588	5530

The computation for a rate of fishing $p = 0.5$ is shown in columns 3–6 of Table 10.1. The sum of instantaneous natural mortality rate and rate of fishing is $0.35 + 0.50 = 0.85$ $(= i)$, and this determines a survival rate of $s = 0.427$ (Appendix II). A stock of 1000 fish on hand at the start of age 3 is reduced to 427 in one year, to 182 the next year, etc. Total deaths each year are found by subtraction, and the fishery takes 0.5/0.85 or 58.8% of these (column 5). These numbers, multiplied by the average weight at each age, give the poundage removals shown in column 6. The total is 5530 lb. per 1000 recruits to age III—a result which is correct within about 100 lb.

Similar calculations for other rates of fishing give the results shown in Table 10.2. Maximum yield is apparently obtained with a rate of fishing slightly greater than 0.5. However, the important conclusion would be that there is a broad range of p-values over which yield varies very little: from 0.35 to 0.8 no really significant change occurs.

TABLE 10.2. Catch and yield per 1000 recruits for different rates of fishing of the population of Table 10.1. Also the average weight of a fish caught, in pounds, and the yield, in weight, per unit of fishing effort, expressed on an arbitrary scale (effort is considered as proportional to rate of fishing).

1 Rate of fishing	2 Catch	3 Yield	4 Av. weight of a fish	5 Yield per unit effort
p	*pieces*	*lb.*	*lb.*	
0.2	363	4600	12.7	100
0.35	500	5370	10.7	67
0.5	588	5530	9.4	48
0.65	650	5400	8.3	36
0.8	695	5270	7.6	29

Although the total poundage taken does not change much, the catch per unit of effort and the average size of the fish caught both change rapidly at the different levels of p shown in Table 10.2. Either one of these might largely determine the most suitable type of regulation, depending on the kind of fishery involved and the commercial or esthetic value of fish of different sizes.

10C. ESTIMATION OF EQUILIBRIUM YIELD—METHOD OF RICKER (1945c)

The mechanics of a direct balancing of growth rate against death rate, in order to compute net change in bulk of a year-class, have been presented in Section 1F. In applying the method to a whole population, a break-down must be made into segments of the life of the fish such that neither growth rate nor mortality rate are changing too rapidly within any period.

The combined estimate of equilibrium yield (Y_E) under given conditions can be represented by the expression below, derived from (1.35):

$$Y_E = \sum_{T=T_R}^{T=T_\lambda} p_T \overline{W}_T \qquad (10.1)$$

The new symbols are as follows:

T successive intervals or periods in the life of the fish (these not necessarily of equal length)

T_R the first period under consideration

T_λ the last period under consideration (usually the last period in which an appreciable catch is made)

Other symbols are as in Section 1C.

The easiest and most useful estimate of average weight of stock, $\overline{W}$, is the arithmetic mean of the initial and final value of W for each interval[2]. Designating the stock at the start and finish of interval T as $W_{T(0)}$ and $W_{T(1)}$, this average is:

$$\overline{W}_T = \frac{W_{T(0)} + W_{T(1)}}{2} = \frac{W_{T(0)}(1 + e^{g_T - i_T})}{2} \tag{10.2}$$

Hence the yield is equal to:

$$Y_E = \sum_{T=T_R}^{T=T_\lambda} \left(\frac{p_T W_{T(0)}(1 + e^{g_T - i_T})}{2} \right) \tag{10.3}$$

Actually the formulae above rather disguise the simplicity of the procedure, which is illustrated in Example 10B. Computations are carried out in tabular form, and are extremely flexible. Age differences in rate of growth, in rate of fishing and in rate of natural mortality, different minimum size limits, and different seasonal distributions of growth, fishing and natural mortality can all be examined easily and directly. Moreover, there is no need to worry about whether growth conforms to some special law, nor is there any restriction on the value of b in the weight-length relationship.

To reduce the number of steps in the computation it will usually be convenient to divide the fish's life into intervals (T) that are of different lengths. At ages where p or g is changing rapidly, it may be desirable to make it as short as a month or two[3], but if these parameters are relatively steady, a year or even several years may be a sufficiently fine division.

COMPUTATION OF BEST MINIMUM SIZE. One important function of computaitions of this sort is to discover the *minimum size* which gives maximum yield from a given weight of recruits. We have defined the *critical size* as the size

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[2] If a stock were increasing or decreasing strictly exponentially, its average size would not be the arithmetic mean (10.2), but rather expression (1.33), which may be written here as:

$$W_T = \frac{W_{T(o)}(e^{g_T - i_T} - 1)}{g_T - i_T} \tag{10.4}$$

Values of this expression can be obtained readily enough, because the factor $(e^{g_T - i_T} - 1)/(g_T - i_T)$ is available in Appendix II: column 5 shows its value for positive values of $g_T - i_T$, and column 4 for negative values, $g_T - i_T$ being equated to the i in column 1. However, mainly because rate of growth decreases throughout the life of a fish, a graph of year-class bulk against time tends to be convex (dome-shaped) with a "tail" to the right, whereas the exponential segments used to approximate it are all concave upward. Even the tail, which is concave upward, is less concave than the individual exponential segments (cf. Fig. 10.1). The result is that the arithmetic mean of the initial and final values of each of these segments is a somewhat better average to use than is (10.4). In practice, when the fish's life is divided into intervals of suitable length, there is very little difference between (10.4) and the arithmetic mean for each interval.

[3] In an analogous computation of the production (sense of Ivlev) of fingerling salmon, Ricker and Foerster (1948) used half-month intervals while the young fish were very small and both the growth rate and the natural mortality rate were changing rapidly.

at which the instantaneous rates of growth and of natural mortality are equal (Section 1F). At that time and size the year-class has its maximum bulk. If the brood could all be cropped at once, that would be the best time to do it. However instantaneous cropping is possible only in piscicultural establishments, where a pond can be drawn down and all the fish removed. If cropping must be spread over a period of time, then some loss in efficiency of cropping occurs. The aim should be to keep such losses to a minimum, and this is done by taking some of the fish when they are less than the critical size, and some when they are greater. The smaller the rate of fishing, the broader the range of sizes that should be taken (Ricker, 1945c)—that is, the smaller should be the mimimum size limit.

SEASONAL INCIDENCE OF NATURAL MORTALITY. In yield computations of all types a persistent minor worry is our (usual) lack of information concerning *when* natural mortality takes place. Often it is advisable to examine two or more possibilities and see what difference there is in the results obtained. If a fishery is restricted to a short season one might, for example, postulate that for practical purposes there was no natural mortality during the fishing season. With a longer season, the instantaneous rate of natural mortality rate might be divided in proportion to the length of time involved—part being combined with the rate of fishing, and the remainder acting by itself.

EXAMPLE 10B. EQUILIBRIUM YIELD OF BLUEGILLS, PER UNIT RECRUITMENT, FOR MUSKELLUNGE LAKE, INDIANA

Data concerning the stock of *Lepomis macrochirus* in Muskellunge Lake are shown in Table 10.3. (Growth and natural mortality were determined from samples taken and experiments made in 1941-42; however the level of fishing shown is that believed characteristic of 1939-40, before the war decline in fishing.) The growth of the fish was read from scales. The computed mean lengths were interpolated on a smooth curve at quarter-year intervals, and were converted to weight using the "year-class-*b*". The "year" in this case is the growth year, which is considered to last 6 months: from about May 1, when new circuli begin to appear on the scales, up to the end of November when the lake is well cooled. Thus the quarter-years of the growth curve are really 1/8 year long on the calendar. Lengths and weights are indicated in columns 3 and 4 of Table 10.3, on this basis, May 1 being considered as the start of the year. Column 5 is the natural logarithm of weight, and the difference between the natural logarithms of two adjacent values is the instantaneous growth rate for the interval concerned (column 6).

Fishing in Muskellunge Lake occurred almost wholly during the period June 16-September 15; records kept in 1941 showed that 66% of the total pole-hours were in June 16-July 31, and 34% were later. (May 1 to June 15 was closed to fishing at that time.) Accordingly, of a total rate of fishing of 0.5, 0.33 is assigned to the second eighth of the year, and 0.17 to the third (column 8). In the year of recruitment not many age 2 individuals would be large enough to be caught during the second eighth, but nearly all would be vulnerable by the end of the third eighth, and the p-values are adjusted accordingly.

Natural mortality is estimated as equal to about 0.6, from tagging and age-composition studies (Ricker, 1945a). There is some evidence that it is at least fairly well distributed throughout the year; and here it is divided up equally: 0.075 is assigned to each of the four summer eighths, and 0.3 to the winter half (column 7). At age 5 the natural mortality is made to increase progressively, because older fish are relatively scarcer.

Column 9 is the resultant of growth and all mortality: i.e., $(g-q-p)$ or $(g-i)$. From this a "change factor" is obtained, equal to e^{g-i}, and obtainable from any exponential table or from Appendix II (column 12 plus unity when $g-i$ is positive; column 3 when it is negative). In column 11 of Table 10.3 the successive population weights are computed, starting with an arbitrary 1000 weight units. Column 12 is the arithmetic average of adjacent stock sizes, and in column 13 these are multiplied by p to give the yield obtained during each interval. Columns 12 and 13 need be computed only for the intervals when there was a fishery.

A convenient check is provided by summing the instantaneous rates for each year, or for the whole series, and comparing with the appropriate figure in column 11. For example, the grand total of $g - i$ is -2.690, and $1000e^{-2.69} = 68$, as in column 11.

The sum of column 13 indicates that 2.29 lb. of bluegills are caught from the lake for every pound of age 2 recruits. (Fish age 6 and older would not add to this appreciably.)

Of the numerous variations of the Table 10.3 conditions that can be examined, we will mention here only the possibility of opening the period May 1 to June 15 to fishing. What would its effect be on yield? In the absence of any increase in total amount of fishing, a likely distribution of rate of fishing under the new conditions would be 0.15, 0.20 and 0.15, respectively, in the first three eighths of the year, for fully-recruited fish. (The actual distribution of course would depend on the fishermen themselves.) Used in a table like 10.3, these rates indicate practically no change in the yield per unit recruitment. In practice, however, opening the spring season would likely increase overall fishing effort for the year, and this results in some increase in computed equilibrium yield (cf. Example 10c).

Example 10c. Equilibrium Yield when Fishing is Considered to Act throughout the Year. Effects of Varying Minimum size and Overall Rate of Fishing

In an earlier treatment of the data of Example 10b, fishing and natural mortality were considered as acting at a uniform instantaneous rate throughout the year; growth was not considered uniform, but the decreasing instantaneous rate was divided among the four *quarters* of the statistical year (instead of the

Table 10.3. Instantaneous rates of growth (g), natural mortality (q) and fishing mortality (p) for bluegills of Muskellunge Lake, distributed according to their observed or (for q) hypothetical seasonal incidence; and the computation of equilibrium yield, in successive fishing seasons, from 1000 weight-units of recruits at age 2.

1 Date	2 Age	3 Length	4 Weight	5 $\log_e$(wt.)	6 g	7 q	8 p	9 $g-p-q$	10 Weight change factor	11 Weight of stock	12 Average weight	13 Yield
	years	*mm.*	*g.*									
May 1...	2	95	13	2.56						1000		
					0.81	0.075	0	+0.735	2.086			
June 16...	2⅛	109	29	3.37						2086		
					0.41	0.075	0.04	+0.295	1.343		2444	98
Aug. 1...	2¼	122	44	3.78						2801		
					0.28	0.075	0.14	+0.065	1.067		2894	405
Sept. 15..	2⅜	135	58	4.06						2988		
					0.17	0.075	0	+0.095	1.100			
Nov. 1...	2½	145	69	4.23						3287		
					0	0.300	0	−0.300	0.741			
May 1...	3	145	69	4.23						2435		
					0.15	0.075	0	+0.075	1.078			
June 16..	3⅛	153	80	4.38						2625		
					0.13	0.075	0.33	−0.275	0.760		2310	762
Aug. 1...	3¼	160	91	4.51						1995		
					0.11	0.075	0.17	−0.135	0.874		1870	318
Sept. 16..	3⅜	165	101	4.62						1744		
					0.08	0.075	0	+0.005	1.005			
Nov. 1...	3½	170	110	4.70						1752		
					0	0.300	0	−0.300	0.741			
May 1...	4	170	110	4.70						1297		
					0.07	0.075	0	−0.005	0.995			

TABLE 10.3 (concluded)

1 Date	2 Age	3 Length	4 Weight	5 log$_e$wt.	6 g	7 q	8 p	9 $g-p-q$	10 Weight change factor	11 Weight of stock	12 Average weight	13 Yield
	years	*mm.*	*g.*									
June 16..	4⅛	175	118	4.77						1291		
					0.07	0.075	0.33	−0.335	0.715		1107	365
Aug. 1...	4¼	178	125	4.84						923		
					0.05	0.075	0.17	−0.195	0.823		841	143
Sept. 16..	4⅜	182	131	4.89						759		
					0.04	0.075	0	−0.035	0.966			
Nov. 1...	4½	185	137	4.93						734		
					0	0.300	0	−0.300	0.741			
May 1...	5	185	137	4.93						544		
					0.04	0.075	0	−0.035	0.966			
June 16..	5⅛	188	143	4.97						525		
					0.03	0.105	0.33	−0.405	0.667		438	144
Aug. 1...	5¼	191	148	5.00						350		
					0.04	0.140	0.17	−0.270	0.763		308	52
Sept. 16..	5⅜	193	153	5.04						267		
					0.03	0.200	0	−0.170	0.844			
Nov. 1...	5½	195	158	5.07						226		
					0	1.200	0	−1.200	0.301			
May 1...	6	195	158	5.07						68		
Totals....					2.51	3.52	1.68	−2.690				2287

TABLE 10.4. Instantaneous rates of growth (*g*), natural mortality (*q*) and fishing mortality (*p*), for bluegills of Muskellunge Lake. In contrast to Table 10.3, fishing as well as natural mortality is divided evenly through the year, while growth is distributed through the whole year but a separate rate is used for each quarter; however the sums of *g*, *q* and *p* are the same in both tables. Recruitment occurs mainly during the age 2½–2¾ interval, to which a reduced value of *p* is assigned. (122 mm. fork length was the legal limit of size, but the fish did not at once become fully acceptable to fishermen.)

1 Age	2 Mean length	3 Mean weight	4 *g*	5 *q*	6 *p*	7 *g-p-q*	8 Weight change factor	9 Weight of stock	10 Average weight	11 Yield
	mm.	*g.*						*kg.*	*kg.*	*kg.*
2	95	13						1000		
			0.81	.15	0	+.660	1.935			
2¼	109	29						1935		
			0.41	.15	0	+.260	1.297			
2½	122	44						2510		
			0.28	.15	.055	+.075	1.078		2608	143
2¾	135	58						2705		
			0.17	.15	.125	−.105	0.901		2572	321
3	145	69						2438		
			0.15	.15	.125	−.125	0.883		2294	287
3¼	153	80						2152		
			0.13	.15	.125	−.145	0.865		2007	251
3½	160	91						1862		
			0.11	.15	.125	−.165	0.848		1720	215
3¾	165	101						1579		
			0.08	.15	.125	−.195	0.823		1439	180
4	170	110						1299		
			0.07	.15	.125	−.205	0.815		1179	147
4¼	175	118						1059		
			0.07	.15	.125	−.205	0.815		961	120
4½	178	125						863		
			0.05	.15	.125	−.225	0.798		776	97
4¾	182	131						689		
			0.04	.15	.125	−.235	0.790		616	77
5	185	137						544		
			0.04	.18	.125	−.265	0.767		480	60
5¼	188	143						417		
			0.03	.34	.125	−.435	0.647		344	43
5½	191	148						270		
			0.04	.50	.125	−.585	0.557		210	26
5¾	193	153						150		
			0.03	.70	.125	−.795	0.452		109	14
6	195	158						68		
Total			2.51	3.52	1.68	−2.690				1981

first four eighths). Table 10.4 is a computation made on this basis[4]. The same total instantaneous rates of growth, fishing and natural mortality are used in each year, but the computed yield is less: 1.98 lb. per pound of recruits, instead of 2.29 lb. Figure 10.1 shows the reason for this difference: Table 10.3 permits the large excess of growth over mortality which exists in spring (May 1-June 15) to increase the stock to a high level, and the fishery acts on it at that high level; also, ⅝ of the natural mortality occurs after the fishing is all over for the year.

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[4] There are minor differences in the earlier computation, notably that growth was estimated by taking tangents at the even years, halves and quarters. Consequently Table 10.4 here is not directly comparable with table 1 of Ricker (1945c).

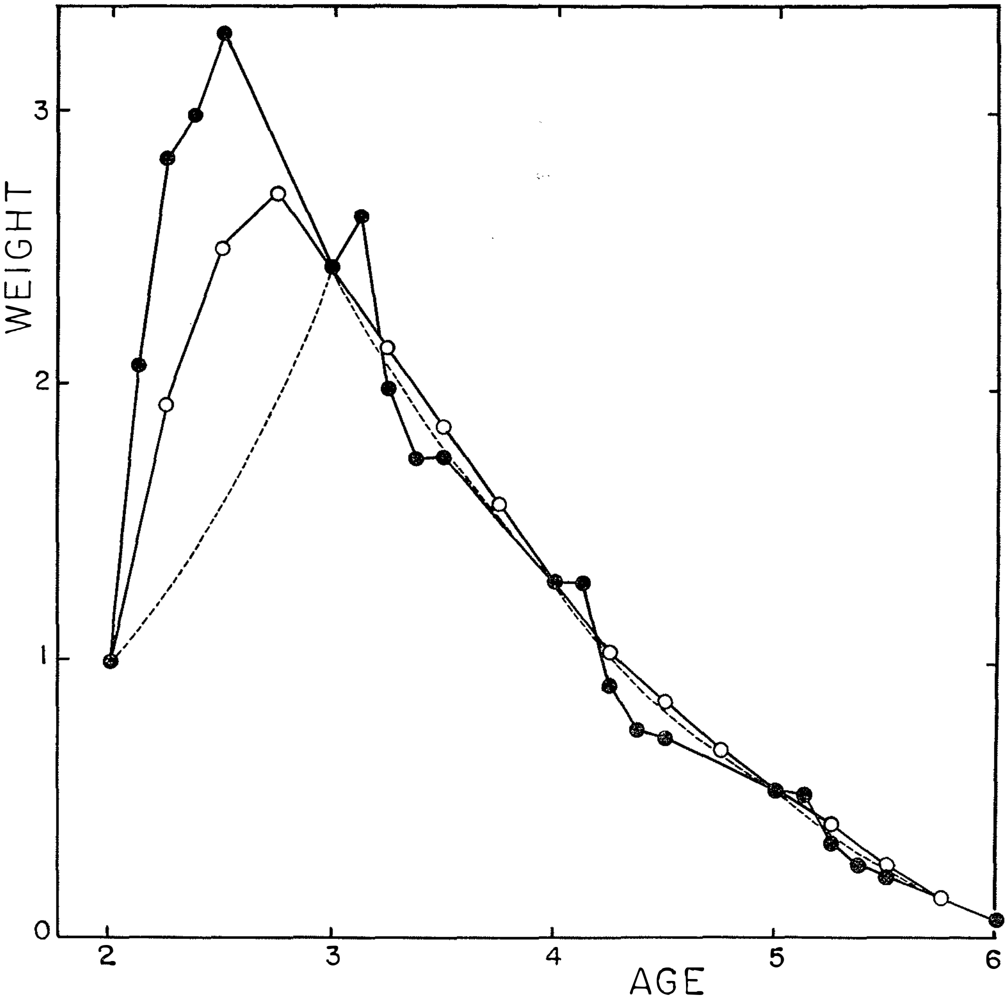

Figure 10.1. Course of change in weight of a year-class in the populations of Table 10.3 (solid circles) and Table 10.4 (open circles). The dotted line comprises successive segments of exponential curves obtained by computation from the net instantaneous rate of increase or decrease for each full year.

In Table 10.4, by contrast, fishing and natural mortality are brought into play with full force from the beginning of the year (for fully-recruited ages).

For some purposes, however, failure to use a true seasonal distribution of these various factors is not important. The absolute level of yield obtained, per unit recruitment, may then be somewhat fictitious; but *changes* in that level will be accurate enough, relatively, and can provide most of the information sought for. In particular, a computation like Table 10.4 is completely suitable for examining effects of an overall increase or decrease in rate of fishing, and reasonably suitable for examining changes in minimum size—though the more realistic Table 10.3 is just as easy to construct.

To determine the yields from a variety of size limits, it is not necessary to repeat the whole of the computation in Table 10.3 or 10.4 each time[5]. Suppose, for example, we were examining, in Table 10.3, the effect of a limit which would protect all age 2 fish. Then the p entries between age $2\frac{1}{8}$ and $2\frac{3}{8}$ become zero, and there are corresponding changes in columns 9-11, while the yield at that age is of course zero. The new regime permits the survival to age $2\frac{3}{8}$ of 3574 weight units of stock ($= 1000e^{1.275}$), instead of the 2988 shown in the table. However, from that age onward these fish are subject to the same conditions as before; so the new yield will be 3574/2988 or 1.196 times the old yield of fish age 3 and older, namely $1.196 \times 1784 = 2134$ weight units. Thus the proposed change would decrease by 7% (from 2287 to 2134) the yield per unit weight of recruits.

Changes in rate of fishing and in minimum size for Muskellunge bluegills were examined (Ricker, 1945c) in a computation similar to Table 10.4. In addition to $p = 50\%$ (applicable to 1939-40), there was used $p = 30\%$ which was close to the 1942 rate of fishing in this lake, and also the rather large value of $p = 100\%$. This last figure constitutes a rather extreme extrapolation from the observed data, but was included for purpose of illustration. The relative yields for these three different rates of fishing, and for six different minimum sizes, were as follows:

Minimum fork length	Rate of fishing (p)		
mm.	0.3	0.5	1.0
102	76	96	110
116	77	99	120
122	76	100	125
128	75	99	128
140	71	95	125
149	65	88	119

The yields shown are relative to 1939-40 conditions ($p = 0.5$), these being taken as 100. As it turned out, the optimum or "eumetric" size limit for getting greatest yield from recruits at the 1939-40 rate of fishing was approximately the legal minimum actually in use. For the reduced fishing of the war years ($p = 0.3$) the best limit would have been somewhat less, and for any rate of fishing substantially greater than 0.5 the best minimum would be somewhat greater than 122 mm. (5 inches total length).

However, what is of most interest is the rather close *agreement* among calculated yields at each rate of fishing. For example, with minima anywhere from 102 to 140 mm., for $p = 0.5$, yield is never less than 95% of the maximum. This same stability has appeared in parallel computations (by this or other methods), for most other fisheries examined to date, and it has a number of implications. For one thing, there is considerable leeway allowed for errors in the data from which the computation of minimum size is made. Secondly, it is evidently not an important matter to determine the *exact* optimum minimum size for maximum yield. Third, if it were known that a certain minimum size is best from the point of view of regulating the size of the stock so as to obtain

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[5] For a worked-out example of this type of computation, see columns 9-11 of table 8 of Chatwin (1958).

optimum recruitment, then a considerable adjustment of the minimum can be made to meet this requirement without sacrificing any significant part of the yield from whatever recruits actually appear. Fourth, if either the individual size of the fish caught, or the catch per unit of effort, are important considerations in respect to the fishery, either of these can be favoured by the regulations to a considerable degree without significant loss of yield. Fifth, if the minimum size has to be specified as what a given mesh of net will catch, rather than a fixed limit based on measurement of individual fish, then this will usually be almost as effective as a sharp cut-off size (though the fate of the rejected fish needs to be considered: whether they survive or die). Finally, if it is desirable to have a uniform minimum standard apply to a number of bodies of water, or even to different kinds of fish, for which the optimum minima are different, this will be possible without any great sacrifice of yield, provided the optima are not *too* diverse.

10D. Estimation of Equilibrium Yield—Method of Baranov (1918)

Baranov (1918, p. 92) developed expressions for yield, applicable to stocks of fish in which growth in length is the same in successive years among the commercial-sized stock, and in which weight is proportional to the cube of length. To facilitate the combination of growth and mortality into one expression, the instantaneous total mortality rate is expressed in terms of the unit of time in which the fish grows a unit of length; so that, in effect, length can be used as a measure of time. The following symbols will be used:

l	fish length, in centimeters for example
d	the annual increase in length of a fish, in the same unit as l
i'	($= i/d$) the instantaneous rate of decrease in numbers of an age-group, referred to the interval of time in which it grows one unit of length (i' = Baranov's K)
L	the length of a fish at recruitment
b	a constant such that the weight of a fish, in grams for example, is equal to bl^3 (b = Baranov's w)
R′	the number of fish recruited at length L during $1/d$ of a year, recruitment being at a constant absolute rate throughout the year
N_0'	a constant; described by Baranov as the (hypothetical) number of fish which appear during time period 0, computed as though the mortality rate i' were constant back to that time. (N_0' is not used in actual calculations.)

From the definitions above:

$$R' = N_0' e^{-i'L}$$

Baranov shows, by argument analogous to that leading to expression (1.27) above, that the *number* of fish of commercial size in a balanced population is:

$$\overline{N} = \int_{l=L}^{l=\infty} N_0' e^{-i'L}\, dl = \frac{N_0' e^{-i'L}}{i'} = \frac{R'}{i'} \qquad (10.5)$$

This is of course equal to the R/i of (1.27).

The *weight* of the commercial population is:

$$\overline{\mathrm{W}} = \int_{l=\mathrm{L}}^{l=\infty} \mathrm{N}_0' b l^3 e^{-i'l} dl$$

$$= \frac{b\mathrm{L}^3\mathrm{N}_0' e^{-i'\mathrm{L}}}{i'} \left(1 + \frac{3}{i'\mathrm{L}} + \frac{6}{(i'\mathrm{L})^2} + \frac{6}{(i'\mathrm{L})^3}\right)$$

$$= b\mathrm{L}^3\overline{\mathrm{N}} \left(1 + \frac{3}{i'\mathrm{L}} + \frac{6}{(i'\mathrm{L})^2} + \frac{6}{(i'\mathrm{L})^3}\right) \tag{10.7}$$

The integration factor which appears in brackets above can be designated by the letter Q for convenience (Baranov's q). Rearranging (10.7):

$$\mathrm{Q} = 1 + \frac{3}{i'\mathrm{L}} + \frac{6}{(i'\mathrm{L})^2} + \frac{6}{(i'\mathrm{L})^3} = \frac{\overline{\mathrm{W}}/\overline{\mathrm{N}}}{b\mathrm{L}^3} \tag{10.8}$$

The numerator of the RHS of (10.8) is the average weight of a fish in the population, while the denominator is the weight of a recruit. Thus Q is a factor which reflects the gain in weight made by an average fish from time of recruitment to time of death.

The mean weight of the commercial stock (10.7) may also be written in terms of recruitment, R′ or R:

$$\overline{\mathrm{W}} = \frac{\mathrm{R}'b\mathrm{L}^3\mathrm{Q}}{i'} = \frac{\mathrm{R}b\mathrm{L}^3\mathrm{Q}}{i} \tag{10.9}$$

Having found the mean population on hand, in numbers and in weight (expressions 10.5 and 10.9), a year's catch is of course obtained by multiplying these by the rate of fishing, p:

$$\text{Catch in numbers} = \mathrm{C} = \frac{p\mathrm{R}}{i} \tag{10.10}$$

$$\text{Yield in weight} = \mathrm{Y} = \frac{pb\mathrm{L}^3\mathrm{QR}}{i} = \mathrm{C}b\mathrm{L}^3\mathrm{Q} \tag{10.11}$$

Expression (10.11) is well adapted to examining the effects of a change in rate of fishing, or in size at recruitment, L. Baranov illustrates the former in his figure 10, and the latter in figure 11.

The assumptions underlying this method are rather restricting, as compared with those of Section 10C. Some of the difficulties which arise are as follows:

1. In some populations growth in length does not in fact remain even approximately constant over the main range of commercial sizes.

2. In some fishes the exponent in the length-weight relationship deviates considerably from 3.

3. There is no flexibility in respect to mortality: all fully-recruited broods must be considered as subject to equally severe attack, whether by man or by natural woes.

4. Usually fish do not suddenly become catchable at some specific size; rather, their vulnerability increases over a range of sizes and ages, which in some instances occupies quite a number of years. This difficulty is minimized by making L the middle of the range of increasing vulnerability, but often this middle value is not too easy to decide, and in any event there may be a need to estimate rate of fishing for each year of recruitment individually.

In spite of these drawbacks, the Baranov method has the advantage of ease and brevity, and there are likely to be many situations where it is of real value, particularly when the effects of only small deviations from existing conditions are being examined. For that matter, calculations involving large deviations will usually be of doubtful applicability, no matter what method is used.

EXAMPLE 10D. POPULATION AND CATCH OF NORTH SEA PLAICE AT VARIOUS RATES OF FISHING AND NATURAL MORTALITY, BY BARANOV'S METHOD

Baranov's application of his method was to North Sea plaice (*Pleuronectes platessa*) as of about 1906, but we will use here the data for modern conditions given by Beverton (1954, pp. 97, 158a-c). The growth in length of plaice is not in fact linear, but it is not far from it over the ages 5 to 10 years which make up the bulk of the catch: the increase averages 3.0 cm. per year over that range. Let us examine first the actual situation where natural mortality, q, is 0.163, and fishing mortality, p, is 0.665 (Beverton's estimates), hence $i = 0.828$. We have:

$d = 3.0$ cm./year

$i' = 0.828/3.0 = 0.276$

$L = 25.2$ cm. (mean length at recruitment)

$i'L = 6.95$

$b = 0.00892$

$bL^3 = 143.4$ g. (mean weight at recruitment)

From the above we calculate the factor Q as:

$$Q = 1 + \frac{3}{6.95} + \frac{6}{6.95^2} + \frac{6}{6.95^3} = 1.574$$

Thus an average fish has a chance to grow in weight by 57%, after recruitment, before it is caught or dies. If R is the annual *number* of recruits, the mean *weight* of stock on hand is, from (10.9):

$$R \times \frac{143.4}{0.828} \times 1.574 = 273 \text{ R } \textit{grams}$$

or 273 times the yearly number of recruits. The yield is, from (10.11):

$$0.665 \times 273 \text{ R} = 182 \text{ R } \textit{grams}$$

that is, 182 times the yearly number of recruits.

To examine the effect, upon yield, of having other average recruitment sizes (obtained by using other sizes of mesh in the trawls), appropriate changes are made in L, bL^3 and $i'L$. Still using $p = 0.665$ and $i = 0.828$, a schedule can be calculated as follows:

1. Mean length at recruitment, in cm. (L)	15	20	25.2	30	40
2. Mean weight at recruitment, in g. (bL^3)	30.1	71.4	143.4	241	571
3. $i'L$	4.14	5.52	6.95	8.28	11.04
4. Yield per recruit, in grams	53	103	182	283	605
5. Survival from a length of 15 cm. to the mean length at recruitment	1.0	0.762	0.575	0.443	0.250
6. Yield per fish reaching 15 cm., in grams	53	78	105	125	151

Lines 5 and 6 above are necessary to put the yields on a comparable basis, because in the pre-recruitment phase the fish are decreasing from natural mortality. The latter is $q = 0.163$, or 0.0543 on a centimeter-of-growth basis. The factors in row 5 are therefore calculated from $e^{-0.0543(L-15)}$, where L is the recruitment size under consideration.

It appears that *increasing* the mesh size would tend to increase yield under these circumstances, which is the same conclusion as comes from Beverton and Holt's method, described below. Quantitatively, by using Baranov's method the estimated yields for small L are somewhat too small, and those for large L too great, because this computation does not take into account that the absolute yearly increase in length actually decreases with increasing age.

10E. ESTIMATION OF EQUILIBRIUM YIELD—METHOD OF BEVERTON AND HOLT

This method has been made available in publications of Graham (1952), Beverton (1953), Parrish and Jones (1953), Beverton and Holt (1956, 1957) and the lecture notes of Beverton (1954). It resembles Baranov's, but uses the more widely applicable Brody-Bertalanffy age-length relationship described in Section 9D. The applicability of this relationship to any population can be tested by plotting a Walford graph. In cases where it adequately describes the growth in length of the commercial-size stock, this procedure removes the first of the difficulties that were mentioned on page 218, though the others remain.

The following symbols are used:

t	age in years; it can be measured from any convenient origin: oviposition, or hatching, or the start of the calendar year in which these occur
t_0	the (hypothetical) age at which the fish would have been zero length if it had always grown according to the Bertalanffy relationship
t_Q	a standard minimum age of reference for the unit number of fish of each year-class which the computations deal with; conveniently it is the average age at which they become acceptable as objects of food, or when they *first* become vulnerable to some common type of fishing (t_ρ of Beverton and Holt)
t_R	age of recruitment (*average* age at which the fish become vulnerable to the gear under consideration) ($t_{\rho'}$ of Beverton and Holt)

Q	yearly number of individuals which reach age t_Q
R	yearly number of recruits which enter the fishery at age t_R (= R′ of Beverton and Holt)
t_λ	"the end of the life-span", or maximum age attained
p	instantaneous rate of fishing—considered constant over the life span after recruitment (F of Beverton and Holt)
q	instantaneous rate of natural mortality—considered constant after time t_Q (M of Beverton and Holt)
i	instantaneous total mortality rate—considered constant after time t_R ($i = p + q$)
C	yield or catch, in numbers (Y_N of Beverton and Holt)
Y	yield in weight units (Y_W of Beverton and Holt)
l_∞	the average asymptotic or average maximum size of a fish, as determined by (9.6) above
w_∞	the average weight of the fish of a brood when its average asymptotic length is l_∞
K	$-\log_e k$, where k is the slope of the Walford line (Section 9D)

Over the period of time before recruitment, the initial number of fish decreases by natural mortality only, so that the number at recruitment is:

$$R = Qe^{-q(t_R - t_Q)} \tag{10.12}$$

This expression is involved whenever the effect of varying the age at recruitment is being examined, but it is convenient to keep it separate from the production equation.

After recruitment, the yield in numbers is the rate of fishing times the average population:

$$C = p\int_{t=t_R}^{t=t_\lambda} Re^{-i(t-t_R)}dt \tag{10.13}$$

and yield in weight is therefore:

$$Y = p\int_{t=t_R}^{t=t_\lambda} Rw_t e^{-i(t-t_R)}dt \tag{10.14}$$

Omitting p, the integral (10.14) above would be the sum of the yearly average bulk of all fish in a year-class, for all the years that it contributes to the fishery. If recruitment is invariable from year to year, this is equal to the weight of commercial stock on hand.

Expression (9.13) of Section 9F describes the weight of a fish at age t, when the growth is of the Brody-Bertalanffy type. Provided this type of growth prevails over the fishable life span, and when growth of the brood is isometric (year-class-$b = 3$), we may write:

$$w_t = w_\infty\left(1 - e^{-K(t-t_0)}\right)^3 \tag{10.15}$$

Expanding (10.15) gives:

$$w_t = w_\infty\left(1 - 3e^{-K(t-t_0)} + 3e^{-2K(t-t_0)} - e^{-3K(t-t_0)}\right) \tag{10.16}$$

Substituting (10.16) for w_t in (10.14), and integrating (Beverton, 1954, p. 45), gives:

$$\begin{aligned} Y = pRw_\infty \Bigg(& \frac{1 - e^{-i(t_\lambda - t_R)}}{i} \\ & - \frac{3e^{-K(t_R-t_0)}\left(1 - e^{-(i+K)(t_\lambda - t_R)}\right)}{i + K} \\ & + \frac{3e^{-2K(t_R-t_0)}\left(1 - e^{-(i+2K)(t_\lambda - t_R)}\right)}{i + 2K} \\ & - \frac{e^{-3K(t_R-t_0)}\left(1 - e^{-(i+3K)(t_\lambda - t_R)}\right)}{i + 3K}\Bigg) \end{aligned} \tag{10.17}$$

This is the expanded form of Beverton's (1953) expression (4), omitting the pre-recruitment period which is here considered separately in (10.12)[6].

For many purposes (10.17) is more complex than is necessary, or even desirable. Selection of the quantity t_λ, the greatest age considered, is always somewhat arbitrary and the terms containing it are all close to unity except when i and $(t_\lambda - t_R)$ are both small. The expression can be simplified by omitting such terms, that is, by making $t_\lambda = \infty$. In that manner we obtain:

$$Y = pRw_\infty\left(\frac{1}{i} - \frac{3e^{-K(t_R-t_0)}}{i + K} + \frac{3e^{-2K(t_R-t_0)}}{i + 2K} - \frac{e^{-3K(t_R-t_0)}}{i + 3K}\right) \tag{10.18}$$

The shortened expression (10.18) can always be used safely when i and t_λ are given values close to those which are characteristic of a reasonably intensive fishery—that is, when $i = 0.5$ or more and when t_λ represents the greatest age observed in a sample of 500 to a few thousand individuals. If, for prediction purposes, i is given a considerably smaller value and t_λ is not changed, the full expression (10.17) then describes a population in which an appreciable fraction of the fish reach age t_λ each year, and then suddenly perish. This is true, for example, of the isopleths to the left of A, approximately, in figure 2 of Beverton (1953), which corresponds to the ascending limb and dome of figure 3 of the same paper.

Although the above danger is avoided by using the reduced expression (10.18)—which implies that the old fish continue to die off gradually and evenly at the same rate as younger fish—this may often be biased somewhat in the opposite direction to (10.17). In a number of populations it has been shown that natural mortality rate increases among mature and older fish (cf. Ricker, 1949a; Kennedy, 1954b; Tester, 1955); and the formulae of the present section do not allow for age variation in this statistic, other than a sudden increase to 100%. For a more exact treatment the method of Section 10C is available.

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[6] Recently Jones (MS, 1957) has outlined a simpler form of the yield equation (10.17) which is evaluated using a table of the incomplete Beta function. This form has the additional advantage that the exponent b in the weight-length relationship need not necessarily be exactly 3.

A typical computation of yields from (10.17), for a fairly long-lived fish, the North Sea plaice, is shown in Beverton's (1953) figure 2. The yield contours or isopleths indicate a ridge of high production which starts near the origin of the graph and curves upward and to the right (cf. Fig. 10.2B). A little above the crest of this ridge the line of *eumetric fishing* can be plotted, cutting each contour at the point where a vertical tangent touches it. This line indicates the best minimum average age of first capture for each rate of fishing.

EXAMPLE 10E. COMPUTATION OF EQUILIBRIUM YIELDS FOR A WINTER FLOUNDER FISHERY, BY THE BEVERTON AND HOLT METHOD. (After Dickie and McCracken, 1955.)

Vital statistics and the Bertalanffy growth parameters for the stock of *Pseudopleuronectes americanus* in St. Mary Bay, Nova Scotia, were obtained by Dickie and McCracken, as follows:

$t_Q = 3$ years
$t_R = 3.5$ years
$t_0 = 0$ years
$t_\lambda = 18$ years
$p = 0.25$
$q = 0.36$
$i = 0.61$
$w_\infty = 2.43$ lb.
$K = 0.40$

Taking $Q = 1{,}000{,}000$ fish of age 3, the survivors at age 3.5 years, the mean time of entry to the fishery, are from (10.12):

$$R = 1{,}000{,}000 \; e^{-0.36 \times 0.5} = 835{,}300 \text{ fish}$$

In computing yield, the short expression (10.18) is appropriate, since the largest of the exponentials containing t_λ (in 10.17) is equal to only 0.00014. From (10.18):

$$Y = 0.25 \times 835{,}300 \times 2.43 \left(\frac{1}{0.61} - \frac{3 \times 0.2466}{1.01} + \frac{3 \times 0.0608}{1.41} - \frac{0.0150}{1.81} \right)$$

$$= 522{,}000 \text{ lb. (per million fish at age 3)}$$

This is the point marked "P" in Figure 10.2A. Computations for other values of t_R and p determine the yield surface defined by the contours shown in the same figure. A somewhat smaller natural mortality rate is examined in Figure 10.2B. Though greater yields are evidently physically possible, Dickie and McCracken point out that the relatively greater fishing effort needed to take them would drive the catch per unit of gear below what is economically profitable at the present time—always provided that recruitment did not change.

Dickie and McCracken also computed the landed value in dollars of the flounders taken at different rates of fishing, given that flounders 30 cm. and over sell for 4 cents per pound, and smaller flounders for half as much. The results are shown in two value-isopleth diagrams (their figure 3). The economic

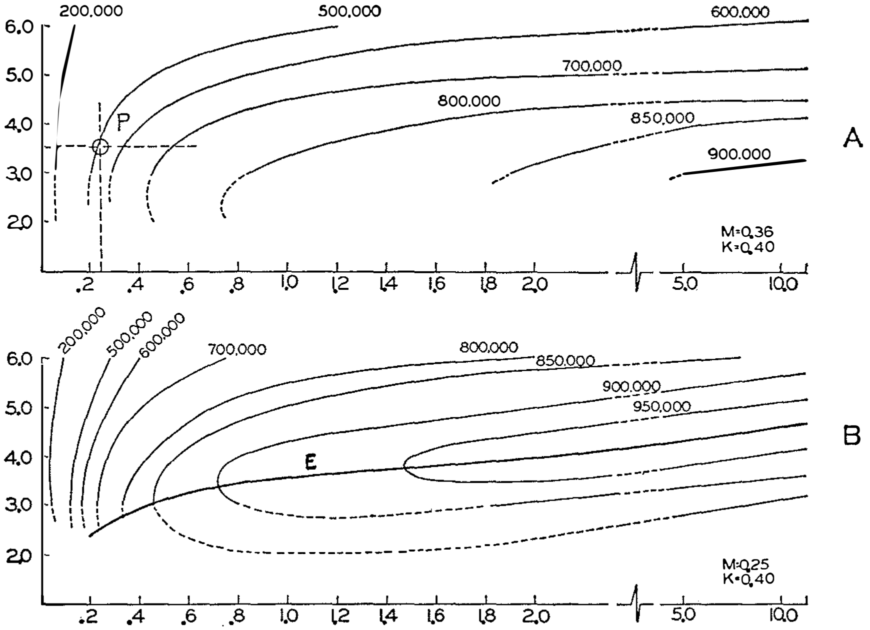

FIGURE 10.2. Contours of equilibrium yield in pounds, for winter flounders of St. Mary Bay, Nova Scotia, for instantaneous natural mortality rates of 0.36 (above) and 0.25 (below). Abscissa: instantaneous rate of fishing. Ordinate: mean age at recruitment. The point P represents the 1953 position of the stock and fishery. The line of eumetric fishing (E) in the lower panel represents the catch which could be taken at each rate of fishing if net mesh size were adjusted to release the smaller flounders at the most favourable average age. (From Dickie and McCracken, 1955, figure 3, slightly modified).

prospects indicated by computations of this type have been examined at greater length by Beverton (1953), Kesteven and Holt (1955) and Holt (1956).

10F. TEMPORARY EFFECTS OF A CHANGE IN THE RATE OF FISHING

The previous Sections of this Chapter have described the *equilibrium* catch to be expected under stated conditions of growth and rate of fishing, with steady recruitment. However, the *immediate* effect of a change in fishing effort is often quite different from its long-term effect.

It is fairly obvious that, in any given season, increased fishing will make for greater catch *at that time*, and less fishing will mean less catch, whatever may happen later. The pattern of change from the immediate yield to the equilibrium yield became known when Baranov (1918) and Huntsman (1918) simultaneously described the effect of a sustained change in mortality rate upon a stock's age composition and upon the catch taken from it. Huntsman showed by pyramidal diagrams that, by imposing an annual fishing mortality rate (m) of $\frac{1}{4}$ upon an unfished stock in which natural mortality rate (n) was $\frac{1}{7}$, the relative number of old fish in the population decreased progressively. Baranov illustrated the same process by examining the effect of an increase in mortality, *a*, from 0.2 to 0.5, using the graph reproduced here as Figure 1.1, and he particularly emphasized the temporary nature of the large increase in catch which follows on such an increase in rate of fishing. Unfortunately neither of these presentations created much impression at the time. Only during the later 1930's, after Thompson and Bell's (1934) excellent exposition and illustrations became available, did a general appreciation of these effects become evident in our fishery literature.

To illustrate these situations, schedules like Table 10.1 or Table 10.3 can be used, but each year must be treated separately during the period of transition

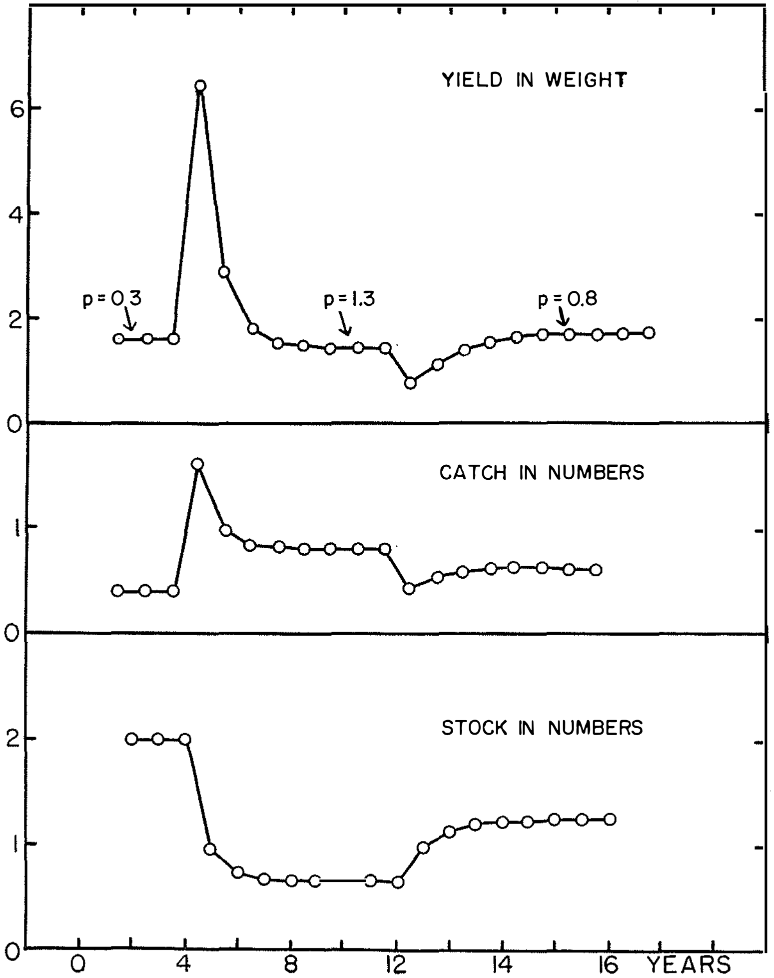

FIGURE 10.3. Trends of yield in weight, catch in numbers, and stock size in numbers, for a stock in which natural mortality, *q*, is 0.2 throughout, and rate of fishing, *p*, changes from 0.3 to 1.3, then to 0.8. The first year of each change is marked by the high peak and low trough respectively, on the yield curve. Values were computed using a model of the type of Table 10.1, with an appropriate age-weight distribution, the same for all years.

from the old to the new rate of fishing. The contrast between equilibrium yields and temporary catch potential is illustrated in Figure 10.3: three very different rates of fishing (p = 0.3, 0.8 and 1.3) have equilibrium levels of yield that are much alike, the intermediate level being slightly the best. A yield *four times* as great, however, is taken in the first year of the change from p = 0.3 to p = 1.3. Similar short-term potentialities exist in any virgin or lightly-fished stock that consists of many age-groups[7]. A stand of virgin timber affords a close analogy.

Familiar and even obvious though these relationships now appear, their discovery in 1918 represented a major feat of imaginative analysis. Furthermore, their practical value to date has probably been greater than that of all the various determinations of equilibrium yield of the kinds described in Sections 10B–10E. This is so for two reasons. 1. The temporary effects of changes in rate of fishing tend to be much greater than the equilibrium effects which are calculated on the basis of constant recruitment, hence it has been easier to check theory against practice and to make useful predictions. 2. Constant recruitment seems unlikely to be a suitable basis for predicting true equilibrium yield at different levels of fishing, in anything more than a minority of stocks (cf. Section 11A); but it is a suitable basis for predicting the *immediate* effect of a change in fishing, because the increased or decreased year-classes resulting from change in stock density (caused by change in fishing) take some years to "grow into" the usable stock.

Moreover, these temporary changes in yield bulk very large in the view of fishermen whenever new regulations are contemplated; and because of this, goals which seem desirable from the equilibrium-yield standpoint must sometimes be approached quite gradually. Conversely, knowledge of the direction and magnitude of expected *temporary* increases or decreases in yield makes it possible to avoid mistaking them for indications of long-term prospects.

EXAMPLE 10F. COMPUTATION OF YIELDS DURING THE PERIOD OF TRANSITION FROM A SMALLER TO A LARGER RATE OF FISHING, FOR THE STOCK OF EXAMPLE 10B.

Table 10.5 shows the effect, upon the population of Table 10.3, of doubling the rate of fishing at all ages. The divisions of the year are condensed to the two fishing periods and the long period between. Column 2 shows the resultants of growth and natural mortality taken from Table 10.3, to which are added the new mortality rates of column 3, giving the new instantaneous rates of population change (column 4) and corresponding change factors (column 5). The latter are applied to previous equilibrium population weights at the *start* of each age shown in column 6 (from column 11 of Table 10.3). The fish of each age decrease in bulk during year 1 as shown in column 7; the average for each period was computed and multiplied by the instantaneous rate of fishing to give the yield

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[7] This effect, perhaps more than any other, accounts for the fisherman's nostalgia for the "good old days" when, for a few years, catch per hour or per set was so much greater than at present. Of course other factors may also be involved. Certain types of relationship between stock density and recruitment can produce a similar effect (Section 11F), though usually less extreme. There may also be increased wariness on the part of the fish, or bad memory on the part of the fisherman (cf. Kennedy, 1956, p. 47). Finally, simply increasing the amount of gear implies a decline even in equilibrium catch per unit, which usually becomes apparent long before the level of maximum sustained yield is reached (cf. Table 10.2).

TABLE 10.5. Effect of doubling the rate of fishing at all ages, upon the population of Table 10.3. (See text for explanation.)

1	2	3	4	5	6	7	8	9	10	11	12	13	14
						Year 1		Year 2		Year 3		Year 4	
Age	g-q	p	g-q-p	Weight change factor	Previous equilibrium weight of stock	Initial weight	Yield	Initial weight	Yield	Initial weight	Yield	Initial weight	Yield
2⅛					2086	2086		2086		2086		2086	
	+0.335	0.08	+0.255	1.290			191		191		191		191
2¼					....	2691		2691		2691		2691	
	+0.205	0.28	−0.075	0.928			726		726		726		726
2⅜					....	2497		2497		2497		2497	
	−0.130	0	−0.130	0.878									
3⅛					2625	2625		2192		2192		2192	
	+0.055	0.66	−0.605	0.546			1339		1118		1118		1118
3¼					....	1433		1197		1197		1197	
	+0.035	0.34	−0.305	0 737			423		353		353		353
3⅜					....	1056		882		882		882	
	−0.300	0	−0.300	0.741									
4⅛					1291	1291		782		654		654	
	−0.005	0.66	−0.665	0.514			645		391		327		327
4¼					....	664		402		336		336	
	−0.025	0.34	−0.365	0.694			191		116		97		97
4⅜					....	461		279		233		233	
	−0.370	0	−0.370	0.691									
5⅛					525	525		319		193		161	
	−0.075	0.66	−0.735	0.480			256		156		94		79
5¼					....	252		153		93		77	
	−0.100	0.34	−0.440	0.644			70		43		26		22
5⅜					....	162		99		60		50	
Totals							3841		3094		2932		2913

shown in column 8. In year 2 the overwinter survivors *of each age* in year 1 are computed and their weight is entered at the start of the next greater age: for example, 2497 × 0.878 = 2192; 1056 × 0.741 = 782; etc. During year 2 fishing occurs and the population decreases at the same rate as in year 1, but the yield is less for age 3 and older. By year 4 the new equilibrium population structure is established, shown in column 13.

The change from the old to the new conditions is completed in four years, which is the number of vulnerable age-groups of fish present in significant numbers. In the first year of change the yield rises to from 2.29 to 3.84 lb. (per pound of age 2 recruits), then falls to 3.09, to 2.93, and finally to the new equilibrium value 2.91 lb.

CHAPTER 11.—RELATION OF RECRUITMENT TO THE SIZE OF THE ADULT STOCK

11A. THE RELATION BETWEEN STOCK AND RECRUITMENT

The reproduction which is accomplished by a fish stock can be assessed at any stage: eggs, larvae, fry, juveniles, smolts, and so on. For practical fishery work what is of most interest is the number of *recruits to the usable stock*.

Considering that fish change their foods and habitats as they grow up, fish of a given age may to varying degrees be in competition with, or be preyed upon by, other ages of the same species. Consequently a completely adequate description of the effect of stock density on recruitment should be based upon measurements of the density of each age-group in the population separately (or combinations of ecologically-equivalent ages). This line of attack was applied experimentally to flour beetle populations at the University of Chicago by Watt (1954), who has also proposed a similar treatment for fish populations (1956). However, such analyses tend to require information on a larger scale than anything yet in sight.

An approximation to this approach (Ricker, 1954a, b) is based on the possibility that, among the population characteristics affecting reproduction and recruitment, the abundance of *mature spawners* is often sufficiently outstanding in importance (or is sufficiently well correlated with other important factors) to make it of real value for analysis and prediction. Although cannibalism of adults on young is possible in many species, it is likely that the effect of parental stock density upon recruitment is usually exerted *via* the density of the eggs or larvae they produce, the survival of the latter being affected by density-dependent competition for food or oxygen, compensatory predation, etc.[1].

1. At low levels of stock abundance and, in some instances, possibly up to quite substantial levels, the progeny (F) produced may vary directly as the abundance of spawners (P). This linear relationship (Fig. 11.1, line A) is described by:

$$F = bP \qquad (11.1)$$

If the variability (variance) of F increases in proportion to the size of P (as is likely to be approximately true) the best value of b is to be found (Deming, 1943, Section 15) from:

$$b = \frac{\Sigma F}{\Sigma P} \qquad (11.2)$$

The equilibrium yield is represented by the distance between line A and the 45° diagonal. Obviously, over the range where it is applicable, increase in yield is obtained by increasing stock as much as possible.

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[1] There is considerable disagreement concerning the role and perhaps even the reality of density dependence, in relation to animal abundance, particularly among entomologists. A recent brief review by Solomon (1957) summarizes the present state of the controversy from a point of view similar to what underlies the argument here; see also Ricker (1955b).

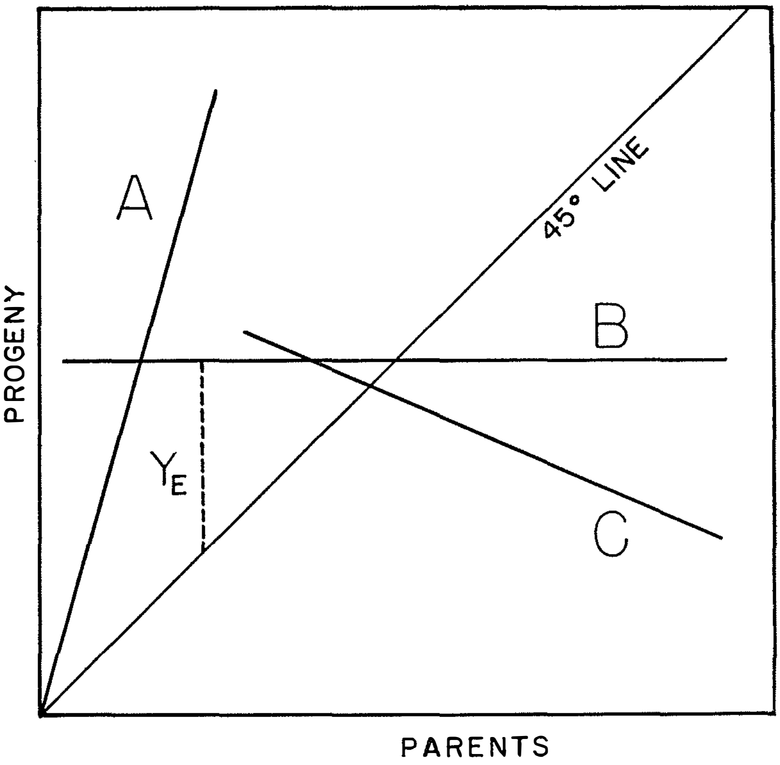

FIGURE 11.1. Some possible types of reproduction relationship. The 45° line represents replacement reproduction at all stock densities.

2. Very often no really low abundance of adult spawners is included in the range of observations available, and these observations may suggest little or no relation between recruitment and size of parent stock over the range examined (Fig. 11.1, line B). In such event, the estimate of average production for all stock densities is simply the mean size of all observed filial generations. Since environmental variability tends to be multiplicative in its action (Section 11B), the *most probable* production is usually much closer to the geometric mean of the observed productions than to their arithmetic mean.

With relationship B, maximum sustained yield is obtained by making the spawning stock as small as possible, since in that way the Y_E distance is maximized. No sustained yield is possible to the right of the 45° diagonal.

3. At very large stock densities the net reproduction may fall off, for a variety of reasons (Fig. 11.1, line C). A separate line can be fitted to this part of the recruitment-parent relationship, if it is represented in the data. Over the range represented by line C, increased yield is obtained by decreasing the size of the spawning stock.

Lines A and B of Figure 11.1, and also line C if it is indicated, can be fitted separately to any body of data, and they may provide useful reproduction norms. However it is unlikely that sharp transitions from one relationship to the other actually occur in nature, so that a single curve fitted to the whole data has at least a theoretical advantage. Fitting a polynomial is always a possibility; in fact very often a quadratic expression is adequate to describe the observed range of observations. On the other hand, a general polynomial is not apt to pass through the origin, so that it may indicate either no recruitment while adult stock is still appreciable (which is possible, though unlikely) or else appreciable recruitment when there is no adult stock (which is impossible). These troubles can be avoided by fitting a polynomial with the restriction that it must pass through the origin; but it is still apt to indicate a *maximum* of breeding stock beyond which reproduction falls below zero—another unlikely situation. Since the purpose of fitting a curve is usually to project the relationship beyond the actual observations, these deficiencies can be disturbing. A simple expression which has some of the more obviously desirable properties for use in this connection is described in the Section 11C. First, however, some comments on effects of environmental variability upon reproduction.

11B. EFFECTS OF ENVIRONMENT UPON RECRUITMENT

The biggest difficulty in examining the effect of stock density upon net reproduction is that year-to-year differences in environmental characteristics usually cause fluctuations in reproduction at least as great as those associated with variation in stock density over the range observed—sometimes much greater. Sometimes these fluctuations show significant correlation with one or more measured physical characteristics of the environment. To the extent that this is so, their effect can be removed from the total variability by some kind of regression analysis.

Detecting relationships between environment and some measure of an animal's reproduction, or abundance, has of course a long history; and the subject has an intrinsic interest quite apart from its use to reduce the variability of the parent-progeny relationship. The procedures most used are described in elementary statistical texts; the discussion here mainly concerns problems of interpretation. More complex methods are beginning to be proposed (e.g., by Doi, 1955a, b) but are not considered here.

In general it is not too difficult to discover correlations, even quite "significant" ones, but it is necessary to be cautious in deducing causal relationships from them. It is well known, for example, that correlations between "time series" are particularly likely to be accidental (involve no causal relationship) when both quantities have a unidirectional trend over a period of years. A correlation is much more apt to have meaning when the two quantities vary the direction of their trend, in parallel fashion. However even these cases sometimes prove to be related (if at all) by way of some third factor whose mode of operation may be unknown and whose very existence is at first unsuspected.

In spite of these dangers, it would be foolish to accept the defeatism of those who argue that because a regression or correlation is based on "the theory of errors", any information it provides is bound to contain error and hence will be of little value. Actually, soundly-considered regression analysis does exactly the opposite: from an originally large variability ("error") whose causes are unknown, it separates out quantitatively the components ascribable to each of a number of factors, so that the unidentified variability or residual error is substantially reduced.

ADDITIVE AND MULTIPLICATIVE EFFECTS. Consider the progemy of a single spawning of a fish stock up to the time they become usable—the recruits of that year-class. The effect of a unit change in an environmental factor might be to change the number of recruits by some constant quantity, or it might change it to some constant multiple or fraction of the initial value, or it might act in some more complex manner. In practice, we should expect the effect of the physical environment normally to be multiplicative rather than additive: if conditions are favorable, all the fry present have a chance of benefitting; if unfavorable, a certain fraction (not a fixed number) will be lost. To make multiplicative effects amenable to linear regression analysis, the logarithm of the observed effect is used rather than its actual value. The logarithms have an additional advantage, that they commonly make the variability of the number of recruits produced (Y-values) more nearly uniform over the observed range of environmental effects (X-values).

These advantages, however, are obtained only at a price; and the price is that the "expected" or "most frequent" value of Y, calculated from the logarithmic relationship for some particular X, is not the arithmetic mean of actual observed Y values at that X: rather, it is their geometric mean, which of course is always less than the corresponding arithmetic mean. Because this situation is so frequently encountered, Table 11.1 has been calculated to show the relation between arithmetic and geometric means for variates whose logarithms are distributed as in the normal frequency distribution[2]. Using it, approximate average reproduction can be estimated from a computed geometric mean and the standard deviation of the logarithms.

A log standard deviation of 0.5 corresponds to a 1-in-20 chance of a single observed reproduction being as small as 1/10 of the geometric mean or as great as 10 times that mean—a total spread of 100:1. When variability in reproduction is greater than this, the concept of an *average* reproduction becomes rather tenuous.

CURVED REGRESSIONS. For any environmental condition there is typically an intermediate most favourable range, with less favourable conditions above and below. For example, water can be either too cold or too warm for successful incubation of eggs: the optimum is intermediate. Consequently a graph of reproduction (Y) against temperature (X) would have a maximum and would probably be dome-shaped; hence it could not be straightened by any simple transformation of either or both scales. The mathematical procedure is then to find the regression of Y (or log Y) on X *and* X^2. Even higher powers of X can be used, but data for fish stocks would rarely warrant it. A simpler procedure is to fit a curved line, or two or three straight lines, freehand to the graph—which can be justified at least for preliminary analysis (Rounsefell, 1958).

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[2] It is computed from the expression:

$$\log_{10}\left(\frac{\mathrm{AM}}{\mathrm{GM}}\right) = 1.1518s^2$$

derived from formula (8) of Jones (1956, p. 35), with $\mu = \mathrm{AM}$, $\bar{x} = \mathrm{GM} = 1$, $(n-1)/n = 1$, $a = 0$, s = the standard deviation of the normally-distributed logarithms. Before discovering this formula, a number of values of AM/GM had been worked out by calculating and averaging actual series, using Pearson's (1924) table II: there was agreement to the second decimal.

SECULAR TRENDS. If the data exhibit any important trend or trends extending over periods of years comparable to the total length of the series, then it is usually necessary to remove this trend before examining the year-to-year effects of environmental factors. Several methods can be used.

TABLE 11.1. Relation between (1) the standard deviation of the base-10 logarithms of variates whose logarithms are normally distributed, and (2) the ratio of the arithmetic mean to the geometric mean of those variates.

Standard deviation of logarithm	Ratio: AM/GM	Standard deviation of logarithm	Ratio: AM/GM
0.05	1.007	0.55	2.230
0.10	1.027	0.60	2.598
0.15	1.061	0.65	3.066
0.20	1.112	0.70	3.667
0.25	1.180	0.75	4.445
0.30	1.270	0.80	5.459
0.35	1.384	0.85	6.794
0.40	1.529	0.90	8.694
0.45	1.711	0.95	10.951
0.50	1.941	1.00	14.183

1. It is sometimes possible to fit a regression of Y against time (of linear, quadratic, or even higher order), calculate the "expected" value for each Y, and subtract this from the actual Y to obtain a series of *residuals* (as was done, for example, by Milne, 1955, p. 476). These residuals can then be plotted and tested against the various environmental factors.

2. If the series is long and the trend irregular, a moving average of 5, 7 or 9 items will provide an "expected" trend line from which the residuals can be measured. Care should be taken that the averaging does not remove variability which can be related to the factors to be examined.

3. A more satisfying procedure is available when the trend in Y is related to a trend in an environmental factor (X) whose influence on Y is well established. In that event the regression of Y on X will take care of the trend, and again residuals can be computed for use with other factors. But this procedure should *not* be used with environmental factors selected only because of their correlation with Y, in the absence of independent evidence of an actual effect on Y, because of the time-series correlation danger discussed above.

EXPLORATORY CORRELATIONS. In general, there can be an indefinitely large number of environmental factors which could be selected for comparison with a record of reproduction or year-class abundance. For example, the temperature, rainfall, etc., in each of a series of months, and in various combinations of months, might be examined (Hile, 1941; Henry, 1953; Dickie, 1955; Ketchen, 1956; and others). The usual way to assess possible relationships is to compute the coefficient of correlation for each. If more than one is tested, however, then the likelihood of accidentally obtaining a "significant" correlation for some one of them increases as the number of factors examined. Thus an investigator is confronted with the paradox that the more factors he tests, the more likely he is to include the effective ones in his search, but the less likely he is to be able to recognize them. If all factors tested seem equally possible a priori, then the level of significance (P-value) for a single effect can be made more realistic by increasing it in relation to the number of factors—at least as an approximation (cf. Fisher, 1937, p. 66). For example, if four factors are examined and one of them is apparently "significant" with a P-value of 0.02, then the probability that this factor is really related to abundance is not 98% but about 92% ($= 1 - 4 \times 0.02$).

However the situation is usually more complicated. There is almost always some provisional hypothesis of a possible relationship behind each correlation tested, even though some may seem far-fetched. Also, we tend to test first the relationships which seem most likely to be appropriate, or which are suggested by gross inspection of the data. Indeed, the very fact that we have thought of testing a factor is some reflection of its possible significance. As a rule, then, the likelihood of one of the first-tested correlations being "real" is much greater than that of (say) the tenth one, tried on the strength of a wild idea, even though the formal statistical probability be the same for both. To help his readers to assess the reality of observed correlations, an investigator should publish details of r and P values for *all* the factors which he has examined, whether they seem significant or non-significant. He should also indicate his a priori estimate of the likelihood of each, even if only in a general way. Scrupulous attention to these matters will avoid many an embarrassing volte-face.

In general, tentative relationships deduced from an exploratory study involving several to many factors must always be confirmed by additional information. This additional information can be more observations of the kind already used, as they accumulate in the future. With fish populations, ten years or so is usually required to obtain confirmation in this manner. To get a quicker answer, experiments or observations can sometimes be made to determine the exact causal nature of any relationship suggested by the correlation—which is very desirable anyway, whenever possible. An observed correlation gains vastly in acceptability if the implied biological process can be demonstrated to occur, even if only qualitatively.

DIFFICULTY OF OBTAINING EVIDENCE OF SIGNIFICANT EFFECTS FROM SHORT SERIES OF OBSERVATIONS. As a rule we expect *several* environmental factors to be fairly important in determining year-class abundance. If so, no one of them can be really outstanding, and none will be apt to have a "significant" correlation when series of less than say 15 to 25 years are available. For example, suppose that five and only five independent and uncorrelated factors determine the variation in reproduction of a fish species, and that they are all of equal importance. Then the "coefficient of determination" (ρ^2) for each is 1/5 or

0.20, and the coefficient of correlation is $\rho = \sqrt{0.20} = 0.447$. Nineteen pairs of values are necessary to establish an estimated correlation of $r = 0.45$ as "significant" at the $P_{0.05}$ level. Hence, if only say 15 years' observations were available, there might be no significant effects demonstrable even though all the pertinent possibilities had actually been examined. In practice, one or two of the five r's above would likely exceed the $P_{0.05}$ level by chance, while the others fell well below it; and adding more years' observations would almost certainly shift the order of these r-values. In such cases the effect which initially seems most "significant" may decrease in apparent relative importance or even subside into insignificance, while some originally "non-significant" effect may become demonstrably important, as future years' data are added to a correlation series. Such shifts have often been observed.

EFFECTS OF TWO OR MORE FACTORS CONSIDERED SIMULTANEOUSLY—MULTIPLE REGRESSION. If measurements of all the environmental characteristics examined are all available for the same period of years, the best method of analysis is that of multiple regression, or its close ally, partial correlation. This is particularly true if all the relationships are reasonably close to linear. For a multiple regression analysis, it is not necessary that the separate factors examined be independent. For example, the joint effects of sea temperature, salinity and wind velocity upon survival of pelagic eggs of a fish might be examined, in a situation where these three are all somewhat correlated among themselves. The "standard regression coefficients" provide estimates of the relative value of each factor for predicting survival. They do *not* tell whether it was temperature, or salinity, or wind, or some unmeasured factor like current speed, or some combination of these, which actually affected survival directly. The square of the adjusted multiple correlation coefficient, R_A^2, represents the fraction of the total variability in survival which is related to all the factors examined, whether or not the latter are correlated.

The superiority of multiple regression over single-factor analysis consists in the fact that it will separate the effects of two correlated factors and indicate their relative value for predictive purposes. This is especially advantageous in connexion with antagonistic effects. Suppose, for example, that fry survival is strongly favored by lower temperatures (over the range examined), and is rather weakly favored by slow currents, but that years of low temperature usually have strong currents. In that event, a simple correlation of fry survival with current speed would be positive in spite of the fact that the biological relationship is negative. When enough years' observations are at hand, multiple regression or partial correlation will uncover the true relationship, and provide an estimate of the importance of each effect in the absence of the other.

Since multiple regressions become cumbersome when more than three or four factors are included, good judgment is required in selecting factors for examination:

1. Preference should be given to factors which are likely to affect the organism directly, as indicated by known or plausible biological relationships.

2. Of two or more closely-correlated factors, only one should be used; if it is impossible to give one of them preference on the basis above, it should be done arbitrarily. "Close" correlation, for this purpose, would be upward from $r = 0.8\text{-}0.9$, depending on the number of other factors which have to be included.

3. Factors represented by fairly accurate quantitative measures are to be preferred to those only grossly or subjectively classified (for example, as 1, 2 and 3, corresponding to light-medium-heavy).

For the use of "path coefficients" in illuminating relationships discovered, see papers by Davidson *et al.* (1943) and by Li (1956), and their references to Wright's contributions.

REGRESSION ANALYSIS BY STAGES. Whether because of the large number of factors to be examined, because of non-linearity of some of the relationships, or because the data are not complete for all factors, it is sometimes necessary to do an analysis in successive stages (Rounsefell, 1958). One or a few factors are used each time, and the "residuals" computed from each fitting are used for the next one. In such work, the environmental factors should themselves first be tested by pairs; any which exhibit moderate correlation *and* seem likely to have independent effects on the Y value should be included in the same multiple regression, if at all possible. Apart from that, factors should preferably be dealt with in the order of the size of each one's correlation (whether positive or negative) with the effect in question, as in this way the variability of the residuals will be reduced most quickly. Probabilities of significance can be estimated from the r or R for each regression; and an overall P-value can be obtained by transforming and combining the separate P's to a χ^2 value (Fisher, 1950, section 21.1).

EXAMPLE 11A. POSSIBLE RELATION OF CHUM SALMON CATCHES IN TILLAMOOK BAY TO WATER FLOW AND OTHER FACTORS. (After Henry, 1953.)

The method of exploratory regression was used by Henry to examine relationships between chum salmon landings and stream flows at the time the eggs which produced each brood were being spawned or were in the redds—that is, in November-April, 4 to $3\frac{1}{2}$ years previously. Of 32 kinds of flow examined, for individual months or combinations, significant or suggestive (P = 0.15 or less) correlations were found only for the maximum flow in early November and for the minimum flow in February (or some combination of months which included February). Further trials indicated that minimum flow from January 15 to March 20 produced a regression with apparent significance of P = 0.01 (this flow index is shown in Table 11.2, p. 240). The correlation coefficient was 0.63, showing that 40% of the variation in catch is associated with this index of stream flow *over the years in question.* The best prediction equation, using this variable, was:

$$\hat{Y} = -493.6 + 2.059x_1 \tag{11.3}$$

where Y is the expected catch in thousands of pounds, taken from the brood affected by the flow in question, and x_1 is the minimum flow in cubic feet per second. However, Henry emphasizes that it is unlikely that as strong a relationship, with precisely this flow index, would persist into the future, though *some* index of minimum flow during the winter might well do so. The biological relation to be postulated is of course that low water in winter exposes eggs to drought, frost, or suffocation.

Henry also combined two factors which exhibited suggestive relationships: maximum water flow early in November (x_2—in cubic feet per second), and maximum air temperature in January or February (x_3—in degrees Fahrenheit), into a multiple regression with the above, as follows:

$$\hat{Y} = 346.5 + 0.9731x_1 + 0.06610x_2 - 7.782x_3 \qquad (11.4)$$

However the application of this expression reduces the residual variability of the catches only slightly, as compared with residuals from expression (11.3).

11C. Characteristics of a Family of Reproduction Curves

The relation between adult stock and resulting recruitment is easiest to examine in certain anadromous species whose habits make it easy to distinguish the contribution of separate year-classes to the catch. Examination of a number of these, and of a few other fishes, suggested a pattern of asymmetrical recruitment curves (Ricker, 1954b). The maximum of recruitment occurred at some intermediate level of abundance, and the "ascending limb" approaching the maximum was steeper than the descending limb beyond it. These curves can usually be fitted approximately by expression (A12) of Appendix I:

$$\frac{F}{F_r} = \frac{P}{P_r} e^{(P_r-P)/P_m} \qquad (11.5)$$

where the symbols are as follows:

F	the filial generation (recruitment), measured at some stage after density-dependent mortality ceases
P	the parental generation
P_r	the "replacement" size of the parental generation, i.e., that which, on the average, just replaces its own numbers
F_r	the (geometric mean) size of the filial generation produced by a parental generation of size P_r
P_m	the level of parental stock which produces the maximum filial generation

When possible, it is simplest to arrange for P and F to be measured in the same units[3], scaled so that $F_r = P_r$; thus the denominators of (11.5) can be disregarded:

$$F = Pe^{(P_r-P)/P_m} \qquad (11.6)$$

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[3] With stocks in which the individual fish are available to the fishery during more than one year, the most generally applicable way to achieve this is probably to convert everything to the basis of eggs spawned or potentially available for spawning. Parental abundance is measured in thousands or millions of eggs actually produced during the year in question. For the progeny, if an estimate of the abundance of the progeny generation in (for example) its first year of recruitment to the fishery is available, its egg production that year is computed, plus the estimated egg production of the survivors during the following year *assuming only natural mortality is in operation*, and so on up to whatever age the survivors are too few to produce an appreciable number of eggs—the sum of these actual and potential egg productions being the abundance of the progeny measured in a unit comparable to that of the parents. Unfortunately the natural mortality rates needed for such a comparison will often be difficult to obtain with sufficient accuracy.

For an estimate of P_m, the size of stock needed for maximum recruitment, it is not necessary that F and P be in comparable units. Using a different measure for F (call it F′) in expression (11.9) merely adds the constant $\log_{10}(F'/F)$ to the RHS of the equation, and P_m can be estimated from the slope as before.

If, in addition, we define $a = P_r/P_m$, $Z = F/P_r$, $W = P/P_r$, two convenient short forms are:

$$F = Pe^{a(1-P/P_r)};\ Z = We^{a(1-W)} \tag{11.7}$$

The curve (11.7) is drawn in Figure 11.2, for several values of a. Some general features which make it flexible and (it seems) often appropriate for describing reproduction are:

1. It passes through the origin: when there is no adult stock there is no reproduction.

2. It falls off asymptotically at high levels of stock, so that there is no point at which reproduction is completely eliminated at high densities. (This is not a logically-necessary requirement of reproduction curves, but it appears reasonable and accords with observations available.)

3. The *rate* of recruitment (F/P) decreases continuously with increase in parental stock (P).

4. The maximum of recruitment may occur at densities less than replacement (when $a > 1$), or at densities greater than replacement (when $a < 1$).

In fitting this curve to data, the convenient method suggested by Rounsefell (1958) is better than the tedious selection of trial positions of the apex as used by Ricker (1954b, p. 618). A straight-line transformation of (11.6) is:

$$\log_e(F/P) = \frac{P_r}{P_m} - \frac{P}{P_m} \tag{11.8}$$

Or, more conveniently:

$$\log_{10}F - \log_{10}P = \frac{0.4343P_r}{P_m} - \frac{0.4343P}{P_m} \tag{11.9}$$

The left side of (11.9), plotted against P, gives a straight line with a negative slope which can be equated to $0.4343/P_m$, while its Y-axis intercept is $0.4343P_r/P_m$. Thus P_m and P_r are estimated.

Note however that the existence of a significant negative slope in a graph of log(F/P) against P in no way contributes any justification for choosing (11.9) as an expression appropriate for describing the parent-progeny relationship. Such a slope occurs partly because a function of P appears as a negative item in the left side of (11.8) and (11.9); in fact this slope is very marked in lines plotted from sequences of F and P values that are paired up quite at random. Observational justification for using (11.9) comes when it significantly reduces the variance of the residuals of log F (that is, observed values of log F less the value computed from the equation), as compared with the simple variance of log F values about their mean.

EXAMPLE 11B. A COMPENSATORY RELATIONSHIP BETWEEN FILIAL AND PARENTAL STOCK, FITTED TO STATISTICS OF TILLAMOOK BAY CHUM SALMON. (Data from Henry, 1953.)

The chum salmon (*Oncorhynchus keta*) of Tillamook Bay mature mostly at age IV, as described in Example 11A, so each year's catch can be considered

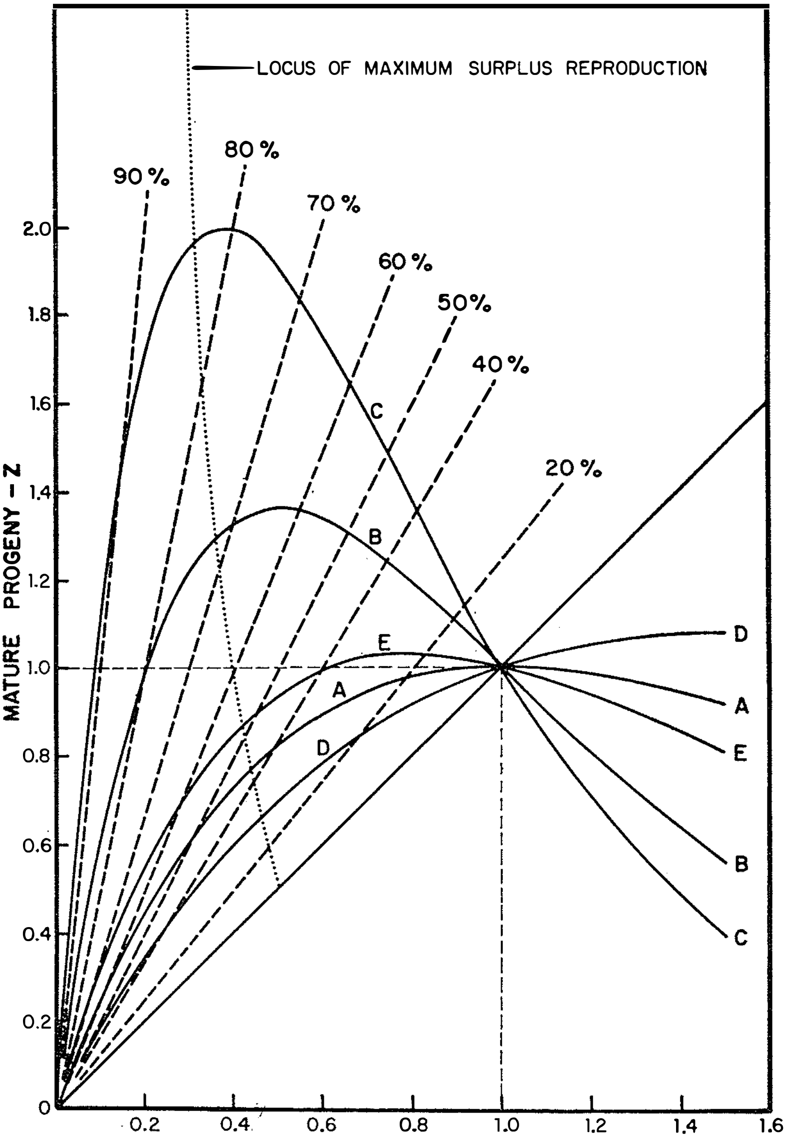

FIGURE 11.2. Reproduction curves conforming to the relationship $Z = We^{a(1-W)}$. Values of a are: D, 0.667; A, 1.0; E, 1.25; B, 2.0; C, 2.678. The point where the curves cut the diagonal is the replacement level of stock and reproduction. The dotted lines from the origin are loci of equilibrium reproduction for the rates of exploitation indicated.

as largely the progeny of the spawning stock of 4 years earlier. Henry says that much the same group of fishermen fished the bay over the years included in Table 11.2, so that year-to-year variation in rate of exploitation was probably not large (except for 1932, see below). For a factual analysis of these data, it

TABLE 11.2. Catches of Tillamook Bay chum salmon, the log data used to fit a reproduction curve of the form (11.9), and the computation of the original and the residual variance of log F (the logarithm of the progeny generation). (Logarithms are to the base 10.) Column 2 is the catch of salmon in thousands of pounds, which is considered also to represent the size of the spawning stock at an estimated rate of exploitation of 50% (see the text *re* 1928 and 1932). Column 4 is the logarithm of the progeny generation, which is estimated as twice the catch (catch plus estimated escapement) 4 years after the brood year shown in column 1. Columns 5 and 6 are the deviations and squares of deviations of the log F values from their mean. Column 7 is the "expected" log F, computed from $\log F = \log P - 0.000392P + 0.630$. Column 8 gives the "residuals" (difference between column 7 and column 4) and column 9 gives their squares. Column 10 was used in Example 11A: it represents the minimum water flow in cubic feet per second in certain spawning streams during the period January 15 to March 20 of the year *following* spawning. Each flow therefore can affect the catch taken in the calendar year 3 years later. (Data from Henry, 1953, and personal communication.)

1 Year	2 P	3 log P	4 log F	5 d	6 d²	7 Computed log F	8 d	9 d²	10 Minimum flow
	10^3 *lb.*								*cfs*
1923	644	2.81	3.55	+.42	.1764	3.19	+.36	.1296	
1924	854	2.93	3.75	+.62	.3844	3.23	+.52	.2704	
1925	931	2.97	3.37	+.24	.0576	3.24	+.13	.0169	
1926	244	2.39	2.67	−.46	.2116	2.92	−.25	.0625	
1927	1764	3.25	3.28	+.15	.0225	3.19	+.09	.0081	
1928	(2804)	....	....	.....	.....	....	.....	.....	
1929	1171	3.07	3.04	−.09	.0081	3.24	−.20	.0400	
1930	234	2.37	2.83	−.30	.0900	2.91	−.08	.0064	
1931	947	2.98	3.06	−.07	.0049	3.24	−.18	.0324	
1932	(89)	....	....	.....	.....	....	.....	.....	
1933	552	2.74	2.94	−.19	.0361	3.15	−.21	.0441	795
1934	336	2.53	3.16	+.03	.0009	3.03	+.13	.0169	380
1935	572	2.76	2.93	−.20	.0400	3.17	−.24	.0576	665
1936	1189	3.08	2.94	−.19	.0361	3.24	−.30	.0900	515
1937	438	2.64	3.54	+.41	.1681	3.10	+.44	.1936	640
1938	725	2.86	3.72	+.59	.3481	3.21	+.51	.2601	821
1939	427	2.63	2.88	−.25	.0625	3.09	−.21	.0441	945
1940	439	2.64	2.86	−.27	.0729	3.10	−.24	.0576	490
1941	1756	3.24	3.19	+.06	.0036	3.18	+.01	.0001	348
1942	2651	3.42	2.98	−.15	.0225	3.01	−.03	.0009	486
1943	379	2.58	2.87	−.26	.0676	3.06	−.19	.0361	344
1944	361	2.56	3.25	+.12	.0144	3.05	+.20	.0400	646
1945	777	2.89	2.94	−.19	.0361	3.22	−.28	.0784	572
1946	482	....	....	.....	.....	....	.....	.....	967
1947	374	....	....	.....	.....	....	.....	.....	....
1948	895	....	....	.....	.....	....	.....	.....	....
1949	436	....	....	.....	.....	....	.....	.....	....
Totals			65.75		1.8644			1.4854	
	Mean and variances		M = 3.131		V = 0.0932			V = 0.0782	

would be necessary to have an estimate of the average rate of exploitation of the stock; this is needed in order to establish a relation between the vertical and horizontal axes in Figure 11.2. For purpose of illustration, we have made the assumption that the catch each year was 50% of the total stock, so that the spawning escapement equalled the catch. However the year 1932 is omitted from both the progeny and parent series, because economic conditions greatly reduced the catch in November and December of that year (Henry, pp. 11, 17; the quantities taken in October suggest that there would have been a better-than-average catch if fishing had continued). This leaves 21 comparisons between parental and progeny years.

The slope of the line of log(F/P) against P is found by least squares to be −0.00039187, and the Y-axis intercept is +0.62952. From (11.9):

$$P_m = \frac{0.4343}{0.00039187} = 1108.3 \text{ thousand lb.}$$

$$P_r = \frac{0.62952}{0.00039187} = 1606.5 \text{ thousand lb.}$$

$$a = P_r/P_m = 1.4495$$

The data and this reproduction curve are shown in Figure 11.3, plotted on logarithmic and on ordinary axes. (The fit is of course based on logarithms of the ordinates.) Fitting the curve reduces the sum of squares from 1.8644 (for deviations from the mean log F) to 1.4854 (for deviations from the log curve).

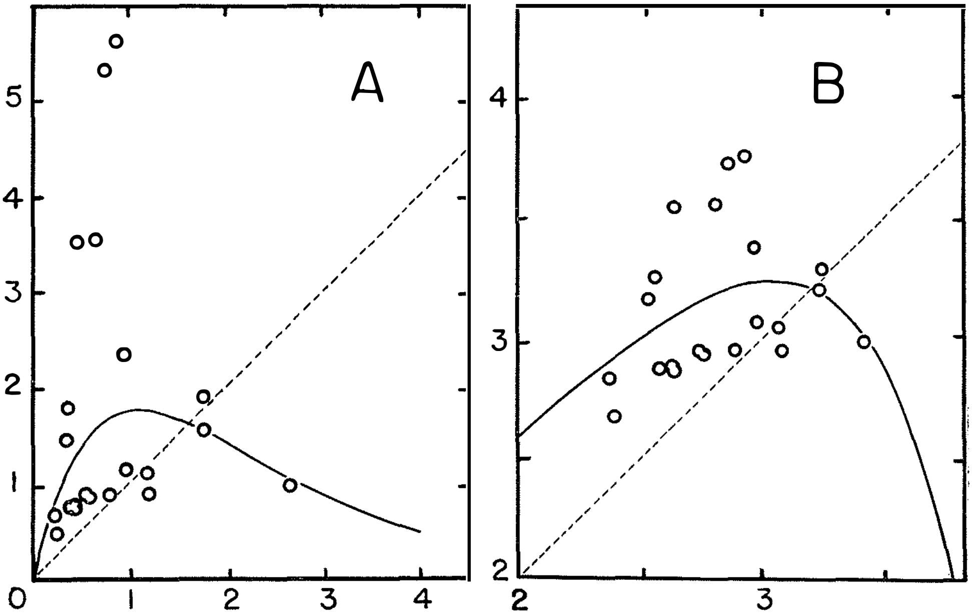

FIGURE 11.3. Twice the catch of Tillamook Bay chum salmon (ordinate) plotted against the catch 4 years earlier (abscissa), on arithmetic (left) and logarithmic (right) axes. The curved lines are fitted by expression (11.9), these being reproduction curves for an "ideal" situation where rate of exploitation is always 50% and the fish mature only at 4 years of age. (Data from Henry, 1953).

The reduction in variance is from 0.0932 to 0.0782—proportionately somewhat less because an extra degree of freedom was used in fitting the line. Thus fitting the curve has not reduced the variance of log F values a great deal, but reproduction is so variable that no conceivable curve could do much better.

Whether or not variability is reduced, such a curve can be used to predict mean log reproduction and estimate a best level of exploitation and escapement. The best escapement is the P-value where the curve of Figure 11.3A has a positive slope of 45°. By eye, this is about 650,000 lb. Also as read from the graph, the geometric mean of the filial generations produced by such a stock is the height of the curve above 650,000—about 1,560,000 lb.; the yield is 890,000 lb., and the rate of exploitation is 57%.

To obtain the above results by computation, expression (A20) of Appendix I can be solved by trial for W_E, given $a = 1.4495$. This comes to $W_E = 0.400$; and, from (11.7), $Z_E = 0.955$. Hence the spawning stock at maximum equilibrium yield is $W_E P_r = 0.4 \times 1{,}606{,}500 = 643{,}000$ lb., the total stock is $Z_E P_r = 0.955 \times 1{,}606{,}500 = 1{,}534{,}000$ lb., the yield is 1,534,000 − 643,000 = 891,000 lb., and the rate of exploitation is 891/1534 = 58.1%.

The arithmetic average yield, of course, will be somewhat greater than the "most probable" estimate obtained in this manner. The standard deviation of the log deviations from the curve is the square root of 0.0782, or 0.28; hence, from Table 11.1, the arithmetic average reproduction should be approximately $1.23 \times 1{,}534{,}000 = 1{,}890{,}000$ lb. At the 58% rate of exploitation, this makes the average yield about 1,100,000 lb.—to which a few very large years would contribute heavily. Theoretically at least, it would be possible to obtain even greater average yields if the stock entering the fishery could be accurately estimated each year and the fishery adjusted so that everything in excess of 643,000 lb. would be harvested. This and other effects of environmental variability upon yield are examined by Ricker (1958*b*).

What relation has this analysis to the relationship between reproduction and environmental factors which was developed in Example 11A? Since in that example the relationship was fitted to the catches themselves, not their logarithms, and a slightly different series of years was used, a repetition of Henry's simpler fitting (expression 11.3) was made using the variables of this example (log F and x_1). The numerical relationship of stream flow to catch is about the same, though somewhat less "significant" than that of (11.3) above ($r = 0.57$ for 12 degrees of freedom).

To test the two factors parental abundance and minimum flow together (still assuming a rate of exploitation of 50%), the residual deviations of the log catches from the curve of Figure 11.3 (shown in column 8 of Table 11.2) were related to the minimum flows three years earlier (column 10 of Table 11.2). However the resulting coefficient of correlation becomes smaller ($r = 0.45$) rather than larger. Thus the two factors mentioned are to some extent "competing" for the same variability in the size of the catch. Only further information would decide which has the more important influence upon reproduction, and whether or not one of them could be ignored, for practical purposes.

11D. OTHER REPRODUCTION CURVES

Reproduction curves differing considerably in shape from any described by (11.5) are quite possible, and may even prove to be in a majority (Ricker, 1954b). Deviations from (11.5) seem most likely to take the form of (a) flatter domes, (b) steeper right limbs, (c) a reduced rate of reproduction at very low stock densities.

A *flatter dome* and more gently inclined limbs would be the usual consequence of division of the population into partially-distinct units, so that effects of density are not uniformly felt throughout the stock. Flattening of the dome also is expected when there is an upper limit of space available to a population which exhibits territorial behaviour, or a limited number of safe habitat niches: in extreme cases the right limb could be horizontal. Flattening of the dome also occurs when there is an upper limit of food supply for which there is a "contest" in the sense of Nicholson (1954)—each successful individual gets enough to complete growth, others die without reducing the food available to the successful ones.

A *steeper right limb* results if there is a "scramble" (Nicholson) for limited food or other requisite, so that all members of a brood get some but many do not get enough to complete development; in the limiting case none get enough and all the brood dies. For example, a large deposition of salmon eggs in a spawning area might have an oxygen demand in excess of the supply, so that no eggs would survive.

A reduced rate of reproduction at low stock densities might result from a need for group activity in the breeding cycle, difficulty of finding mates in a scattered population, relatively higher losses from predation when the stock is at a low level, etc. Neave (1954) has discussed this possibility and has observed it in pink salmon reproduction. This effect and the preceding one, working together, tend to produce a *narrow* dome, and a very narrow dome is in fact indicated by the reproduction data for Skeena sockeye salmon (Shepard and Withler, 1958).

If expectation or observation suggests some irregular type of reproduction curve, a freehand line fitted to the stock-reproduction data may be the most useful curve to use. For *any* line, empirical relationships can be computed similar to what are developed in Appendix I for the expression (11.5). In particular, the maximum equilibrium catch always occurs at the point[4] where the curve has a slope of 45° and a tangent of +1, and where its absolute vertical distance from the 45° diagonal is greatest.

11E. RELATION OF EQUILIBRIUM YIELD TO RATE OF FISHING, FOR DIFFERENT REPRODUCTION CURVES

The practical importance of the shape of a reproduction curve is best realized by comparing the maximum equilibrium yields which different ones will provide. Figure 11.4 shows the sustained yields obtainable from stocks A, B and C of Figure 11.2, at different rates of fishing. The very great difference in yield potential is obvious: Curve C can provide about 5 times as great a catch as A, although the two stocks were of the same size before exploitation. The rate of fishing necessary to achieve maximum yield increases from A to C (i.e., with increasing values of the coefficient $a = P_r/P_m$). However the catch increases even more rapidly than the necessary rate of fishing, so that the catch per unit effort at maximum sustained yield would be greater for C than for A, by about 55%.

The yield curves of Figure 11.4 fall off more rapidly on the right side than on the left, and this feature becomes much more marked if the rate of exploitation

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[4] In exceptional circumstances there could be two such points (theoretically even more), in which event there would be two possible stable levels of stock for some limited range of values of the rate of exploitation (see Neave, 1954; Ricker, 1954b, figure 30).

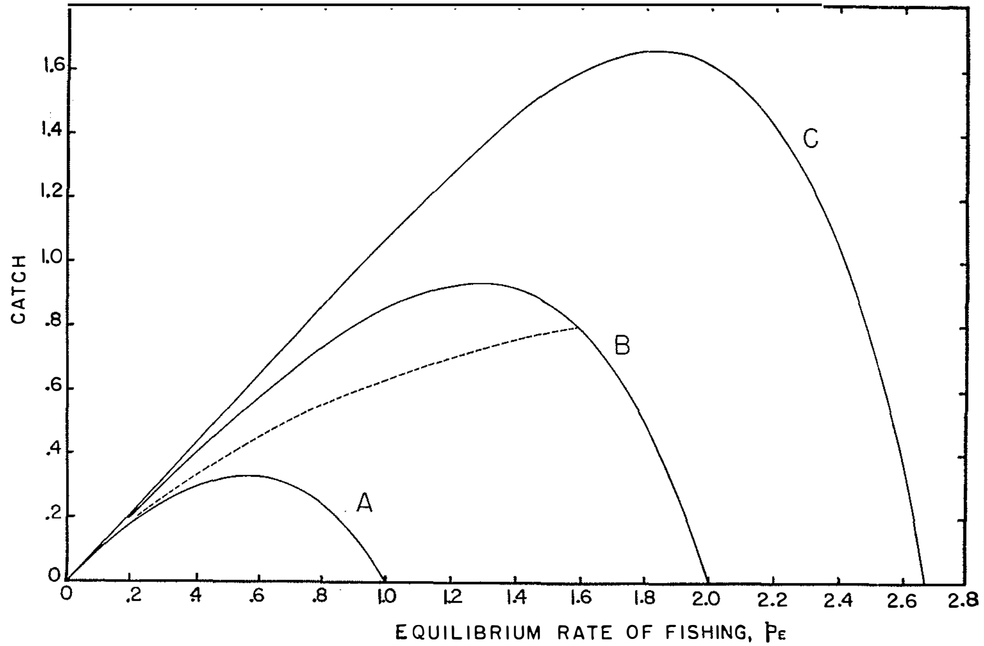

FIGURE 11.4. Equilibrium yield from populations described by Curves A-C of Figure 11.2, for different rates of fishing (p_E). The curves give the equilibrium catch as a fraction of the replacement abundance of the stock, for the situation where the fish neither grow nor suffer natural mortality while vulnerable to fishing (a situation which is approximated by many salmon fisheries). Catch is shown as a fraction of the replacement level of stock, calculated from (A17) and (A19) of Appendix I with $p_E = -\log_e(1-u_E)$. The three stocks have the same (geometric) mean abundance when there is no fishing. At any point, the rate of fishing would be approximately proportional to the fishing effort needed to take the catch indicated.

is used on the abscissa, instead of the rate of fishing. With curves of this sort, consequently, obtaining the maximum yield will always be a bit tricky—with a more drastic penalty for too much fishing than for too little.

Comparable graphs can be constructed for other types of reproduction curves, most readily by direct measurement of yield from the curve to the diagonal. In Figure 11.4 the dotted line shows the catch from a reproduction curve which coincides with Curve B up to the replacement level of reproduction, but with further increase in spawners produces no additional recruits.

11F. RELATION OF THE REPRODUCTION CURVE TO THE PROGRESS OF A NEW FISHERY

Curves like those of Figure 11.4 show equilibrium yields, but in many fisheries equilibrium catch is known for very few levels of exploitation, or none at all. Consequently it is desirable to examine the effects of changing exploitation rates upon these population parameters, for the situation where the stock available to the fishery is determined solely by the reproduction curve. We will deal with *increasing* exploitation, because for many salmon fisheries a history of catch under increasing exploitation is available.

Figures 11.5 and 11.6 show the catch history of a new fishery attacking a species which has a single age of maturity and is vulnerable only near maturity. Three model populations are shown, characterized by the reproduction Curves A, B and C of Figure 11.2[5]. Each starts out from the replacement level of

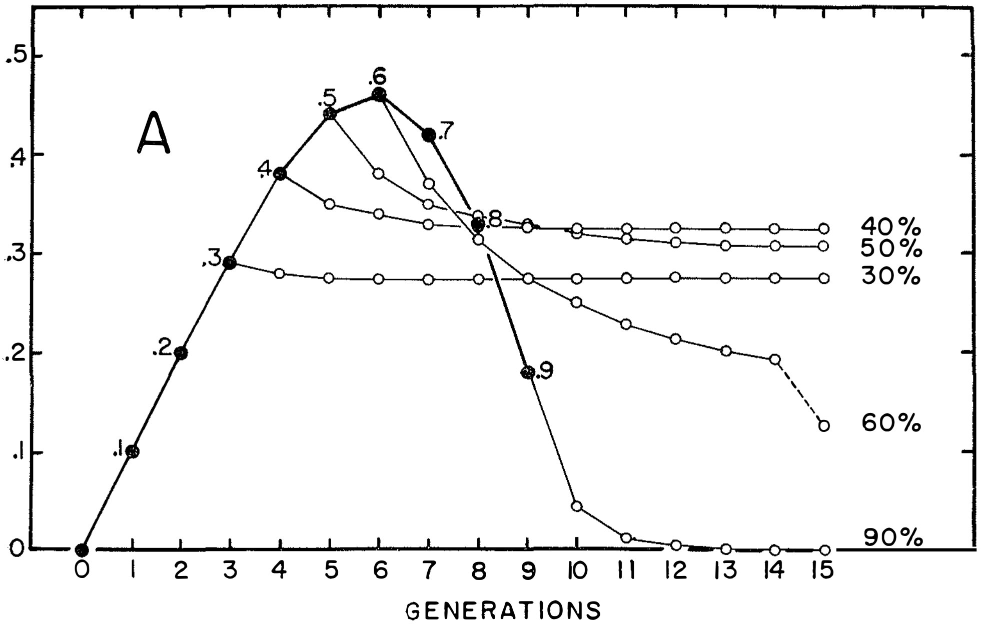

FIGURE 11.5. Catches obtained from a stock whose reproduction is described by Curve A of Figure 11.2. *Solid dots:* catches obtained when the rate of exploitation has successive absolute increases of 10% per generation, starting with a stock at the replacement level. *Open circles:* catches obtained when the rate of exploitation remains constant at the levels shown, starting from the position described by the solid dot to which it is joined. The maximum sustained yield is obtained at 43%, and is very slightly higher than the equilibrium level shown for 40%.

stock and is subjected to an exploitation of 10% in the first generation, 20% in the second, and so on. The solid points indicate the course of events when the increase in exploitation is continued up to 90%. Stabilization of fishing at 90% would soon exterminate stocks A and B, but the C curve can support removals somewhat greater than 90%.

In practice, fishing is more likely to level off at some intensity less than 90%. This level will be determined either by the increasing cost of the fishing effort per unit catch, or by regulations resulting from the alarm provoked by a reduced absolute yield. Various stabilized levels are indicated by dotted lines in Figures 11.5 and 11.6, while the equilibrium yield corresponding to *any* rate of exploitation can be calculated from expressions (A17) and (A19) of Appendix I.

For population A, whereas the maximum equilibrium catch is achieved at 43% exploitation, and 50% gives almost as much, a further increase to only 60%

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[6] Numerical characteristics of these curves are given in Table A1, page 268.

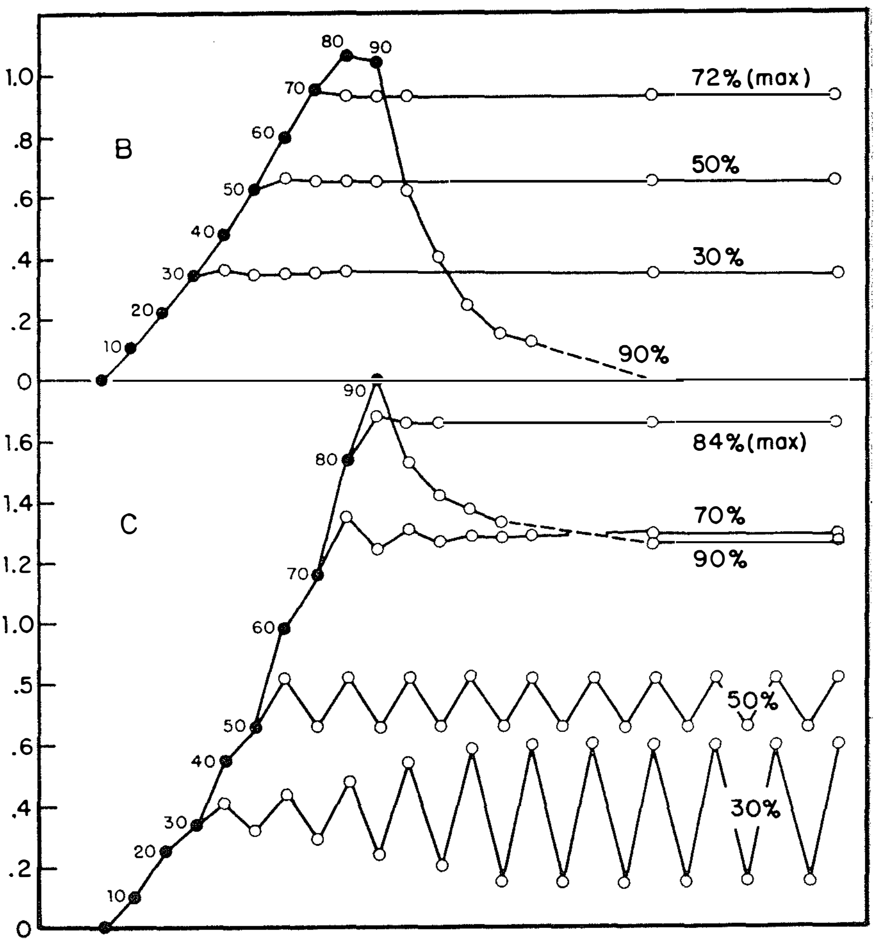

FIGURE 11.6. Catches obtained from stocks whose reproduction is described by Curves B and C of Figure 11.2. Symbols as in Figure 11.5.

eventually cuts the yield to less than half the maximum, while 63% gradually reduces the stock to zero.

For population B (Fig. 11.6), stabilizing the fishery at any level up to 70% exploitation means that catch becomes stabilized practically at the level already achieved—with very minor fluctuations. Maximum equilibrium catch is 0.935 of the replacement reproduction, and is achieved at 72% exploitation.

Population C is inherently oscillatory in the absence of fishing[6]. Even if the fishery happened to begin when the stock was at the replacement level, it would develop somewhat jerkily (Fig. 11.6)—quite apart from any fluctuations due to environmental causes. If exploitation levelled off at 30%, the catches of alternate years would become more and more different until they came to a

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[6] This is because of the effect discovered by Moran (1950), that when the right limb of a reproduction curve crosses the replacement line at a steeper slope than 45°, there is no stable equilibrium level of abundance (see Ricker, 1954b, figure 7).

stable alternation between 0.15 and 0.60 (of replacement). At 50% exploitation a smaller oscillation would be established at once. At 70% a small oscillation would quickly be damped to a steady catch of 1.29. At 90% the catch would fall asymptotically to the stable level 1.27. Maximum sustained yield is 1.66, obtained with 84% exploitation.

In all the above sequences, if the rate of exploitation during the developmental period increases steadily to a value greater than that required for maximum sustained yield, then the equilibrium catch will be less than the peak catch. What is less expected, is that for Curve A there will be a maximum of catch during the developmental period even if the optimum rate of exploitation is not exceeded. In the sequence shown (Fig. 11.5) the first year's catch at 40% exploitation is 15% greater than the maximum equilibrium yield. However, the magnitude of this historical peak in landings will depend on the speed with which optimum exploitation is approached. In the extreme situation, if the A population is all at once subjected to the optimum rate of exploitation (43%), its first year catch is 30% higher than the sustainable yield [= (0.43 − 0.33)/0.33]. Even higher peaks are possible without exceeding the optimum level of fishing, with stocks in which the parameter a is less than 1.

EFFECTS ON MANAGEMENT. For the fishery manager, different kinds of reproduction curves will present different problems:

1. For the steep Curve C the possible equilibrium *catch* is 66% greater than the original average *population.* If stabilization occurs at moderate values of exploitation, the catch from year to year will have an inherent tendency to fluctuate—though the stock as a whole will be more stable than before fishing started. These fluctuations will be superimposed on those caused by environmental variability, and will prove confusing until the slope of the reproduction curve is finally determined.

2. For the Curve B stocks, maximum sustained yield is a little less than the original abundance. Stabilization of the fishing leads immediately to stabilization of catch, up to quite high values of rate of exploitation. Management should be easiest in this situation, although, if the fishery initially develops beyond the point of maximum yield, some of the problems below will be encountered.

3. A population close to Curve A will present more puzzling management problems. A steadily increasing fishery will take an increasing catch up to a point considerably beyond the point of maximum sustained yield. For example, suppose exploitation increases by 10% per generation in a fish which has a 5-year generation, and the unfished equilibrium population is 1000 tons. After 25 years the average catch will have risen to 440 tons per year, taken at 50% exploitation. This is considerably greater than the possible permanent yield of 330 tons per year, but there is no way for anyone to know it. Catch has been increasing continuously. It is true that catch per unit effort will have decreased by a third or a little more, but that will scarcely be noticeable because of the fortuitous

variability which would exist in any real situation. Even if noticed, it would likely be disregarded, because few expect fishing in a developed fishery to be as good as when fishermen were scarce. Thus there will seem to be no harm in continuing to fish at least at the 50% rate, or perhaps even harder.

Actually, there is no way to avoid a decrease in catch once exploitation has reached 50%. If by good luck fishing is held steady at that level, the decrease in catch will be gradual, and the final level will be only about 30% less than the highest level achieved, or about 10% less than the possible maximum equilibrium value. But it is a critical time. If exploitation were to rise from 50% to only 60%, the catch again rises slightly, but in succeeding years it falls. Decreasing rapidly at first, then more slowly, it moves toward equilibrium at a catch about 27% of the maximum achieved (60% line in Fig. 11.5). Concurrently catch per unit effort will fall to as low as 14% of what it was originally, or 28% of what it was at maximum catch. This really will be noticeable, and a search for causes and remedies will get under way. In a salmon fishery where there is information on abundance of spawners on the redds, there will be an additional indication of scarcity: the spawners will be only 8% as numerous as in the unfished stock, or 27% as numerous as when catch was greatest. All these signs will point toward "depletion" by rule of thumb reasoning, and hence restrictions on fishing are likely to be imposed. Restrictions mean temporary sacrifices, and they may or may not be made effective enough to get back to the level of maximum equilibrium catch—which, of course, has yet to be determined. However, no amount of restriction will ever get a sustained catch as large as the maximum of the developmental period, even if the optimum rate of exploitation has not been exceeded.

The above discussion applies directly to species which are taken only at the conclusion of their lives. If the fish of each brood are vulnerable over a period of years, similar relationships may apply, but changes in abundance are so complicated by fishing-up effects (Section 10F) that there is not much likelihood of determining the form of the reproduction curve from statistics of catch alone. It is worth noticing that an early maximum of yield in a developing fishery, a phenomenon which has in the past usually been attributed solely to the fishing-up effect, is also to be associated with rather flat reproduction curves such as D, A or E of Figure 11.2, even when the best rate of fishing is never exceeded.

Example 11c. HISTORY OF THE SKEENA RIVER SOCKEYE SALMON FISHERY. (Data from Milne, 1955.)

Table 11.3 shows the catches of sockeye salmon (*Oncorhynchus nerka*) in the Skeena River fishing area, averaged by 5-year periods, and an adjusted index of fishing effort which may be fairly close to "effective" effort (from Milne, 1955, table 3). Though exact statistics of early catches are lacking, the commercial fishery had a fairly steady growth from the early 1870's. The general picture up to 1937 is similar to the lines in Figure 11.5, showing a rise in catch up to a moderate level of exploitation (50% or 60%) and a subsequent decline when that level is maintained. Unlike the Figure 11.5 model, the Skeena rate of fishing

TABLE 11.3. Five-year averages of number of gill-net boats fishing on the Skeena (Milne's adjusted index); their sockeye salmon catch in thousands of cases (C); the instantaneous rates of fishing (i) computed as proportional to number of boats, using 0.69 in 1945-49 as a base; the corresponding rates of exploitation (u); the average size of stock (S) computed from C/u; and the average escapement ($E = S - C$). Prior to 1905 the number of boats is known for only occasional years, and the values given are interpolated. (Data from Milne, 1955; 1 case = 72 lb. round weight, approximately, or 7–8 fish.)

	Boats	i	u	C	S	E
				cases	*cases*	*cases*
1870–74	25	0.02	0.02			
1875–79	70	0.06	0.06			
1880–84	140	0.16	0.15			
1885–89	330	0.29	0.25			
1890–94	420	0.36	0.30			
1895–99	500	0.43	0.35			
1900–04	750	0.65	0.48			
1905–09	980	0.82	0.56	101	180	79
1910–14	1028	0.89	0.59	119	202	83
1915–19	1128	0.98	0.62	110	177	67
1920–24	1193	1.02	0.64	104	163	59
1925–29	1217	1.05	0.65	71	109	38
1930–34	1263	1.11	0.67	72	107	35
1935–39	1097	0.94	0.61	58	95	37
1940–44	891	0.76	0.53	65	123	58
1945–49	812	0.69	0.50	71	142	71
1950–54	....	0.62	0.46	69	150	81

decreased after 1937, and the catch and stock increased following the appropriate lag period (Table 11.3). As a matter of fact it is possible to choose, from among the reproduction curves described by expression (11.6), the one which best conforms to the Skeena fishery in respect to the interval between maximum catch and minimum catch and in respect to the percentage decline during that interval. The curve has the form:

$$F = Pe^{1.119(1-P/234{,}000)}$$

where F is the total stock (in cases) produced by parental generation P (see Appendix I, Fig. A1). For this curve the average maximum sustained yield is 98,000 cases, taken from a stock of 196,000 cases at 50% exploitation; the replacement size of stock is $P_r = 234{,}000$ cases. This is of course a very preliminary estimate of the potential of this fishery[6].

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[6] Shepard and Withler (1958) have now worked out the empirical average reproduction curve for this stock, using year-by-year catch and effort statistics and a division of each catch into its component age categories. The curve rises more slowly and has a much narrower dome than Figure A1. The indicated maximum sustained yield (for constant rate of exploitation) is 1.4 million sockeye or about 120,000 cases, obtained at a rate of exploitation close to 60%. They point out, however, that the shape of the curve is such that yearly adjustment of the rate of fishing to provide the optimum number of spawners would be particularly desirable. If this could be done precisely, an average yield somewhat greater than the above would be obtained (cf. Ricker, 1958b).

CHAPTER 12.—DIRECT ESTIMATION OF THE RELATION OF EQUILIBRIUM YIELD TO SIZE OF STOCK AND RATE OF FISHING

12A. GENERAL CONDITIONS

The final step in evaluating vital statistics of a fish population (of mixed ages and maturities) will be to bring changing recruitment into the picture along with growth and mortality, so that equilibrium yield under different fishing conditions can be computed. This has not yet been attempted on an analytical basis, because concurrent data on the variation of both growth and recruitment, in relation to abundance, are not yet available for any fishery. However we may look for it in the near future.

Meantime there have been a number of attempts to relate stock density to yield directly. These methods all involve the reasonable postulate that a fish stock produces its greatest harvestable surplus when it is at some intermediate level of abundance, not when it is at maximum abundance. Though perhaps not *always* true, this must be fairly generally so. The principal reasons for lessened surplus production at higher stock densities are three:

1. Near maximum stock density efficiency of reproduction is reduced, and quite commonly the actual number of recruits is less than at smaller densities. In the latter event, reducing the stock will increase recruitment.

2. When food supply is limited, food is less efficiently converted to fish flesh by a large stock than by a smaller one. Each fish of the larger stock gets less food individually, hence a larger fraction is used merely to maintain life, and a smaller fraction is used for growth.

3. An unfished stock tends to contain more older individuals, relatively, than a fished stock. This makes for decreased production, in at least two ways. (a) Larger fish tend to eat larger foods, so an extra step may be inserted in the food pyramid, with consequent loss of efficiency of utilization of the basic food production. (b) Older fish convert a smaller fraction of the food they eat into new flesh—partly, at least, because mature fish annually divert much substance to maturing eggs and milt.

Under reasonably stable natural conditions the net increase of an unfished stock is zero, at least on the average: its growth is balanced by natural deaths. Introducing a fishery increases production per unit of stock by one or more of the methods above, and so creates a surplus which can be harvested. In these ways "a fishery, acting on a fish population, itself creates the production by which it is maintained" (Baranov). Notice that effects 1 and 3 above may often increase the *total* production of fish flesh by the population—it is not merely a question of diverting some of the existing production to the fishery, though that also occurs.

The question of the interaction of a fish stock and its food supply had occupied Petersen (1922) and others, but apparently the first comprehensive attempt at a numerical computation and catch predictions based on these relationships was by Baranov (1926). He applied them to two fisheries: the North Sea plaice and the Caspian vobla. Following Petersen, he assumed a constant production of fish food in the environment, all of which was consumed at all possible densities of stock—to be used partly for the maintenance of the stock, partly for growth in excess of natural mortality. In both of his examples the reaction of the stock to the reduced fishery of world war I, and to the subsequent increase in fishing, provided the basis for the numerical computations. In its details, unfortunately, the argument of this paper suffers from errors of logic, and there are serious practical difficulties in its application, both of which aspects have already been discussed at length (see Edser, 1926; Monastyrsky, 1940). Here we will only add that the computation of the 1913 stock of plaice (assumed to be in equilibrium with the fishery) was made by dividing the catch by the rate of exploitation, instead of by the rate of fishing; the latter procedure would be correct because the fishery is pursued practically throughout the year. For this reason the estimate of stock is exaggerated (since $u = 0.44$, whereas $p = 0.70$).

If Baranov's computation for plaice is put on a rational basis it becomes very similar to the method of Schaefer (Example 12D below); but when this is done, no obvious relation of yield-plus-maintenance to the assumed constant food supply can be detected. Similarly, Monastyrsky found that when the Baranov computation for the vobla was followed through the late 1920's, eventually in 1931 the catch exceeded the estimated supply! Thus the details of Baranov's computation seem now to be only of historical interest, but it has stimulated investigation of the problem posed.

Another influential work has been that of Hjort, Jahn and Ottestad (1933). Discounting any likelihood of significant variation in rate of growth, these authors concluded that a stable unfished stock has either a smaller absolute reproduction or a greater absolute mortality (or more likely both these) than has a stock of less than maximum size; and that the maximum stable catch would be available at less than maximum stock abundance. Their numerical computation is not a very convenient one, however, and they applied it only to the case of a whale stock for which catch continuously exceeded reproduction—that is, no equilibrium was established.

12B. Fitting a Parabolic Surplus Production Curve and Logistic Growth Curve—Method of Graham

It remained for Graham (1935) to introduce a simple and consistent numerical model based on reasoning like the above. He postulates that the instantaneous rate of surplus production of a stock (the resultant of recruitment, growth and natural mortality) is directly proportional to the difference between the actual density and the maximum density which the area will support.

Further, when fishing removes the surplus production at the same rate as it is produced, it becomes the yield from a stock held in equilibrium. Consider:

W_t	the weight of the stock at some equilibrium condition t
W_∞	the maximum possible equilibrium stock
k	the instantaneous rate of increase of the stock ($= g+z-q$), *at minimal densities* (k = V of Graham)
p_t	the rate of fishing which maintains the stock in equilibrium at size W_t

In these symbols, Graham's postulate above is that the equilibrium yield at any stock density W_t is equal to:

$$p_t W_t = W_t\left(\frac{k(W_\infty - W_t)}{W_\infty}\right) \tag{12.1}$$

$$= kW_t - \left(\frac{k}{W_\infty}\right) W_t^2 \tag{12.2}$$

The form (12.2) shows that the relation between equilibrium stock and equilibrium yield is a parabola: an example is shown in Figure 12.1B. Notice that maximum yield is obtained, with this model, when the stock is at exactly half of its maximum equilibrium level.

Fitting expression (12.1) to statistics of an actual fishery can be done from several combinations of information. Required for all methods is:

(1) The absolute size of the stock, W_t, and the rate of fishing, p_t, at a stable level of abundance (i.e., when the stock is in equilibrium with the fishery).

Easiest to combine with (1) is:

(2) The level of stock, W_∞, characteristic of no fishing. Under suitable conditions this can be found by relating W_∞ to the stable W_t, proportionately to the catch per unit effort for each situation. (Strictly speaking, W_∞ can exist only when there is no catch, but an early stage of a fishery can be considered as corresponding approximately to the natural equilibrium. However the "suitable conditions" just postulated may not often occur, for it is notorious that the catch per unit effort at the start of exploitation may overestimate the true abundance of the stock.) Example 12A illustrates the use of these two pieces of information.

(3) In place of the value W_∞, a second equilibrium level of exploitation and stock may be combined with (1). Either the new W_t and p_t may be estimated independently; or, with greater risk, the new W_t may be related to that determined in (1) by using the catch per unit effort for the two situations, and p_t may be considered proportional to gear in use in each case. Example 12B illustrates this procedure.

INFORMATION FROM RATE OF INCREASE OF THE STOCK. If the surplus production in (12.1) is allowed to accumulate instead of being taken by the fishery, the stock grows and eventually approaches its maximum size. At least as a mathematical proposition, the hypothesis we are using indicates that (12.1) defines the rate at which this growth will occur; using t now to indicate time, in years, it may be written:

$$\frac{dW_t}{dt} = W_t\left(\frac{k(W_\infty - W_t)}{W_\infty}\right) \qquad (12.3)$$

In integrated form, this is the S-shaped "logistic" curve of Verhulst:

$$W_t = \frac{W_\infty}{1 + e^{-k(t-t_0)}} \qquad (12.4)$$

t_0 is a constant which adjusts the time scale to an origin at the inflexion point of the curve: i.e., $t - t_0 = 0$ when $W_t = W_\infty/2$. For some purposes it is useful to transform (12.4) to a straight-line relationship in t:

$$\log_e\left(\frac{W_\infty}{W_t} - 1\right) = kt_0 - kt \qquad (12.5)$$

EXAMPLE 12A. FITTING A PARABOLIC SURPLUS-PRODUCTION CURVE, GIVEN W_∞ AND ONE EQUILIBRIUM LEVEL OF FISHING

This illustration and the two to follow are freely adapted from Graham's (1935) data and computations concerning the North Sea demersal fish stocks. However the absolute level of stock indicated is fictitious.

A fishery, many years in a state of steady effort and yield, is characterized by a yearly catch (Y_t) of 40,000 tons, of which 30,000 tons consist of fish which were already vulnerable at the start of the year. The rate of exploitation of these fully-vulnerable individuals is found by tagging to be 30%. The vulnerable stock present at the start of the year is therefore 30,000/0.3 = 100,000 tons, and since the stock is in equilibrium with the fishery, this represents also the vulnerable stock continuously on hand. The rate of fishing, p_t, is therefore 40,000/100,000 = 40%, and this must also be the instantaneous rate of surplus production (rate of recruitment plus rate of growth less rate of natural mortality).

Catch per unit effort is currently 10 tons per boat per day. However some years earlier, immediately following a long fishing respite, catch was 22 tons per day. Considering Y/f proportional to stock, the stock charcteristic of no fishing was therefore 100,000×22/10 = 220,000 tons.

The instantaneous rate of fishing, p_t, is equal to $k(W_\infty - W_t)/W_\infty$ in (12.1); hence $k = 0.40 \times 220{,}000/120{,}000 = 0.733$. The relationship of equilibrium yield to size of stock is therefore, from (12.2):

$$Y_t = 0.733\ W_t - \frac{0.733\ W_t^2}{220{,}000} \qquad (12.6)$$

EXAMPLE 12B. FITTING A PARABOLIC SURPLUS PRODUCTION CURVE GIVEN TWO EQUILIBRIUM LEVELS OF FISHING

Suppose that W_∞ is not known, but that a second level of equilibrium yield is available along with the one described in Example 12A. The data for the two are as follows:

First level	Second level
$W_t = 100{,}000$ tons	$W_t = 60{,}000$ tons
$Y_t = 40{,}000$ tons	$Y_t = 32{,}000$ tons
$p_t = 0.40$	$p_t = 0.53$

For a trial $W_\infty = 200{,}000$, the value of k is estimated for each level, using (12.2):

First level: $k = 0.40 \times 200{,}000/100{,}000 = 0.80$

Second level: $k = 0.53 \times 200{,}000/140{,}000 = 0.76$

Further trials show that $W_\infty = 220{,}000$ makes the two estimates of k equal, its value being 0.733. The best descriptive equation can then be found as in Example 12A: it will prove to be (12.6). The two levels of stock and yield are indicated in Figure 12.1B.

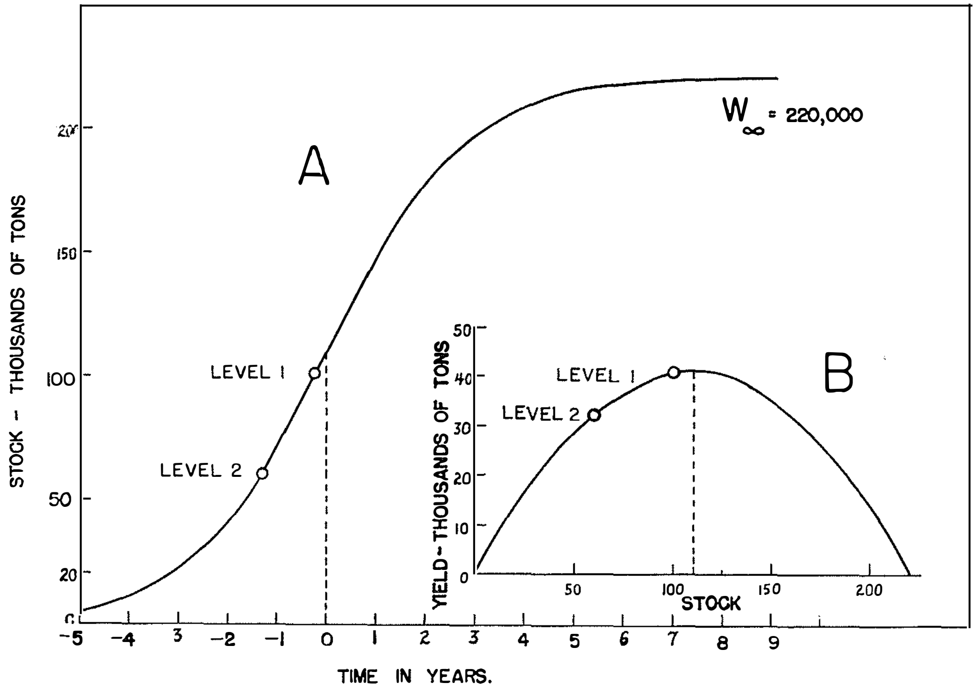

FIGURE 12.1. A. Logistic curve of increase for the population of Examples 12A-12C. B. The concomitant parabolic relationship of yield to stock density. The abscissal scale of A indicates the rate at which the stock, in the absence of fishing, would move toward the asymptotic level W_∞.

As an example of the kind of conclusion which Graham (1935) arrived at, notice that the equation (12.6) indicates a maximum catch at stock density $W_\infty/2 = 110{,}000$ tons, and at a rate of fishing of $k/2 = 0.733/2 = 0.366$. The maximum equilibrium catch is therefore $110{,}000 \times 0.366 = 40{,}300$ tons. Hence at both of the stable levels of stock postulated in this example, extra fishing effort is being devoted to reducing the size of the annual catch. Even at the "first level", where the catch (40,000 tons) is *almost* the maximum, this same amount could be obtained from a higher level of stock at a rate of fishing of 0.333, hence with a saving of effort of $(0.4 - 0.333)/0.4 = 17\%$.

EXAMPLE 12C. FITTING A PARABOLIC SURPLUS PRODUCTION CURVE AND LOGISTIC POPULATION GROWTH CURVE, GIVEN ONE EQUILIBRIUM LEVEL OF STOCK AND ITS INCREASE DURING A PERIOD OF NO FISHING

Consider again the equilibrium state of Example 12A; characterized by:

$$\begin{aligned} Y_t &= 40{,}000 \text{ tons} \\ u_t &= 0.30 \\ W_t &= 100{,}000 \text{ tons} \\ p_t &= 0.40 \end{aligned}$$

After some years of this, fishing suddenly ceased: let this be time $t = 0$. During 2.7 subsequent years of no fishing, yield per unit effort had increased from 10 tons per boat per day to 19 tons. Considering this as proportional to stock, the final stock is estimated as 190,000 tons. There is no direct evidence whether stock was yet at its maximum equilibrium size, but this would seem unlikely to have occurred in so short a time.

The procedure is to use a trial value of W_∞, and compute a trial k from $p = 0.40$, using (12.1). For trial $W_\infty = 250{,}000$, $k = 0.40 \times 250{,}000/150{,}000 = 0.667$. Substituting in (12.5), at time $t = 0$:

$$\log_e\left(\frac{250{,}000}{100{,}000} - 1\right) = 0.667 t_0$$

Hence the trial t_0 is 0.61, which determines a trial relationship of the type (12.4):

$$W_t = \frac{250{,}000}{1 + e^{-0.667(t-0.61)}}$$

Substituting $t = 2.7$, we obtain $W_t = 200{,}000$ tons, which is higher than the observed 190,000 tons. Further trials show that $W_\infty = 220{,}000$ tons, $k = 0.733$ and $t_0 = 0.25$ give the best fit to the data; the corresponding logistic equation of stock growth is:

$$W_t = \frac{220{,}000}{1 + e^{-0.733(t-0.25)}} \qquad (12.7)$$

Notice that the data of Example 12A or 12B are also adequate to compute (12.7), subject to the reservations already given. The value $t_0 = 0.25$ indicates that the equilibrium state of Example 12A is 1/4 year to the left of or "previous to" the inflexion point of the logistic curve, the latter occurring when $W_t = 110{,}000$ tons. Having obtained this t_0, it is convenient to use the inflexion point as the origin of the logistic graph, and let $W_t = 100{,}000$ correspond to $t = -0.25$. This is the abscissal scale indicated in Figure 12.1A. The corresponding equation is:

$$W_t = \frac{220{,}000}{1 + e^{-0.733t}} \qquad (12.8)$$

12C. Relation of Surplus Production to Size of Stock and Rate of Fishing, using the Yearly Increase or Decrease of the Stock—Method of Schaefer

Schaefer (1954) introduced a method of estimating surplus production or "equilibrium catch" for each year individually[1]. This is, in effect, to divide each year's catch in pounds, Y, by its rate of fishing, p, in order to obtain an estimate of mean stock, $\overline{\mathrm{W}}$, present during the year. The level of stock at the turn of a year is approximately the average of the mean stocks of the year just completed and the year ahead. The difference between two initial stocks is the increase for the year in question; that is, the increase in year 2 is approximately:

$$\frac{Y_3/p_3 + Y_2/p_2}{2} - \frac{Y_2/p_2 + Y_1/p_1}{2} = \frac{Y_3/p_3 - Y_1/p_1}{2} \qquad (12.9)$$

The surplus production or equilibrium yield, Y′, for year 2 above is therefore:

$$Y_2' = Y_2 + \frac{Y_3/p_3 - Y_1/p_1}{2} \qquad (12.10)$$

The values of p needed in (12.9) are most directly obtained by estimating p (for at least one year) by tagging or by one of the other methods described in earlier chapters; from it the catchability, c, is estimated, and the other p's are estimated as proportional to effective fishing effort ($p_t = cf_t$ for each year).

Determined in this way, surplus production can be plotted against stock density, independently of any hypothesis relating the two. If a well-defined curve for a reasonably wide range of stock densities is obtained, it can be used quite empirically to define the position of maximum yield for the stock—particularly if the fish in question have a short life history and react quickly to density changes. With long-lived fishes a big danger lies in the lag in the reaction of surplus production to stock density; in this respect this method has the same weakness as that of Example 12c.

If a graph of surplus production against size of stock does not cover the whole of the range which is of interest, some kind of curve must be fitted to it to permit extrapolation. For this purpose Schaefer, like Graham, has used the parabola, though with the reservation that a curve skewed to the left seems to have some support from observation to date.

An alternative plan is to plot surplus production against rate of fishing (p_t) or even against (effective) fishing effort (f_t). Dividing both sides of (12.1) by W_t gives an expression for p_t in terms of W_t. From this, W_t can be expressed

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[1] In an interesting paper, Thompson (1950) applied the concept of a "normal catch" to the Pacific halibut fisheries. The catch selected as normal was the average yield for a period of time after the original fishing-up of accumulated stock was completed—1926-33 on the southern halibut grounds and 1926-36 on the western grounds. From the definition of normal, removals in excess of the norm were accompanied by a decrease in stock density (as shown by decrease in catch per unit effort), while catches less than the norm were accompanied by increase in catch per unit effort, during those years. There is a superficial similarity between this treatment and Schaefer's, because the latter also proceeds from a definition that catches in excess of surplus production (his "equilibrium catch") in any year must result in a decrease in stock, and vice versa. However the difference between the two approaches is more important than the resemblance: whereas Thompson is impressed by the apparent constancy of the "normal" catch over the indicated intervals of time, Schaefer joins with Baranov, Hjort and Graham in emphasizing that equilibrium catch must change as size of stock changes. Actually, of course, the normal levels used by Thompson did not remain normal in later years, and in addition some of the population statistics computed from them are seriously at odds with those derived from the age structure of the population or from the results of tagging experiments.

in terms of p_t and substituted in (12.2). The resulting expression for surplus production or equilibrium yield is:

$$Y'_t = p_t W_t = W_\infty \left(p_t - \frac{p_t^2}{k} \right) \tag{12.11}$$

Thus the graph of surplus production against rate of fishing is a parabola, just as is its graph against size of stock (on the assumptions used). Similarly, cf_t can be substituted for p_t in (12.11), giving a parabola of Y' against f:

$$Y'_t = cW_\infty f_t - \left(\frac{c^2 W_\infty}{k} \right) f_t^2 \tag{12.12}$$

More recently Schaefer (1957) has shown that (12.12) can be fitted by iteration when there is no independent information on the numerical value of the catchability, c. If (12.12) is divided through by f_t, the parabolic relationship takes the straight-line form:

$$\frac{Y'_t}{f_t} = cW_\infty - \left(\frac{c^2 W_\infty}{k} \right) f_t \tag{12.13}$$

Thus a plot of "equilibrium yield per unit effort" against effort, each year, approximates a straight line whose slope is $c^2 W_\infty / k$ and whose intercept is cW_∞; and the least-squares fit of the line will give the "prediction" form of the relationship[2]. However a trial estimate of c is needed in order to estimate the Y' values, from (12.10), which are used on the LHS of (12.13). Using several trial estimates of c (Schaefer's k_2), graphical interpolation will give an estimate of the value for which mean square deviation from the line of fit of (12.13) is least.

In the yellowfin tuna example (Schaefer, 1957, fig. 4) a rather wide range of c values (those corresponding to rates of fishing from $p = 0.92$ to $p = 1.61$ at the 1954 level of fishing effort) all gave very similar lines of the form (12.13). This means, on the one hand, that this method does not estimate c with any precision but, on the other hand, even an approximate estimate of c suffices to give as good an estimate of the relationship between Y' and f as the data are capable of providing.

Example 12D. COMPUTATION OF SURPLUS PRODUCTION FOR HALIBUT, AND FITTING A SYMMETRICAL CURVE. (From Schaefer, 1954.)

Table 12.1 illustrates the method of calculating surplus production for the Pacific halibut in the southern area; it is based on Schaefer's table I, but it is arranged to correspond better to the usages of this Handbook. The significant step is to convert catch (column 2) into mean stock (column 6) by dividing by rate of fishing (column 5). The latter is scaled to the results of tagging experiments, which indicated an instantaneous fishing mortality rate, p, of about 0.615 in 1926[3]. The values for p in other years are calculated as proportional to

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[2] Schaefer first (p. 256) shows a method of estimating the "functional" form, which however gives a closely similar result.

[3] The figure used by Schaefer is 0.635, corresponding to an annual mortality rate (m) of 0.47. However Schaefer referred this 0.635 to the old estimate of 494,000 skates of gear in 1926, rather than to the 477,000 skates which the revised data of his table indicate, so I have adjusted the rate of fishing in order to make the table consistent. Note that even 0.615 is greater than the 0.57 estimated for fully-vulnerable fish in Example 5F.

TABLE 12.1. Sample computations of equilibrium yield (surplus production) for the Area 2 halibut stock. (From Schaefer, 1954, table 1, where the complete schedule is given.) The year 1926 is the base year for rate of fishing.

1	2	3	4	5	6	7	8	9
	Catch Y	Effort f	Catch per skate Y/f	Rate of fishing, p	Mean stock $\overline{W}$	Initial stock W	Change of stock ΔW	Surplus production Y'
	10^6 *lb.*	10^3 *skates*	*lb.*		10^6 *lb.*	10^6 *lb.*	10^6 *lb.*	10^6 *lb.*
1915	44.0	374	117.5	0.481	91.4		....	....
						90.1		
1916	30.3	265	114.1	0.341	88.8		−14.1	16.2
						76.0		
1917	30.8	379	81.3	0.488	63.2		−10.5	20.3
						65.5		
1918	26.3	302	87.0	0.388	67.7		+ 0.2	26.5
						65.7		
1919	26.6	325	81.8	0.418	63.6		−1.4	25.2
						64.3		
1920	32.4	388	83.6	0.499	65.0		....	....
......	......	......	......	......	......	......	......	......
1926	24.7	477	51.7	0.615	40.2	....	....	....

effort, *f*. The mean stocks shown in column 6 are averaged between successive years to obtain approximate estimates of initial stock (column 7), and differences between the latter show the estimated change in stock during each year (column 8). Adding the catch to the latter gives the net additions to the stock during the year (column 9), which is the "equilibrium catch" or "surplus production". These equilibrium catches are plotted against mean stock density in the upper panel of Figure 12.2. There is some tendency for the years of smallest stock to have a small surplus production, hence Schaefer concludes that the stock in those years was probably less than what would produce a maximum surplus and maximum equilibrium catch.

This conclusion is independent of the exact nature of the relation of surplus production to stock size; and, in fact, the scatter of the points gives little clue concerning the form of the complete surplus production curve. However, for illustration Schaefer computed an equilibrium-yield parabola for the graph of Y' against $\overline{W}$ by least squares (the aberrant 1916 value is omitted). This parabola is also drawn on our Figure 12.2A. For comparison of symbols and calculations, note the following equivalents:

$\overline{fP}$ of Schaefer = Y' here
k_1 of Schaefer = k/W
k_2 of Schaefer = c or p/f (catchability)

Schaefer's formula for the equilibrium-yield parabola is, in our notation (expression 12.1):

$$Y'_t = W_t\left(\frac{0.931(121\times10^6-W_t)}{121\times10^6}\right)\text{ lb.}$$

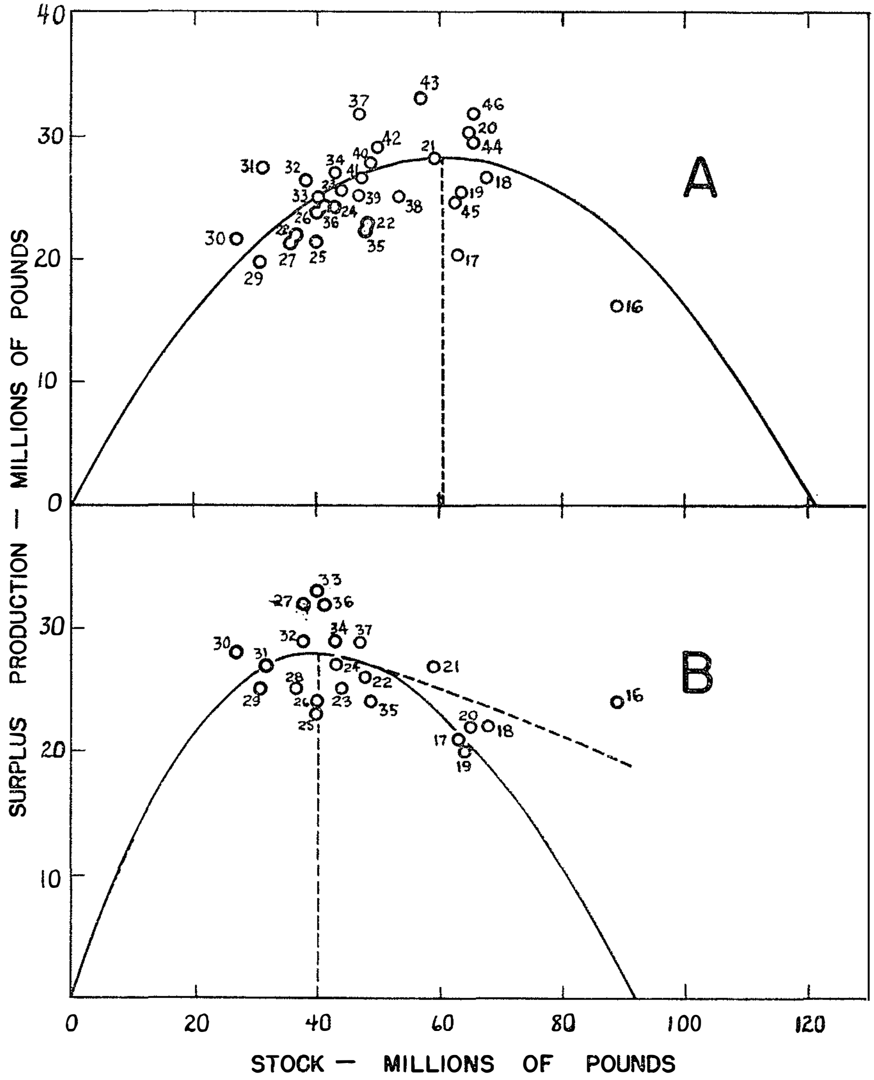

FIGURE 12.2. A. Surplus production (equilibrium catch) of Pacific halibut in Area 2, plotted against stock density in the same year, with a production parabola fitted to average values (after Schaefer, 1954, fig. 2). B. The same surplus productions plotted against stock density 9 years previously (the latter identified by the years beside the points). The dotted curve is drawn freehand, while the solid curve is fitted by expression (A19). The 1916 point was omitted in fixing the position of both of the computed curves, but was allowed to influence the freehand curve.

where W_t is the stock present at any time and 121×10^6 lb. is the maximum level of stock. The *k* value, 0.931, is the instantaneous rate of surplus production by the stock at minimal densities, and is the initial slope of the parabola in Figure 12.2A.

An unavoidable weakness of the procedure above is the fact that it is very unlikely that halibut could adjust their growth or mortality to stock size rapidly enough to make a plot of surplus production against the current size of the stock meaningful (cf. Example 12E).

12D. Asymmetrical Surplus Production Curves

Graham and Schaefer have, quite naturally, worked with a symmetrical surplus production curve, since this is the simplest form available and since their observations give little clue concerning the actual shape. However recruitment is a component of surplus production, and most of the available recruitment curves are asymmetrical (Ricker, 1954b). The theoretical reproduction curves of Figure 11.2 can be converted to surplus production curves by computing $Z-W$ for equilibrium situations ($=C_E = Z_E - W_E$: see formula (A19) of Appendix I). When values of C_E are plotted against W_E (Fig. 12.3) the resulting figures constitute surplus-production graphs for the situation where surplus production depends solely on recruitment. All the graphs shown are somewhat asymmetrical—skewed to the left. Further, asymmetry in this direction is not just a special characteristic of the curves described by expression (11.5); it is obtained with most reasonable-looking reproduction graphs, and it can be more extreme than the examples of Figure 12.3. Consequently when surplus production depends mainly on increased recruitment, we should anticipate that its graph against population density will usually be skewed to the left. The corresponding graphs of surplus production against rate of exploitation or rate of fishing are, of course, skewed to the right, as in Figure 11.4.

The quadratic surplus-production expression (12.2) might be modified to describe this situation by substituting for W_t^2 some higher power of W_t—the exponent being not necessarily an integer. Alternatively, expression (A19) can be tried.

Example 12E. Computation of an Asymmetrical Surplus Production Curve for a Halibut Stock. (Data from Schaefer, 1954.)

The Area 2 Pacific halibut of Example 12D start to become important commercially at about age V, and they make their maximum contribution to the catch at about age IX (though this has varied by a few years). The halibut catch has not been divided up by ages, over the years, so no true graph of the parent-progeny relationship is available[4]. However if as an approximation the surplus production or "equilibrium catch" (Y') is plotted against parental stock density 9 years previously, there is little or no indication that stock density has been below the optimum, *in so far as surplus production may depend on recruitment* (Fig. 12.2B).

A surplus production curve derived from (11.7) can be fitted approximately to such a figure, and it will have the form of the equilibrium yield curve (A19 of Appendix I). The simplest way to fit this is by selecting a trial value for maximum surplus production and the parental stock which produces it—in other words, the position of the apex of the curve of Figure 12.2B. The condition for maximum equilibrium yield is shown in (A20). To use (A19) and (A20), our figures must

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[4] Even if available, it would be desirable to adjust the total weight contribution of each year-class to the fishery by the estimated natural mortality after the start of recruitment. With a variable rate of fishing, the fraction of each brood (by number) which has been caught has varied considerably, but the weight contribution per unit recruitment would vary much less because of the excess of growth over natural mortality at younger ages.

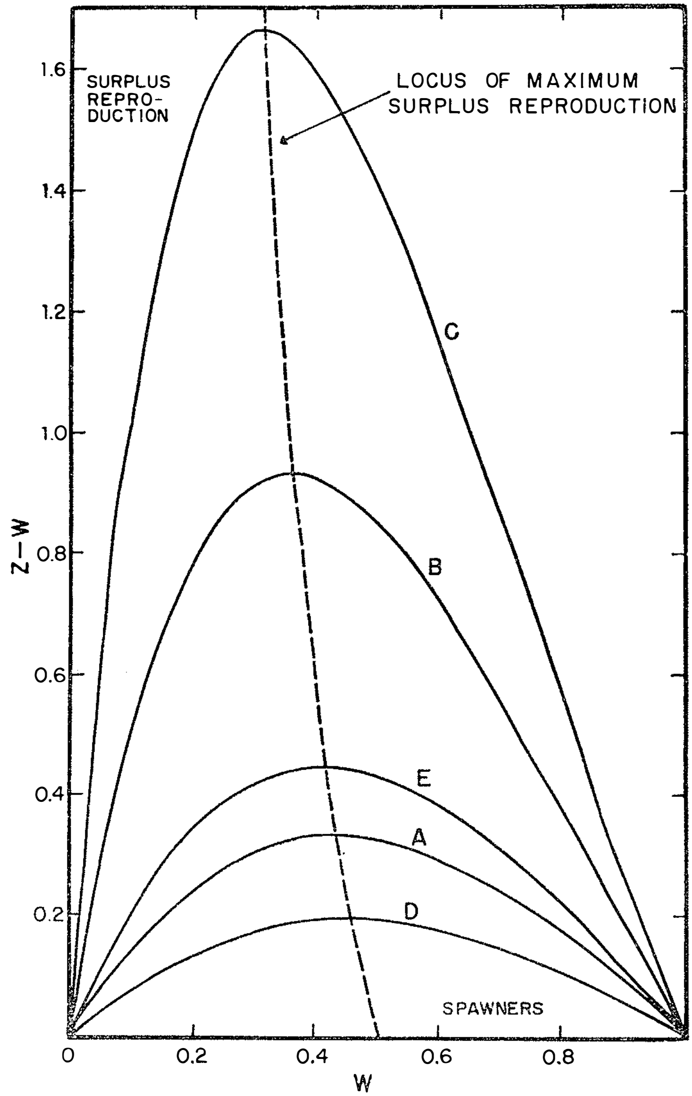

FIGURE 12.3. Curves of surplus production (equilibrium production less adult stock, or Z — W), plotted against adult stock density (W), for the five curves of Figure 11.2. The unit for both axes is the replacement level of production.

be divided by the (unknown) replacement level of stock P_r. Estimating the maximum surplus as 28.5 million pounds, taken at a stock density of 40 million pounds, (A19) and (A20) are equivalent to:

$$\frac{28.5}{P_r} = \frac{40e^{a(1-40/P_r)}}{P_r} - \frac{40}{P_r}$$

$$(1 - 40a/P_r)e^{a(1-40/P_r)} = 1$$

Solving these simultaneously gives:

$$a = 0.954$$
$$P_r = 91.8 \text{ million pounds}$$

This is the solid curve drawn on Figure 12.2B, and would describe the trend reasonably well except for 1916 (a point which gives trouble in 12.2A also).

However it is unlikely that this halibut fishery will prove to follow a relationship as simple as those shown in either A or B of Figure 12.2. One reason is that the age composition of the stock has changed over the years: it contained more old fish during the years of fishing-up, to say 1920, more young fish during the period 1921-40, and recently a lot of older fish again. These qualitative changes in the stock affect catch per unit effort and hence the positions of the points on these graphs (the younger fish are less vulnerable); they may also affect recruitment; and they obviously should modify the lag period used in Figure 12.2B, though the latter can be adjusted without changing the picture greatly. Since no true equilibrium situation has ever existed during the period of record, the attempt to define the position of maximum equilibrium yield must be extremely tentative, quite apart from the possibility of significant variation in environmental influence on reproduction. Data for years subsequent to those used in Figure 12.2 tend to put the apex of either curve somewhat higher and at greater stock densities.

APPENDIX I. DEVELOPMENT OF MODEL REPRODUCTION CURVES ON THE BASIS OF A THEORY OF PREDATION AT RANDOM ENCOUNTERS[1]

Using formula (11.6) of Chapter 11 can be justified only by its applicability to observed information on reproduction. However it is instructive to consider what kind of theoretical situation can produce such a relationship. One such approach[2] is from consideration of predation upon the eggs or young of the species, when this occurs (on the average, if not necessarily on each occasion) as though at random encounters between predator and prey. That is, the relative (or absolute) abundance of predator and prey does not affect the expectation of capture of an individual of the prey species by an individual predator.

The consequences of random searching for insect prey by hymenopterous parasites (really predators) has been examined by Nicholson (1933). Much the same concept is involved here.

Consider a predator-prey system in which the prey density is governed by a predator species or assemblage of species early in its life, and the abundance or effectiveness of these predators is affected by or is related to the abundance of the prey in some direct manner. The predators are not wholly or even mainly dependent for food on this prey. The prey is not necessarily killed by these predators alone, but these include all the predators which are responsible for governing prey abundance: any other causes of death of prey are non-compensatory.

Specifically, think in terms of a fish having pelagic eggs, larvae and juveniles, during which stages all compensation is assumed to occur. This seems fairly realistic because relative year-class strength usually varies little after a fish becomes of commercial size.

For predation to be compensatory, it is necessary that the abundance or effectiveness of the predators in question increase with increase in the abundance of the prey. For the mathematical development below, we assume that the average abundance of the predators (during the time of their contact with the prey) varies, from year to year, as some constant fraction of the *initial* abundance of prey (fish eggs or larvae, etc., at whatever stage compensation begins), but that the predators have a minimum abundance which is sustained by their other foods. This relationship is most easily pictured when the parents of the eggs or larvae in question are themselves the controlling predators, but it seems fairly appropriate for other possible compensatory agents.

It may be objected that predators ordinarily don't take all the food which they encounter, but feed to satiation and then stop. This is perhaps typical of warm-blooded predators, but for fishes a much greater range of daily rations is consistent with maintaining life, and the evidence of stomach analysis seems to be that fishes almost always eat considerably less than they *could*. The same probably applies to other poikilothermic organisms. In any event, if a predator becomes satiated at some density of prey and ceases to function as a control, that merely shifts a part of the compensatory mechanism to some other predator or other agent which can function at the higher density.

An important feature of the conditions just outlined is that there is a certain *time lag* in the adjustment of abundance (or effectiveness) of the controlling predators to the abundance of the prey. For simplicity we have assumed that the predators are able to adjust themselves in response to the *initial* prey abundance, but obviously their numbers might become more nearly proportional to some slightly later stage of the predator-prey interaction. For example, if a

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[1] Material in this appendix was presented as part of a series of Lectures on Population Dynamics at the Scripps Institution of Oceanography, September 6-8, 1955.

[2] A different approach which, making appropriate assumptions as to details, also leads to the relationship (A13), is developed by Beverton and Holt (1957, p. 55). The situation which they describe is one where competition for food reduces the growth rate of the denser broods during their first year of life, and the rate of predation on a brood at any given interval after hatching is inversely related to the average size of its members at that time.

herring population were regulated by way of the consumption of its larvae by comb-jellies, the abundance[3] of the ctenophores might be able to adjust itself in a given year so that its average level corresponded best not to the initial larval abundance, but to the abundance of larvae a week after the hatch (say). If however (as seems unlikely on biological grounds) the ctenophores were able to adjust their abundance continuously, day by day, to the changes in herring larval abundance, then the resulting reproduction curves would be quite different from the types obtained below[4].

The hypothesis to be examined requires that *with sufficiently high initial prey densities* the predators must be or must become so numerous that in the later part of the predation period they consume enough prey to actually decrease the absolute number of prey survivors (by comparison with survivors of some smaller initial prey density).

The following symbols are used:

M	mean abundance of predators which are involved in compensatory predation, during the time they affect the prey. (These will be called "controlling predators".)
M_0	abundance of controlling predators when the prey species is at zero abundance and hence no prey eggs are produced
P	abundance of adults of the prey species at spawning
E	number of eggs produced per adult (both sexes)
k_1, k_2, K	parameters; $k_1k_2 = K$
F	number of adults of a filial generation (of the prey) produced by parental abundance P
F_m	maximum reproduction (filial abundance) of prey
P_m	parental abundance of prey which results in maximum reproduction
F_r	replacement reproduction of prey
P_r	parental abundance of prey which results in replacement reproduction ($F_r = P_r$ when, as here, parents and progeny are in equivalent units)
Z	F/F_r
Z_m	F_m/F_r
W	P/P_r
a	P_r/P_m
i_0	instantaneous mortality rate of prey from causes other than the controlling predators
s_c	survival rate of prey from compensatory predation
s_n	survival rate of prey from all non-compensatory causes (including controlling predators up to density M_0)
E	used as a subscript, denotes an equilibrium level of stock, exploitation or yield

The average abundance of controlling predators at prey egg density PE and hence adult prey density (at spawning) P is:

$$M = M_0 + k_1P \tag{A1}$$

The total instantaneous mortality rate of the prey is:

$$i_0 + k_2(M_0 + k_1P) = i_0 + k_2M_0 + k_1k_2P \tag{A2}$$

Hence:

$$s_n = e^{-(i_0+k_2M_0)} \tag{A3}$$

$$s_c = e^{-k_1k_2P} = e^{-KP} \tag{A4}$$

The abundance of the filial generation of prey, F, produced by a parental generation, P, is:

$$F = PEs_ns_c = PEs_ne^{-KP} \tag{A5}$$

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[3] Or better, the "predation potential" of the ctenophores, which would involve their size, for example, as well as their abundance.

[4] They are, in fact, of the type described in the Addendum to this Appendix, page 268.

In order to evaluate K, consider the condition for maximum reproduction, found by differentiating (A5) and equating to zero:

$$-PKe^{-PK} + e^{-PK} = 0$$

Since e^{-PK} cannot $= 0$, $1 - PK = 0$ when P produces maximum F; hence:

$$K = 1/P_m \qquad \text{(A6)}$$

Substituting this in (A5) gives:

$$F = PEs_n e^{-P/P_m} \qquad \text{(A7)}$$

Maximum reproduction, when $P = P_m$, then becomes:

$$F_m = P_m E s_n e^{-1} \qquad \text{(A8)}$$

Parenthetically, this indicates that survival rate at maximum reproduction ($= F_m/P_mE$) is e^{-1} or 37% of s_n, that is, 37% of what it is when stock density approaches zero.

Dividing each side of (A7) by the corresponding side of (A8):

$$\frac{F}{F_m} = \frac{P}{P_m} e^{1-P/P_m} \qquad \text{(A9)}$$

This is the equation (10) of Ricker (1954b), showing reproduction in terms of its maximum.

However it is usually more convenient to put (A9) into terms of replacement reproduction, F_r, because at replacement $P_r = F_r$ and the two axes of the relationship have the same scale. From (A9), at the replacement level of stock:

$$\frac{F_r}{F_m} = \frac{P_r}{P_m} e^{1-P_r/P_m} \qquad \text{(A10)}$$

Dividing (A10) into (A9) on both sides:

$$\frac{F}{F_r} = \frac{P}{P_r} e^{P_r/P_m - P/P_m} \qquad \text{(A11)}$$

Since $F_r = P_r$:

$$F = Pe^{P_r/P_m - P/P_m} \qquad \text{(A12)}$$

(A11) can also be shortened to:

$$Z = We^{a(1-w)} \qquad \text{(A13)}$$

Relation of maximum reproduction to replacement reproduction. Given (A13), maximum reproduction can be found by differentiating and equating to zero:

$$-aWe^{a(1-w)} + e^{a(1-w)} = 0 \qquad \text{(A14)}$$

Since $e^{a(1-w)}$ cannot equal 0, at maximum reproduction $aW = 1$ and $W = 1/a$. Substituting these in (A13), the ratio of maximum reproduction to replacement reproduction is:

$$Z_m = \frac{e^{a-1}}{a} \qquad \text{(A15)}$$

This expression can also be used in reverse to compute a from a given value of Z_m. The solution has to be by interpolation in a table of exponentials or logarithms; and for each value of Z_m there are two possible values of a—one greater than unity and one less. Suppose, for example, that we want a curve in which the maximum recruitment is twice the replacement recruitment, i.e., $Z_m = 2$. The maximum can come either when the spawning stock is greater than the replacement level or when it is less. Solving (A15), $a = 2.678$ or 0.232; substituting these in (A13), the two curves can be calculated.

Equilibrium exploitation. Consider any reproduction curve, for example that of Figure A1. For any position of a stock *to the left of the 45-degree line,* there is a rate of exploitation which will maintain the stock in equilibrium at that position. Let A be any point on the curve and AC a perpendicular cutting the 45-degree line at B. At equilibrium the portion BC of the

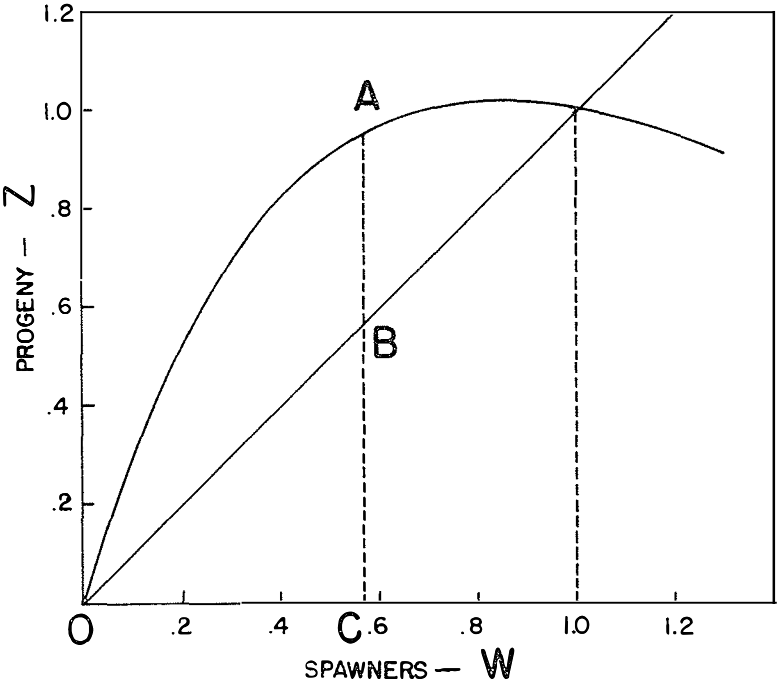

FIGURE A1. An example of a reproduction curve of the type $Z = We^{a(1-W)}$, with $a = 1.119$. The point A is any point on the curve, the distance AB representing the surplus reproduction which must be removed by fishing if the stock is to remain in equilibrium at this level. The distance AB becomes a maximum a little farther to the left on the curve.

recruitment must be used for spawning (since BC = OC), while AB is taken by the fishery. Representing such equilibrium values by the subscript E, the equilibrium rate of exploitation is:

$$u_E = \frac{AB}{AC} = \frac{Z_E - W_E}{Z_E} = \frac{W_E e^{a(1-W_E)} - W_E}{W_E e^{a(1-W_E)}} = 1 - e^{-a(1-W_E)} \tag{A16}$$

This can be reorganized to indicate directly the number of spawners, W_E, needed to sustain a rate of exploitation u_E:

$$W_E = 1 + \frac{\log_e(1-u_E)}{a} \tag{A17}$$

EQUILIBRIUM EXPLOITATION IN TERMS OF SLOPE. The slope, S′, of a line joining point A to the origin is AC/OC, or Z/W. From (A16) we may write:

$$u_E = 1 - \frac{1}{Z_E/W_E} = 1 - \frac{1}{S'_E} \tag{A18}$$

It follows that the locus of any given u_E is a straight line from the origin lying within the top left half of the recruitment graph: a number of these are drawn on Figure 11.2. These loci are applicable, of course, regardless of what may be the shapes of the reproduction curves under consideration.

CATCH AT EQUILIBRIUM. Knowing W_E from (A17), the equilibrium catch, C_E, corresponding to any equilibrium rate of exploitation, u_E, is:

$$C_E = u_E Z_E = Z_E - W_E = W_E e^{a(1-W_E)} - W_E \tag{A19}$$

Maximum equilibrium catch. The maximum catch which can be taken under equilibrium conditions is estimated by differentiating (A19) and equating to zero:

$$-\ aW_Ee^{a(1-W_E)} + e^{a(1-W_E)} - 1 = 0$$

$$(1 - aW_E)e^{a(1-W_E)} = 1 \quad \text{(when } C_E \text{ is a maximum)} \qquad \text{(A20)}$$

For any given a, (A20) can be solved by trial to give the value of W_E which gives maximum equilibrium yield, the corresponding Z_E is calculable from (A13), and the maximum sustained yield is $Z_E - W_E$.

The locus of maximum equilibrium yields is drawn on Figure 11.2 as the fine dotted line. It of course marks the point at which each of the curves has a tangent of 1, corresponding to a slope of 45°; in fact (A20) can also be obtained by equating the differential of (A13) to unity (instead of to zero as was done in A14). To the left of this point, the absolute magnitude of the reproduction decreases more rapidly than does the spawning stock needed to produce it.

Spawners needed for maximum equilibrium catch. As $a \rightarrow 0$ and the reproduction curve approximates to the 45-degree line, the locus of stock sizes which produce maximum sustained yields, calculated from (A20), approaches a terminal value at $W = Z = 0.5$ (Fig. 11.2). This means that, with reproduction curves of this type, *the size of the spawning stock which gives maximum sustained yield will in no case be greater than half of the replacement number of spawners.* That is, a fully-developed smoothly-functioning fishery should operate with less than half the average spawning stock which characterized the pre-exploitation population. From tests with other reproduction curves of various types, it appears that the above rule is true of practically all of the likely-looking kinds.

On the other hand, with curves described by (A13) best yield is obtained when W is no *less* than about 0.25, because for any smaller values the corresponding curve would become unreasonably steep. However this limit does *not* apply to certain other possible kinds of curves, for example Curve 2a of Ricker, 1954b, p. 564.

Reproduction curve corresponding to a given rate of exploitation at maximum equilibrium catch. The rate of exploitation, u, is equal to $(Z - W)/Z$, hence $Z/W = 1/(1 - u)$. From (A13) we may write:

$$Z/W = 1/(1 - u) = e^{a(1-W)} \qquad \text{(A21)}$$

Substituting this in the condition for maximum equilibrium catch (A20):

$$1 - aW_E = 1 - u_E$$

Hence, at MEC:

$$u_E = aW_E \qquad \text{(A22)}$$

Taking logarithms of (A21):

$$a - aW = -\log_e(1-u) \qquad \text{(A23)}$$

Substituting (A22) in (A23), at MEC:

$$a = u_E - \log_e(1-u_E) \qquad \text{(A24)}$$

Expression (A24) indicates the value of a from which can be computed a reproduction curve whose maximum equilibrium catch will be at a given rate of exploitation u_E.

Limiting equilibrium rate of exploitation. As the equilibrium rate of exploitation, u_E, increases, the corresponding equilibrium abundance of spawners, W_E, decreases. Eventually W_E becomes zero if u_E is sufficiently increased; and this happens at a point where u_E still has some positive value less than unity. This value is the limiting, or maximum, equilibrium rate of exploitation—that which cannot be reached without eventually exterminating the population. Substituting $W_E = 0$ in (A16), the limiting equilibrium rate of exploitation becomes:

$$u_E = \frac{e^a - 1}{e^a} = 1 - e^{-a} \quad \text{(when } W \rightarrow 0\text{)} \qquad \text{(A25)}$$

The limiting equilibrium instantaneous rate of fishing is therefore (in the absence of natural mortality during fishing):

$$p_{\mathrm{E}} = a \quad \text{(when } \mathrm{W} \to 0) \tag{A26}$$

It is also easy to show that the slope of the reproduction curve at the origin (W = 0) is equal to:

$$e^{a} \tag{A27}$$

Some characteristic statistics of each of the 5 curves of Figure 11.2 are shown in Table A1. 1. When $a < 1$, as in Curve D, the dome of the reproduction curve is to the right of the "45-degree line"—that is, maximum reproduction occurs when the spawners are more numerous than their replacement level. Starting a fishery immediately reduces the size of stock, but the stock comes to equilibrium at the reduced density defined by (A17), provided the rate of exploitation does not exceed $1 - e^{-a}$ (expression A25). The best rate of exploitation is that which brings the spawning population to the density defined by (A20), and thus gives maximum equilibrium catch. 2. The above is true also when $a = 1$ (Curve A) and the replacement density of stock is also the maximum density. 3. When $a > 1$ (Curves B, C, E), starting a fishery *increases* absolute reproduction for some time, but if exploitation is increased far enough reproduction eventually decreases again. The formulae for maximum catch and limiting rate of exploitation still apply.

TABLE A1. Characteristics of 5 reproduction curves of the type $Z = We^{a(1-W)}$, when the replacement level of stock is taken as 1000. The curves are plotted in Figure 11.2, page 239.

	Reproduction curve				
	D	A	E	B	C
Value of a (= P_r/P_m)	$\frac{2}{3}$	1	1.25	2	2.678
Maximum stock (replacement stock = 1000)	1072	1000	1027	1359	2000
Spawners needed for max. stock (1000/a)	1500	1000	800	500	373
Maximum equilibrium catch (MEC)	198	330	447	935	1656
Spawners needed for MEC	456	433	415	361	314
Stock density (before fishing) at MEC	654	763	862	1296	1970
Rate of exploitation at MEC	0.304	0.433	0.519	0.722	0.841
Limiting equilibrium rate of exploitation	0.486	0.632	0.714	0.865	0.932

ADDENDUM. Beverton and Holt (1957, pp. 49-55) develop a theoretical relationship between egg production, E, and resulting recruits, R, based on the postulate that rate of decrease from egg to recruit is, at successive intervals, proportional to the sum of (1) a density-independent mortality rate and (2) a compensatory mortality rate which is proportional to the number of larvae surviving at successive intervals. These assumptions lead to a relationship with two parameters:

$$\mathrm{R} = \frac{1}{\alpha + \beta/\mathrm{E}} \tag{A28}$$

With this expression the largest recruitments are at the highest values of E, and in fact recruitment asymptotically approaches the value $1/\alpha$. Inverted, (A28) becomes:

$$\frac{1}{\mathrm{R}} = \alpha + \frac{\beta}{\mathrm{E}} \tag{A29}$$

One way to fit the expression to data is therefore to plot values of 1/R against 1/E; the slope of the line is an estimate of β and the intercept is an estimate of α. (The fact that 1/R instead of R is used to fit the line is an advantage, because 1/R is likely to be more symmetrically distributed than is R itself. However the computed R values are reciprocals of the mean of 1/R for the given E, rather than a mean of R-values themselves.) Another method of evaluating β (Beverton and Holt, 1957, figures 15.14, 15.18) gives lower expected values of R for high E.

To put (A28) into a form comparable to (A13), values of R can be multiplied by a factor, x, which adjusts them to the same unit as E. Calling the new values R′, we have:

$$\frac{1}{\mathrm{R}'} = \frac{\alpha}{x} + \frac{\beta/x}{\mathrm{E}} \tag{A30}$$

At the replacement level of reproduction $\mathrm{R}' = \mathrm{E}$; let this particular value of E be represented by E_r. If observed values of R′ and of E are divided by E_r, they then represent reproduction and spawning stock, respectively, in terms of replacement stock. For these quantities we have been using the symbols Z and W; hence:

$$\frac{1}{\mathrm{Z}} = \frac{\alpha \mathrm{E}_r}{x} + \frac{\beta/x}{\mathrm{W}} \tag{A31}$$

Now at replacement $\mathrm{Z}=\mathrm{W}=1$, so that $\beta/x = 1 - \alpha \mathrm{E}_r/x$. Letting $A = \alpha \mathrm{E}_r/x$ for convenience, (A31) becomes:

$$\frac{1}{\mathrm{Z}} = A + \frac{1 - A}{\mathrm{W}} \tag{A32}$$

which is an expression with one parameter, comparable to (A13). In inverted form it is:

$$\mathrm{Z} = \frac{\mathrm{W}}{1 + A(\mathrm{W} - 1)} \tag{A33}$$

This expression illustrates the relation of the asymptotic reproduction $1/A$ to the replacement reproduction (which is unity). Its practical use would hinge on obtaining an estimate of this

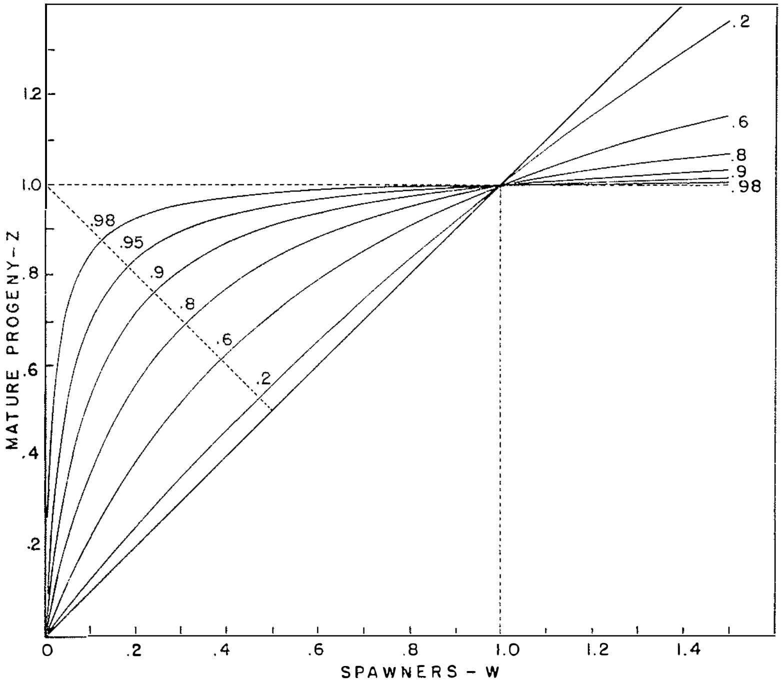

FIGURE A2. Reproduction curves corresponding to the relationship $\mathrm{Z} = \frac{\mathrm{W}}{1 + A(\mathrm{W} - 1)}$, for the values of A indicated on the corresponding curves. Both the progeny, Z, and the spawning stock, W, are expressed in terms of the replacement density of stock, which is 1. The diagonal from the ordinate value $\mathrm{Z} = 1.0$ is the locus of maximum equilibrium yields.

relationship, but it is instructive to compare populations described by different values of A but having the same equilibrium density in the absence of exploitation, in a manner similar to Figures 11.2 and 11.4.

Some curves conforming to (A33) are shown in Figure A2. To the left of the replacement density, all the curves are symmetrical about a diagonal running from (0, 1) to (0.5, 0.5). The limiting forms of the curve are the 45° diagonal when $A = 0$, and a right-angled "curve" when A has its maximum value, 1. With values of A greater than about 0.9, expression (A33) describes reproduction curves quite unlike any described by (A13): that is, situations in which reproduction rises rapidly to a point close to *but not exceeding* the asymptotic level and changes little thereafter.

Statistics can readily be derived from (A33) which are similar to those calculated above for (A13). We will note only that the slope of (A33) is given by its differential:

$$\frac{1 - A}{[1 + A(\mathrm{W} - 1)]^2} \tag{A34}$$

The position of 45° slope, which is the position of maximum equilibrium yield, is obtained by equating this to 1 (tan 45°). Using the subscript E to represent equilibrium situations, the positive root of the quadratic above is:

$$\mathrm{W_E} = \frac{A - 1 + \sqrt{1 - A}}{A} \quad \text{(when } \mathrm{Z_E} - \mathrm{W_E} \text{ is a maximum)} \tag{A35}$$

The value of (A35), the $\mathrm{W_E}$ corresponding to maximum sustained yield, has an upper limit of 0.5 as $A \rightarrow 0$. Hence the maximum equilibrium yield is obtained with a spawning stock no greater than half of its primitive replacement level, for all curves of this family—the same conclusion as discovered for the (A13) family. The locus of maximum equilibrium catches is in fact the NW-SE diagonal (Fig. A2).

In contrast to (A13), plausible *simple* biological situations which would result in (A33) are apparently not easy to visualize; but in biology complex situations seem to be at least as frequent as simple ones (Section 11D). On the observational side, the available information for North Sea plaice evidently suggests that recruitment has no detectable trend over a wide range of stock densities (Beverton and Holt, 1957, p. 270), a condition which could be described well by (A33) when A equals 0.95 or more. Because of their large year-to-year variability in reproduction, some existing series of reproduction observations could be described almost equally well by (A33) and by (A13).

APPENDIX II. TABLE OF EXPONENTIAL FUNCTIONS AND DERIVATIVES

Functions frequently needed in the calculations of this Handbook are given in terms of the instantaneous mortality rate, i, the annual mortality rate, a, and the annual survival rate, s.

$$(1 - a) = s = e^{-i}$$

Note that column 5, headed a/is, is also equal to $(e^{i} - 1)/i$.

In general, the accuracy of the figures tabulated does not exceed about 0.05%, so that the fourth significant figure is not always wholly reliable.

The short schedule below gives a few values of i for even values of a:

a	i	a	i	a	i	a	i
0.00	0.0000	0.25	0.2877	0.50	0.6391	0.75	1.3863
0.05	0.0513	0.30	0.3567	0.55	0.7985	0.80	1.6094
0.10	0.1054	0.35	0.4308	0.60	0.9163	0.85	1.8971
0.15	0.1625	0.40	0.5108	0.65	1.0498	0.90	2.3026
0.20	0.2231	0.45	0.5978	0.70	1.2040	0.95	2.9957

1 i	2 a	3 s	4 a/i	5 a/is	6 a^2	7 i^2	8 a^2/i^2	9 $i-a$	10 $a^2/(i-a)$	11 $i^2/(i-a)$	12 e^i-1	13 i
.01	.0100	.9900	.9950	1.005	.0001	.0001	.9900	.0000	1.988	2.007	.0101	.01
.02	.0198	.9802	.9901	1.010	.0004	.0004	.9800	.0002	1.973	2.013	.0202	.02
.03	.0296	.9704	.9851	1.015	.0009	.0009	.9704	.0004	1.961	2.020	.0305	.03
.04	.0392	.9608	.9803	1.020	.0015	.0016	.9609	.0008	1.948	2.027	.0408	.04
.05	.0488	.9512	.9754	1.025	.0024	.0025	.9514	.0012	1.935	2.034	.0513	.05
.06	.0582	.9418	.9706	1.031	.0034	.0036	.9417	.0018	1.922	2.041	.0618	.06
.07	.0676	.9324	.9658	1.036	.0046	.0049	.9327	.0024	1.909	2.047	.0725	.07
.08	.0769	.9231	.9610	1.041	.0059	.0064	.9234	.0031	1.896	2.053	.0833	.08
.09	.0861	.9139	.9563	1.046	.0074	.0081	.9148	.0039	1.844	2.060	.0942	.09
.10	.0952	.9048	.9516	1.052	.0090	.0100	.9050	.0048	1.871	2.067	.1052	.10
.11	.1042	.8958	.9470	1.057	.0108	.0121	.8967	.0058	1.860	2.074	.1163	.11
.12	.1131	.8869	.9423	1.062	.0128	.0144	.8880	.0069	1.848	2.081	.1275	.12
.13	.1219	.8781	.9377	1.068	.0149	.0169	.8792	.0081	1.835	2.087	.1388	.13
.14	.1306	.8694	.9332	1.073	.0171	.0196	.8708	.0094	1.824	2.094	.1503	.14
.15	.1393	.8607	.9286	1.079	.0194	.0225	.8622	.0107	1.812	2.101	.1618	.15
.16	.1479	.8521	.9241	1.084	.0219	.0256	.8540	.0121	1.800	2.108	.1735	.16
.17	.1563	.8437	.9196	1.090	.0244	.0289	.8457	.0137	1.789	2.115	.1853	.17
.18	.1647	.8353	.9152	1.096	.0271	.0324	.8372	.0153	1.776	2.122	.1972	.18
.19	.1730	.8270	.9107	1.101	.0300	.0361	.8294	.0170	1.765	2.129	.2092	.19
.20	.1813	.8187	.9063	1.107	.0329	.0400	.8215	.0187	1.754	2.136	.2214	.20
.21	.1894	.8106	.9020	1.113	.0359	.0441	.8136	.0206	1.743	2.142	.2337	.21
.22	.1975	.8025	.8976	1.119	.0390	.0484	.8057	.0225	1.732	2.149	.2461	.22
.23	.2055	.7945	.8933	1.124	.0422	.0529	.7980	.0245	1.721	2.157	.2586	.23
.24	.2134	.7866	.8890	1.130	.0455	.0576	.7904	.0266	1.710	2.163	.2712	.24
.25	.2212	.7788	.8848	1.136	.0489	.0625	.7829	.0288	1.699	2.170	.2840	.25
.26	.2289	.7711	.8806	1.142	.0524	.0676	.7754	.0310	1.688	2.177	.2969	.26
.27	.2366	.7634	.8764	1.148	.0560	.0729	.7680	.0334	1.677	2.184	.3100	.27
.28	.2442	.7558	.8722	1.154	.0596	.0784	.7607	.0358	1.667	2.191	.3231	.28
.29	.2517	.7483	.8679	1.160	.0633	.0841	.7535	.0383	1.656	2.198	.3364	.29
.30	.2592	.7408	.8639	1.166	.0672	.0900	.7464	.0408	1.646	2.205	.3499	.30
.31	.2666	.7334	.8598	1.172	.0710	.0961	.7393	.0434	1.635	2.212	.3634	.31
.32	.2739	.7261	.8558	1.179	.0750	.1024	.7324	.0462	1.625	2.219	.3771	.32
.33	.2811	.7189	.8517	1.185	.0790	.1089	.7255	.0489	1.614	2.226	.3910	.33
.34	.2882	.7118	.8477	1.191	.0831	.1156	.7187	.0518	1.604	2.233	.4049	.34
.35	.2953	.7047	.8437	1.197	.0872	.1225	.7119	.0547	1.595	2.240	.4191	.35
.36	.3023	.6977	.8398	1.204	.0914	.1296	.7052	.0577	1.585	2.247	.4333	.36
.37	.3093	.6907	.8359	1.210	.0956	.1369	.6986	.0607	1.575	2.254	.4477	.37
.38	.3161	.6839	.8319	1.216	.0999	.1444	.6921	.0639	1.565	2.261	.4623	.38
.39	.3229	.6771	.8281	1.223	.1043	.1521	.6857	.0671	1.555	2.268	.4770	.39
.40	.3297	.6703	.8242	1.230	.1087	.1600	.6793	.0703	1.546	2.275	.4918	.40
.41	.3364	.6636	.8204	1.236	.1131	.1681	.6730	.0736	1.536	2.282	.5068	.41
.42	.3430	.6570	.8166	1.243	.1176	.1764	.6667	.0770	1.526	2.289	.5220	.42
.43	.3495	.6505	.8128	1.250	.1221	.1849	.6606	.0805	1.517	2.297	.5373	.43
.44	.3560	.6440	.8090	1.256	.1267	.1936	.6545	.0840	1.508	2.305	.5527	.44
.45	.3623	.6376	.8053	1.263	.1313	.2025	.6485	.0876	1.498	2.311	.5683	.45

1	2	3	4	5	6	7	8	9	10	11	12	13
i	a	s	a/i	a/is	a^2	i^2	a^2/i^2	$i-a$	$a^2/(i-a)$	$i^2/(i-a)$	e^i-1	i
.46	.3687	.6313	.8016	1.270	.1360	.2116	.6425	.0913	1.489	2.318	.5841	.46
.47	.3750	.6250	.7979	1.277	.1406	.2209	.6366	.0950	1.480	2.325	.6000	.47
.48	.3812	.6188	.7942	1.283	.1453	.2304	.6308	.0988	1.471	2.332	.6161	.48
.49	.3874	.6126	.7906	1.291	.1501	.2401	.6250	.1026	1.463	2.340	.6323	.49
.50	.3935	.6065	.7869	1.297	.1548	.2500	.6194	.1065	1.454	2.347	.6487	.50
.51	.3995	.6005	.7833	1.304	.1596	.2601	.6136	.1105	1.444	2.354	.6653	.51
.52	.4055	.5945	.7798	1.312	.1644	.2704	.6081	.1145	1.436	2.362	.6820	.52
.53	.4114	.5886	.7762	1.319	.1692	.2809	.6025	.1186	1.427	2.368	.6989	.53
.54	.4173	.5827	.7727	1.326	.1741	.2916	.5971	.1227	1.419	2.377	.7160	.54
.55	.4230	.5770	.7691	1.333	.1789	.3025	.5915	.1270	1.409	2.382	.7333	.55
.56	.4288	.5712	.7657	1.341	.1839	.3136	.5864	.1312	1.401	2.390	.7507	.56
.57	.4345	.5655	.7622	1.348	.1888	.3249	.5811	.1355	1.393	2.398	.7683	.57
.58	.4401	.5599	.7588	1.355	.1937	.3364	.5758	.1399	1.384	2.405	.7860	.58
.59	.4457	.5543	.7554	1.363	.1986	.3481	.5707	.1443	1.377	2.412	.8040	.59
.60	.4512	.5488	.7520	1.370	.2036	.3600	.5655	.1488	1.368	2.419	.8221	.60
.61	.4566	.5434	.7486	1.378	.2085	.3721	.5603	.1534	1.359	2.426	.8404	.61
.62	.4621	.5379	.7453	1.386	.2135	.3844	.5555	.1579	1.352	2.434	.8589	.62
.63	.4674	.5326	.7419	1.393	.2185	.3969	.5504	.1626	1.344	2.441	.8776	.63
.64	.4727	.5273	.7386	1.401	.2234	.4096	.5455	.1673	1.336	2.448	.8965	.64
.65	.4780	.5220	.7353	1.409	.2285	.4225	.5408	.1720	1.328	2.456	.9155	.65
.66	.4831	.5169	.7320	1.416	.2334	.4356	.5358	.1769	1.319	2.462	.9348	.66
.67	.4883	.5117	.7288	1.424	.2384	.4489	.5312	.1817	1.312	2.471	.9542	.67
.68	.4934	.5066	.7256	1.432	.2434	.4624	.5265	.1866	1.303	2.478	.9739	.68
.69	.4984	.5016	.7224	1.440	.2484	.4761	.5217	.1916	1.296	2.485	.9937	.69
.70	.5034	.4966	.7191	1.448	.2534	.4900	.5177	.1966	1.289	2.492	1.0138	.70
.71	.5084	.4916	.7160	1.456	.2585	.5041	.5127	.2016	1.282	2.500	1.0340	.71
.72	.5132	.4868	.7128	1.464	.2634	.5184	.5081	.2068	1.274	2.507	1.0544	.72
.73	.5181	.4819	.7097	1.473	.2684	.5329	.5037	.2119	1.267	2.515	1.0751	.73
.74	.5229	.4771	.7066	1.481	.2734	.5476	.4993	.2171	1.259	2.522	1.0959	.74
.75	.5276	.4724	.7035	1.489	.2784	.5625	.4949	.2224	1.252	2.530	1.1170	.75
.76	.5323	.4677	.7004	1.498	.2833	.5776	.4905	.2277	1.244	2.537	1.1383	.76
.77	.5370	.4630	.6974	1.506	.2884	.5929	.4864	.2330	1.238	2.545	1.1598	.77
.78	.5416	.4584	.6944	1.515	.2933	.6084	.4821	.2384	1.230	2.552	1.1815	.78
.79	.5462	.4538	.6913	1.523	.2983	.6241	.4780	.2438	1.224	2.560	1.2034	.79
.80	.5507	.4493	.6883	1.532	.3033	.6400	.4739	.2493	1.216	2.567	1.2255	.80
.81	.5551	.4448	.6854	1.541	.3081	.6561	.4698	.2548	1.209	2.575	1.2479	.81
.82	.5596	.4404	.6824	1.550	.3132	.6724	.4658	.2604	1.203	2.582	1.2705	.82
.83	.5640	.4360	.6795	1.558	.3181	.6889	.4618	.2660	1.196	2.590	1.2933	.83
.84	.5683	.4317	.6765	1.567	.3230	.7056	.4578	.2717	1.189	2.597	1.3164	.84
.85	.5726	.4274	.6736	1.576	.3279	.7225	.4538	.2774	1.182	2.605	1.3396	.85
.86	.5768	.4232	.6707	1.585	.3327	.7396	.4498	.2832	1.175	2.612	1.3632	.86
.87	.5810	.4190	.6679	1.594	.3376	.7569	.4460	.2890	1.168	2.619	1.3869	.87
.88	.5853	.4148	.6651	1.603	.3426	.7744	.4421	.2948	1.162	2.627	1.4109	.88
.89	.5893	.4107	.6622	1.612	.3472	.7921	.4383	.3007	1.155	2.634	1.4351	.89
.90	.5934	.4066	.6594	1.622	.3521	.8100	.4347	.3066	1.148	2.642	1.4596	.90

1	2	3	4	5	6	7	8	9	10	11	12	13
i	a	s	a/i	a/is	a^2	i^2	a^2/i^2	$i-a$	$a^2/(i-a)$	$i^2/(i-a)$	e^i-1	i
.91	.5975	.4025	.6566	1.631	.3570	.8281	.4311	.3125	1.142	2.650	1.4843	.91
.92	.6015	.3985	.6538	1.641	.3618	.8464	.4275	.3185	1.136	2.657	1.5093	.92
.93	.6054	.3946	.6510	1.650	.3665	.8649	.4239	.3246	1.129	2.665	1.5345	.93
.94	.6094	.3906	.6483	1.660	.3714	.8836	.4203	.3306	1.123	2.673	1.5600	.94
.95	.6133	.3867	.6455	1.669	.3761	.9025	.4167	.3367	1.117	2.680	1.5857	.95
.96	.6172	.3829	.6429	1.679	.3809	.9216	.4133	.3429	1.111	2.688	1.6117	.96
.97	.6209	.3791	.6401	1.688	.3855	.9409	.4097	.3491	1.104	2.695	1.6379	.97
.98	.6247	.3753	.6374	1.698	.3903	.9604	.4064	.3553	1.098	2.703	1.6645	.98
.99	.6284	.3716	.6348	1.708	.3949	.9801	.4029	.3616	1.092	2.710	1.6912	.99
1.00	.6321	.3679	.6321	1.718	.3996	1.0000	.3996	.3679	1.086	2.718	1.7183	1.00
1.01	.6358	.3642	.6295	1.728	.4042	1.0201	.3962	.3742	1.080	2.726	1.7456	1.01
1.02	.6394	.3606	.6269	1.738	.4088	1.0404	.3929	.3806	1.074	2.734	1.7732	1.02
1.03	.6430	.3570	.6243	1.749	.4134	1.0609	.3897	.3870	1.068	2.741	1.8011	1.03
1.04	.6465	.3535	.6217	1.759	.4180	1.0816	.3865	.3935	1.062	2.749	1.8292	1.04
1.05	.6501	.3499	.6191	1.769	.4226	1.1025	.3833	.3999	1.057	2.757	1.8577	1.05
1.06	.6535	.3465	.6166	1.780	.4271	1.1236	.3801	.4065	1.051	2.764	1.8864	1.06
1.07	.6570	.3430	.6140	1.790	.4316	1.1449	.3770	.4130	1.045	2.772	1.9154	1.07
1.08	.6604	.3396	.6115	1.801	.4361	1.1664	.3739	.4196	1.039	2.780	1.9447	1.08
1.09	.6638	.3362	.6090	1.811	.4406	1.1881	.3708	.4262	1.034	2.788	1.9743	1.09
1.10	.6671	.3329	.6065	1.822	.4450	1.2100	.3678	.4329	1.028	2.795	2.0042	1.10
1.11	.6704	.3296	.6040	1.833	.4494	1.2321	.3647	.4396	1.022	2.803	2.0344	1.11
1.12	.6737	.3263	.6015	1.843	.4539	1.2544	.3618	.4463	1.017	2.811	2.0649	1.12
1.13	.6770	.3230	.5991	1.855	.4583	1.2769	.3589	.4530	1.012	2.819	2.0957	1.13
1.14	.6802	.3198	.5966	1.866	.4627	1.2996	.3560	.4598	1.006	2.826	2.1268	1.14
1.15	.6834	.3166	.5942	1.877	.4670	1.3225	.3531	.4666	1.001	2.834	2.1582	1.15
1.16	.6865	.3135	.5918	1.888	.4713	1.3456	.3503	.4735	0.995	2.842	2.1899	1.16
1.17	.6896	.3104	.5894	1.899	.4755	1.3689	.3474	.4804	0.990	2.850	2.2220	1.17
1.18	.6927	.3073	.5870	1.910	.4798	1.3924	.3446	.4873	0.985	2.857	2.2544	1.18
1.19	.6958	.3042	.5847	1.922	.4841	1.4161	.3419	.4942	0.980	2.865	2.2871	1.19
1.20	.6988	.3012	.5823	1.933	.4883	1.4400	.3391	.5012	0.974	2.873	2.3201	1.20
1.21	.7018	.2982	.5800	1.945	.4925	1.4641	.3364	.5082	0.969	2.881	2.3535	1.21
1.22	.7048	.2952	.5777	1.957	.4967	1.4884	.3337	.5152	0.964	2.889	2.3872	1.22
1.23	.7077	.2923	.5754	1.969	.5008	1.5129	.3310	.5223	0.959	2.897	2.4212	1.23
1.24	.7106	.2894	.5731	1.980	.5050	1.5376	.3284	.5294	0.954	2.904	2.4556	1.24
1.25	.7135	.2865	.5708	1.992	.5091	1.5625	.3258	.5365	0.949	2.912	2.4903	1.25
1.26	.7163	.2836	.5685	2.005	.5131	1.5876	.3232	.5436	0.944	2.921	2.5254	1.26
1.27	.7192	.2808	.5663	2.017	.5172	1.6129	.3207	.5508	0.939	2.928	2.5609	1.27
1.28	.7220	.2780	.5640	2.029	.5213	1.6384	.3182	.5580	0.934	2.936	2.5966	1.28
1.29	.7247	.2753	.5618	2.041	.5252	1.6641	.3156	.5653	0.929	2.944	2.6328	1.29
1.30	.7275	.2725	.5596	2.054	.5293	1.6900	.3132	.5725	0.924	2.952	2.6693	1.30
1.31	.7302	.2698	.5574	2.066	.5332	1.7161	.3107	.5798	0.920	2.960	2.7062	1.31
1.32	.7329	.2671	.5552	2.079	.5371	1.7424	.3083	.5871	0.915	2.968	2.7434	1.32
1.33	.7355	.2645	.5530	2.091	.5410	1.7689	.3058	.5945	0.910	2.975	2.7810	1.33
1.34	.7382	.2618	.5509	2.104	.5449	1.7956	.3034	.6018	0.906	2.984	2.8190	1.34
1.35	.7408	.2592	.5487	2.117	.5488	1.8225	.3011	.6092	0.901	2.992	2.8574	1.35

1	2	3	4	5	6	7	8	9	10	11	12	13
i	a	s	a/i	a/is	a^2	i^2	a^2/i^2	$i-a$	$a^2/(i-a)$	$i^2/(i-a)$	$e^{i}-1$	i
1.36	.7433	.2567	.5466	2.129	.5525	1.8496	.2987	.6167	0.896	2.999	2.8962	1.36
1.37	.7459	.2541	.5444	2.142	.5564	1.8769	.2964	.6241	0.891	3.007	2.9354	1.37
1.38	.7484	.2516	.5423	2.155	.5601	1.9044	.2941	.6316	0.887	3.015	2.9749	1.38
1.39	.7509	.2491	.5402	2.169	.5639	1.9321	.2919	.6391	0.882	3.023	3.0149	1.39
1.40	.7534	.2466	.5381	2.182	.5676	1.9600	.2896	.6466	0.878	3.031	3.0552	1.40
1.41	.7558	.2441	.5361	2.196	.5712	1.9881	.2873	.6541	0.873	3.039	3.0960	1.41
1.42	.7582	.2417	.5340	2.209	.5749	2.0164	.2851	.6617	0.869	3.047	3.1371	1.42
1.43	.7607	.2393	.5319	2.223	.5787	2.0449	.2830	.6693	0.864	3.055	3.1787	1.43
1.44	.7631	.2369	.5299	2.237	.5823	2.0736	.2808	.6769	0.860	3.063	3.2207	1.44
1.45	.7654	.2346	.5279	2.250	.5858	2.1025	.2786	.6846	0.856	3.071	3.2631	1.45
1.46	.7678	.2322	.5259	2.265	.5895	2.1316	.2766	.6922	0.852	3.079	3.3060	1.46
1.47	.7701	.2299	.5239	2.279	.5931	2.1609	.2745	.6999	0.847	3.087	3.3492	1.47
1.48	.7724	.2276	.5219	2.293	.5966	2.1904	.2724	.7076	0.843	3.096	3.3929	1.48
1.49	.7746	.2254	.5199	2.306	.6000	2.2201	.2703	.7154	0.839	3.103	3.4371	1.49
1.50	.7769	.2231	.5179	2.321	.6036	2.2500	.2683	.7231	0.835	3.112	3.4817	1.50
1.51	.7791	.2209	.5160	2.336	.6070	2.2801	.2662	.7309	0.830	3.120	3.5267	1.51
1.52	.7813	.2187	.5140	2.350	.6104	2.3104	.2642	.7387	0.826	3.128	3.5722	1.52
1.53	.7835	.2165	.5121	2.365	.6139	2.3409	.2622	.7465	0.822	3.136	3.6182	1.53
1.54	.7856	.2144	.5101	2.379	.6172	2.3716	.2602	.7544	0.818	3.144	3.6646	1.54
1.55	.7878	.2122	.5082	2.395	.6206	2.4025	.2583	.7622	0.814	3.152	3.7115	1.55
1.56	.7899	.2101	.5063	2.410	.6239	2.4336	.2564	.7701	0.810	3.160	3.7588	1.56
1.57	.7920	.2080	.5044	2.425	.6273	2.4649	.2545	.7780	0.806	3.168	3.8066	1.57
1.58	.7941	.2060	.5026	2.440	.6306	2.4964	.2526	.7860	0.802	3.176	3.8550	1.58
1.59	.7961	.2039	.5007	2.456	.6338	2.5281	.2507	.7939	0.798	3.184	3.9037	1.59
1.60	.7981	.2019	.4988	2.470	.6370	2.5600	.2488	.8019	0.794	3.192	3.9530	1.60
1.61	.8001	.1999	.4970	2.486	.6402	2.5921	.2470	.8099	0.790	3.201	4.0028	1.61
1.62	.8021	.1979	.4951	2.502	.6434	2.6244	.2452	.8179	0.787	3.209	4.0531	1.62
1.63	.8041	.1959	.4933	2.518	.6466	2.6569	.2434	.8259	0.783	3.217	4.1039	1.63
1.64	.8060	.1940	.4915	2.534	.6496	2.6896	.2415	.8340	0.779	3.225	4.1552	1.64
1.65	.8080	.1921	.4897	2.549	.6529	2.7225	.2398	.8421	0.775	3.233	4.2070	1.65
1.66	.8099	.1901	.4879	2.566	.6559	2.7556	.2380	.8501	0.772	3.242	4.2593	1.66
1.67	.8118	.1882	.4861	2.583	.6590	2.7889	.2363	.8582	0.768	3.250	4.3122	1.67
1.68	.8136	.1864	.4843	2.598	.6619	2.8224	.2345	.8664	0.764	3.258	4.3656	1.68
1.69	.8155	.1845	.4825	2.615	.6650	2.8561	.2328	.8745	0.760	3.266	4.4195	1.69
1.70	.8173	.1827	.4808	2.632	.6680	2.8900	.2311	.8827	0.757	3.274	4.4739	1.70
1.71	.8191	.1809	.4790	2.648	.6709	2.9241	.2394	.8909	0.753	3.282	4.5290	1.71
1.72	.8209	.1791	.4773	2.665	.6739	2.9584	.2278	.8991	0.750	3.290	4.5845	1.72
1.73	.8227	.1773	.4756	2.682	.6768	2.9929	.2261	.9073	0.746	3.299	4.6407	1.73
1.74	.8245	.1755	.4738	2.700	.6798	3.0276	.2245	.9155	0.743	3.307	4.6973	1.74
1.75	.8262	.1738	.4721	2.716	.6826	3.0625	.2229	.9238	0.739	3.315	4.7546	1.75
1.76	.8280	.1720	.4704	2.735	.6856	3.0976	.2213	.9320	0.736	3.324	4.8124	1.76
1.77	.8297	.1703	.4687	2.752	.6884	3.1329	.2197	.9403	0.732	3.332	4.8709	1.77
1.78	.8314	.1686	.4670	2.770	.6912	3.1684	.2182	.9486	0.729	3.340	4.9299	1.78
1.79	.8330	.1670	.4654	2.787	.6939	3.2041	.2166	.9570	0.725	3.348	4.9895	1.79
1.80	.8347	.1653	.4637	2.805	.6967	3.2400	.2150	.9653	0.722	3.356	5.0496	1.80

1	2	3	4	5	6	7	8	9	10	11	12	13
i	a	s	a/i	a/is	a^2	i^2	a^2/i^2	i-a	$a^2/(i-a)$	$i^2/(i-a)$	e^i-1	i
1.81	.8363	.1636	.4621	2.825	.6994	3.2761	.2135	.9736	0.718	3.364	5.1104	1.81
1.82	.8380	.1620	.4604	2.842	.7022	3.3124	.2120	.9820	0.715	3.373	5.1719	1.82
1.83	.8396	.1604	.4588	2.860	.7049	3.3489	.2105	.9904	0.712	3.381	5.2339	1.83
1.84	.8412	.1588	.4572	2.879	.7076	3.3856	.2090	.9988	0.708	3.390	5.2965	1.84
1.85	.8428	.1572	.4555	2.898	.7103	3.4225	.2075	1.0072	0.705	3.398	5.3598	1.85
1.86	.8443	.1557	.4539	2.915	.7128	3.4596	.2060	1.0157	0.702	3.406	5.4237	1.86
1.87	.8459	.1541	.4523	2.935	.7155	3.4969	.2046	1.0241	0.699	3.415	5.4883	1.87
1.88	.8474	.1526	.4508	2.954	.7181	3.5344	.2032	1.0326	0.695	3.423	5.5535	1.88
1.89	.8489	.1511	.4492	2.973	.7206	3.5721	.2017	1.0411	0.692	3.431	5.6194	1.89
1.90	.8504	.1496	.4476	2.992	.7232	3.6100	.2003	1.0496	0.689	3.439	5.6859	1.90
1.91	.8519	.1481	.4460	3.011	.7257	3.6481	.1989	1.0581	0.686	3.448	5.7531	1.91
1.92	.8534	.1466	.4445	3.032	.7283	3.6864	.1976	1.0666	0.683	3.456	5.8210	1.92
1.93	.8549	.1451	.4429	3.052	.7309	3.7249	.1962	1.0751	0.680	3.465	5.8895	1.93
1.94	.8563	.1437	.4414	3.072	.7332	3.7636	.1948	1.0837	0.677	3.473	5.9588	1.94
1.95	.8577	.1423	.4398	3.091	.7356	3.8025	.1935	1.0923	0.673	3.481	6.0287	1.95
1.96	.8591	.1409	.4383	3.111	.7381	3.8416	.1921	1.1009	0.670	3.490	6.0993	1.96
1.97	.8605	.1395	.4368	3.131	.7405	3.8809	.1908	1.1095	0.667	3.498	6.1707	1.97
1.98	.8619	.1381	.4353	3.152	.7429	3.9204	.1895	1.1181	0.664	3.506	6.2427	1.98
1.99	.8633	.1367	.4338	3.173	.7453	3.9601	.1882	1.1267	0.661	3.515	6.3155	1.99
2.00	.8647	.1353	.4323	3.195	.7477	4.0000	.1869	1.1353	0.659	3.523	6.3891	2.00
2.01	.8660	.1340	.4308	3.216	.7500	4.0401	.1856	1.1440	0.656	3.532	6.463	2.01
2.02	.8673	.1327	.4294	3.237	.7523	4.0804	.1844	1.1527	0.653	3.540	6.538	2.02
2.03	.8687	.1313	.4279	3.258	.7546	4.1209	.1831	1.1613	0.650	3.548	6.614	2.03
2.04	.8700	.1300	.4265	3.280	.7568	4.1616	.1819	1.1700	0.647	3.557	6.691	2.04
2.05	.8713	.1287	.4250	3.301	.7591	4.2025	.1806	1.1787	0.644	3.565	6.768	2.05
2.06	.8725	.1274	.4236	3.323	.7613	4.2436	.1794	1.1874	0.641	3.573	6.846	2.06
2.07	.8738	.1262	.4221	3.345	.7636	4.2849	.1782	1.1962	0.638	3.582	6.925	2.07
2.08	.8751	.1249	.4207	3.368	.7657	4.3264	.1770	1.2049	0.635	3.591	7.004	2.08
2.09	.8763	.1237	.4193	3.390	.7679	4.3681	.1758	1.2137	0.632	3.600	7.085	2.09
2.10	.8775	.1225	.4179	3.412	.7701	4.4100	.1746	1.2225	0.630	3.607	7.166	2.10
2.11	.8788	.1212	.4165	3.435	.7722	4.4521	.1734	1.2312	0.627	3.616	7.248	2.11
2.12	.8800	.1200	.4151	3.458	.7743	4.4944	.1723	1.2400	0.624	3.624	7.331	2.12
2.13	.8812	.1188	.4137	3.481	.7764	4.5369	.1711	1.2488	0.622	3.633	7.415	2.13
2.14	.8823	.1177	.4123	3.504	.7785	4.5796	.1700	1.2577	0.619	3.641	7.499	2.14
2.15	.8835	.1165	.4109	3.528	.7806	4.6225	.1689	1.2665	0.616	3.650	7.585	2.15
2.16	.8847	.1153	.4096	3.551	.7826	4.6656	.1677	1.2753	0.614	3.658	7.671	2.16
2.17	.8858	.1142	.4082	3.575	.7847	4.7089	.1666	1.2842	0.611	3.667	7.758	2.17
2.18	.8870	.1130	.4069	3.599	.7867	4.7524	.1655	1.2930	0.608	3.675	7.846	2.18
2.19	.8881	.1119	.4055	3.623	.7887	4.7961	.1644	1.3019	0.606	3.684	7.935	2.19
2.20	.8892	.1108	.4042	3.648	.7907	4.8400	.1634	1.3108	0.603	3.692	8.025	2.20
2.21	.8903	.1097	.4028	3.672	.7926	4.8841	.1623	1.3197	0.601	3.701	8.116	2.21
2.22	.8914	.1086	.4015	3.697	.7946	4.9284	.1612	1.3286	0.598	3.709	8.207	2.22
2.23	.8925	.1075	.4002	3.721	.7965	4.9729	.1602	1.3375	0.596	3.718	8.300	2.23
2.24	.8935	.1065	.3989	3.747	.7984	5.0176	.1591	1.3465	0.593	3.726	8.393	2.24
2.25	.8946	.1054	.3976	3.772	.8003	5.0625	.1581	1.3554	0.590	3.735	8.488	2.25

1 i	2 a	3 s	4 a/i	5 a/is	6 a^2	7 i^2	8 a^2/i^2	9 i-a	10 $a^2/(i-a)$	11 $i^2/(i-a)$	12 e^i-1	13 i
2.26	.8956	.1044	.3963	3.798	.8022	5.1076	.1571	1.3644	0.588	3.744	8.583	2.26
2.27	.8967	.1033	.3950	3.823	.8040	5.1529	.1560	1.3733	0.585	3.752	8.679	2.27
2.28	.8977	.1023	.3937	3.849	.8059	5.1984	.1550	1.3823	0.583	3.761	8.777	2.28
2.29	.8987	.1013	.3925	3.876	.8077	5.2441	.1540	1.3913	0.581	3.770	8.875	2.29
2.30	.8997	.1003	.3912	3.902	.8095	5.2900	.1530	1.4002	0.578	3.778	8.974	2.30
2.31	.9007	.0993	.3899	3.928	.8113	5.3361	.1520	1.4093	0.576	3.786	9.074	2.31
2.32	.9017	.0983	.3887	3.955	.8131	5.3824	.1511	1.4183	0.573	3.795	9.176	2.32
2.33	.9027	.0973	.3874	3.982	.8149	5.4289	.1501	1.4273	0.571	3.804	9.278	2.33
2.34	.9037	.0963	.3862	4.009	.8166	5.4756	.1491	1.4363	0.569	3.812	9.381	2.34
2.35	.9046	.0954	.3849	4.036	.8184	5.5225	.1482	1.4454	0.566	3.821	9.486	2.35
2.36	.9056	.0944	.3837	4.064	.8201	5.5696	.1472	1.4544	0.564	3.829	9.591	2.36
2.37	.9065	.0935	.3825	4.092	.8218	5.6169	.1463	1.4635	0.562	3.838	9.697	2.37
2.38	.9074	.0926	.3813	4.120	.8235	5.6644	.1454	1.4726	0.559	3.847	9.805	2.38
2.39	.9084	.0916	.3801	4.148	.8251	5.7121	.1444	1.4816	0.557	3.855	9.913	2.39
2.40	.9093	.0907	.3789	4.176	.8268	5.7600	.1435	1.4907	0.555	3.864	10.023	2.40
2.41	.9102	.0898	.3777	4.205	.8284	5.8081	.1426	1.4998	0.552	3.872	10.134	2.41
2.42	.9111	.0889	.3765	4.234	.8301	5.8564	.1417	1.5089	0.550	.3881	10.246	2.42
2.43	.9120	.0880	.3753	4.263	.8317	5.9049	.1408	1.5180	0.548	3.890	10.359	2.43
2.44	.9128	.0872	.3741	4.292	.8333	5.9536	.1400	1.5272	0.546	3.898	10.473	2.44
2.45	.9137	.0863	.3729	4.322	.8349	6.0025	.1391	1.5363	0.543	3.907	10.588	2.45
2.46	.9146	.0854	.3718	4.352	.8364	6.0516	.1382	1.5454	0.541	3.916	10.705	2.46
2.47	.9154	.0846	.3706	4.382	.8380	6.1009	.1374	1.5546	0.539	3.924	10.822	2.47
2.48	.9163	.0837	.3695	4.412	.8395	6.1504	.1365	1.5637	0.537	3.933	10.941	2.48
2.49	.9171	.0829	.3683	4.442	.8410	6.2001	.1356	1.5729	0.535	3.942	11.061	2.49
2.50	.9179	.0821	.3672	4.473	.8426	6.2500	.1348	1.5821	0.533	3.950	11.182	2.50
2.51	.9187	.0813	.3660	4.504	.8441	6.3001	.1340	1.5913	0.530	3.959	11.305	2.51
2.52	.9195	.0805	.3649	4.535	.8456	6.3504	.1332	1.6005	0.528	3.968	11.429	2.52
2.53	.9203	.0797	.3638	4.567	.8470	6.4009	.1323	1.6097	0.526	3.977	11.554	2.53
2.54	.9211	.0789	.3626	4.598	.8485	6.4516	.1315	1.6189	0.524	3.985	11.680	2.54
2.55	.9219	.0781	.3615	4.630	.8499	6.5025	.1307	1.6281	0.522	3.994	11.807	2.55
2.56	.9227	.0773	.3604	4.662	.8514	6.5536	.1299	1.6373	0.520	4.003	11.936	2.56
2.57	.9235	.0765	.3593	4.695	.8528	6.6049	.1291	1.6465	0.518	4.011	12.066	2.57
2.58	.9242	.0758	.3582	4.728	.8542	6.6564	.1283	1.6558	0.516	4.020	12.197	2.58
2.59	.9250	.0750	.3571	4.760	.8556	6.7081	.1275	1.6650	0.514	4.029	12.330	2.59
2.60	.9257	.0743	.3560	4.794	.8570	6.7600	.1268	1.6743	0.512	4.038	12.464	2.60
2.61	.9265	.0735	.3550	4.827	.8583	6.8121	.1260	1.6835	.5098	4.046	12.599	2.61
2.62	.9272	.0728	.3539	4.861	.8597	6.8644	.1252	1.6928	.5078	4.055	12.736	2.62
2.63	.9279	.0721	.3528	4.895	.8610	6.9169	.1245	1.7021	.5059	4.064	12.874	2.63
2.64	.9286	.0714	.3518	4.929	.8624	6.9696	.1237	1.7114	.5039	4.073	13.013	2.64
2.65	.9293	.0707	.3507	4.964	.8637	7.0225	.1230	1.7206	.5020	4.081	13.154	2.65
2.66	.9300	.0699	.3496	4.999	.8650	7.0756	.1222	1.7299	.5000	4.090	13.296	2.66
2.67	.9307	.0693	.3486	5.034	.8663	7.1289	.1215	1.7392	.4981	4.099	13.440	2.67
2.68	.9314	.0686	.3476	5.069	.8676	7.1824	.1208	1.7486	.4962	4.108	13.585	2.68
2.69	.9321	.0679	.3465	5.105	.8688	7.2361	.1201	1.7579	.4943	4.116	13.732	2.69
2.70	.9328	.0672	.3455	5.141	.8701	7.2900	.1194	1.7672	.4924	4.125	13.880	2.70

1	2	3	4	5	6	7	8	9	10	11	12	13
i	a	s	a/i	a/is	a^2	i^2	a^2/i^2	i-a	$a^2/(i$-$a)$	$i^2/(i$-$a)$	e^i-1	i
2.71	.9335	.0665	.3444	5.177	.8714	7.3441	.1186	1.7765	.4905	4.134	14.029	2.71
2.72	.9341	.0659	.3434	5.213	.8726	7.3984	.1179	1.7859	.4886	4.143	14.180	2.72
2.73	.9348	.0652	.3424	5.250	.8738	7.4529	.1172	1.7952	.4867	4.152	14.333	2.73
2.74	.9354	.0646	.3414	5.287	.8750	7.5076	.1166	1.8046	.4849	4.160	14.487	2.74
2.75	.9361	.0639	.3404	5.325	.8762	7.5625	.1159	1.8139	.4831	4.169	14.643	2.75
2.76	.9367	.0633	.3393	5.362	.8774	7.6176	.1152	1.8233	.4812	4.178	14.800	2.76
2.77	.9373	.0627	.3384	5.400	.8786	7.6729	.1145	1.8327	.4794	4.187	14.959	2.77
2.78	.9380	.0620	.3374	5.438	.8798	7.7284	.1138	1.8420	.4776	4.196	15.119	2.78
2.79	.9386	.0614	.3364	5.477	.8809	7.7841	.1132	1.8514	.4758	4.204	15.281	2.79
2.80	.9392	.0608	.3354	5.516	.8821	7.8400	.1125	1.8608	.4740	4.213	15.445	2.80
2.81	.9398	.0602	.3344	5.555	.8832	7.8961	.1118	1.8702	.4723	4.222	15.610	2.81
2.82	.9404	.0596	.3335	5.595	.8843	7.9524	.1112	1.8796	.4705	4.231	15.777	2.82
2.83	.9410	.0590	.3325	5.634	.8855	8.0089	.1106	1.8890	.4687	4.240	15.945	2.83
2.84	.9416	.0584	.3315	5.674	.8866	8.0656	.1099	1.8984	.4670	4.249	16.116	2.84
2.85	.9422	.0578	.3306	5.715	.8877	8.1225	.1093	1.9078	.4653	4.257	16.288	2.85
2.86	.9427	.0573	.3296	5.756	.8887	8.1796	.1086	1.9173	.4635	4.266	16.462	2.86
2.87	.9433	.0567	.3287	5.797	.8898	8.2369	.1080	1.9267	.4618	4.275	16.637	2.87
2.88	.9439	.0561	.3277	5.838	.8909	8.2944	.1074	1.9361	.4601	4.284	16.814	2.88
2.89	.9444	.0556	.3268	5.880	.8919	8.3521	.1068	1.9456	.4584	4.293	16.993	2.89
2.90	.9450	.0550	.3258	5.922	.8930	8.4100	.1062	1.9550	.4568	4.302	17.174	2.90
2.91	.9455	.0545	.3249	5.964	.8940	8.4681	.1056	1.9645	.4551	4.311	17.357	2.91
2.92	.9461	.0539	.3240	6.007	.8950	8.5264	.1050	1.9739	.4534	4.320	17.541	2.92
2.93	.9466	.0534	.3231	6.050	.8961	8.5849	.1044	1.9834	.4518	4.328	17.728	2.93
2.94	.9471	.0529	.3222	6.094	.8971	8.6436	.1038	1.9929	.4501	4.337	17.916	2.94
2.95	.9477	.0523	.3212	6.138	.8981	8.7025	.1032	2.0023	.4485	4.346	18.106	2.95
2.96	.9482	.0518	.3203	6.182	.8990	8.7616	.1026	2.0118	.4469	4.355	18.298	2.96
2.97	.9487	.0513	.3194	6.226	.9000	8.8209	.1020	2.0213	.4453	4.364	18.492	2.97
2.98	.9492	.0508	.3185	6.271	.9010	8.8804	.1015	2.0308	.4437	4.373	18.688	2.98
2.99	.9497	.0503	.3176	6.316	.9020	8.9401	.1009	2.0403	.4421	4.382	18.886	2.99
3.00	.9502	.0498	.3167	6.362	.9029	9.000	.1003	2.0498	.4405	4.391	19.086	3.00

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