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Fish Population Dynamics in Tropical Waters: A Manual for Use with Programmable Calculators

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INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

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Table of Contents

List of Figures

Appendix Figures

List of Tables

Appendix Tables

Foreword

Fifteen years ago, in Jamaica, I purchased my first electronic calculator, a typewriter-sized affair which had four functions and no memory, and it revolutionized my life. The cheapest of the modern hand-held calculators do more, for less than one hundredth of the price that I paid in 1979. Around the same period, I was using a mainframe computer manned by an army of staff to perform yield-per-recruit computations. The reader will find that their hand-held programmable calculators will execute such computations in a few seconds, by the touch of a button.

It is a feature of our times that new hardware becomes outmoded with remarkable speed. The reader who purchases this book will find that models of the calculators for which the programs were originally written are already difficult to acquire, as they have been replaced by faster and more sophisticated models (which will still run the programs presented here). Likewise, programmable calculators are already being replaced by microcomputers and many readers will wish to translate the programs contained in this book into computer languages.

The scientist working in a sophisticated fisheries laboratory will be aware that many of the routines incorporated in this book are already available in the memories of the mini- or mainframe computers to which they have access and for such individuals, the programs given here will be useful for on-the-spot calculations without moving to a terminal. Convenient yes, but not a remarkable benefit. However, fisheries scientists, particularly in the developing countries, who are working in small, modestly-equipped laboratories, remote from the advanced electronic gadgetry of this decade, will find that their lives and working abilities are radically changed by this book because it will now be possible to do complex analyses of data in the remotest field station or even at sea, and in places without regular power supplies, programmers and systems analysts.

Doubtless, many disastrously erroneous analyses will emerge when inappropriate or poor sample data are used to generate estimates, and the dictum of "garbage in → garbage out" will more frequently be seen in operation—but this will be a small price to pay for the real advances, improved scientific output and scientifically-based fisheries management decisions which will emerge as a result of the publication of this book.

Additionally, ecologists in fields other than fisheries will find that many of the routines given here are easily adapted to non-fisheries applications—which will hopefully help to overcome the needless dichotomy which has tended to separate fisheries science from the rest of ecology.

This book is doubly welcome because, while there are numerous texts which give clear instructions on how to collect data, there are remarkably few which give any instructions on how to analyze what has been collected. W.E. Ricker's *Handbook of Computations and Interpretation of Biological Statistics of Fish Populations* and John Gulland's *Manual of Fish Stock Assessment* have been the mainstays of fish population dynamics for many years and both are sufficiently intimidating—in terms of their mathematics—to have cured many biologists of any inclination to pursue a career in the quantitative aspects of fisheries science. In contrast, readers will not fail to be impresssed by the lucidity and incisiveness which characterizes this manual and which will rightfully earn Dr. Pauly a permanent niche in the annals of fisheries science.

J.L. Munro
Manila
March 1984

Acknowledgements

I wish to express my gratitude to John Munro, Saul Saila and Erik Ursin for reading the entire draft of this book, and for suggesting various improvements, and to John Gulland and Jorge Csirke, who read and proposed changes for several draft chapters.

Thanks are also due to Lourdes "Deng" Palomares for tracing the program listings by hand, and to Aye Pyo for checking the computational examples.

I would like also to express my most sincere appreciation of the efforts of Per Sparre and John Hoenig. Per not only read the entire draft but also checked the derivation of each equation, spotting in the process a frighteningly large number of errors and ill-defined notions, and developing *en passant* two new models that he was kind enough to let me incorporate into Chapter 5 of this book. John, on the other hand, accepted the dreary task of checking the galley proofs; his efforts led similarly to the identification of a number of errors of the most insidious kind, all of which would have been most deleterious; I would have hated to see them in the printed version.

It must be stressed here that neither he, nor Per, nor the other reviewers agreed entirely with the selection of items presented here, or with my interpretation of them. Here, I bear full responsibility, as I do with regard to any remaining errors, typographical or other, which readers may spot.

Daniel Pauly
Manila
March 1984

Abstract

This manual is a selection, from the entire field of fish population dynamics, of methods which are applicable to tropical fish and fisheries and can be implemented with the help of programmable calculators.

The methods selected cover the following areas: length-weight relationships, mesh selection, growth, mortality, population size estimation by various methods (e.g., tagging, virtual population analysis), yield-per-recruit assessments, stock-recruitment relationships, surplus-yield models, the rate of increase of populations and aspects of multispecies stocks and fisheries.

The program listing and user instructions of thirty programs for use with HP 67/97 programmable calculators are included; the translation of these programs for use with other types of calculators especially HP 41 and TI 59 is discussed. Sixty computational examples including complete keystroke sequences are provided to illustrate the methods presented in the text. These examples are drawn exclusively from subtropical and tropical stocks and fisheries.

1. How to Use this Manual

Students of fishery biology in tropical developing countries generally find their textbooks replete with cod and haddock, salmon and trout. There is not even one little example pertaining say, to the chub mackerels, the scads or the various demersal percoids, although these fish often support significant and well-documented fisheries throughout the tropics (Marr 1978).

A manual, such as the one presented here, cannot alone compensate for this sad state of affairs. What this manual will do, however, is demonstrate that:

i. there are at present enough original publications on tropical fish and fisheries to exemplify most aspects of fish population dynamics and stock assessment,

ii. there is no further need, when investigating tropical stocks, to compare one's results with those obtained in temperate areas of the world—"lateral" comparisons, involving several similar tropical stocks being generally far more illuminating.

At this point, the question might arise as to what fish population dynamics are all about. A now classic axiom, formulated by Russel (1931) may be used to answer this question. This axiom states that

$$B_2 = B_1 + (R^* + G^*) - (M^* + Y) \qquad \ldots 1.1)$$

where B_1 and B_2 are the total weights of the exploited phase of a fish stock (or population) at the beginning and end, respectively, of a given time period, while R denotes the recruitment (in weight) to the exploited phase, G^* the growth of individuals in the exploited phase, M^* the biomass of fish that died due to natural causes in the exploited phase, and Y the yield or catch (in weight) during the aforementioned time period. In other words, the axiom states that in a "closed" population (no emigration, no immigration), the primary factors responsible for weight increments to the stock are recruitment and growth, while the factors responsible for weight loss are natural mortality and capture by the fishery (see also Fig. 1.1).

Population dynamics now can be simply defined as the quantitative study of the four primary factors listed in Russel's axiom. *Tropical* fish population dynamics, then, can be more specifically defined as the set of methods which can be used quantitatively to interpret data on: 1) stock sizes, 2) recruitment, 3) growth and 4) natural mortality of tropical fish, such that potential catches can be predicted or such that existing fisheries can be knowledgeably managed.

As will be seen, the dynamics of tropical fish are not very different from those of their temperate counterparts, the major differences being: 1) the ranges of sizes are generally smaller, 2) the time periods are shorter, 3) the intensity of seasonal phenomena is reduced.

Accounting for the differences between tropical and temperate systems is therefore basically a question of adjusting one's scales, the "trick" with tropical fish being to turn what appears to be a liability (i.e., that they operate on scales different from those of temperate fish) into an asset.

For example, the fact that many demersal stocks in tropical waters consist of short-lived fish sometimes prevents aging by means of annuli, but allows one to follow the growth and decay of a cohort within a period of 12 months. When there are well-defined spawning seasons (as is often the case), one can then:

— determine growth from length-frequency data without encountering many of the problems of applying this method to long-lived temperate fishes,

— estimate the age, in days, of individual fish,

— estimate absolute recruit numbers from the relationship of yield per recruit with the catch, and

— neglect time-lag effects when fitting surplus-production models to catch-and-effort data.

Also, the extremely large number of species often encountered in the tropics (especially in demersal fisheries), which many authors have generally considered a major problem, may be viewed as a beautiful set of replicates from which not only one, but several sets of parameter estimates can

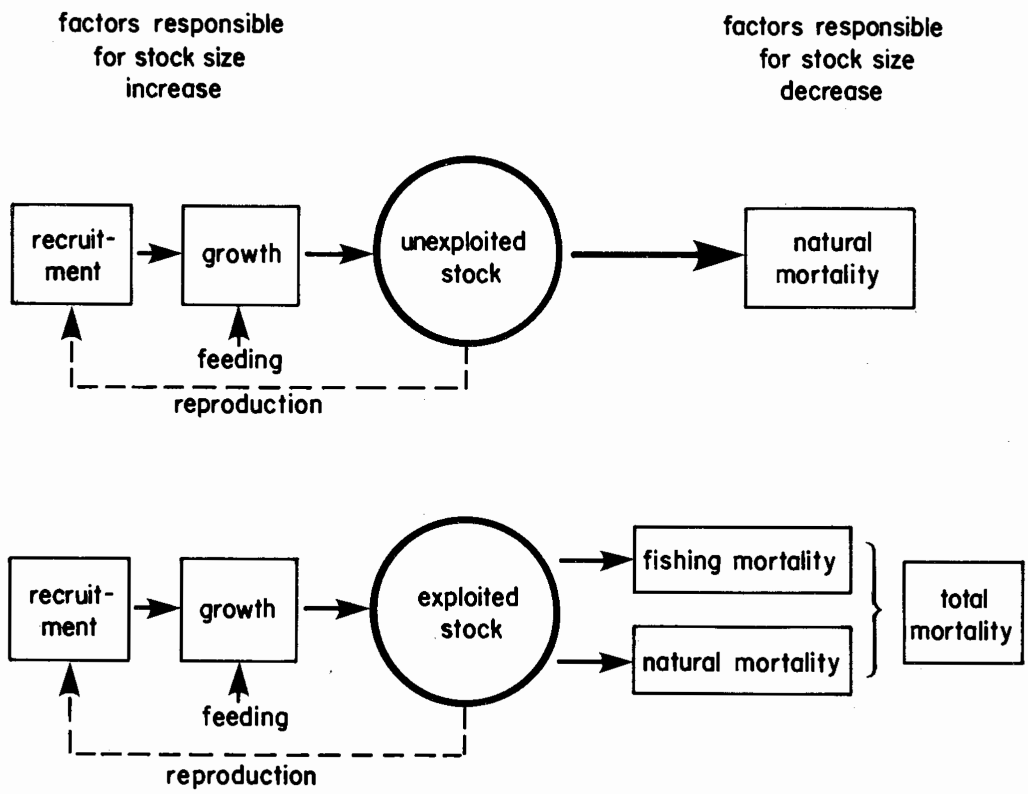

Fig. 1.1. Factors responsible for size increase and decrease in exploited and unexploited stocks (modified after Ricker 1975).

be obtained, for example, to assess the impact of fishing on a multispecies stock (see Chapter 12).

The next 10 chapters of this manual deal with single-species stocks, and only the last chapter deals explicitly with multispecies problems. This 10 to 1 ratio should not conceal the fact that most tropical stocks are part of a multispecies community, and that the other species inevitably affect the dynamics of the stocks under investigation. Chapter 12 is, therefore, very important.

The thirty programs presented here are all original, although a few of them are built around, or incorporate routines written by other authors; the latter are acknowledged in the program descriptions (Appendix II).

The astute reader will note that many, if not all of the programs presented here could be written more elegantly, shortened or otherwise improved. It is only after writing these programs that the author came across such excellent books on calculator programming as Smith (1977), Ball (1978) and Green and Lewis (1979).

Statistical problems *per se* are given little emphasis in this book, for two reasons. First, fish population dynamics, despite recent improvements, are still mainly based on deterministic models (i.e., on models which assume the input data are known perfectly, and which thus ignore the stochastic nature of the inputs). Second, statistics are best learnt from texts explicitly devoted to that subject. Such texts as Draper and Smith (1966), Snedecor and Cochran (1967), Gomez and Gomez (1976), Weber (1980) or Sokal and Rohlf (1981), include both the theoretical background to some of the approaches used for the programs presented here and methods by which these sometimes crude approaches could be refined.

Some possible improvements and refinements are as follows:

— the use of model II instead of model I regressions (or "GM" instead of "AM" regressions) in a number of cases where the former might be more appropriate (Ricker 1973; Laws and Archie 1981),
— the correction of bias in cases where certain parameters are estimated via linear regression by taking the inverse of the variables,
— the correction of bias where a parameter is derived by taking the antilog of a regression intercept (Sprugel 1983),
— the computation of the standard error of parameter estimates where such routines are missing.

Chatterjee and Price (1977) should be consulted for simple methods to deal with these biases, as well as for a detailed account of residual analysis, a method that is extremely useful whenever regression analysis is applied.

Several programs included in this manual provide approximate estimates of standard error (s.e.) for a number of statistics. These were obtained from the square root of the variance in those cases where an equation was readily available which gave the variance of a given statistic, on the assumption that the statistic in question has a normal distribution.

When equations for the estimation of the variance of a given statistic are missing, approximate values of the standard errors can be obtained using the "jackknife" method of Tukey (1977), which is presented in Appendix I.

Confidence intervals are computed by multiplying the "t-statistic" by the standard error. When a large number of degrees of freedom are available, the confidence intervals of a given statistic, A, are thus computed from:

$$A \pm 1.96 \cdot \text{s.e.}_{(A)} = 95\% \text{ confidence interval of A} \qquad \ldots 1.2)$$

or

$$A \pm 2.58 \cdot \text{s.e.}_{(A)} = 99\% \text{ confidence interval of A} \qquad \ldots 1.3)$$

For low numbers of degrees of freedom (d.f. $\leqslant$ 50), table values of the t-statistic must be used.

It is recalled here, finally, that the term "standard error" is used for the square root of the variance *of a given statistic*, while the term "standard deviation" is used for the square root of the variance of *a set of values* of a given variable (see Sokal and Rohlf 1981).

Two types of readers will make use of this manual: those who "believe" in fish population dynamics, and in whatever comes out of a computer (or calculator), and those who don't.

For the latter, little instruction is needed since they already will know how to deal with the contents of this book. The "believer" readers are likely to be students or unfortunate colleagues who might think that given the equations in this book, and the programs to solve them, all they have to do is press the appropriate buttons of their calculator. Clearly, this would be a recipe for disaster. Fish population dynamics are at present in a state of flux and virtually all of the assumptions, approaches and methods presented here have been challenged at least once by highly competent scientists. Furthermore, the application of many of these methods to tropical stocks is rather new, and their overall applicability to all stocks in many cases still needs to be confirmed, especially the new methods presented in this manual.

To give a "feel" of this, several equally legitimate methods and/or equations are usually presented to solve a given problem; these methods generally give somewhat different results, for reasons that are not obvious in the majority of cases. This will help the "believers" appreciate that nothing can replace one's own thorough knowledge of the various aspects of a given problem. Also, it is imperative when using any of the methods and approaches presented herein to read the *original literature;* references are given throughout the text and in a special "recommended reading" section in each of the following chapters.

The methods presented in this book are illustrated by at least one example, based in all cases on data obtained in the tropics or subtropics (Fig. 1.2). Altogether, 60 examples are provided. All include a full keystroke sequence for HP 67/97 calculators and results, to which a brief comment has generally been added. These examples can also be used for testing the programs numbered FB 1 to FB 30 after they have been entered from the listings in Appendix II, into a calculator. The examples can be easily located in the colored pages at the end of Chapters 2-12. Holders for 30 HP 67/97 (and HP 41C) program cards are provided at the end of this book.

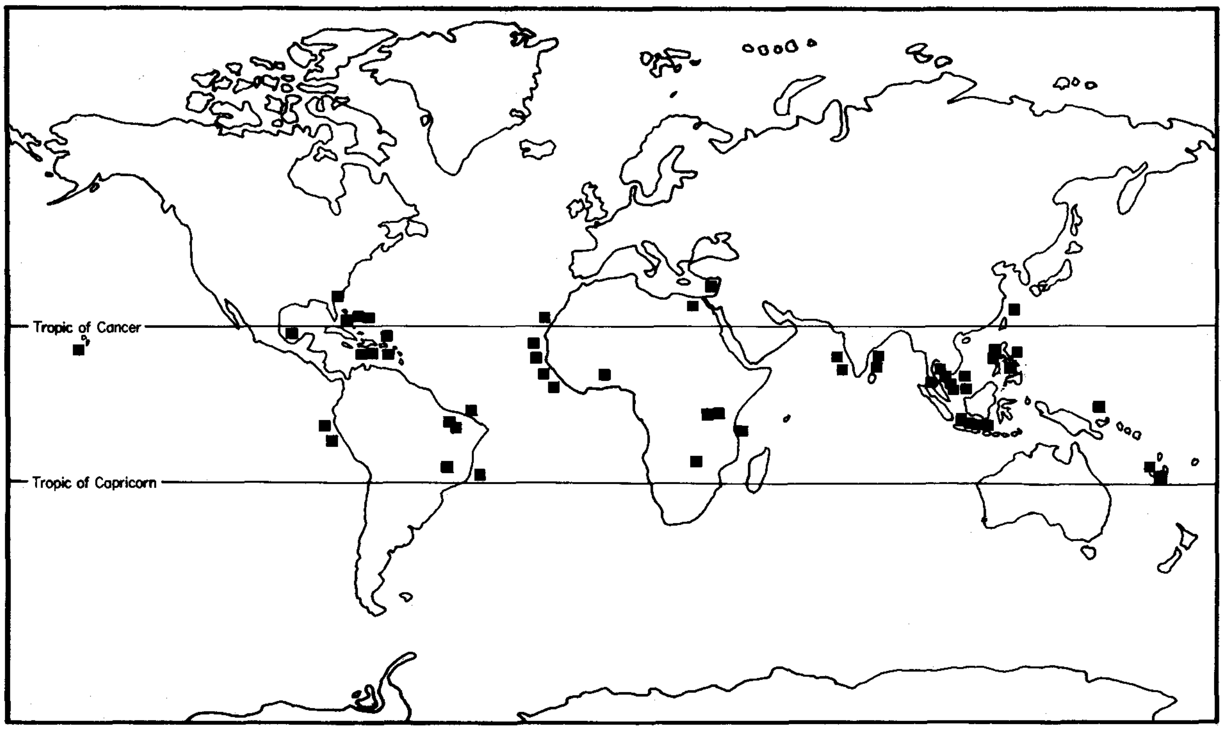

Fig. 1.2. Geographic distribution of examples used in this book, showing that most examples are drawn from the intertropical belt.

The user should follow the procedures below when using this manual and the programs it contains:

1) always read the original literature on the models and approaches presented here,
2) use (whenever possible) several methods to estimate the value of a given parameter and try to identify the sources of the differences in the estimates when such differences occur,
3) estimate standard errors, using the jackknife where appropriate, and perform sensitivity analyses (see Appendix I),
4) always check whether the results obtained make biological sense,
5) try to identify possible sources of biases in the model used here and attempt to improve Programs FB 1 to FB 30,
6) consider that more rigorous methods for estimating certain parameters are possible, and
7) do not blame the author for the nonsensical results that may result from thoughtless applications of the methods and programs given here.

2. Length-Weight Relationships

INTRODUCTION

The relationship between the length (L) and the weight (W) of fish can generally be expressed by the equation:

$$W = a \cdot L^b \qquad \ldots 2.1)$$

where *a* is a factor discussed below and the exponent b lies between 2.5 and 3.5, usually close to 3. Carlander (1969, 1977) has demonstrated from an extraordinarily large number of length-weight data, stemming from a wide variety of fishes, that values of $b < 2.5$ or $b > 3.5$ are generally based on a very small range of sizes and/or that such values of b are most likely to be erroneous. When $b = 3$, weight growth is called *isometric*, meaning that it proceeds in the "same" dimension as the cube of length. When $b \neq 3$, weight growth is *allometric*, meaning that it proceeds in a "different" dimension (differing from L^3). Allometric growth can be either positive ($b > 3$) or negative ($b < 3$). Another way of relating length and weight is to define a condition factor (c.f.) such that

$$\text{c.f.} = W \cdot 100/L^3 \qquad \ldots 2.2)$$

When weight growth is isometric ($b = 3$), we also have

$$\text{c.f.}/100 = a \qquad \ldots 2.3)$$

where a is the multiplicative factor in equation (2.1). The reason for the multiplication by 100 in equation (2.2), it may be mentioned, is to bring the value of the condition factor of fishes with a "normal" shape close to unity when grams are used to express the weight, and centimeters to express the length. It must be emphasized, however, that the c.f. in a given fish species or stock can be compared to that of another species or stock only if the same units and definitions have been used (e.g., total length in cm and live or ungutted weight in g). The units and definitions must always be stated.

In addition many factors, such as sex, time of year, stage of maturity, stomach contents and others influence the numerical magnitude of the condition factor. Comparisons should only be made when these factors are roughly equivalent among samples to be compared.

The values of a in equation (2.1), on the other hand, cannot be used for interspecies or interstock comparisons, even when the same units and definitions are used, unless the values of b are exactly the same. The values of b, finally, are not affected by the units or definitions used.

PARAMETER ESTIMATION

The values of a and b in equation (2.1) are estimated in Program FB 1 by means of a "linearized" form of that equation, namely

$$\log W = \log a + b \cdot \log L \qquad \ldots 2.4)$$

that is by taking (base 10) logarithms on both sides and by estimating the values of log a and of b by means of a linear regression.

This procedure of using ordinary least-square regression to estimate a and b only approximate these parameters, and results in estimates of the standard errors that are not very reliable; alternative procedures, e.g., the use of non-linear least-squares estimations should be considered where possible.

Program FB 1 also calculates single values of c.f. when L/W data are entered, computes an individual or mean c.f. value after one or several pairs of L/W values have been entered and estimates L from W and/or W from L when values of a and b, or an estimate of the condition factor are available.

When expression (2.4) is fitted to data, the coefficient of determination (r^2) is also estimated by program FB1. This coefficient has the value of the correlation coefficient squared, and is used in all those programs that are presented here in which an estimator of the goodness of fit is given. It has the advantage over the correlation coefficient that it expresses directly the proportion of the variance that is "explained" by the regression (e.g., of log W on log L). For example, $r^2 = 0.92$ means that 92% of the variance in a set of values is accounted for, or explained, by a regression, while 100 — 92 = 8% remains "unexplained", that is, must be attributed to other cause(s), e.g., to random variability.

As will be seen in the following chapters, a number of models (= equations) used in fish population dynamics assume that the exponent of the length-weight relationship is equal to 3. Also some models can be considerably simplified when this exponent is actually equal to 3. For these reasons, Program FB 1 incorporates a routine which calculates the value of $\hat{t}$ that can be used to test whether a value of b calculated by this program is significantly different from 3. The equation used to compute the t-statistic is

$$\hat{t} = \frac{s.d._{(x)}}{s.d._{(y)}} \cdot \frac{|b-3|}{\sqrt{1-r^2}} \cdot \sqrt{n-2} \qquad \ldots 2.5)$$

where $s.d._{(x)}$ is the standard deviation of the log L values, and $s.d._{(y)}$ the standard deviation of the log W values, n being the number of fish used in the computation. The value of b is different from 3 if $\hat{t}$ is greater than the tabled value of t for n — 2 d.f. (see Example 2.1).

Table 2.1 presents data which can be used for establishing a length-weight relationship (see also Example 2.1).

Table 2.1. Data for establishing a length-weight relationship for the threadfin bream *(Nemipterus marginatus)* from the southern tip of the South China Sea (live weight in g).

#	TL (cm)	W (g)	#	TL (cm)	W (g)
1	8.1	6.3	9	16.6	65.5
2	9.1	9.6	10	17.7	69.4
3	10.2	11.6	11	18.7	76.4
4	11.9	18.5	12	19.0	82.5
5	12.2	26.2	13	20.6	106.6
6	13.8	36.1	14	21.9	113.8
7	14.8	40.1	15	22.9	169.8
8	15.7	47.3	16	23.5	173.3

When large numbers of fish have been measured, entering the L/W data pairs can become quite tedious. In such cases, a common practice is to arrange the data by length groups, and to calculate the mean weight for each length class. The data should then look as in Table 2.2.

Using Program FB 1, the length-weight relationship and/or the mean condition factor may be calculated with the L/W data pairs having been "weighted" by the sample size. Example 2.2 shows how the data of Table 2.2 may be used in this context. Example 2.3, finally, shows how a single data pair (one value each of L and W) can be used to obtain a preliminary estimate of c.f.

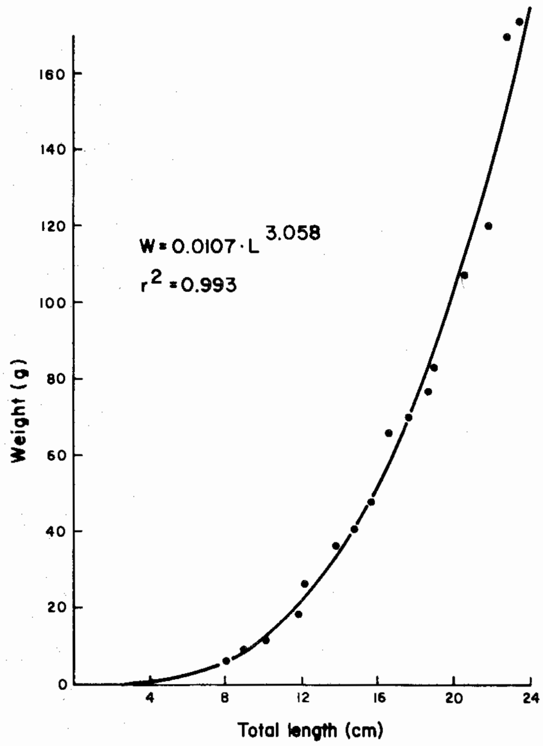

Fig. 2.1. Length-weight relationship for the threadfin bream *(Nemipterus marginatus)* from the South China Sea (based on data in Table 2.1 and Example 2.1).

Table 2.2. Data for establishing the length-weight relationship of *Leiognathus splendens* from the Eastern Java Sea (total length in cm, live weight in g).

#	Class limits low high	Class midlength	Mean weight	n
1	6.00-6.49	6.25	5.28	1
2	6.50-6.99	6.75	4.07	1
3	7.00-7.49	7.25	6.91	11
4	7.50-7.99	7.75	8.46	26
5	8.00-8.49	8.25	10.15	26
6	8.50-8.99	8.75	11.88	23
7	9.00-9.49	9.25	13.77	16
8	9.50-9.99	9.75	17.13	2
9	10.00-10.49	10.25	19.29	7
10	10.50-10.99	10.75	22.57	9
11	11.00-11.49	11.25	25.54	7
12	11.50-11.99	11.75	28.66	3
13	12.00-12.49	12.25	34.02	7
—	12.50-12.99	12.75	—	0
14	13.00-13.49	13.25	46.73	1
—	13.50-13.99	13.75	—	0
15	14.00-14.49	14.25	55.91	1
16	14.50-14.99	14.75	65.63	1
17	15.00-15.49	15.25	61.72	1

Recommended reading: The following papers and books contain useful reviews of aspects of the length-weight relationships of fish: Kesteven (1947), Le Cren (1951), Carlander (1969, 1977), Weatherley (1972), Ricker (1973, 1975), Balon (1974).

Suggested research topics: Estimating a and b in various commercially exploited fish stocks, plotting c.f. values of adults of similar sizes against month of the year to detect changes due to spawning, and comparing the c.f. values of fishes of similar sizes, both parasitized and unparasitized.

Several of the models discussed in the following chapters of this manual require estimates of the mean size at first capture, that is the length at which 50% of the fish entering a trawl net are retained by the gear (L_c).

The parameter L_c is particularly interesting in that it is the length at which the numbers of smaller fish caught retained by the cod end compensate for the number of larger fish not yet retained by the cod end (see shaded areas in Fig. 3.1).

While L_c can be estimated graphically, a more precise method is to order the catch data as in Table 3.1 and to estimate L_c from

$$L_c = L_{n+1} - \Sigma p_i \qquad \ldots 3.1)$$

where L_n is the lower limit of the highest length class considered (when this equation is used the fish must be grouped in classes of width equal to unity, e.g., 1 cm), while Σp_i is the sum of the fractions retained, as shown in Table 3.1 (see also Example 3.1).

Another method to estimate L_c is to fit the retention data with a logistic curve of the form

$$P = 1/(1 + e^{-r_m (L - L_c)}) \qquad \ldots 3.2)$$

where P is the probability of capture, L the midpoint of a length class and r_m is a constant whose value increases with the steepness of the selection curve; both equations (3.1) and (3.2) assume the selection curve to be symmetrical or nearly so.

A program is provided here (FB 29) which can be used to fit a logistic curve to data obtained by a trawl selection experiment (Example 3.2). However, this approach gives best results when the selection curve is symmetrical about the L_c value, and it is thus necessary to first plot the data to check if the requirement for symmetry is at least reasonably met (see Example 3.2 and Fig. 3.1).

In general, L_c can be considered proportional to the mesh size of the cod-end meshes; the proportionality constant is called the selection factor (S.F.). When known, it can be used to estimate L_c from the relationship

$$L_c = \text{S.F.} \times \text{mesh size} \qquad \ldots 3.3)$$

It has been demonstrated by several authors that the selection factor of fishes is generally related to their overall shape, i.e., slender fishes have high selection factors while bulky fishes have low selection factors. This property has been used by the author to derive a nomogram (Fig. 3.2), based on a large number of published results of selection experiments, and which can be used to estimate approximate values of selection factors of fishes, given their "girth factor" (maximum girth/total length) or their "depth ratio" (standard length/maximum body depth). (See Table 3.2 and Example 3.3).

GILLNET SELECTION

Whereas trawl selection is essentially a one-sided affair (with only smaller fish having a reduced probability of capture), gillnets tend to select negatively both small and large fish. The former simply go through the mesh without getting caught, while the latter are too big to insert themselves into a mesh. Thus, when the fish are actually "gilled" (that is caught with their head in the mesh, with the net's twine retaining the fish by their operculum), the resulting selection curve has the shape of a normal distribution, and the length at optimum efficiency (optimum length) will be proportional to mesh size. The selection curve of gillnets can be estimated, when the fish are "gilled" as described above, by using two gillnets of different mesh sizes, if the following applies:

— both selection curves are normally distributed,

Fish Population Dynamics in Tropical Waters: A Manual for Use with Programmable Calculators

To Sandra, Ilya and Angela

Table 3.2. Morphometric data for *Leiognathus equulus* for rapid estimation of mean length at first capture (L_c).[a]

	Total length (cm)	Standard length (cm)	Maximum girth (cm)	Maximum body depth (cm)
	10.2	8.2	9.9	4.5
	10.5	8.6	10.6	5.0
	11.3	9.0	11.1	4.8
	14.0	11.5	14.2	6.3
	14.3	11.8	14.0	6.1
	14.4	11.8	13.7	6.0
	16.4	13.2	16.3	7.6
	16.7	13.2	16.5	7.4
	18.4	14.9	18.3	8.4
	22.1	17.8	22.8	10.5
Σ	148.3	120.0	147.4	66.6
$\bar{x}$	14.83	12.00	14.74	6.66

[a]Based on samples from Mombasa Harbour, obtained during the FAO/DANIDA Training Course on the Methodology of Fisheries Sciences (Biology), held in Mombasa, Kenya, 19 May-14 June 1980.

— the two selection curves have the same standard deviation,
— optimum length is proportional to mesh size,
— the two nets have overlapping selection ranges.

In such cases, given catches obtained by the smaller mesh of size A and the larger mesh of size B, the optimum length corresponding to A (L_A) and the optimum length corresponding to B (L_B) can be estimated from the catch by length class of each mesh (C_A, C_B) through a linear regression of the form y = a + bx, where

$$y = \ln \frac{C_B}{C_A} \qquad \ldots 3.4)$$

$$x = L \text{ (class midpoint)} \qquad \ldots 3.5)$$

The ratio C_A/C_B is called the catch ratio.

The intercept and slope of this regression can then be used to estimate the optimum lengths from

$$L_A = \frac{-2a \cdot A}{b\,(A + B)} \qquad \ldots 3.6)$$

and

$$L_B = \frac{-2a \cdot B}{b\,(A + B)} \qquad \ldots 3.7)$$

while the standard deviation of both selection curves is estimated from

$$\text{s.d.} = \sqrt{\frac{2a\,(A - B)}{b^2\,(A + B)}} \qquad \ldots 3.8)$$

Once L_A, L_B and s.d. have been estimated, the probability of capture (P) at a given length (L) is given for mesh A by

$$P_A = \exp\left(-\frac{(L - L_A)^2}{2\ \text{s.d.}^2}\right) \qquad \ldots 3.9)$$

and for mesh B by

$$P_B = \exp\left(-\frac{(L - L_B)^2}{2\ \text{s.d.}^2}\right) \qquad \ldots 3.10)$$

The derivation of these equations may be found in Gulland (1969, p. 90-92); this method was proposed by Holt (1963) on the basis of pioneering work by Baranov (1914).

Although the method gives reasonable results in the case of the example provided here (Example 3.4, Table 3.3, Figs. 3.3 and 3.4), various authors have shown that gillnet selection curves frequently have shapes other than normal (= bell-shaped). This applies especially to large, spiny fishes, which, in addition to being gilled often entangle themselves, which results in asymmetrical selection curves. In such cases, it may be necessary to use more elaborate methods to estimate the selectivity of the net(s) under investigation, e.g., those of Gulland and Harding (1961), or Hamley (1975).

When the selection curves for a given fish species are only slightly asymmetrical and drawn to the right, it is still possible to apply the Baranov/Holt method outlined above using the logarithm

Table 3.3. Catch by length of two gillnets to estimate their selection for *Tilapia esculenta* in Lake Victoria. Simplified from Table 1 in Garrod (1961).

Midpoint of length group (in cm)	Mesh sizes (cm) 8.1	9.1[a]	
18.5	7	—	not used, no catch with 9.1-cm meshes
19.5	90	1	used, n = 5
20.5	199	9	
21.5	182	53	
22.5	119	290	
23.5	29	357	
24.5	17	225	not used, see Fig. 3.3
25.5	3	82	
26.5	—	19	not used, no catch with 8.1-cm meshes
27.5	—	10	

[a]Note that, when comparing two nets, only those lengths can be used for which there are non-zero catch data on both sides.

of the lengths (and of the mesh sizes) instead of the lengths (and mesh sizes) in all computations. This approach is illustrated in Example 3.5, which is based on the data pertaining to *Tilapia galilaea* caught in Volta Lake, Ghana (Table 3.4). As might be seen in Fig. 3.5A, the plot of the natural logarithm of catch ratio against length is not linear (thus suggesting that the simple Baranov/Holt model is inappropriate). The plot of the natural logarithm of catch ratio against that of length (Fig. 3.5B) is linear however, and provides parameters from which asymmetrical selection curves can be drawn (Fig. 3.6).

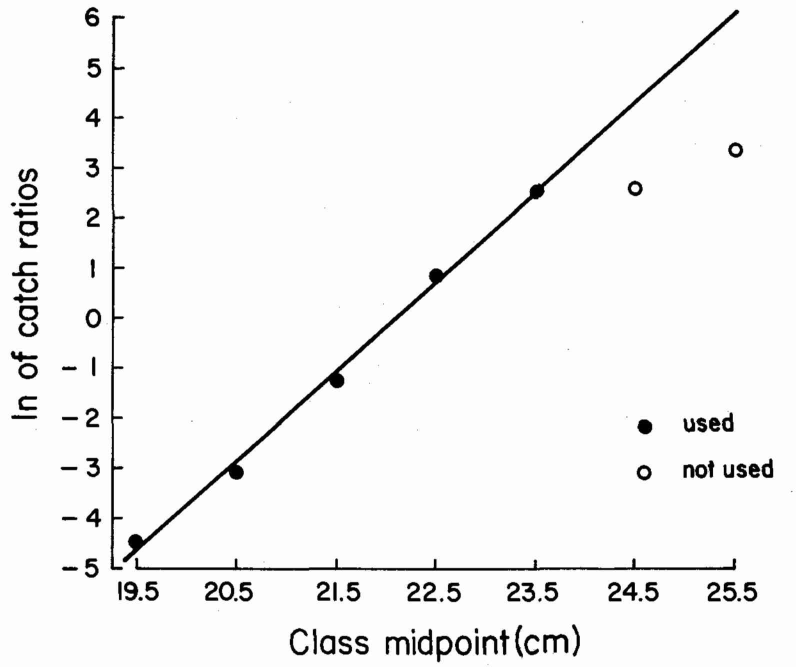

Fig. 3.3. Logarithm of catch ratios plotted for length in *Tilapia esculenta* caught with gillnets of two different mesh sizes (based on data in Table 3.3 and Example 3.4). (Note that one could also argue that the logarithmic model in Fig. 3.5 would fit the data better than the simpler model used here.)

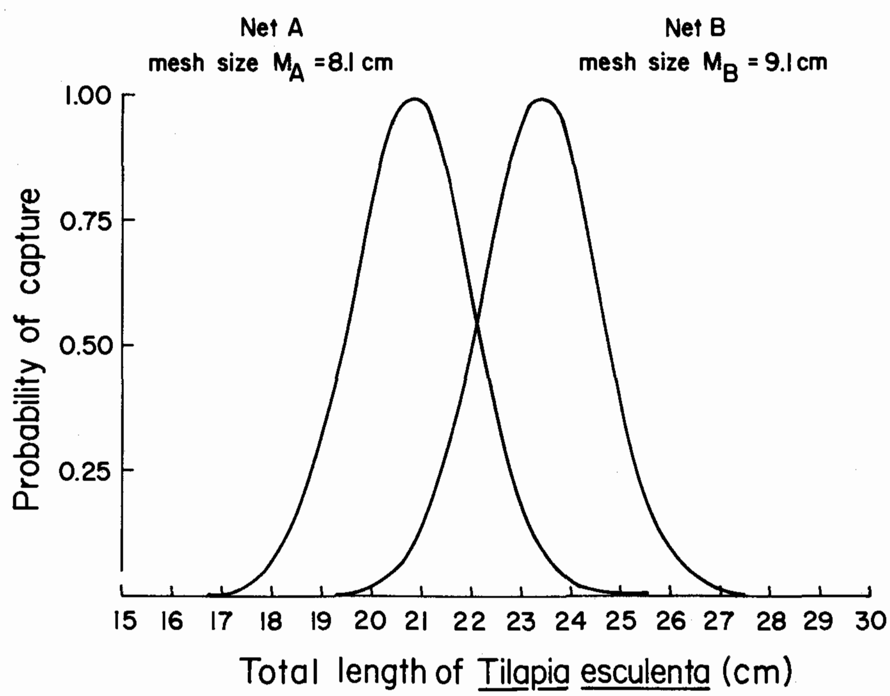

Fig. 3.4. Selection curves for *Tilapia esculenta* caught with gillnets of two different mesh sizes (based on Example 3.4).

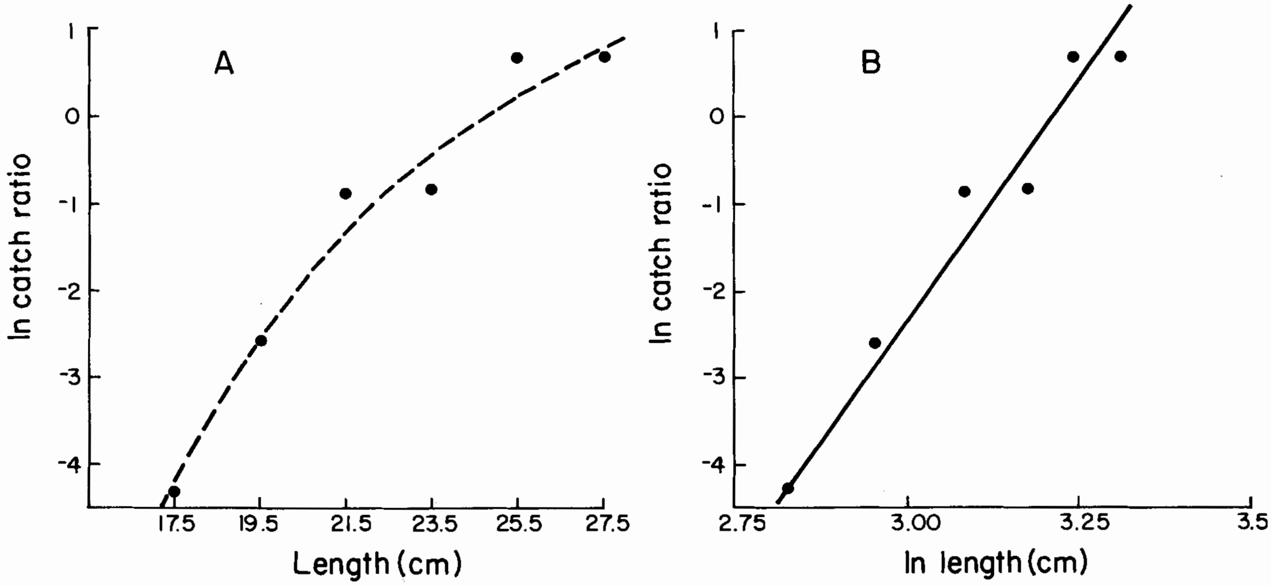

Fig. 3.5. Plot of natural logarithms of catch ratios against length (A) and ln length (B) to show effect of logarithmic transformation of length. Based on data of Table 3.4. Note non-linearity of relationship A (dotted line drawn by eye); see also Example 3.5 and text.

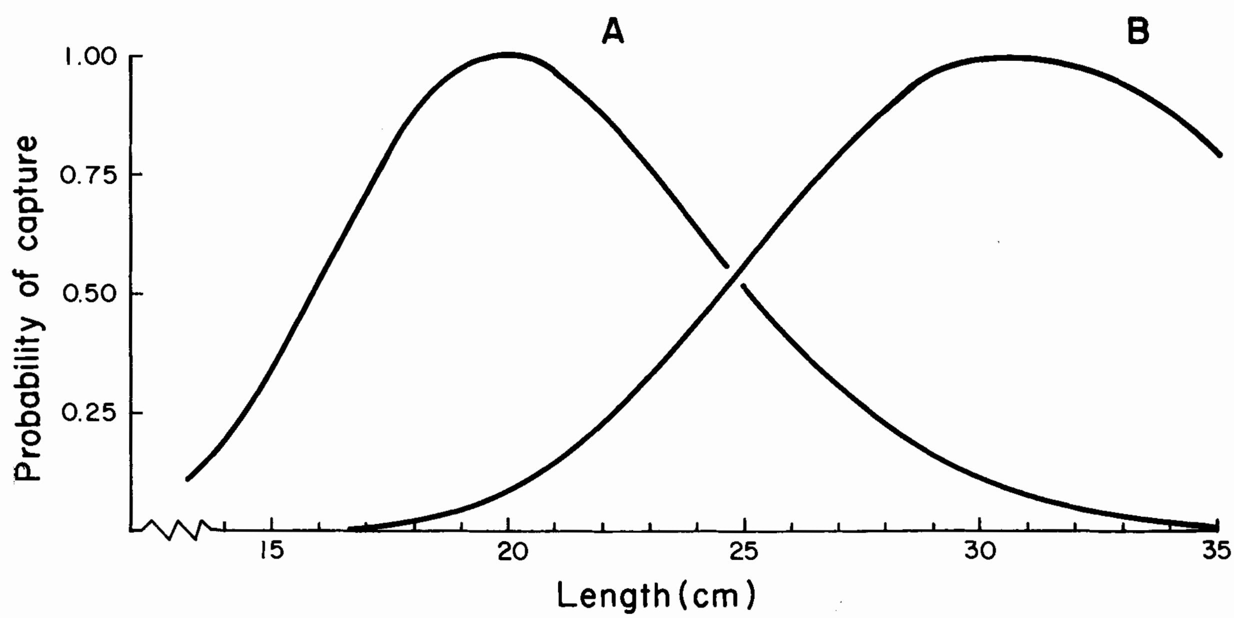

Fig. 3.6. Selection curve of *Tilapia galilaea* caught with gillnets of two mesh sizes (A = 7.6 cm, B = 10.2 cm). Based on data in Table 3.4 and Example 3.5.

Table 3.4. Catch by length of two gillnets for estimation of their selection for *Tilapia galilaea* in Volta Lake, Ghana.[a]

Midpoint of length class (cm)[b]	Mesh sizes (cm) 7.6	10.2	Probability of capture at mesh sizes 7.6 cm	10.2 cm
	No. of fish caught			
17.5	75	1	0.803	0.016
19.5	95	7	0.994	0.068
21.5	36	15	0.929	0.190
23.5	14	6	0.705	0.391
25.5	5	10	0.457	0.633
27.5	2	4	0.262	0.849

[a]Data read off Fig. 1 in Lelek and Wuddah (1969), including only those lengths for which both mesh sizes had non-zero catches.
[b]Data regrouped in 2-cm classes to reduce number of classes with zero catches.

USING A SELECTION CURVE TO ADJUST CATCH SAMPLES

Conducting and interpreting selection experiments, e.g., with the models proposed above, represent only half of the work that must be done to obtain catch samples that are representative of a given fish population. The other half of the work, obviously, is to use the selection curves obtained to adjust the available samples. Such adjustment is done by simply dividing the number of fish caught, for each length class, by the probability of capture of that length class, i.e., using the relationship

$$\text{true relative abundance in the population} = \frac{\text{relative abundance in sample}}{\text{probability of capture}} \quad \ldots 3.11)$$

Fig. 3.7 shows, as an example, the catch sample of *Tilapia galilaea* in Table 3.4 (7.6-cm meshes) and the computed true (relative) abundances in the population.

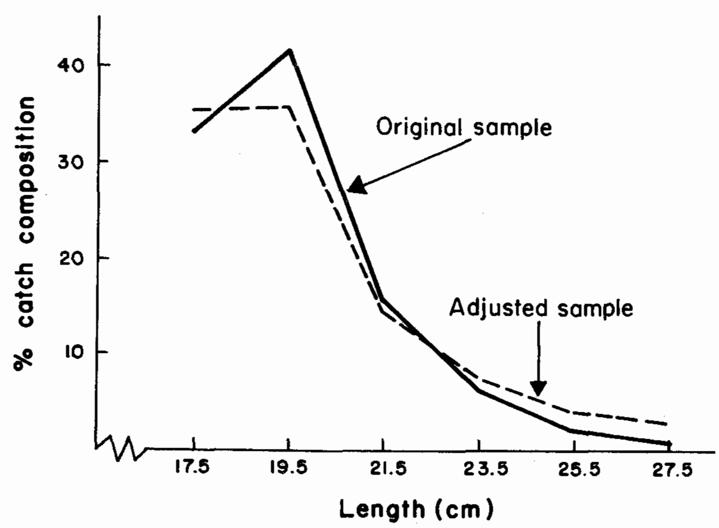

Fig. 3.7. Difference between a gillnet sample and the same sample, adjusted for mesh selection (based on data of Table 3.4, 7.6-cm meshes and Example 3.5). The difference between the two samples is relatively small in this example, but can be quite dramatic when large ranges of sizes are represented in the catch.

Recommended reading: Mesh selection for both trawl and gillnets is discussed in Gulland (1969, p. 84-95) who derives the various equations presented in this chapter. For trawl selection, further details may be found in Beverton and Holt (1957, p. 221-233) and Pope et al. (1975), while McCombie and Fry (1960), Gulland and Harding (1961) and Hamley (1975) describe methods for assessing the selectivity of gillnets when the assumptions of the models presented above are not met, e.g., when the selection curves are strongly asymmetrical.

It is extremely important for fishery biologists to have a good knowledge of the gears used in a given fishery, and of the properties of such gears. Brandt (1972) and Baranov (1976) may be consulted for gear descriptions and the study of gear properties, respectively.

Passive gears, such as traps, longlines, gillnets, etc. tend to interfere with each other and to become saturated. These and related problems are reviewed in Munro (1974) and Eggers et al. (1982).

Suggested research topics: Estimate selection ogives, L_c, and selection factors of important commercial species. In multispecies fisheries, use the knowledge gained in the fashion of Sinoda et al. (1979).

EXAMPLE 3.1

Estimation of the mean length at first capture (L_c) and selection factor of *Leiognathus equulus* by means of a trawl selection experiment.

Data from Table 3.1

Computation

1) Read sides 1 and 2 of Program FB 2

2) Keystrokes

8 f a 4 ↑ 0A 35 ↑ 2A 198 ↑ 22A 170 ↑ 56A 76 ↑ 42A 45 ↑ 34A 25 ↑ 19A 7 ↑ 21A 0 ↑ 12A 1 ↑ 3A 0 ↑ 5A 0 ↑ 5A 0 ↑ 3A 0 ↑ 1A 0 ↑ 1A 0 ↑ 1A

	Keystrokes	Results	
3) Calculate L_c	fb	13.88	(L_c)
4) Calculate the selection factor (S.F.) (i.e., divide by the mesh size used):	7.88 ÷	1.76	(S.F.)

See Example 3.2 for another method to estimate S.F., also applied to *Leiognathus equulus*.

EXAMPLE 3.2

Fitting the logistic curve to trawl selection data.

Data from Table 3.1 (but note that midpoints are used instead of the lower class limits)

Computations

1) Read side 1 of Program FB 29

2) Keystrokes

1 f a .054 ↑ 9.5 A .1 ↑ 10.5 A .248 ↑ 11.5 A .356 ↑ 12.5 A .43 ↑ 13.5 A .432 ↑ 14.5 A .75 ↑ 15.5 A
(note that midlengths above 15.5 were skipped; see below)

3) Estimate goodness of fit and L_c.

Keystroke	Results
E	0.938 (r^2)
	0.591 (r_m)
	14.002 (L_c)

4) To draw curve as in Fig. 3.2 enter class midpoint, and obtain fraction retained, as follows

	Keystrokes	Results
	7.5 C	0.021 (frac. retained)
	8.5 C	0.037 (frac. retained)
	... etc.	
and	14.002 C	0.500 (as expected)

5) Divide L_c by the mesh size used (here 7.88 cm) to estimate the selection factor.

Keystrokes	Results
14.002 ↑	–
7.88 ÷	1.777 (S.F.)

The value of L_c obtained here (14 cm) is very close to the value obtained earlier (13.9 cm). However, this was achieved by omitting all values associated with lengths higher than 15.5 cm. This step was necessary because the program used here does not allow for the entry of 1.00 as a fraction retained. The selective removal of all such values, on the other hand, would cause a bias in the curve estimation. Thus, the best solution here was to omit all lengths from the first which couldn't be entered. As Fig. 3.1 shows, the resulting curve gives a good fit to the data.

EXAMPLE 3.3

Estimation of the selection factor of *Leiognathus equulus* by means of morphometric data and a nomogram (Fig. 3.2).

Data from Table 3.2

1) Calculate the "girth factor" (maximum girth/total length)
   Keystrokes: 14.74 ↑ 14.83 ÷
   girth factor = 0.99

2) Calculate the "depth ratio" (standard length/maximum body depth)
   Keystrokes: 12 ↑ 6.66 ÷
   depth ratio = 1.80

3) Use the calculated "girth factor" and "depth ratio" to estimate two values of S.F. via the nomogram in Fig. 3.2. This results in a mean estimate of S.F. of ≈ 1.8 which compares well with the values of 1.76 and 1.78 estimated in Examples 3.1 and 3.2, respectively.

EXAMPLE 3.4

Estimation of the selection curves for *Tilapia esculenta* caught with gillnets of two different mesh sizes.

Data from Table 3.3

Computation

1) Read sides 1 and 2 of Program FB 2

2) Keystrokes

   8.1 ↑ 9.1 fe 90 ↑ 1 ↑ 19.5 C 199 ↑ 9 ↑ 20.5 C 182 ↑ 53 ↑ 21.5 C 119 ↑ 290 ↑ 22.5 C
   29 ↑ 357 ↑ 23.5 C

3) Calculate parameters of selection curves

Keystrokes	Results	
E	0.996	(r^2)
	−39.801	(a)
	1.801	(b)
	20.818	(L_A)
	23.388	(L_B)
	1.195	(s.d.)

4) Obtain P-values to draw selection curves

Keystrokes	Results	
17 D	0.006	(P)
18 D	0.062	(P)
etc.		

Step 4 allows the quick estimation of values of P (= probability of capture) for any length, using mesh A; to obtain values pertaining to mesh B, enter the length value and press fd (see Users' Instruction for Program FB 2 and Fig. 3.4 for selecting the curves pertaining to this example).

EXAMPLE 3.5

Estimation of asymmetrical selection curves for *Tilapia galilaea* caught with gill-nets of two different sizes.

Data from Table 3.4

Computation

1) Read sides 1 and 2 of Program FB 2

2) Keystrokes

fSTF1 7.6 ↑ 10.2 fe 75 ↑ 1 ↑ 17.5 C 95 ↑ 7 ↑ 19.5 C 36 ↑ 15 ↑ 21.5 C 14 ↑ 6 ↑ 23.5 C 5 ↑ 10 ↑ 25.5 C 2 ↑ 4 ↑ 27.5 C

3) Calculate parameters of selection curves

Keystrokes	Results	
E	0.941	(r^2)
	−36.024	(a)
	11.224	(b)
	19.936	(L_A)
	30.774	(L_B)
	0.197	(s.d.)

(but note that s.d. is expressed in $\log_e$ units)

4) Obtain P-values to draw selection curve for mesh A

Keystrokes	Results	
17.5 D	0.803	(P)
19.5 D	0.994	(P)

etc. (see Table 3.4 and Fig. 3.6)

For mesh B, enter midpoints and press fd instead of D; remember that all computations in this example must be performed *with flag 1 set*, and that it should be cleared to get back to linear plots of ln catch ratio on length and to symmetrical selection curves.

4. Fish Growth

INTRODUCTION

Growth may be defined as the change over time of the body mass (≅ body weight) of a fish, being the net result of two processes with opposite tendencies, one building-up body substances (anabolism) and the other breaking these substances down (catabolism) or

$$dw/dt = HW^d - kW \qquad \ldots 4.1)$$

where dw/dt is the change in body weight per unit time, H is the coefficient of anabolism and k is the coefficient of catabolism. The process of anabolism is here viewed as being proportional to a certain power (d) of the fish weight (W), while catabolism is proportional to weight itself (von Bertalanffy 1938; Pauly 1981).

Equation (4.1) is a differential equation which may be integrated in two ways:

a) by setting the value of d at 2/3. This leads to what is widely known as the *V*on *B*ertalanffy *G*rowth *F*ormula (VBGF), which is here called *special* VBGF.
b) by allowing d to take a certain range of values, including 2/3. This leads to what will be called the *generalized* VBGF (Pauly 1981).

Most growth-related programs in this manual allow the use of both forms of the VBGF, and there is no need to fear that the use of a "new" growth equation will complicate things. The reason why the generalized VBGF is introduced here is that this form of the growth equation allows smaller deviations when fitting growth data and a biological interpretation of the equation parameters, as intended by von Bertalanffy (1951) (see Pauly 1981).

Details on the integration of expression (4.1) to a growth curve have been presented in Taylor (1962) and Pauly (1979a). It suffices to mention here that, in the course of this integration, the weights in expression (4.1) are replaced by length such that

$$HW^d = pL^a \qquad \ldots 4.2a)$$

and

$$W = qL^b \qquad \ldots 4.2b)$$

Also a "surface factor D" is defined such that

$$D = b - a = b\,(1 - d) \qquad \ldots 4.3)$$

The integration for length growth yields the equation

$$L_t{}^D = L_\infty{}^D\,(1 - e^{-KD\,(t - t_o)}) \qquad \ldots 4.4)$$

or

$$L_t = L_\infty\,(1 - e^{-KD\,(t - t_o)})^{1/D} \qquad \ldots 4.5)$$

where

L_∞ is the asymptotic length, that is the mean length the fish of a given stock would reach if they were to grow indefinitely.

K is a growth constant which may be conceived as a "stress factor", with K = k/3 (relative) age". Table 4.3 gives an example of such data. From such data, L_∞, (or W_∞) and K may be estimated, but not t_o, which is due to the fact that what is really known are age *differences*, not actual ages. To obtain estimates of t_o, a knowledge of the absolute age of fish of given size is necessary, as might be obtained, e.g., from aging by means of daily otolith rings (Pannella 1971) or from a detailed knowledge of the life-history of a fish, inclusive of the exact spawning season.

Table 4.3. A set of length-at-(relative) age data, pertaining to male Nile carps *(Labeo niloticus)* from a freshwater body near Alexandria (Egypt).[a]

Age group (relative age, in years)	Length (cm)	N
I	19.6	184
II	37.4	73
III	45.7	11
IV	51.0	3

[a]From Hashem (1972).

Throughout most of this manual, I have used the term size-at-age both for data on size at *absolute* and at *relative* age, and distinguished between the two only when the distinction was essential to the point being made.

Size-at-age data (in the wider sense) are required in this manual for Programs FB 3 (von Bertalanffy Plot), FB 4 (Ford-Walford Plot) and FB 7 (seasonal length growth).

Data on size increase in time may be typically represented by the tagging-recapture data of Table 4.4. With this type of data, we do not know the age of any fish, nor do we even have a series of sizes at relative ages. Still, it is possible to derive from data of this type an estimate of asymptotic size and K, given values of D, by means of Program FB 5 (Gulland and Holt Plot) or Program FB 6 (Munro Plot).

This manual, it must be stressed here, shows how to interpret growth data, not how to obtain them. Introductions into the literature on fish aging, including validation techniques applicable to tropical fish, are given by Mohr (1927, 1930 and 1934), Graham (1929), Suvorov (1959), Menon (1950), Bagenal (1974), Pauly (1978), by Brothers (1980), who also reviews techniques for aging tropical fish by means of daily otolith rings, and most recently by Beamish and McFarlane (1983).

METHODS FOR PARAMETER ESTIMATION

A method for obtaining first estimates of asymptotic size

Various authors, notably Beverton (1963) and Taylor (1958), have noted that there is generally a good agreement in various fish stocks, between L_{max}, the largest length recorded from a given stock and L_∞, the asymptotic length estimated for that stock.

Taylor (1958) in fact suggested the rule of thumb

$$L_{max}/0.95 \approx L_{(\infty)} \qquad \ldots 4.16)$$

which for weight becomes

$$W_{max}/0.86 \approx W_{(\infty)} \qquad \ldots 4.17)$$

and where $L_{(\infty)}$ and $W_{(\infty)}$ are used (instead of L_∞ and W_∞) to distinguish such preliminary estimates from values of asymptotic size obtained from growth data, e.g., by means of a Ford-Walford plot (see below).

Two problems are associated with this method to obtain preliminary estimates of asymptotic size. The first problem is that of properly defining L_{max} (or W_{max}); S. Garcia, FAO (pers. comm.) suggests L_{max} and W_{max} should be derived by averaging the sizes of several large specimens from a well-sampled stock, whenever possible, rather than using only one single value. In either case, it is important to distinguish L_{max} (and W_{max}) from $L_{max.\ ever}$ (and $W_{max.\ ever}$), i.e., to distinguish the maximum size on record from a *given stock* from the maximum size recorded from a given *species* of fish (see e.g., Intern. Game Fish Assn. 1978). Obviously, values of $L_{max.\ ever}$, or $W_{max.\ ever}$ will not do for use with equation (4.16) or (4.17), because the "record" fish will most probably have grown under environmental conditions different from those applying to the stock under investigation.

The second problem associated with the use of expression (4.16) or (4.17) to obtain preliminary estimates of asymptotic size lies in the fact that in fish capable of reaching very large sizes, the use of the special VBGF implies that $L_\infty \gg L_{max}$ (and $W_\infty \gg W_{max}$), as shown in Pauly (1981) (see also Example 4.9 and Fig. 4.5). The reason for this is that the assumption embedded in the special VBGF that D = 1, which is more or less erroneous in most fish, is most erroneous in those fish that are capable of reaching large sizes (see Fig. 4.1). Using D = 1, instead of the appropriate value of D has in these fish the effect of generating values of asymptotic sizes much larger than the maximum known from the stocks in question (Pauly 1981). Thus, in fish capable of reaching large sizes (> 50 cm) it is imperative, when using expression (4.16) or (4.17) to compute and use the appropriate value of D.

The von Bertalanffy plot

Historically, the first method for estimating the parameters of the VBGF was that proposed by von Bertalanffy (1934). The method requires the use of a set value for the asymptotic size ($L_{(\infty)}$, or $W_{(\infty)}$).

The generalized VBGF

$$L_t{}^D = L_{(\infty)}{}^D \cdot (1 - e^{-KD\,(t - t_o)}) \qquad \ldots 4.18)$$

can also be written

$$(L_t/L_{(\infty)})^D = 1 - e^{-KD\,(t - t_o)} \qquad \ldots 4.19)$$

and

$$1 - (L_t/L_{(\infty)})^D = e^{-KD\,(t - t_o)} \qquad \ldots 4.20)$$

or

$$-\ln [1 - (L_t/L_{(\infty)})^D] = -KDt_o + KDt \qquad \ldots 4.21)$$

Expression (4.21) has the form of a linear regression, y = a + bx,

where

$$y = -\ln [1 - (L_t/L_{(\infty)})^D] \qquad \ldots 4.22)$$

and

$$x = t \qquad \ldots 4.23)$$

which, given a set of length-at-age data, a value of D and an estimate of $L_{(\infty)}$, provides values of intercept (a) and slope (b) which can be used to obtain K and t_o through

$$K = b/D \qquad \ldots 4.24)$$

and

$$t_o = -a/b \qquad \ldots 4.25)$$

Also, a value of r^2 is generated which estimates the goodness of fit and which can be used to test whether the use of a different value of $L_{(\infty)}$ improves the linearity of the regression. The latter

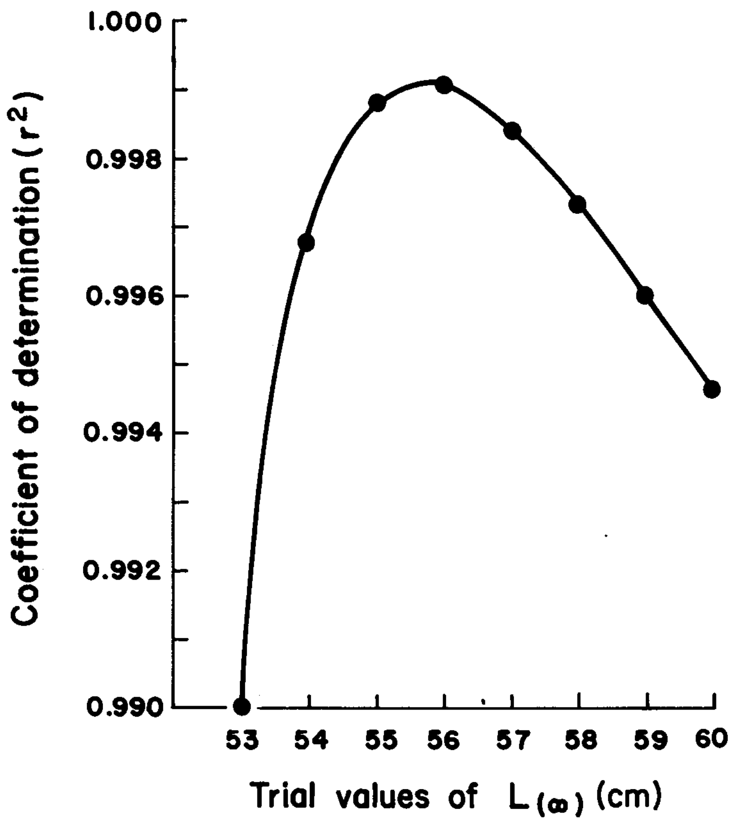

Fig. 4.3. Relationship between the goodness of fit of a von Bertalanffy plot (expressed by the coefficient of determination) and the selected value of $L_{(\infty)}$ (based on data in Table 4.3 and Example 4.2).

feature, therefore, can be used to obtain by trial and error the value of $L_{(\infty)}$ which brings r^2 to its maximum. See Example 4.2 and Fig. 4.3.

The use of a von Bertalanffy plot has the following advantages:

a) the values of t (ages) do not need to be equidistant (see Example 4.1)
b) the mean length values used in the regression can be weighed by sample size (as in Example 4.2)
c) the value of t_o is estimated directly when absolute ages are provided (as in Example 4.1)
d) the use of a forcing value of $L_{(\infty)}$ helps in obtaining (rough) estimates of K even when the growth data are not asymptotic.

The Ford-Walford plot

Of all methods used for estimating the parameters of the VBGF, the Ford-Walford plot (Ford 1933; Walford 1946) is the most commonly used. The method is based on a rewritten version of the VBGF:

$$L_{t+1}{}^{D} = a + bL_t{}^{D} \qquad \ldots 4.26)$$

from which is derived

$$L_\infty = \left(\frac{a}{1-b}\right)^{1/D} \qquad \ldots 4.27)$$

and

$$K = -\frac{\ln b}{D} \qquad \ldots 4.28)$$

Here, $L_t{}^D$ and $L_{t+1}{}^D$ pertain to length separated by a constant time interval (1 = year, month or week, etc.). Table 4.4 shows how size-at-age data need to be rearranged for use in a Ford-Walford plot.

A point must be mentioned which pertains to the regression model used in conjunction with the Ford-Walford plot. The linear regression models normally used in this manual (as well as in the HP 67/97 Standard PAC) are arithmetic mean (AM) regressions, also called type I, or predictive regressions. In this regression type, it is implied that the ordinate (y) values are measured with error, or have natural variability, while the abscissa value (x) are measured without error or not to have natural variability. This assumption applies in the case of the von Bertalanffy plot. In the case of the Ford-Walford plot, however, the use of an AM regression introduces a bias, due to the fact that both the y values (= $L_{t+1}{}^D$) and the x values (= $L_t{}^D$) are measured with the same error (they are indeed the same data, used twice!). In such a case, a geometric mean (GM) regression (also called type II, or functional regression) has to be used (Ricker 1973; Laws and Archie 1981).

In practice this consists in calculating the a, b and r^2 values of an AM regression, then calculating the GM slope (b′) from

$$b' = b/r \qquad \ldots 4.29)$$

and the GM intercept (a′) from

$$a' = \bar{y} - (b'\bar{x}) \qquad \ldots 4.30)$$

where $\bar{x}$ is the mean of the $L_t{}^D$ values and $\bar{y}$ the mean of the $L_{t+1}{}^D$ values. The values of a′ and b′ are then inserted into equation (4.27) and equation (4.28) instead of the values of a and b.

Table 4.4. Length-at-age data for the Atlantic yellowfin *(Thunnus albacares)*[a] off Senegal for use with a Ford-Walford plot.

Age (years)	FL (cm)	Rearrangement for Ford-Walford plot	
		L_t (= x)	L_{t+1} (= y)
1	35		
2	55	35	55
3	75	55	75
4	90	75	90
5	105	90	105
6	115	105	115

[a]From Postel (1955), who also gives L_{max} = 146.5, corresponding to a value of $W_{max} \approx 60$ kg.

The computations outlined here are all performed by Program FB 4 and data are provided in Table 4.4 for calculating Example 4.3 (see also Figs. 4.4 and 4.5). The Ford-Walford plot has a few advantages over the von Bertalanffy plot—an estimate of L_∞ is obtained immediately, and it is relatively easy to compute.

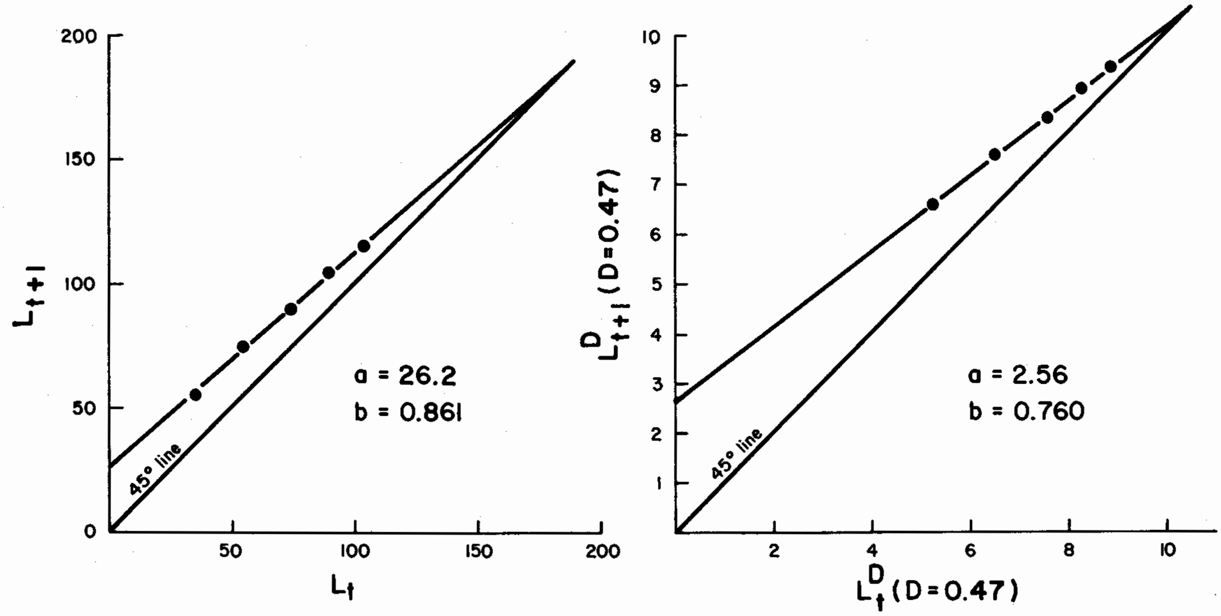

Fig. 4.4. Two Ford-Walford plots for Atlantic yellowfin *(Thunnus albacares)*, based on the special and generalized VBGF (based on Table 4.4 and Example 4.3).

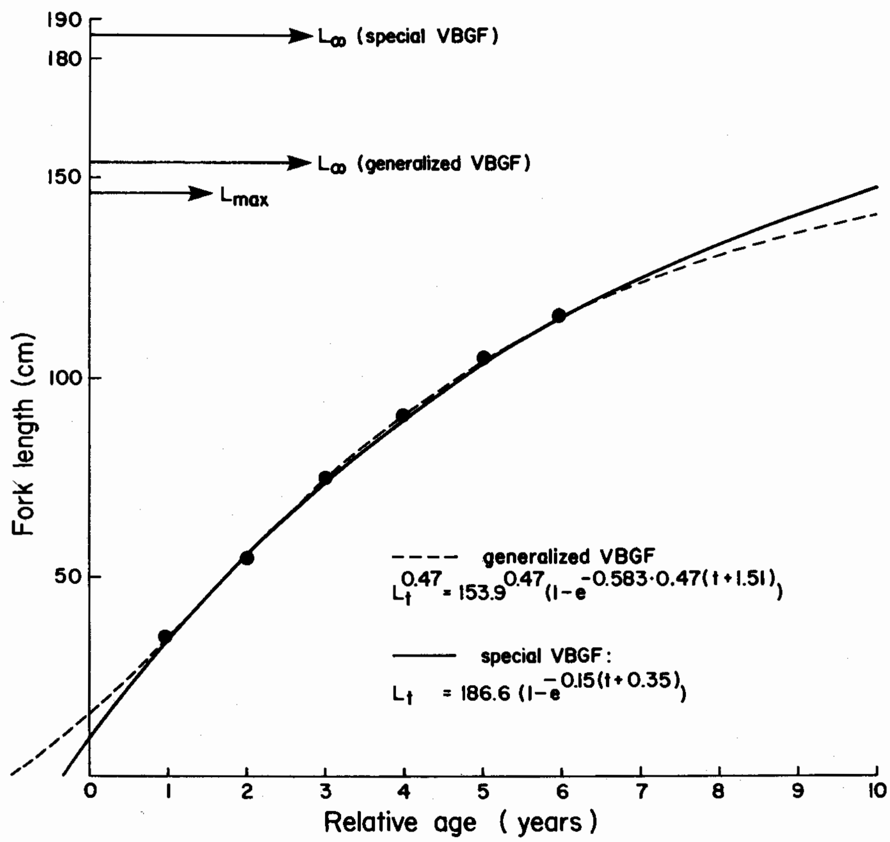

Fig. 4.5. Differences between the special and generalized VBGF as applied to growth data for Atlantic yellowfin *(Thunnus albacares)* (based on Example 4.3).

These advantages, as it seems, are outweighed by the disadvantages of this method, namely:

- The plot requires that the data are equidistant in time (the time between size values being years, months, weeks, etc.).
- The points are unevenly spaced along the plot (see Fig. 4.4) which introduces a slight bias when calculating the regression parameters.
- The points, being combined from *two* values of size-at-age cannot be readily weighed by sample size.
- One value of size-at-age is always lost (because it has no corresponding value of L_{t+1}).
- The value of t_o must be estimated separately.

Variants of the basic Ford-Walford plot have been published (e.g., Gulland 1969; Hohendorf 1966), but the negative features of this plot can hardly be compensated for; it would appear that the Ford-Walford plot is in fact inferior to the original von Bertalanffy plot.

The Gulland and Holt plot

Another method for estimating L_∞ and K from growth data is provided by the feature that a plot of size increments per unit time against mean size (for the increment in question) gives a straight line, whose slope—with sign changed—closely corresponds to the value of K, or including the parameter D:

$$\frac{L_2^D - L_1^D}{t_2 - t_1} \approx a - KD\bar{L}^D \qquad \ldots 4.31)$$

where $\bar{L}^D = (L_1^D + L_2^D)/2$, and where L_1 and L_2 are successive lengths, pertaining to times t_1 and t_2, respectively (Gulland and Holt 1959).

Table 4.5 gives an example of data of this kind, which are typically obtained from tagging studies or from length-frequency data. The method uses normal size-at-age data, at equal or unequal

Table 4.5. Length at tagging (L_1), length at recapture (L_2) and time at large for tagged ocean surgeon fish *(Acanthurus bahianus)* from the Virgin Islands.[a]

No.	L_1 (cm)	L_2	Days out	Annual K[b]	Mean temp.[c] (in °C)
1	9.7	10.2	53	0.370	27.48
2	10.5	10.9	33	0.518	28.61
3	10.9	11.8	108	0.385	27.79
4	11.1	12.0	102	0.419	29.29
5	12.4	15.5	272	0.808	28.37
6	12.8	13.6	48	1.007	28.89
7	14.0	14.3	53	0.405	27.55
8	16.1	16.4	73	0.500	27.99
9	16.3	16.5	63	0.407	27.54
10	17.0	17.2	106	0.321	28.00
11	17.7	18.0	111	0.707	28.30
			$\bar{K}$ =	0.532	
			C.V. =	0.408	

[a] Adapted from Table 3 of Randall (1962). Data included pertain to fishes which grew at least 2 mm while at large, which accounts for small measurement errors and cases of no-growth due to tagging wounds.

[b] As calculated from a Munro plot (see Example 4.6) with $L_{(\infty)}$ = 19.25 cm and D = 1 (Fig. 4.9).

[c] As computed from the mean monthly temperatures and the dates at tagging and recapture in Randall (1962), who also gives 29.4°C as highest mean monthly temperature (T_s), 27.2°C as lowest mean monthly temperature (T_w) and 28.5°C as annual mean ($\bar{T}$).

intervals, granted that the values of $(t_2 - t_1)$ stay small in relation to the longevity of the fish (Gulland and Holt 1959).

Equation (4.31), it will be noted, has the form of a linear regression y = a + bx with

$$x = \bar{L}^D \qquad \ldots 4.32)$$

and

$$y = \frac{L_2^D - L_1^D}{t_2 - t_1} \qquad \ldots 4.33)$$

the intercept (a) and slope (b) of which provide values of K and L_∞ through the relationships

$$K = -b/D \qquad \ldots 4.34)$$

and

$$L_\infty = \left(\frac{a}{KD}\right)^{1/D} \qquad \ldots 4.35)$$

Sometimes, the method does not provide reasonable parameter estimates, when the $\bar{L}^D$ data are too close to each other (Table 4.6, Fig. 4.6). In such a case, a set value of $L_{(\infty)}$ may be used in connec-

Table 4.6. Length at tagging (L_1), length at recapture (L_2) and days at large of tagged Queen parrot fish *(Scarus vetula)* from the Virgin Islands.[a]

No.	L_1 (cm)	L_2	Days out	$\bar{L}$	cm/day
1	14.0	16.9	48	15.45	0.0604
2	20.8	27.6	189	24.2	0.0360
3	24.8	26.5	48	25.65	0.0354
				$\bar{x}$ = 21.77 ;	$\bar{y}$ = 0.0439

[a]Adapted from Table 17 in Randall (1962). Randall (1968) gives for this stock a value of L_{max} = "20 inches", hence $L_{(\infty)}$ = 20·2.54/0.95 = 53.5 cm.

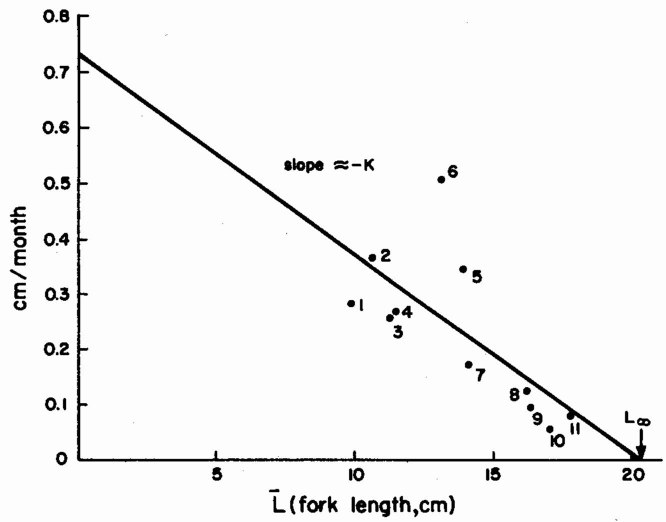

Fig. 4.6. Estimation of growth parameters for the ocean surgeon fish *(Acanthurus bahianus)* off the Virgin Islands by means of a Gulland and Holt plot (based on data in Table 4.5 and Example 4.4).

tion with the means of all $\bar{L}^D$ values ($\bar{x}$) and of all $\frac{L_2^D - L_1^D}{t_2 - t_1}$ values ($\bar{y}$) to obtain an estimate of K through

$$K \approx \frac{\bar{y}}{(L_\infty^D - \bar{x}) \cdot D} \qquad \ldots 4.36)$$

This method, called a "forced" Gulland and Holt plot, allows the estimation of K even when only *one* pair of x and y values is available.

Program FB 5 provides estimation of L_∞ and K, or W_∞ and K given appropriate data (as exemplified in Tables 4.5 and 4.6 and Fig. 4.8). When values of $L_{(\infty)}$, or of $W_{(\infty)}$ are supplied, only K is estimated (Examples 4.4 and 4.5).

Care should be taken, when using tagging data in conjunction with a Gulland and Holt plot, to identify and reject those data pertaining to fish whose growth was severely reduced or halted, e.g., as a result of tagging wounds. It is generally necessary to draw a scattergram prior to all calculations to identify such values of x and y (see Fig. 4.7 for an example). For this purpose, Program FB 5 has been given a routine which provides for the output of the x and y values.

The Munro plot

Munro (1982) suggested that

$$\log_e (L_\infty - L_a) - \log_e (L_\infty - L_b) = K (b - a) \qquad \ldots 4.37)$$

which becomes, in the notation used here, and in terms of the generalized VBGF

$$\ln (L_{(\infty)}{}^D - L_1{}^D) - \ln (L_{(\infty)}{}^D - L_2{}^D) = KD (t_2 - t_1) \qquad \ldots 4.38)$$

Given a value of D and trial values of $L_{(\infty)}$, this equation can be used to calculate single values of K (one for each triplet of L_1, L_2 and time values). The calculated values of K are close to each other when an optimal value of $L_{(\infty)}$ has been selected, and differ widely from each other when the selected value of $L_{(\infty)}$ is too high or too low.

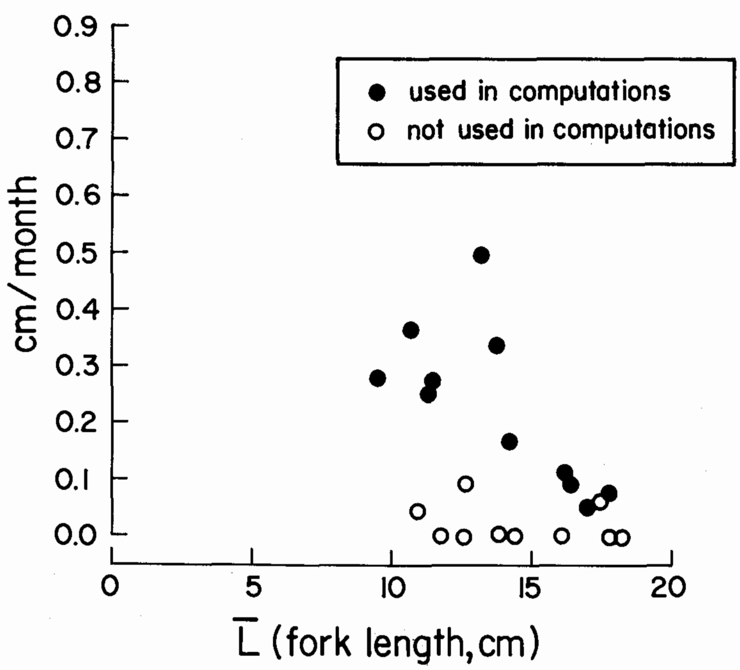

Fig. 4.7. Scattergram of growth increment for ocean surgeon fish *(Acanthurus bahianus)*, as obtained from tagging data (the selection of points used was done using a rigorous criterion, see Table 4.5).

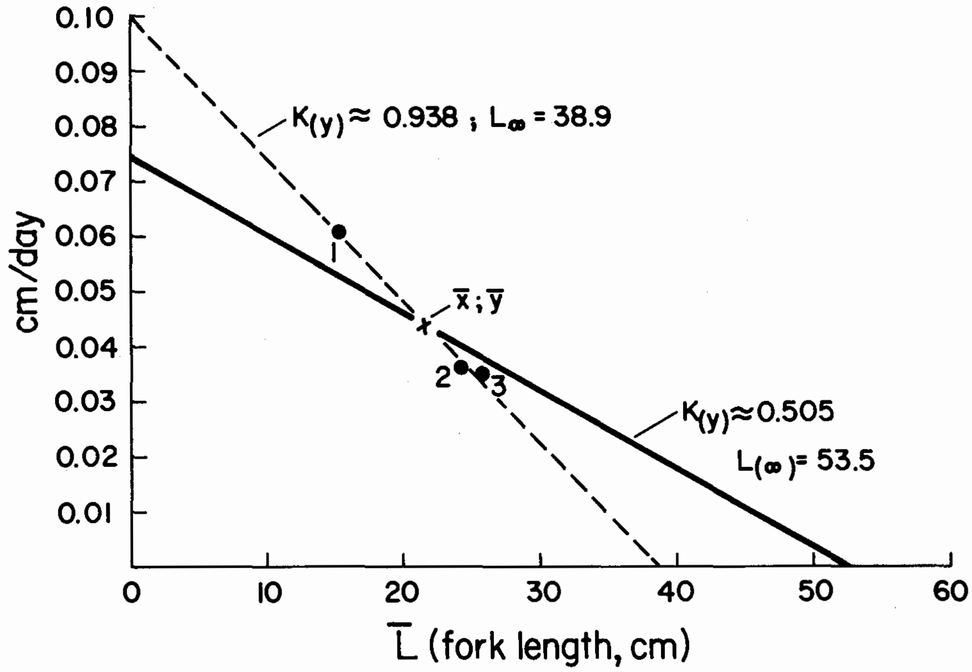

Fig. 4.8. Gulland and Holt plot (dotted line) and "forced" Gulland and Holt plot (solid line) for the Queen parrot fish *(Scarus vetula)* off the Virgin Islands (based on data in Table 4.6 and Example 4.5).

Thus, by calculating, for a given value of $L_{(\infty)}$, the coefficient of variation of the K-values (C.V. of K = $\frac{\text{standard deviation of the K-values}}{\text{mean value of K}}$), one may select by trial and error the value of $L_{(\infty)}$ which produces the lowest coefficient of variation for a given set of data. Program FB 6 (Munro plot) can be used for this purpose (see Table 4.5, Example 4.6, Fig. 4.9).

This method resembles the (forced) Gulland and Holt plot in that data for unequal time intervals can be used, e.g., tagging data. It has, however, the distinct advantage over the Gulland and Holt plot of providing accurate solutions (K values) irrespective of the length of the time interval(s) ($t_2 - t_1$ values).

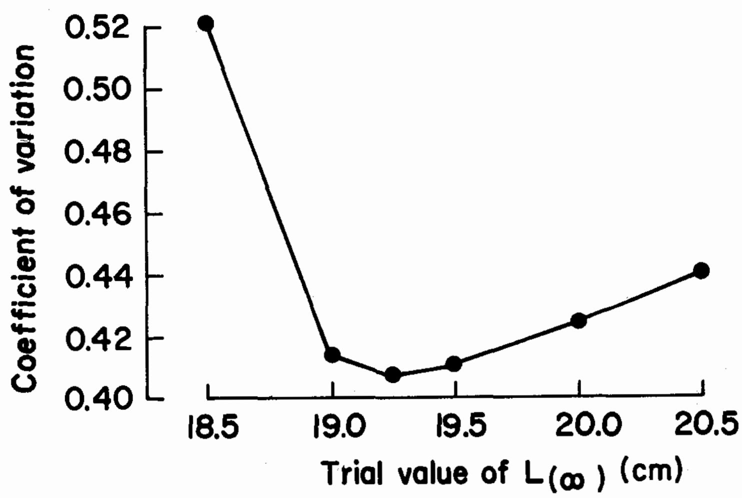

Fig. 4.9. Graph showing how the coefficient of variation (C.V.) of the K-values obtained from a Munro plot depends on the selected value of $L_{(\infty)}$ (based on data in Table 4.5 and Example 4.6).

Alternatively, when a value of L_∞ is reliably known (e.g., as obtained by the procedure outlined above), single values of K can be output (see Table 4.5) which can be compared and/or plotted against any variable likely to affect the growth of individual fish (e.g., mean water temperature during time at large).

Fitting seasonally oscillating length-growth data

In sub-tropical waters, and even more so in temperate waters, the growth of fish is fastest in summer time when temperatures are highest, and slowest in winter time when temperatures are lowest, the growth oscillation roughly following a sine wave curve of period one year (Fig. 4.10).

The inclusion of a sinusoid element of period one year into the VBGF has, therefore, the effect of considerably improving the fit of a growth curve and the accuracy of estimated values of the growth parameters in cases of growth seasonality (Pauly and Gaschütz 1979; Gaschütz et al. 1980).

The "seasonalized" version of the generalized VBGF has the form

$$L_t^D = L_\infty^D \left(1 - e^{-[KD(t - t_o) + C \frac{KD}{2\pi} \sin 2\pi (t - t_s)]}\right) \qquad \ldots 4.39)$$

Where L_∞, D, K and t_o are parameters of the "unseasonalized" VBGF while C expresses the amplitude of the growth oscillations and t_s the start of the sinusoid growth oscillations with respect to $t = 0$.

The value of C is defined such that, if $C = 1$, the growth rate (dl/dt) is zero exactly once a year.[a] Values of $0 < C < 1$ indicate a slowing down of the growth rate in winter time without dl/dt ever reaching zero, while $C = 0$, finally corresponds to the unseasonalized VBGF. The para-

[a]Values of $C > 1$ do not imply that the length of fish is reduced in winter, but rather that the period of no-growth lasts over several weeks or months. This case should not occur in the tropics, however.

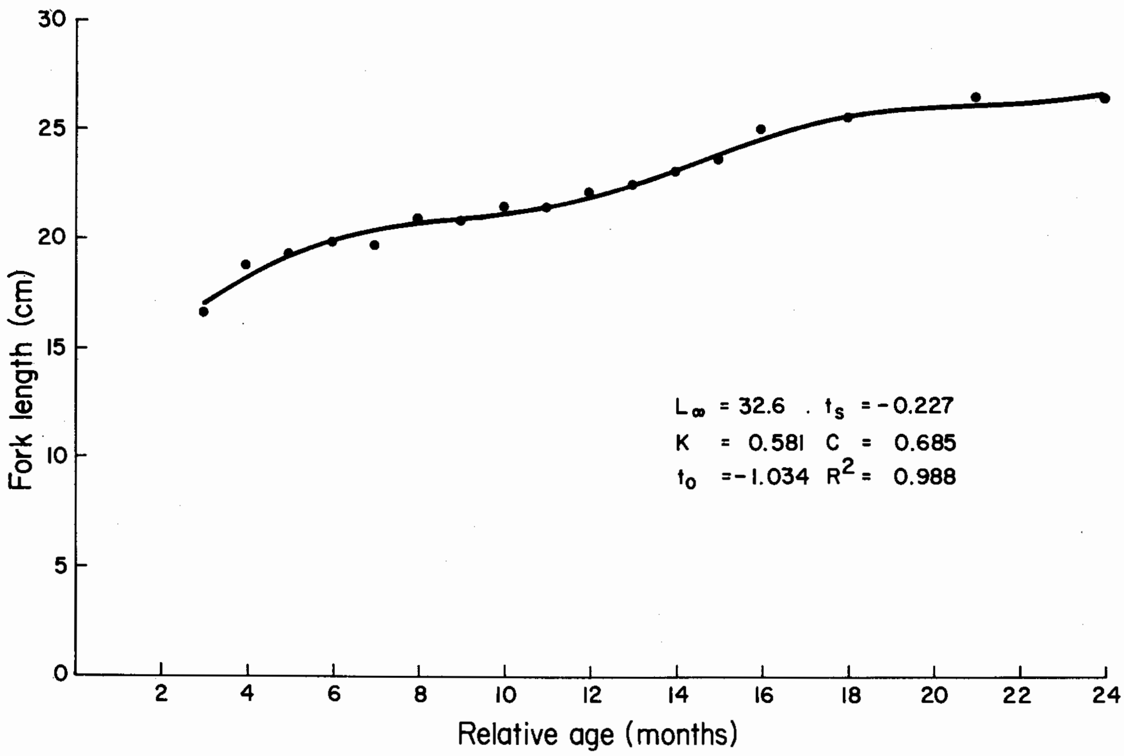

Fig. 4.10. Seasonally oscillating growth of the halfbeak *(Hemirhamphus brasiliensis)* off Florida (based on data in Table 4.7 and Example 4.7).

meter t_s is defined such that $t_s + 0.5$ = "winter point", i.e., the time of the year when growth is slowest.

Given values of $L_{(\infty)}$, D and a set of seasonally oscillating length-at-age data, the parameters K, C, t_o and t_s of equation (4.39) can be easily estimated from a multiple linear regression of the form

$$y = a + b_1x_1 + b_2x_2 + b_3x_3 \qquad \ldots 4.40)$$

where $y = \ln(1 - L_t^D/L_\infty^D)$ ... 4.41)

$x_1 = t$ (age must be always expressed in years) ... 4.42)

$x_2 = \sin 2\pi t$ ... 4.43)

and $x_3 = \cos 2\pi t$ ... 4.44)

and where the parameters K, t_o, C and t_s are estimated from the relationships

$$a = KDt_o \qquad \ldots 4.45)$$

$$b_1 = -KD \qquad \ldots 4.46)$$

$$b_2 = -KD\frac{C}{2\pi}\cos 2\pi t_s \qquad \ldots 4.47)$$

$$b_3 = KD\frac{C}{2\pi}\sin 2\pi t_s \qquad \ldots 4.48)$$

and $t_s = \{\arctan(-b_3/b_2)\}/2\pi$ ... 4.49)

The only parameters which cannot be estimated directly from the seasonally oscillating growth data are $L_{(\infty)}$ and D. The input value of $L_{(\infty)}$, however, can be improved by means of the same trial and error techniques suggested for the von Bertalanffy and the Munro plots, because Program FB 7 has a routine for computing R^2 (multiple coefficient of determination, analogous to r^2) the value of which may be maximized by means of a few plots with different estimates of $L_{(\infty)}$ (see Table 4.7, Example 4.7 and Fig. 4.11). Hoenig and Choudary (1983) give a method to derive standard errors of the parameters of equation (4.39).

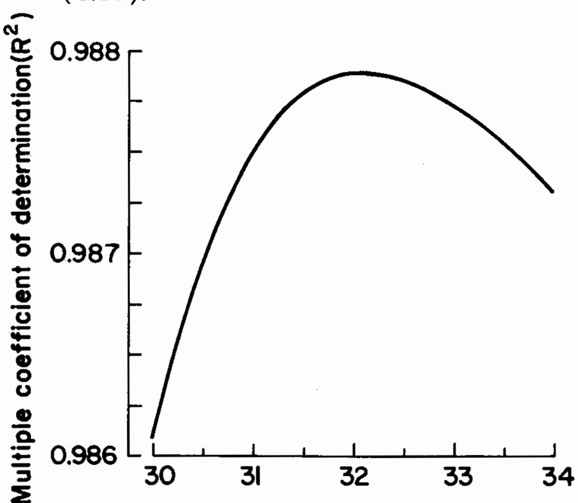

Fig. 4.11. Graph showing how an optimal value of $L_{(\infty)}$ can be selected when fitting seasonally oscillating length-growth data (based on data in Table 4.7 and Example 4.7).

Table 4.7. Seasonal growth of halfbeak *(Hemirhamphus brasiliensis)* off Western Florida, U.S.A.[a]

Relative age in months	FL (cm)	Relative age in months	FL (cm)
3	16.8	12	22.2
4	18.9	13	22.5
5	19.4	14	23.2
6	20.0	15	23.6
7	19.8	16	25.0
8	21.0	18	25.5
9	20.8	21	26.4
10	21.5	24	26.4
11	21.5	—	—

[a]As read off Fig. 5 in Berkeley and Houde (1978), who also give 31 cm for FL_{max}.

Program FB 7, as opposed to the other programs for estimating the parameters of the VBGF, cannot be used to fit weight growth data, even after conversion of W to $W^{1/b}$, because weight oscillations have in fish a structure different from that of length oscillations (see Shul'man 1974).

Extended Gulland and Holt plot

The seasonally oscillating growth model presented above (equation 4.39) is very sensitive, even to small seasonal oscillations. Using this model, growth oscillations have been demonstrated using data previously thought to depict growth patterns unaffected by the relatively small oscillations of environmental factors that occur in the tropics (Pauly and Ingles 1981). For this reason, it becomes necessary to consider growth oscillations not only with regard to size-at-age data, but also with regard to size increment data (i.e., tagging data), which have been frequently used to estimate the growth parameters of tropical fish.

The method proposed here is a modification of the Gulland and Holt plot, discussed earlier in this chapter. The new method may be called "extended Gulland and Holt plot"; it consists of extending the earlier method

$$\frac{L_2{}^D - L_1{}^D}{t_2 - t_1} = a + bX \qquad \ldots 4.50)$$

where b = —KD and x = $(L_1{}^D + L_2{}^D)/2$ into a multiple regression of the form

$$y = a + b_1\, x_1 + b_2\, x_2 \qquad \ldots 4.51)$$

where $y = (L_2{}^D - L_1{}^D)/(t_2 - t_1)$, and $x_1 = (L_1{}^D + L_2{}^D)/2$, as in the Gulland and Holt plot, and where x_2 is the value, during the time $t_1 - t_2$, of the environmental factor most likely to affect the growth of the fish while at large. (Obviously, the expression may be extended to any number of additional terms, up to $b_n\, X_n$, but this will not be investigated here.)

As shown in Fig. 4.12, the amplitude of seasonal growth oscillations in different fishes is extremely well correlated with the difference between annual minimum and maximum temperature of the water masses they inhabit, for which reason the most meaningful factor to insert for X_2 in expression (4.51) is the average temperature encountered by the fishes while at large (between times t_1 and t_2).

Thus, the model becomes

$$\frac{L_2{}^D - L_1{}^D}{t_2 - t_1} = a + b_1 \left(\frac{L_1{}^D + L_2{}^D}{2}\right) + b_2 T \qquad \ldots 4.52)$$

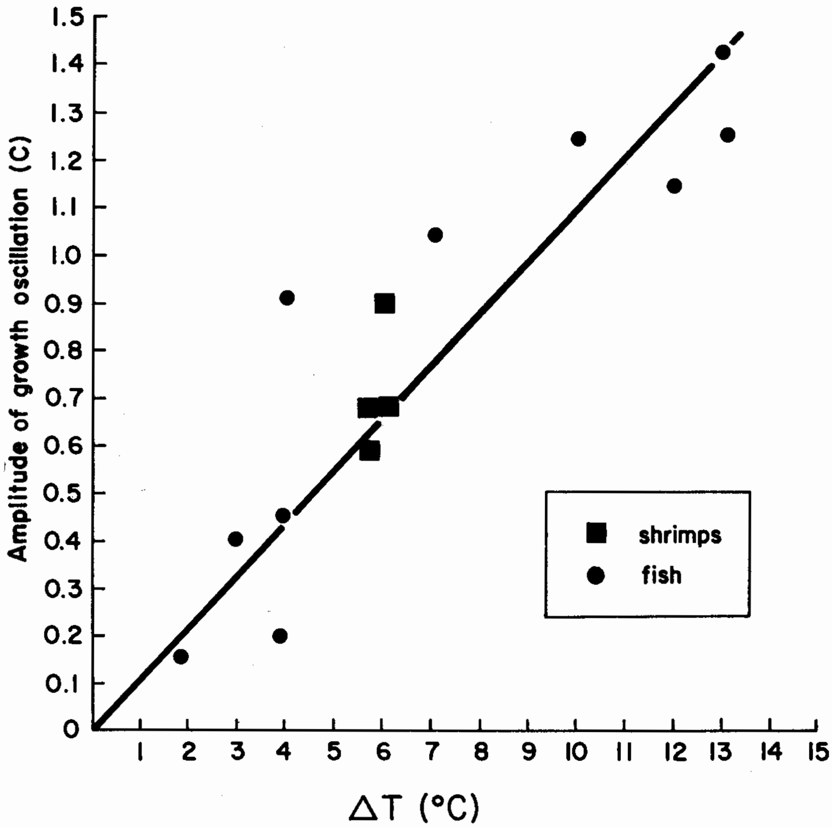

Fig. 4.12. Relationship between the amplitude of seasonal growth oscillations (C) of fish and shrimps and the difference between highest and lowest mean monthly temperature of their habitats (ΔT). Adapted from Pauly et al. (in press).

where T is the mean environmental temperature in °C during an interval t_1 to t_2. From this, the value of L_∞ corresponding to the mean annual temperature ($\bar{T}$) (hence, to a value of L_∞ unaffected by temperature fluctuations) can be estimated as:

$$L_\infty = \left(\frac{a + (b_2 T_m)}{-b_1} \right)^{1/D} \qquad \ldots 4.53)$$

while K and C can be estimated from

$$K = -b_1/D \qquad \ldots 4.54)$$

and

$$C = \frac{b_2 (T_s - T_w)}{2 [a + (b_2 \bar{T})]} \qquad \ldots 4.55)$$

respectively, T_s ("summer") being the highest and T_w ("winter") the lowest mean monthly temperature of the water body in question.

The method, as might be seen from Example 4.8, is extremely sensitive and can detect and quantify temperature effects that are extremely slight.

In analogy to the "forced Gulland and Holt plot", the method can also be used to estimate K (while accounting for seasonal growth oscillations) with a forcing value of $L_{(\infty)}$, using

$$K \approx [a + (b_2 T_m)]/L_{(\infty)}{}^D \qquad \ldots 4.56)$$

(See Example 4.8.).

GROWTH: A CONCLUDING PROGRAM

More methods suitable to estimate growth parameters by means of HP 67/97 calculators are available, especially from the HP "Users Library". The six methods proposed here are quite sufficient, however, for most problems and this chapter concludes with a straightforward, but hopefully helpful program.

Program FB 9 simply gives solutions for the generalized versions of the VBGF and their derivatives and also estimates the parameters d and D from equations (4.8) and (4.9). Table 4.8 gives an overview of the various output values that are calculated, given an appropriate set of values for the parameters needed for the calculation (see Examples 4.9 and 4.10).

Table 4.8. Constants to be stored for each of the solutions of the generalized von Bertalanffy Growth Formula (see Program FB 9).

		Constants required in stores							
Label	Values estimated	L_∞	W_∞	K	D	t_o	b	Input	Output
A	length at a given age	X	—	X	X	X	—	t	L_t
B	weight at a given age	—	X	X	X	X	X	t	W_t
C	age at a given length	X	—	X	X	X	—	L_t	t
c	age at a given weight	—	X	X	X	X	X	W_t	t
E	t_o for given length and age[a]	X	—	X	X	—	—	L_t, t	t_o
e	t_o for given weight and age[a]	—	X	X	X	—	X	W_t, t	t_o
a	length at inflexion point of curve[b]	X	—	X	X	—	—	—	L_i
b	weight at inflexion point of curve	—	X	X	X	—	X	—	W_i
D	growth rate at a given length	X	—	X	X	—	X	L_t	dl/dt
d	growth rate at a given weight	—	X	X	X	—	X	W_t	dw/dt
7	values of d and D	—	—	—	—	—	—	W_{max}[c]	d, D
	Stores:	A	B	1	D	O	E		

[a]The values of t_o may be summed up (Σ+), then averaged ($\bar{x}$).
[b]Applicable only when $D < 1$.
[c]W_{max} must be expressed in grams.

This program, although consisting of very simple steps, can help save a considerable amount of time to whomever has to draw various growth and related curves.

Recommended reading: The literature on fish growth is immense, and a list of recommended reading on this subject is necessarily highly subjective. Nevertheless, here are some useful references: von Bertalanffy (1938), Beverton and Holt (1959), Cushing (1981), Taylor (1962), Pannella (1971), Fryer and Iles (1972), Weatherley (1972), Bagenal (1974), Shul'man (1974), Ricker (1975, Chapter 9), Lowe-McConnell (1975, Chapter 9), Jones (1976a), Ricker (1979), Brothers (1980) and even Pauly (1981).

Suggested research topics: Estimate growth parameters of commercially exploited fishes, and of little-investigated groups (e.g., coral reef fish). Compare growth curves obtained with the special VBGF with growth curves obtained using the generalized VBGF, especially in tuna. Estimate the age of fish by means of daily rings in their otoliths (see Brothers 1980). Assess the intensity of seasonal growth oscillations in tropical fish, and establish the cause for these oscillations.

Reanalyze previously published length-frequency data (or data on file somewhere) by new methods (see, e.g., Pauly and David 1981) and use the resulting growth prameters to derive growth-related parameters (e.g., mortality rates; see next chapter).

EXAMPLE 4.3

Estimation of L_∞ and K for *Thunnus albacares* off Senegal by means of a Ford-Walford plot, special and generalized VBGF.

Data from Table 4.4

Computations

Case I, with D = 1

1) Read sides 1 and 2 of Program FB 4

2) Keystrokes

35 ↑ 1 f a 55 A 75 A 90 A 105 A 115 A

	Keystrokes	Results	
3) Compute r^2, K and L_∞	E	0.996	(r^2)
		0.150	(K)
		186.6	(L_∞)

Case II, with D = 0.47*

4) Keystrokes

35 ↑ .47 f a 55 A 75 A 90 A 105 A 115 A

5) Compute r^2, K and L_∞	E	0.998	(r^2)
		0.583	(K)
		153.9	(L_∞)

Note the slight improvement of the goodness of fit (0.998 > 0.996), the higher value of K and the lower value of L_∞ ($\approx L_{max}$ = 146.5 in Postel 1955) resulting from the use of the generalized VBGF. See Fig. 4.5 for a view of the differences between the special and generalized VBGF.

*Obtained from W_{max} = 60 kg and equation 4.10 (see Fig. 4.1 and Program FB 9).

EXAMPLE 4.4

Using a Gulland and Holt plot to estimate L_∞ and K for ocean surgeon fish *(Acanthurus bahianus)* from the Virgin Islands.

Data from Table 4.5

Computation

1) Read sides 1 and 2 of Program FB 5.

2) Keystrokes

1 f a 9.7 ↑ 10.2 ↑ 53 A 10.5 ↑ 10.9 ↑ 33 A 10.9 ↑ 11.8 ↑ 108 A 11.1 ↑ 12 ↑ 102 A 12.4 ↑ 15.5 ↑ 272 A 12.8 ↑ 13.6 ↑ 48 A 14 ↑ 14.3 ↑ 53 A 16.1 ↑ 16.4 ↑ 73 A 16.3 ↑ 16.5 ↑ 63 A 17 ↑ 17.2 ↑ 106 A 17.7 ↑ 18 ↑ 111 A

3) Calculate r^2, K and L_∞

	Keystrokes	Results	
	E	0.496	(r^2)
		0.001	(K)
		20.336	(L_∞)
4) Putting K on an annual basis	X ⇋ Y	0.001	
	365 x	0.432	(K)

Hence, the growth parameters are L_∞ = 20.4 and K = 0.432 (see Fig. 4.6). For plotting the data and results on a graph (such as Figs. 4.6, 4.7) press C; the procedure is then as follows (data of Table 4.6):

Keystrokes:	Output:	$\bar{L}$	$\Delta L/\Delta t$	i
14 ↑ 16.9 ↑ 48 A		15.45	0.060	1
20.8 ↑ 27.6 ↑ 189 A		24.20	0.036	2
24.8 ↑ 26.5 ↑ 48 A		25.65	0.035	3
etc.		. . .	. . .	. . .

The intercept and slope of the regression line are in STO A and STO B, respectively, and may be recalled to trace the line.

EXAMPLE 4.5

Using a "forced" Gulland and Holt plot to estimate K when a value of L_{max} and growth increment data are available.

Tagging data from Table 4.6. Also, Randall (1968) gives for the fish in question a value of L_{max} = "20 inches".

Computations

1) Read sides 1 and 2 of Program FB 5.

2) Estimation of $L_{(\infty)}$, in cm

Keystrokes	Results	
20 ↑		
0.95 ÷	21.053	
2.54 x	53.474	($L_{(\infty)}$)

3) Estimation of K

Keystrokes:	Results	
1 f a 14 ↑ 16.9 ↑ 48 A 20.8 ↑ 27.6 ↑ 189 A 24.8 ↑ 26.5 ↑ 48 A 53.5 f c	0.001 (rounded up)	(K)

4) Putting K on an annual basis: 365 x — 0.505 (K)

Hence, the growth parameters are $L_{(\infty)} \approx 53.5$ cm and $K \approx 0.505$. See Example 4.6 on how to draw the graph.

EXAMPLE 4.6

Calculating values of K, and using these to improve a first trial value of $L_{(\infty)}$ for ocean surgeon fish *(Acanthurus bahianus)* by means of a Munro plot.

Data from Table 4.5

Computations

1) Read side 1 of Program FB 6.

2) Select trial value of $L_{(\infty)}$, e.g., as obtained from a Gulland and Holt plot; try $L_{(\infty)}$ = 20 cm.

3) Keystrokes

   20 ↑ 1 f a 9.7 ↑ 10.2 ↑ 53 A 10.5 ↑ 10.9 ↑ 33 A 10.9 ↑ 11.8 ↑ 108 A 11.1 ↑ 12 ↑ 102 A 12.4 ↑ 15.5 ↑ 272 A ↑ 12.8 ↑ 13.6 ↑ 48 A 14 ↑ 14.3 ↑ 53 A 16.1 ↑ 16.4 ↑ 73 A 16.3 ↑ 16.5 ↑ 63 A 17 ↑ 17.2 ↑ 106 A 17.7 ↑ 18 ↑ 111 A

4) Calculate mean value of K and C.V.

Keystrokes	Results	
E	0.448	($\overline{K}$)
	0.425	(C.V.)

5) Compute $\overline{K}$ and C.V. for $L_{(\infty)}$ = 18.5, 19.0, 19.5, 20.5 and plot C.V. values. The results should look as in Fig. 4.9, which allows for an estimate of best $L_{(\infty)}$ (hence, L_∞) = 19.25, corresponding to $\overline{K}$ = 0.532 and C.V. 0.408.

6) To obtain single values of K, select a good value of $L_{(\infty)}$ and perform:

Keystrokes	Results	
19.25 ↑ 1 f a fSTFO ↑ 9.7 ↑ 10.2 ↑ 53A	0.370	(K_1)
10.5 ↑ 10.9 ↑ 33 A	0.518	(K_2)
10.9 ↑ 11.8 ↑ 108 A	0.385	(K_3)
etc. (see Table 4.5, right column)		

The estimates of K may then be plotted against variables likely to influence growth rate (e.g., water temperature while at large).

EXAMPLE 4.7

Determination of growth parameters from seasonally oscillating length-at-age data for the halfbeak *(Hemirhamphus brasiliensis)*.

Data from Table 4.7 (and using D = 1)

Computations

1) Read sides 1 and 2 of Program FB 7 (a).

2) Compute preliminary value of $L_{(\infty)}$ from L_{max} = 31 cm.

Keystrokes	Results	
31 ↑		
.95 ÷	32.6	($L_{(\infty)}$)

3) Initialize and enter length-at-age data

Keystrokes

10 ↑ 5y^x f a 3 ↑ 12 ÷ 16.8 ↑ 32.6 A 4 ↑ 12 ÷ 18.9 ↑ 32.6 A 5 ↑ 12 ÷ 19.4 ↑ 32.6 A 6 ↑ 12 ÷ 20 ↑ 32.6 A 7 ↑ 12 ÷ 19.8 ↑ 32.6 A 8 ↑ 12 ÷ 21 ↑ 32.6 A 9 ↑ 12 ÷ 20.8 ↑ 32.6 A 10 ↑ 12 ÷ 21.5 ↑ 32.6 A 11 ↑ 12 ÷ 21.5 ↑ 32.6 A 12 ↑ 12 ÷ 22.2 ↑ 32.6 A 13 ↑ 12 ÷ 22.5 ↑ 32.6 A 14 ↑ 12 ÷ 23.2 ↑ 32.6 A 15 ↑ 12 ÷ 23.6 ↑ 32.6 A 16 ↑ 12 ÷ 25 ↑ 32.6 A 18 ↑ 12 ÷ 25.5 ↑ 32.6 A 21 ↑ 12 ÷ 26.4 ↑ 32.6 A 24 ↑ 12 ÷ 26.4 ↑ 32.6 A

4) Read sides 1 and 2 of Program FB 7 (b).

5) Perform:

Keystrokes	Results	
A	0.98783	(R^2)
E	0.58094	(K · D)
	–1.03386	(t_o)
	–0.27326	(old t_s)
	–0.68498	(–C)

6) Adjust t_s and C values (see User's Instruction FB 7 (b))

Keystrokes	Results	
CHS	0.68498	(C)
0.273 CHS	–0.273	(old t_s)
0.5 +	0.227	(new t_s)

7) Repeat steps 3-6 with different values of $L_{(\infty)}$ and plot resulting R^2 values against the $L_{(\infty)}$. A figure similar to Fig. 4.11 should emerge from which the best value of L_∞ can be selected. (The best value of $L_{(\infty)}$ happens to 32.6 cm.)

8) To trace the growth curve follow User's Instruction FB 7 (b).

EXAMPLE 4.8

Estimating the growth parameters and the seasonal growth oscillations of *Acanthurus bahianus* from the Virgin Islands.

Data from Table 4.5

1) Read sides 1 and 2 of Program FB 8.

2) D is set equal to unity.

3) Keystrokes

1 f a 9.7 ↑ 10.2 ↑ 53 ↑ 27.48 A 10.5 ↑ 10.9 ↑ 33 ↑ 28.61 A 10.9 ↑ 11.8 ↑ 108 ↑ 27.79 A 11.1 ↑ 12 ↑ 102 ↑ 29.29 A 12.4 ↑ 15.5 ↑ 272 ↑ 28.37 A 12.8 ↑ 13.6 ↑ 48 ↑ 28.89 A 14 ↑ 14.3 ↑ 53 ↑ 27.55 A 16.1 ↑ 16.4 ↑ 73 ↑ 27.99 A 16.3 ↑ 16.5 ↑ 63 ↑ 27.54 A 17 ↑ 17.2 ↑ 106 ↑ 28 A 17.7 ↑ 18 ↑ 111 ↑ 28.3 A

4) Estimate R^2, intercept and slopes

	Keystrokes	Results	
	E	0.648	(R^2)
		−0.065	(a)
		0.001	(b_1)
		0.003	(b_2)

5) Calculate value of L_∞ corresponding to the mean annual temperature ($\overline{T}$) and K

	Keystrokes	Results	
	28.5 C ($\overline{T}$)	22.079	(L_∞)
		0.001	(K_d)
to put value of K on annual basis do:	365 x	0.387	(K_y)

6) To estimate value of C, enter T_s, T_w and $\overline{T}$

	Keystrokes	Results	
	29.4 ↑		
	27.2 ↑		
	28.5 f c	0.146	(C)

7) To estimate value of K based on a forcing value of asymptotic length do

	Keystrokes	Results	
(value of $L_{(\infty)}$ in Example 4.4 =)	20.4 ↑		
(T_m =)	28.5 f e	0.001	(K_d)
to put value of K on an annual basis do:	365 x	0.419	(K_y)

This last result (K = 0.419) corresponds well with that obtained with the same data used in conjunction with a simple Gulland and Holt plot (see Example 4.4, where a value of K = 0.432 was estimated for L_∞ = 20.4.)

5. Total, Natural and Fishing Mortalities

INTRODUCTION

In fishery biology, the most useful manner of expressing the decay (= decrease) through time of a group of fish born at the same time (a cohort) is by means of "instantaneous" rates. These rates, of which there are three (Z, M, F), are defined by the following two expressions:

$$N_t = N_o \cdot e^{-Zt} \qquad \ldots 5.1)$$

where N_o is the (initial) number of fish at time zero, and N_t is the number of remaining fish at the end of time t; Z is the instantaneous rate of total mortality. An advantage of such decay rates is that they can be added or subtracted. Thus we have

$$Z = M + F \qquad \ldots 5.2)$$

where M is the instantaneous rate of natural mortality and F the instantaneous rate of fishing mortality. Obviously, when F = 0, Z = M, which means that natural and total mortality have the same value when there is no fishing, i.e., in an unexploited stock (Fig. 5.1).

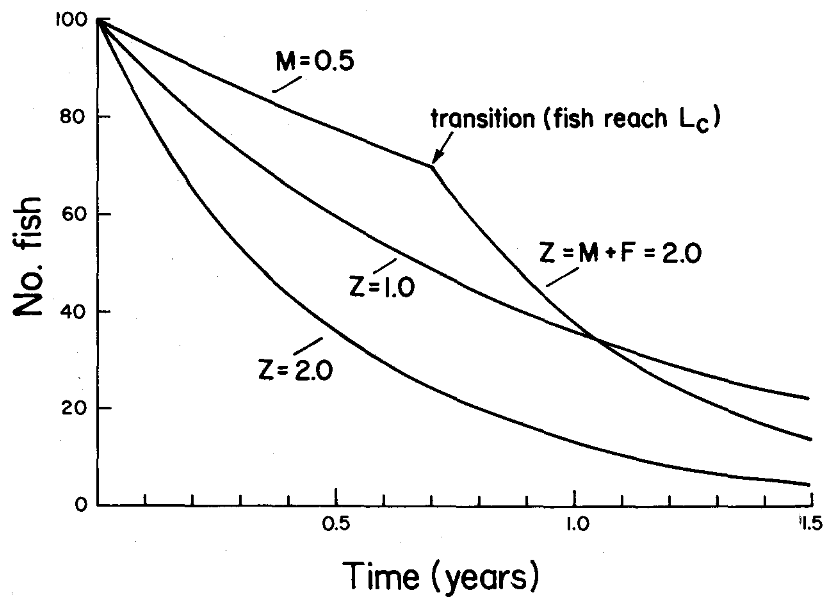

Fig. 5.1. Decrease of a cohort of 100 fish (initially), subjected to different levels of mortality; L_c = mean length at first capture.

Instantaneous rates (i.e., "exponential" rates) of mortality can be converted to the fraction surviving through equations such as

$$S = \frac{N_t}{N_o} \qquad \ldots 5.3)$$

where S is the fraction surviving after time t, while

$$A = 1 - S \qquad \ldots 5.4)$$

is the fraction of the stock dead after time t. Although used by a number of authors, percentage mortalities are not further discussed in this book, because they are too cumbersome to handle in comparison with instantaneous rates (see Beverton and Holt 1956, p. 68 for reasons).

Mortalities, whether expressed as instantaneous rates or as fractions, always refer to a certain period of time. Throughout this book, the *year* is used as the conventional unit, unless mentioned otherwise.

Fishery biologists have two main jobs as far as mortalities are concerned:

a) to estimate total mortality;
b) to split their estimates of total mortality where appropriate into separate estimates of natural and fishing mortalities.

A number of methods are proposed here by which these aims can be achieved, given suitable inputs.

Ecologists, on the other hand, will be pleased to know that Z, as defined here, is equivalent to the inverse of the mean age of the animals in a population (computed from the age when Z is more or less constant) and, hence, as shown by Allen (1971) equal to their "turnover rate", i.e., to the production/biomass ratio (P/B ratio) that is so difficult to estimate reliably using the various methods described in the ecological literature (e.g., Chapman 1968; Winberg 1971).

ESTIMATING TOTAL MORTALITY

Total mortality from the oldest animal in the catch

Following a number of earlier authors who had demonstrated the existence of a strong relationship between the longevity of fish (in the wild) and their mortality, Hoenig (1984) assembled data on a large number of aquatic animals (molluscs, fish and cetaceans) from which he derived the relationship

$$\ln Z = 1.44 - 0.984 \ln t_{max} \qquad \ldots 5.5)$$

where t_{max} is the maximum age (in years) observed in a given stock, and Z is defined as above.

Although the "fit" of equation (5.5) is rather good ($r^2 = 0.82$ for 130 data pairs), it should be realized, when using this equation, that the estimates of Z thus obtained are very approximate, possibly biased downward (J.M. Hoenig, pers. comm.) and should therefore be revised as additional information becomes available. Table 5.1 gives examples of the application of equation (5.5) which, given its simplicity, needs not be illustrated by a computational example.

When, in addition to t_{max} and t_c the size of the sample (n) from which t_{max} was determined is also known, it becomes possible to estimate Z and its standard error (s.e.$_{(Z)}$) from the relationships derived by Hoenig and Lawing (1982),

$$Z = \frac{1}{c_1 \cdot (t_{max} \cdot t_c)} \qquad \ldots 5.6)$$

and

$$s.e._{(Z)} = \sqrt{c_2 \cdot Z^2} \qquad \ldots 5.7)$$

where c_1 and c_2 are coefficients whose values depend on n (see Table 5.2).

Hoenig and Lawing (1982), whose paper should be consulted for the derivation of equations (5.6), (5.7) and of Table 5.2, stress that "fast growing, short-lived species with minimal variability in length about age are best suited for this method". This is so because in such cases, n, the sample size, is *not* the number of fish actually aged, but the number of fish from which a subsample, consisting of the largest fish was taken. Thus, if say, 200 fish have been inspected, from which the 20 largest were selected for aging, then the value of n will be 200, not 20 (this assumes, obviously that the oldest fish of the sample of 200 will be among the 20 largest). This feature appears particularly valuable in all those cases where fish must be aged by the tedious procedure of counting daily rings (Hoenig and Lawing 1982).

Table 5.1. Maximum observed size (L_{max}, W_{max}), maximum observed age (t_{max}) and estimated mortality (Z) for 12 coral reef fish of New Caledonia.[a]

Family	Species	L_{max} (standard length, in cm)	W_{max} (live weight, in g)	t_{max} (in years)	Z^b
Holocentridae					
	Adioryx spinifer	25.8	572	13	0.34
Serranidae					
	Epinephelus summana	20.8	263	16	0.28
Carangidae					
	Caranx ignobilis	76.4	10,765	9	0.49
Lutjanidae					
	Lutjanus argentimaculatus	60.7	5,870	18	0.25
	Lutjanus gibbus	37.0	1,735	18	0.25
	Lutjanus sebae	69.5	13,810	35	0.13
Pomadasyidae					
	Plectorhynchus chaetodonoides	43.1	2,715	21	0.21
	Plectorhynchus pictus	39.2	1,970	11	0.40
	Pomadasys hasta	31.8	87.3	12	0.37
Lethrinidae					
	Lethrinus harak	24.3	450	15	0.29
	Lethrinus obsoletus	25.0	501	14	0.31
	Monotaris grandoculis	39.2	2,730	11	0.40

[a]Size and age data adapted from Loubens (1980, Table VI); the values of t_{max} are based on limited samples (sample sizes not given) which, however contained large-sized adults.

[b]Estimated from Equation (5.5).

Table 5.2. Table of coefficients for estimating Z and its standard error using equations (5.6) and (5.7) (from Hoenig and Lawing 1982).

n^a	c_1	c_2	n^a	c_1	c_2
5	0.583	0.416	110	0.200	0.050
10	0.405	0.196	120	0.196	0.048
15	0.344	0.142	140	0.190	0.045
20	0.311	0.117	160	0.185	0.043
25	0.290	0.102	180	0.181	0.041
30	0.274	0.091	200	0.178	0.040
35	0.263	0.084	250	0.171	0.037
40	0.253	0.078	300	0.165	0.035
45	0.245	0.074	350	0.161	0.033
50	0.239	0.070	400	0.157	0.032
55	0.233	0.067	450	0.155	0.031
60	0.228	0.064	500	0.152	0.030
65	0.224	0.062	600	0.148	0.028
70	0.220	0.060	700	0.144	0.027
75	0.217	0.058	800	0.142	0.026
80	0.214	0.057	900	0.139	0.025
90	0.208	0.054	1,000	0.137	0.025
100	0.204	0.052			

[a]Interpolate for intermediate values of n.

Table 5.3 gives values of Z and its standard error as obtained by application of equations (5.6) and (5.7); the method is also illustrated in Example 5.1.

Table 5.3. Maximum reported age and estimated total mortality of selected Brazilian freshwater (F) and marine fish (M).[a]

Family	Species	t_{max} (yr)	n	Location, sampling date(s)	Author(s)	Estimated Z	s.e.(Z)
Auchenipteridae							
	Trachychorystes galeatus ♀	3.5	83	Banabuiú Reservoir	Nomura	1.35	0.32
	Trachychorystes galeatus ♂	3.5	99	Caera State, 1971 (F)	et al. (1976)	1.40	0.32
Characidae							
	Prochilodus scrofa ♀	13	451	Mossi Guassu River,	Godoy	0.50	0.09
	Prochilodus scrofa ♂	9	485	São Paulo State, 1947 (F)	(1959)	0.73	0.13
Sciaenidae							
	Plagioscion squamosissimus ♀	6	103	Amanari Reservoir,	Nomura and	0.82	0.19
	Plagioscion squamosissimus ♂	7	134	Caera State, 1960-2 (F)	Oliviera (1976)	0.74	0.16
	Micropogon furnieri ♀	6	229	Off Iguape, Caera	Rodrigues	0.96	0.19
	Micropogon furnieri ♂	7	115	State, 1966-7 (M)	(1968)	0.72	0.16
	Macrodon ancylodon ♀ & ♂	11	9,947	Off São Paulo, 1975-6 (M)	Lara (1951)	0.66	0.11

[a]Total mortality and its standard error estimated from equations (5.6) and (5.7), with t_c set at zero because very small fish were included in the catch samples.

Total mortality from the mean size in the catch

The following expression (Beverton and Holt 1957; Gulland 1969) can be used to estimate Z from the mean weight ($\overline{\overline{W}}$) of fish in the catch from a given population:

$$\overline{\overline{W}} = W_\infty \left\{ 1 - \frac{3Z \exp(-a)}{Z + K} + \frac{3Z \exp(-2a)}{Z + 2K} - \frac{Z \exp(-3a)}{Z + 3K} \right\} \qquad \ldots 5.8)$$

where $a = K \cdot (t_c - t_o)$, with K and W_∞ pertaining to the special VBGF (i.e., when D = 1) and where t_c is the mean age at first capture (corresponding to L_c as defined in Chapter 2) obtained by a given gear. Equation (5.8) it will be noted, can be solved for Z only iteratively (Program FB 10, Example 5.2). Also, the equation requires an estimate of t_o, which may sometimes be difficult to obtain.

Another equation, proposed by Beverton and Holt (1956), is more generally used to estimate Z from the mean size in the catch. When used in conjunction with the generalized VBGF, it has the form

$$Z = \frac{KD\,(L_\infty^D - \overline{L}^D)}{\overline{L}^D - L'^D} \qquad \ldots 5.9)$$

where $\overline{L}$ is the mean length of all fish $\geqslant L'$, the latter being (a length not smaller than) the smallest length of fish fully represented in the length-frequency data at hand. L' is always $> L_c$, as defined in Chapter 2, except in true cases of "knife-edge selection", where $L' = L_c$. [A method is given further below in connection with a discussion of length-converted catch curves to obtain reasonable estimates of L' from a set of length-frequency data.]

A sensitivity analysis of this widely-used equation is given in Appendix I; on the average, equation (5.9) gives results (values of Z) which are equal to those obtained with length-converted catch curves (see below).

Occasionally, data are available in the literature where the mean length has been computed from the whole range of length in the catch rather than from L′ upward. In such cases, minimum estimates of Z can still be obtained, using

$$Z_{min} = \frac{KD\,(L_\infty^D - \bar{\bar{L}}^D)}{\bar{\bar{L}}^D - L_c^D} \qquad \ldots 5.10)$$

where $\bar{\bar{L}}$ is the overall mean length and L_c is the 50% retention length. See Chapter 2 for various methods to compute L_c.

Another type of widely available data is mean weights of fish, as obtained by simply weighing ing a haul, counting the fish caught and dividing the weight by the number caught. Such values of $\bar{\bar{W}}$, however, do not represent the weight corresponding to a given value of $\bar{\bar{L}}$; rather, they are biased upward. This effect should partly offset the negative bias in equation (5.10) such that

$$Z \approx \frac{KD\,(W_\infty^{D/3} - \bar{\bar{W}}^{D/3})}{\bar{\bar{W}}^{D/3} - W_c^{D/3}} \qquad \ldots 5.11)$$

where W_∞ and W_c are the weights corresponding to L_∞ and L_c, respectively. It will be realized that this equation gives quite approximate results, and that, as in the case of equation (5.5), every effort should be made to revise the estimates of Z based on it as soon as additional information become available.

Example 5.3 presents applications of equations (5.9), (5.10) and (5.11).

Although computationally convenient, simple equations such as (5.9 to 5.11) have two disadvantages, one of them major. Equations (5.9 to 5.11) require estimates of L_c or L′; the first of these parameters involves either conducting selection experiments, or using shape measurements and the nomogram presented in Chapter 2. The second of these parameters, on the other hand, can be estimated from length-frequency data; this, however, involves plotting the data in a form akin to a length-converted catch curve, at which point it will be more appropriate to estimate Z from the catch curve itself (see below).

The major objection to the use of mean size data for estimating Z is, however, that one quite literally doesn't *see* what one is doing. While computation of one single value of Z from the mean of a wide range of sizes implies that mortality is constant, the assumption itself cannot be verified. The semi-graphical methods presented further below, particularly the length-converted catch curves, do allow verification of this assumption. Also, they allow the selection of data points to use in the estimation of Z, and hence the estimation of values of Z applying only to certain ranges of size something which cannot be done using summary statistics, such as mean lengths or mean weights. [Mean sizes can be used directly to draw inferences on the status of a stock or fishery without being expressed in terms of Z. Henderson (1972) provides a theoretical background for this approach which was applied to tropical fish by Ita (1980), but won't be discussed here.]

Estimation of Z from cumulative plots

When length-frequency data or catch-at-length data are available which were obtained over a period during which conditions can be considered constant, several methods can be used to estimate Z which are less crude than the ones presented above. The first of these was proposed by Jones (1981) to estimate Z/K; it is presented here, however, among methods for the estimation of Z because it led to another method, developed by Sparre (MS) which is closely related to Jones' method, but allows direct estimation of Z.

The basic equation in Jones' method, expressed in terms of the generalized VBGF, has the form of a linear regression,

$$\ln C\,(L_i, \infty) = a + \frac{Z}{KD} \cdot \ln\,(L_\infty^D - L_i^D) \qquad \ldots 5.12)$$

where $C(L_i, \infty)$ is the cumulative catch (computed from the highest length class with non-zero catch) corresponding to a given length class, and L_i is the lower limit of that length class, the ∞ symbol expressing that the catch considers a range from L_i to all larger sizes.

However, as shown in Fig. 5.2, the plot of the $\ln C(L_i, \infty)$ values on the $\ln(L_\infty^D - L_i^D)$ values is linear only over the central part of its range and deviates markedly from linearity when very large and very small fish are considered.

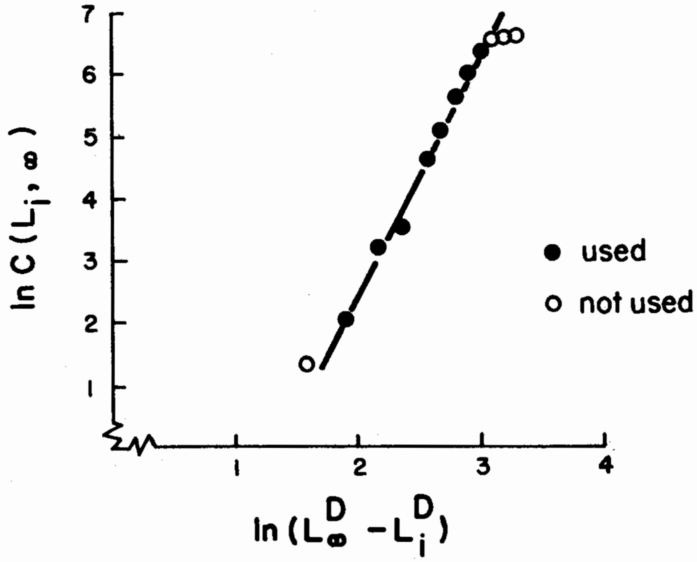

Fig. 5.2. Jones' cumulative plot for the estimation of Z/K (or Z), as applied to the data of Table 5.4. The points to be included in the regression are selected after transformation and plotting of the data (see Example 5.4).

Thus, when applying this method, it is necessary to draw a scattergram of the computed values and to select visually the points belonging to the straight segment of the plot (see Example 5.4). Sparre's modification of equation (5.12) resembles a catch curve (see below for definition) in that the ages (or relative ages) are used for the x-axis and that Z (or Z/K) is estimated from the slope of a descending series of points. The equation used has the form

$$\ln C(L_i, \infty) = a + bt' \qquad \ldots 5.13)$$

where $\ln C(L_i, \infty)$ is defined as above and t' is the (relative) age corresponding to L_i, while b, with sign changed, provides an estimate of Z (the relative ages are estimated through conversion from length to age) based on the straight part of the plot. A routine has been incorporated in Program FB 11 which produces values of $C(L_i, \infty)$ and t' such that a scattergram can be drawn, from which the values usable in the estimation of Z can be selected (see Fig. 5.3 and Example 5.5).

When K is not known, Sparre's method can still be used; in this case, a value of one (unity) has to be used instead of K, which results in the relative ages being defined as

$$t' = (t - t_o) \cdot K \qquad \ldots 5.14)$$

The slope (b in equation 5.13) will then be equal to Z/K.

Both Jones' and Sparre's methods are extremely ingenious methods which lead to exact values of Z or Z/K, given suitable data and appropriate selection of data points to be included in the regression. However, both methods give results which, because of the cumulation of the catches, are extremely sensitive to the values of the catches in the largest size groups, even when they are not included in the linear regression. Thus, these methods should not be used when the catch composition data used were obtained from gears that markedly select for or against very large fish.

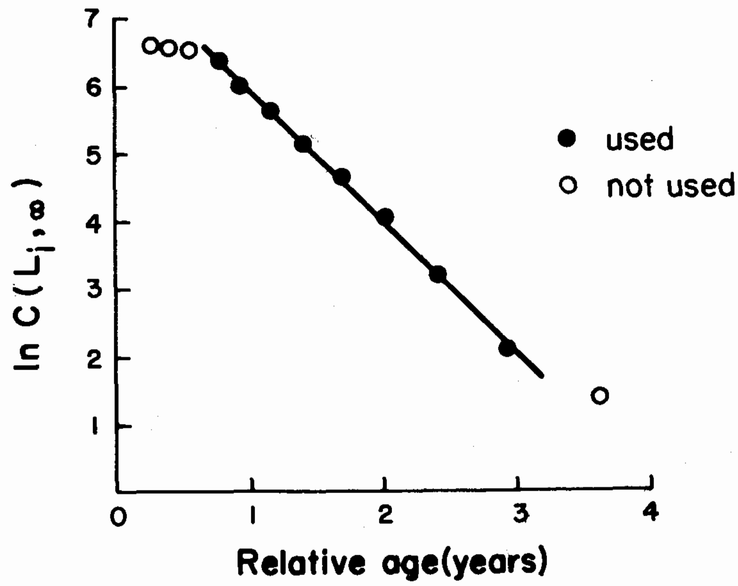

Fig. 5.3. Sparre's cumulative plot for the estimation of Z (or Z/K), as applied to the data of Table 5.4 (see Example 5.5).

Catch curves and length-converted catch curves

One of the methods most commonly applied in temperate waters to estimate the total mortality of fish is the "catch curve" method, which has been reviewed in Beverton and Holt (1956), Chapman and Robson (1960), Robson and Chapman (1961) and Ricker (1975, Chapter 2).

Essentially, the method consists of a plot of the natural logarithm of the number of fish in various age groups (N_t) against their corresponding age (t), or

$$\ln N_t = a + bt \qquad \ldots 5.15)$$

Z being estimated from the slope b, with sign changed, or the descending, right arm of the plot (Fig. 5.4).

The following assumptions are involved here:

1) Z is the same in all age groups used in the plot,
2) all age groups used in the plot were recruited with the same abundance (or the recruitment fluctuations have been small and of random character),
3) all age groups used in the plot are equally vulnerable to the gear used for sampling,
4) the sample used is large enough and covers enough age groups to effectively represent the average population structure over the period of time considered.

The authors of this method should be consulted for more detailed treatment of the assumptions involved in catch curves.

Often, in order to broaden the data base from which inferences are drawn (i.e., in order to meet assumption 4 above), the samples used for catch-curve analysis are constructed in three steps, as follows:

i) record the lengths of very large samples of fish,
ii) age a subsample of fish, and construct an "age-length key", and
iii) separate the large length-frequency sample into an age-frequency sample by means of the age-length key obtained in (ii).

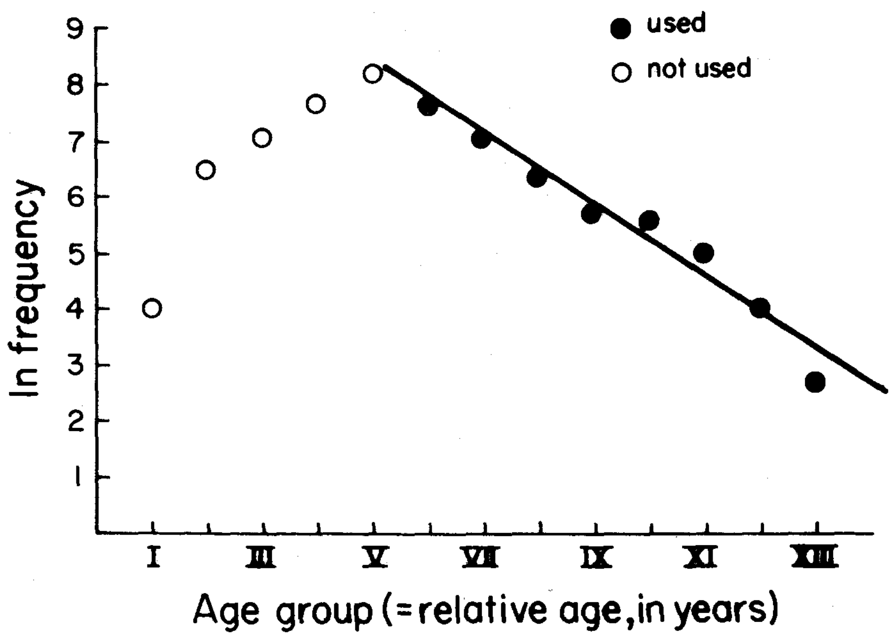

Fig. 5.4. Catch curve for red porgy *(Pagrus pagrus)* caught off North and South Carolina, U.S.A. The curve is based on 13,120 measured specimens, of which 222 were actually aged. Note slight non-linearity of curve which, on the average, suggests a value of Z = 0.65 (adapted, with modifications, from Manooch and Huntsman 1977, Fig. 3).

This indirect procedure was introduced by Fridrikson (1934) and is discussed in detail in Gulland (1966) and Allen (1966), and was applied by Manooch and Huntsman (1977) in their study of red porgy mortality (see Fig. 5.4). However, it has hardly ever been used in tropical waters, where the very few authors who have used catch curves have tended to construct them directly, based on relatively small samples of aged fish. As shown by Kimura (1977), there are several cases where this procedure is indeed more appropriate.

A major disadvantage of the age-structured catch curves represented by equation (5.15) is that they cannot be used in conjunction with animals that presently cannot be aged individually, such as shrimps, lobsters and some molluscs.

"Length-converted catch curves", as will be shown below, allow the use of catch curves with animals that cannot be aged; moreover, the method, being based solely on length-frequency samples, allows the use of large samples without construction of age-length keys.

The estimation of Z from a length-converted catch curve involves the following steps:

i) pooling of length-frequency samples to obtain a single, large length-frequency sample representative of the population for the period under consideration;
ii) construction of the catch curve proper, using the large sample in (i) and a set of growth parameters (see below);
iii) estimation of Z from the descending right arm of the catch curve.

Pooling of length-frequency samples (e.g., of monthly samples) over a longer period of time (at least one year) is particularly needed in short-lived fish and shrimps, because their whole population structure is affected by seasonal "pulses" of recruitment, generally one or two per year (Pauly and Navaluna 1983). Also, to prevent a single, larger (monthly) sample from unduly affecting the total (annual) sample, the various samples may be given the same weight, by conversion to percentages prior to adding to obtain a single overall sample.

There are many alternatives to a scheme where each sample is given the same weight. For example, it might be more appropriate to weigh the samples by the square root of their size when the fishery catch is not known, or by the catch when it is known. However, empirical studies concerning appropriate sample sizes and weighing factors for length-converted catch curves are still lacking. Table 5.5 is given here to suggest sample sizes which at present seem appropriate.

Table 5.4. Data for the estimation of Z/K and Z for the banded grouper *(Epinephelus sexfasciatus)* of the Visayan Sea, Philippines (from Pauly and Ingles 1981).[a]

Lower class limit (cm)	Midpoint of class (cm)	N^b
4	5	5
6	7	29
8	9	114
10	11	161
12	13	143
14	15	118
16	17	61
18	19	50
20	21	32
22	23	17
24	25	4
26	27	4

[a]To be used in conjunction with $L_\infty = 30.9$, $K = 0.51$ and $D = 1$.
[b]As obtained by pooling a number of samples representing a whole year.

Table 5.5. Criteria for assessing the suitability of length-frequency samples for estimating Z (modified from Munro and Thompson 1973).

Total sample size (no. fish)	Time (in months) over which data for total sample were accumulated[a]				
	1	2	4	6	12
1 — 99	0	0	0	0	0
100 — 499	0	0	1	2	2
500 — 999	1	1	2	3	4
1,000 — 1,499	1	2	3	4	5
1,500 — ∞	2	3	4	5	5+

0 = not usable; 1 = poor; 2 = fair; 3 = good; 4 = very good; 5 = excellent

[a]It is here assumed (1) that the samples cover a wide range of lengths, (2) that gear selection is accounted for and (3) that the sizes of the monthly samples are more or less equal if the total sample is accumulated over more than one month.

There are also several methods by which a length-converted catch curve may be constructed. However, they all must account for the fact that fish growth in length is not linear, but slows down as length and age increase. This slowing down has the effect that older *size groups* contain more age groups than do younger *size groups.* In other words, it takes larger fishes longer to "leave" a certain size group, they "pile-up" (Baranov 1918), or "stack-up" (van Sickle 1977) in the size classes pertaining to old, large, slow-growing fish. Correcting fôr this effect is rather straightforward, and three methods by which this can be achieved here will be discussed here.

The first approach, analogous to but improved upon those discussed in Ricker (1975, p. 33 and p. 60-64) and van Sickle (1977), consists of multiplying the number in each length class by the growth rate of the fish in that class. This results in a catch curve equation of the form

$$\log N_i \cdot (dl_i/dt) = a + bt_i' \qquad \ldots 5.16)$$

where dl_i/dt is the growth rate and t_i' the relative age corresponding to length class (i), respectively. In practice (dl_i/dt) can be estimated from the VBGF as the growth rate pertaining to the median length, or "midlength" of length class (i), while t' can be estimated as the relative age corresponding to the median of class (i) as estimated, using the appropriate growth parameters, through conversion using the VBGF. "Relative" ages are used here because using t_o (which leads to *absolute* ages) is not necessary in conjunction with catch curves, where Z is estimated from a *slope*.

Fig. 5.5 gives an example of such catch curve, constructed from the data in Table 5.4 and using Program FB 9 with which values of dl_i/dt and t' can be computed (see Example 5.6).

Equation (5.16) allows ready estimation of the bias caused by *not* accounting for the "pile-up" effect mentioned above. This is done by first rewriting equation (5.16) as

$$\ln N - \ln (dl/dt) = a + bt' \qquad \ldots 5.17)$$

or

$$\ln N = a + bt' - \ln (dl/dt) \qquad \ldots 5.18)$$

Now, in terms of the generalized VBGF, the growth rate can be expressed as

$$dl/dt = \ln (K \cdot D \cdot L_\infty^D) + KD\,(t' - t_o) \qquad \ldots 5.19)$$

where K, D, L_∞ and t_o are parameters of the generalized VBGF, and relative t' is the age corresponding to a given midlength. Inserting (5.19) in (5.13) gives

$$\ln N = a + bt' - \ln (KDL_\infty^D) - KD\,(t' - t_o) \qquad \ldots 5.20)$$

or

$$\ln N = a + bt' - \ln (KDL_\infty^D) - KDt' + KDt_o \qquad \ldots 5.21)$$

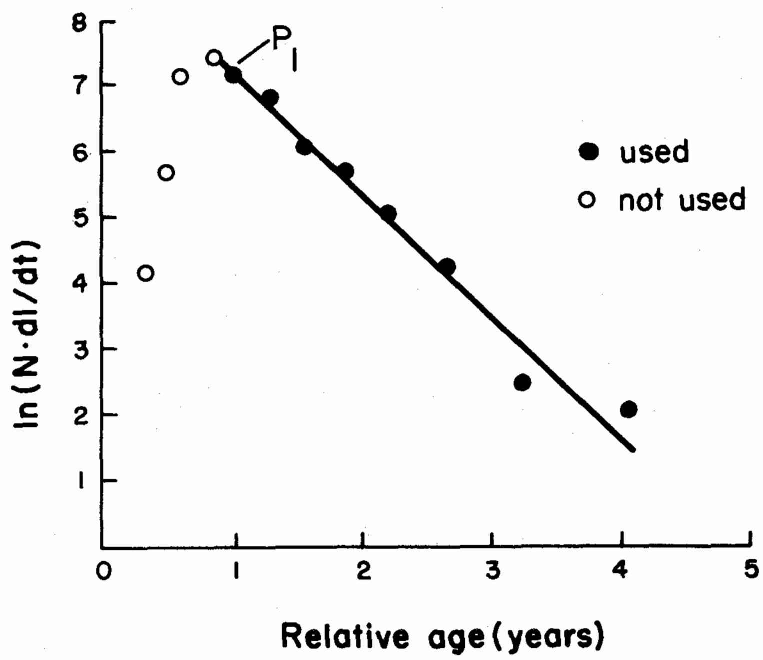

Fig. 5.5. A length-converted catch curve, based on the data of Table 5.4. The first point to be included in the estimation of Z (P_1) is clearly defined (see text). Note that each point is independent of all others and thus could be deleted singly from the computation of Z.

Equation (5.21), it will be noted, has 3 constant terms with regard to the variable N and t′, namely a, ln (KDL_∞^D) and KDt_o. Since Z in equation (5.16) is estimated as a slope, these 3 constant terms can be grouped into one single new term (a′) which becomes the intercept of a new equation of the form

$$\ln N = a' + bt' - KDt' \qquad \ldots 5.22)$$

which gives, rearranged

$$\ln N = a' + (b - KD)\, t' \qquad \ldots 5.23)$$

as a new equation for a length-converted catch curve. Therefore,

$$-b + KD = Z \qquad \ldots 5.24)$$

It follows from this that the bias resulting from the non-consideration of the "pile-up" effect (i.e., resulting from using ln N instead of ln (N · dl/dt) as ordinate of a length-converted catch curve) is equal to KD, or to K when the special VBGF is used (i.e., when D = 1). (See Example 5.7.)

Two practical applications of this finding come to mind:

(i) It becomes possible to correct biased values of Z obtained by various authors who didn't account for the "pile-up" effect (by simply adding K times D to their (biased) estimate of Z) (see e.g., Berry 1970; Nzioka 1983).

(ii) The estimation of Z from a length-converted catch curve becomes simpler, since one can first ignore the "pile-up" effect then compensate for it by addking K · D to the absolute value of the curve's slope (see Example 5.7).

When K is not known, equations such as (5.16) and (5.24) can still be used; in such cases, a value of unity (one) should be used instead of K when computing the relative ages, which are then defined by equation (5.14). The slope of the catch curve, with sign changed, will then be equal to (Z/K)−1.

Another type of length-converted catch curve is defined by the equation

$$\ln N_i/\Delta t_i = a + bt'_i \qquad \ldots 5.25)$$

where N_i and t'_i are defined as in equation (5.16), and where Δt_i is the time needed, on the average by the fish to grow through length class i. This equation accounts for the "piling-up" effect through division of the N_i-values by Δt_i, the inverse of the growth rates by which the N_i values are multiplied in equation (5.16). Hence, equation (5.25) is a slightly modified version of (5.16), and its properties, e.g., with regard to not accounting for the "piling-up" effect are the same.

Since equations (5.16) and (5.25) are equivalent, only one Program (FB 12) is given here for the computation of length-converted catch curves. This program implements equation (5.25) rather than (5.16) because the former has already been presented and discussed elsewhere (Pauly 1980a, 1982a, 1983; Pauly and Ingles 1981; Gulland 1983).

Example 5.8 shows the application of equation (5.25) and Program FB 12 to the data of Table 5.4. It will be noted that as in the earlier models, the points of a length-converted catch curve must be drawn for selection of the values to include in the regression equation. This selection must account for two features of a length-converted catch curve:

- as in age-structured catch curves, the points belonging to the ascending, left arm of the curve must not be included because they represent incompletely selected and/or incompletely recruited animals, and
- the conversion of length to (relative) ages by means of the VBGF, when involving fish whose length is very close to L_∞, generates unrealistically high "ages" which cannot be included either.

Suggested criteria for the selection of points to be included in the computation of Z are:

1) the first point to be included (P_1 on Figs. 5.5, 5.6 and 5.7) should be the point immediately to the right of the highest point. The latter may still be affected by incomplete selection and/or recruitment and is considered to be part of the ascending, left part of the curve;
2) points should be deleted that were obtained through conversion from lengths within 5% of L_∞ (see Fig. 5.6 for an example of such points);
3) the points selected should fit along, or close to, a straight line, and one *single* outlier may be excluded, particularly when it is based on few fish only.

Concerning the first of these criteria, it might be added that point P_1 corresponds to the length class whose lower class limit represents an estimate of L′ as required for equation (5.9). The third of these criteria must not be misunderstood to provide an excuse for the wholesale deletion of points until one's preconceived notion of linearity is achieved; rather it allows deletion of *one* point. When

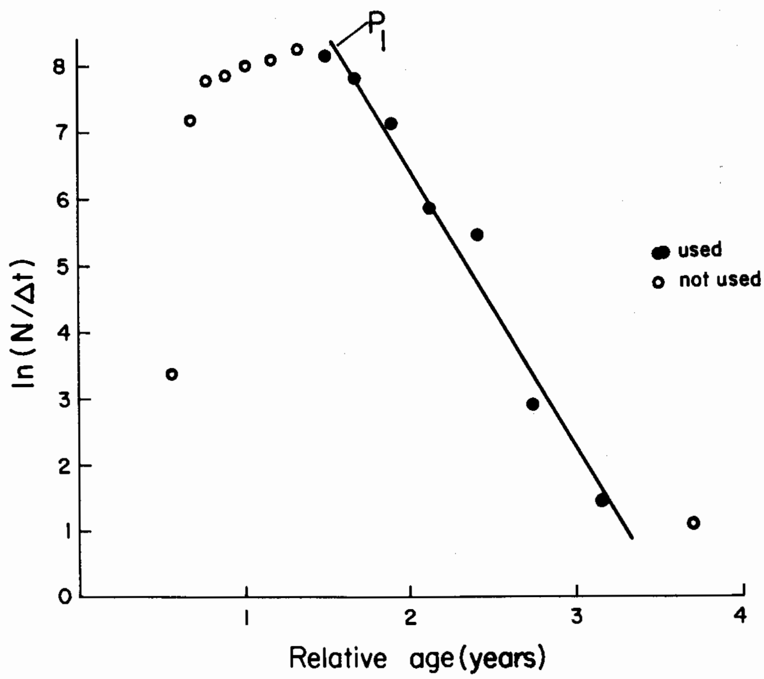

Fig. 5.6. Length-converted catch curve for yellow striped goatfish *(Upeneus vittatus)* from Manila Bay, Philippines, showing a point pertaining to a length close to L_∞ which should not be used in the computation of Z (from Pauly 1982a).

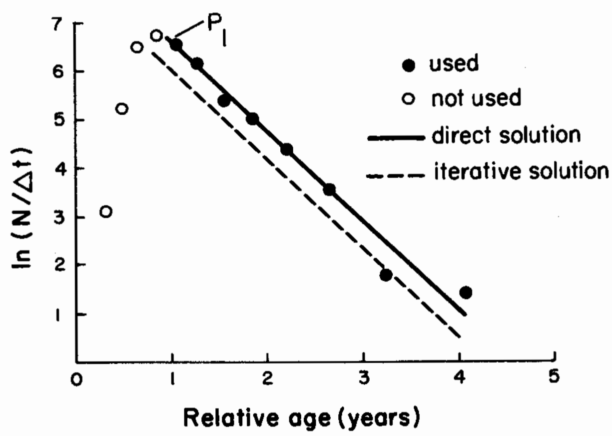

Fig. 5.7. Length-converted catch curve, based on equation (5.25) and the data of Table 5.4. The broken line, which parallels the catch curve, was obtained using equation (5.28). As shown in Example 5.9, the two lines provide virtually identical estimates of Z.

the curve as a whole seems to deviate from linearity, the appropriate approach should be to test whether this deviation is significant or not, using any of the statistical tests available for this purpose (e.g., Guilford and Fruchter 1978, p. 277-280).

Non-linearity of length-converted catch curves (see e.g., Fig. 5.4), that is their response to systematic changes in fishing effort or recruitment are akin to those of age-structured catch curves. The exhaustive discussions of the general properties of catch curves in Beverton and Holt (1956) and Ricker (1975) also apply to length-converted catch curves.

When reviewing the draft of this book, P. Sparre (pers. comm.) derived a form of a length-converted catch curve which involves none of the approximations in (5.16) and (5.25), by defining

- $N(t_1, t_2)$ = number of fish caught between ages t_1 and t_2, with $\Delta t = t_2 - t_1$
- $t_{L'}$ = the age corresponding to L′ (see above for definition of L′)
- $E = F/Z$ (see below for a more detailed definition)

from which

$$N(t_1, t_2) = N_{t'} \, e^{-Z(t_1 - t_{L'})} \cdot E(1 - e^{-Z\Delta t}) \qquad \ldots 5.26)$$

or

$$\ln N(t_1, t_2) = -Zt_1 + Zt_{L'} + \ln\{N_{t'} \cdot E(1 - e^{-Z\Delta t})\} \qquad \ldots 5.27)$$

which leads, with some rearrangement, to a new equation for a length-converted catch curve of the form

$$\ln \frac{N_i}{(1-e^{-Z\Delta t_i})} = a - Zt'_i \qquad \ldots 5.28)$$

where N_i is the number of fish in a given length class i; Δt_i the time needed to growth through class i and t'_i the relative age corresponding to the *lower* limit of class i.

Equation (5.28), although it can be solved only iteratively, has the definite advantage that no approximation is involved, as opposed to equation (5.25) where both the division of N_i by Δt_i and the use of relative ages corresponding to the midlengths of the length classes involve approximations.

Thus, equation (5.28) can be used to test the accuracy of the results obtained through equation (5.16) or (5.25). Example 5.8, which is typical of the many cases investigated so far, shows that equation (5.25) (and consequently 5.16 also) provide values of Z which differ only by a small fraction (less than 1%) from those obtained iteratively from equation (5.28). Therefore, the simpler model (5.25) generates results which are estimates of Z, and not only "proportional to Z", as suggested in Gulland (1983).

Further inferences from length-converted catch curves

Length-converted catch curves, in addition to allowing for the direct estimation of Z from length-frequency data, have the added advantage over "age-structured" catch curves of allowing a number of inferences to be drawn through detailed examination of the left, ascending arm of the curve, which is generally ignored in catch-curve analysis.

When the selection curve of the gear used to sample the data at hand is known, M can be estimated from the left side of a catch curve (Munro 1984). Conversely, when natural mortality is known, the selection curve of the gear can be inferred from the shape of the ascending arm of a length-converted catch curve. Only the latter of these two methods will be discussed here, as Munro's method, although quite elegant, has data requirements which limit its applicability.

Table 5.6 illustrates the derivation of selection data (probabilities of capture, by length) based on the left side of a selection curve and an estimate of M. The computational steps involved here are as follows:

(i) Set up a table which draws together all information needed for further analysis (these values are in square brackets in Table 5.6).

(ii) Compute times to grow from one class midpoint to the next and write Δt values as in Table 5.6.

(iii) Interpolate mortalities (Mortality I in Table 5.6) between Z and M (whose values should pertain to the highest length class with zero catch; see Table 5.6). The step size for the interpolations is estimated from $(Z - M)/(n + 1)$ where n is the number of classes for which mortality must be interpolated (here, $n = 4$).

(iv) The mortalities estimated in (iii) are estimates of the mortality *within* a given length class. The mortality *between* adjacent length classes (Mortality II) are estimated by taking means between adjacent length classes (see Table 5.6).

(v) Compute numbers available from equation given in Table 5.6, starting with number of fish in the first class where the probability of capture is equal to unity (i.e., corresponding to point P_1).

(vi) Obtain probabilities of capture by dividing, for each length class, the number caught (C_i) by the number available (N_i).

The method as outlined here is extremely useful in that it derives quantities which are normally obtained from costly selection experiments from readily obtained length-frequency samples and a reasonable estimate of M, which is easy to obtain when growth parameters are available (see below).

In stocks that are unexploited, the estimate of Z obtained from the catch curve can serve as the estimate of M; otherwise, the computations remain the same except, obviously that the interpolations between Z and M are superfluous because the same value of Z = M is used throughout. The special case, Z = M, formed the basis of the approach of Pauly et al. (in press) to estimate approximate selection curves from the backward projection of the straight segment of a length-con-

Table 5.6. Derivation of a selection curve from the left side of a length-converted catch curve (all values in square brackets must be available before attempting to complete table).

Class limits[a] Lower	Upper	Midpoint	Numbers caught (C_i)	Δt (class midpoint to midpoint)[b]	Mortality I ($M \rightarrow Z$)[c]	Mortality II (means)	Numbers available (N_i)[d]	$P = C_i/N_i$
2	4	3	[0]	—	[M = 1.14]	—	—	[0]
4	6	5	5	0.158	1.28	1.35	448	0.0112
6	8	7	29	0.171	1.42	1.49	362	0.0801
8	10	9	114	0.188	1.56	1.63	281	0.4057
10	12	11	161	0.208	1.70	1.77	207	0.7778
12=L′	14	13	[143][e]	—	[Z = 1.84]	—	[143][e]	[1.00]

[a]Actual upper class limits are 3.999, 5.999, etc., but are rounded for convenience.

[b]Computed from $\frac{1}{KD} \ln \left\{ \frac{L_\infty^D - L_2^D}{L_\infty^D - L_1^D} \right\}$ where L_1, L_2 are the lower and upper class limits, respectively.

[c]Values between Z and M interpolated linearly.

[d]Computed from $N_i = N_{i+1} e^{Z\Delta t}$, where N_{i+1} is the number available in a given length class and N_i the number available in the next lower length class.

[e]This number may be taken as the actual number caught in the first length class that is fully selected (i.e., corresponding to P_1). However, a better approach is to compute this number from the equation of the catch curve, for the midpoint in question. In this example, the two values of N are similar.

verted catch curve. This approach is now superseded by the more versatile and accurate method illustrated by Table 5.6.

The accuracy of the method outlined here depends critically on the following assumption being met:

(i) The gear in question is a trawl or has a selection curve similar to that of a trawl (where it is only the smaller fish that are selected against).
(ii) The smallest fish caught (L_{min}) are fully recruited.
(iii) The value of M used for the fish just below L_{min} and the mortalities generated by interpolation between M and the Z value for the fully selected animals are accurate.

The first of these assumptions can be easily verified. The second, which will often be violated, implies that the resulting probabilities will not strictly refer to a *selection* curve, but to a *resultant* curve, i.e., to the product of a selection with a recruitment curve (Gulland 1969). Whether this assumption is met or not will thus affect the *interpretation* of the results, but not their computation.

The third of these assumptions can be assessed quite straightforwardly. The effects of changes in the value of M used on the probabilities of capture are easy to compute (see Appendix I for a brief introduction to sensitivity analysis). Anon. (1982) compared estimates of length at first capture obtained from selection experiments with length at first capture estimated through the approach proposed here (but using the special case where M is set equal to Z, see above) and obtained a good match for the cases investigated, Mediterranean sardines and hakes.

Chapter 2 should be consulted for the interpretation and use of selection curves, notably for the computation of mean lengths at first capture.

Estimating Z from a pseudo-catch curve

When the average size of the animals of a population under investigation displays a significant relationship to the water depth, or distance from the coast (or any other environmental gradient), it will generally be difficult to obtain size-frequency samples representative of the population as a whole. Various schemes of stratified sampling may be applied to deal with such a situation. However, as far as the estimation of Z is concerned, the best approach may be to actually *use*, in conjunction with a "pseudo-catch curve" as defined in Pauly (1980c), the gradient along which the population is distributed.

Here the method is applied to the case where the mean size of fish increases and their numbers decrease with water depth—the environmental gradient one is most likely to encounter.

To apply the pseudo-catch curve method, the following items are required:

1) data allowing quantification of the size-depth relationship (this might be a relationship involving mean length and depth, or mean weight and depth; in the case of the former a length-weight relationship is also needed). An example of such relationship is given as Fig. 5.8;

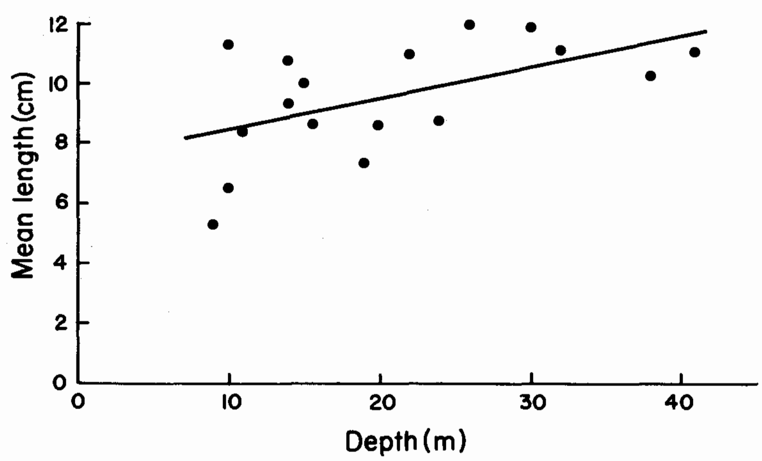

Fig. 5.8. Relationship between mean length and water depth in slipmouths *(Leiognathus splendens)* caught off Southeast Kalimantan, Indonesia (from Pauly 1980c).

2) catch-per-effort data stratified by depth and representative of the whole depth range inhabited by the investigated population. An example of such data is given as Fig. 5.9;
3) the growth parameters L_∞, K (or W_∞, K) and D of the VBGF.

The method consists of (1) using the size-depth relationship and the growth parameters to compute the mean (relative) age corresponding to the size at each depth for which a catch-per-effort value is available; (2) dividing the mean weight at depth into the corresponding c/f value to obtain the average "number at depth"; (3) plotting the natural logarithm of the numbers at depth against the corresponding relative age (see Fig. 5.10 for an example), and estimating (—)Z from the slope.

The computations involved are outlined in Example 5.9.

This method, as emphasized in Pauly (1980c), was developed mainly to estimate Z from data which have been gathered and/or published for miscellaneous purposes and which could not be used directly for the construction of a real length-converted catch curve.

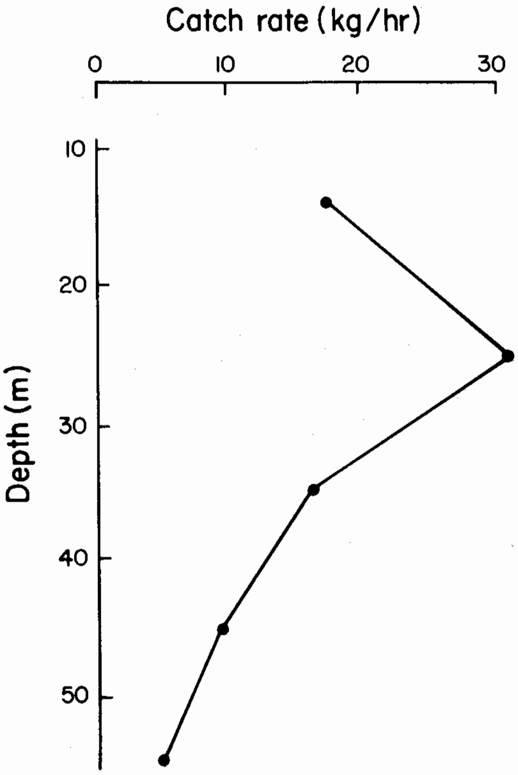

Fig. 5.9. Relationship between average catch per effort of *Leiognathus splendens* and water depth in western Indonesian waters (from Pauly 1977).

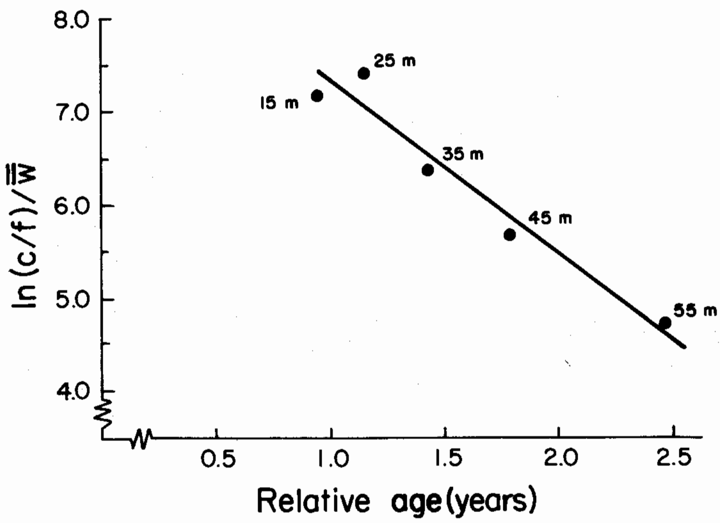

Fig. 5.10. Pseudo-catch curve for *Leiognathus splendens* in western Indonesian waters (see Example 5.9 for derivation and interpretation).

SIMULTANEOUS ESTIMATION OF Z AND K

Saila and Lough (1981), based on a model developed by Ebert (1973), presented a method for the estimation of total mortality which has the advantage of also estimating the value of K of the VBGF given a set value for the asymptotic length $L_{(\infty)}$, an assumed value for the length at recruitment (L_r) and two successive mean lengths ($\bar{L}_1$, $\bar{L}_2$) obtained twice within a year (t_1, t_2) at times that are as far apart as possible.

Given these inputs (and a value of D when the generalized VBGF is used), K can be estimated from

$$K = \frac{\ln \dfrac{L_\infty^D - \bar{L}_2^D}{L_\infty^D - \bar{L}_1^D}}{(t_1 - t_2) \cdot D} \qquad \ldots 5.29)$$

while Z is estimated iteratively as the value which fulfills

$$\frac{\sum\limits_{x=0}^{N} e^{-Zx} - b \cdot \sum\limits_{x=0}^{N} e^{-(KD\,(t_1 + x) + Zx)}}{\sum\limits_{x=0}^{N} e^{-Zx}} = \frac{\bar{\bar{L}}_1^D}{L^D_{(\infty)}} \qquad \ldots 5.30)$$

and

$$\frac{\sum\limits_{x=0}^{N} e^{-Zx} - b \cdot \sum\limits_{x=0}^{N} e^{-(KD\,(t_2 + x) + Zx)}}{\sum\limits_{x=0}^{N} e^{-Zx}} = \frac{\bar{\bar{L}}_2^D}{L^D_{(\infty)}} \qquad \ldots 5.31)$$

where

$$N = \text{integer part of } \{\, [-(\ln 0.0001)/Z] + 1 \,\} \qquad \ldots 5.32)$$

and

$$b = (L^D_{(\infty)} - L^D_r)/L^D_{(\infty)} \qquad \ldots 5.33)$$

A table (5.7) is provided here from which t_1, t_2 values can be read off, given the months of sampling and of recruitment (i.e., the months during which the length-frequency data were sampled from which $\bar{\bar{L}}_1$, $\bar{\bar{L}}_2$ and L_r were estimated). Assumptions of this method are that (a) the VBGF and equation (5.1) describe the growth and mortality, respectively, of the investigated stock; (b) recruitment occurs during a brief period of time, and only once a year; (c) interannual variations of recruitment are negligible, i.e., the stock has a stable population with a stationary age distribution; and (d) $\bar{\bar{L}}_1$, $\bar{\bar{L}}_2$, L_r and $L_{(\infty)}$ are good estimates of the actual values.

Of these assumptions, (c) may be the most crucial one, and the one whose validity may be the most difficult to assess. It must be understood, however, that this assumption is made not only here,

Table 5.7. Values of t_1 and t_2 for use with L_1 and L_2 values, given the month of recruitment.[a]

Sampling months (for L_1 and L_2)	Month of recruitment J	F	M	A	M	J	J	A	S	O	N	D
J	0	1	0.909	0.818	0.727	0.636	0.546	0.455	0.364	0.273	0.182	0.091
F	0.091	0	1	0.909	0.818	0.727	0.636	0.546	0.455	0.364	0.273	0.182
M	0.182	0.091	0	1	0.909	0.818	0.727	0.636	0.546	0.455	0.364	0.273
A	0.273	0.182	0.091	0	1	0.909	0.818	0.727	0.636	0.546	0.455	0.364
M	0.364	0.273	0.182	0.091	0	1	0.909	0.818	0.727	0.636	0.546	0.455
J	0.455	0.364	0.273	0.182	0.091	0	1	0.909	0.818	0.727	0.636	0.546
J	0.546	0.455	0.364	0.273	0.182	0.091	0	1	0.909	0.818	0.727	0.636
A	0.636	0.546	0.455	0.364	0.273	0.182	0.091	0	1	0.909	0.818	0.727
S	0.727	0.636	0.546	0.455	0.364	0.273	0.182	0.091	0	1	0.909	0.818
O	0.818	0.727	0.636	0.546	0.455	0.364	0.273	0.182	0.091	0	1	0.909
N	0.909	0.818	0.727	0.636	0.546	0.455	0.364	0.273	0.182	0.091	0	1
D	1	0.909	0.818	0.727	0.636	0.546	0.455	0.364	0.273	0.182	0.091	0

[a]To use this table, select appropriate column (= month of recruitment, and read from that column values of t_1 and t_2, given the month at which sampling for L_1 and L_2 took place (t_1 can be, but is not necessarily, the month of recruitment). Values may be interpolated linearly for dates of the month; in this case, recruitment and table values should be viewed as pertaining to the 15th of the corresponding month. Interpolation must not be done between 1 and 0.

but also in the various equations used to estimate Z from mean size data, as well as in all "catch curve" related methods (see above). The validity of assumption (b), on the other hand, can be assessed quite straightforwardly, e.g., by plotting the available length-frequency data and inspecting them visually for the pattern of recruitment (see Fig. 5.11). Assumption (a) is made throughout this manual and requires no further comment.

The method presented here for estimating Z and K simultaneously, as incorporated in Program FB 13, generates results that are very sensitive to small errors affecting the input parameters, particularly the values of $\bar{\bar{L}}_1^D - L_r^D$ and $\bar{\bar{L}}_2^D - L_r^D$. On the other hand, the values of t_1 and t_2 have a comparatively smaller effect on the results. Still, they will be improved by using exact values of t_1, t_2 for which reason a table (5.7) was included here which can be used to obtain directly the appropriate values of t_1, t_2, given the months of recruitment and sampling. The table also allows for interpolations when the exact dates in the months are known.

As this method—and a number of other methods discussed in this manual—involve the use of mean lengths, a routine has been included in Program FB 13 which can be used to compute rapidly the weighted mean lengths (or mean weights, or any weighted mean for that matter) from size-frequency data. The routine also computes the standard deviation of the variates and the standard error of the mean. This use of the routine is illustrated in Example 5.3 (see also Table 5.8).

Table 5.8. Length-frequency data for the goby *(Glossogobius giurus)* from Cardona, Laguna de Bay, Philippines.[a]

Lower class limit (cm)	1958 A	S	O	N	D	1959 J	F	M	A	M	J	J
4	1	3	—	—	—	—	—	—	—	—	—	—
6	138	113	1	9	2	—	—	—	—	—	—	—
8	153	62	40	65	126	12	5	6	—	—	—	—
10	49	36	111	49	127	55	52	56	21	—	—	—
12	9	25	43	20	65	50	84	77	50	6	3	8
14	—	7	3	1	14	25	36	38	53	37	6	36
16	—	1	—	—	3	9	4	8	26	43	17	18
18	—	—	—	—	—	—	—	3	12	15	13	4
20	—	—	—	—	—	—	—	1	4	6	5	3
22	—	—	—	—	—	—	—	—	1	4	—	2
24	—	—	—	—	—	—	—	—	—	1	—	—
Σ	350	247	198	144	337	151	181	189	167	112	44	71
Mean length	8.58	8.93	11.07	10.15	10.83	12.52	12.80	10.99	14.69	16.89	17.50	15.99
Inputs	$\bar{\bar{L}}_1$ = 9.5 (Sept)									$\bar{\bar{L}}_2$ = 16.8 (June)		

[a]Adapted from data in Marquez (1960).

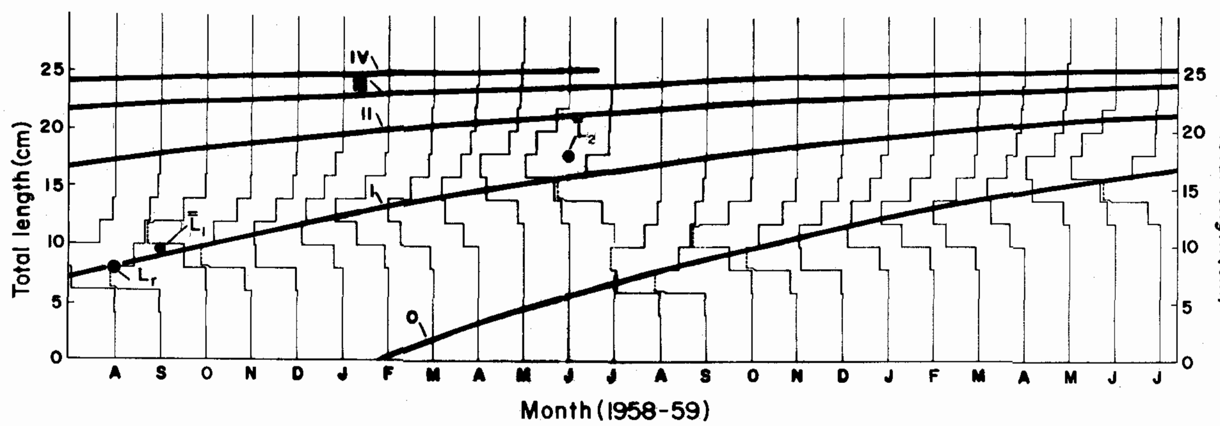

Fig. 5.11. Growth curve of the white goby *(Glossogobius giurus)* in Laguna de Bay, Philippines as estimated using Ebert's method (based on data in Table 5.8 and Example 5.10).

ESTIMATION OF Z/K

While the estimation of Z requires either a knowledge of the growth parameters of a stock, or that the age of at least a few fish is known, a number of methods exist which allow for the estimation of a parameter—Z/K—which is closely related to Z, yet require no information on age or growth for its estimation.

A few of these methods have been presented above (cumulative plots, length-converted catch curves); in these, use of 1 (one) instead of the value of K leads to the estimation of Z/K instead of Z.

Powell (1979) derived a general model for the estimation of Z/K from which he derived four special cases, as follows:

1st case: the Beverton and Holt formula of 1956

Probably the simplest method for estimating Z/K is to rewrite equation (5.9) such that

$$Z/K = \frac{D\,(L_\infty^D - \bar{L}^D)}{\bar{L}^D - L'^D} \qquad \ldots 5.34)$$

where all parameters are defined as in (5.9). This model is illustrated in Example 5.11. However, the reservations mentioned earlier with regards to (5.9) apply to this model also.

2nd case: using the variance of the mean length

Powell (1979) derived for the estimation of Z/K the equation

$$Z/K = \frac{2\,C^2}{1 - C^2} \qquad \ldots 5.35)$$

where in terms of the special VBGF

$$C^2 = (\text{s.d.}_{(L)})^2/(\bar{L} - L')^2 \qquad \ldots 5.36)$$

where $\bar{L}$ and L' are defined as previously, and where $\text{s.d.}_{(L)}$ is the standard deviation of the L values used in computing $\bar{L}$.

Several applications of equation (5.36) suggest that this model produces values of Z/K which are generally biased downward (see Example 5.11). On the other hand, the model does not require any estimate of asymptotic size, which might be viewed as an advantage over equation (5.34).

3rd case: using a nomogram and the mean weight of fish in the catch

Fig. 5.12 reproduces a nomogram presented by Powell (1979) to roughly estimate Z/K from the mean weight of fish in the catch and a few ancillary values.

4th case: estimating Z/K from the shape of the length-frequency distribution

Fig. 5.13 gives a redrawn version of Fig. 110 in Powell (1979), which may be used to obtain a crude, preliminary estimate of Z/K given a set of length-frequency data representative of a given population in which individual growth is described by the special VBGF.

The main reasons why Powell's graphs (Figs. 5.12 and 5.13) are given here is not their feature of allowing crude estimates of Z/K. Rather these graphs, particularly Fig. 5.13, have been included because they *show* how Z/K is related to major properties of fish stocks.

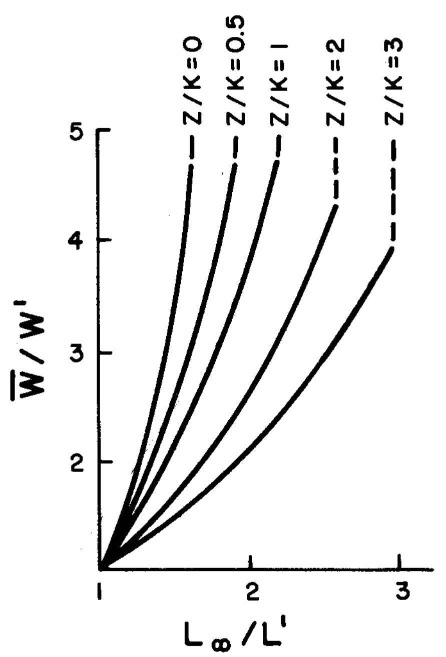

Fig. 5.12. Powell's nomogram for the estimation of Z/K (special VBGF) from the relationship between the mean weight ($\overline{W}$) in the catch, the asymptotic length and the lowest size at full retention (L′ and W′).

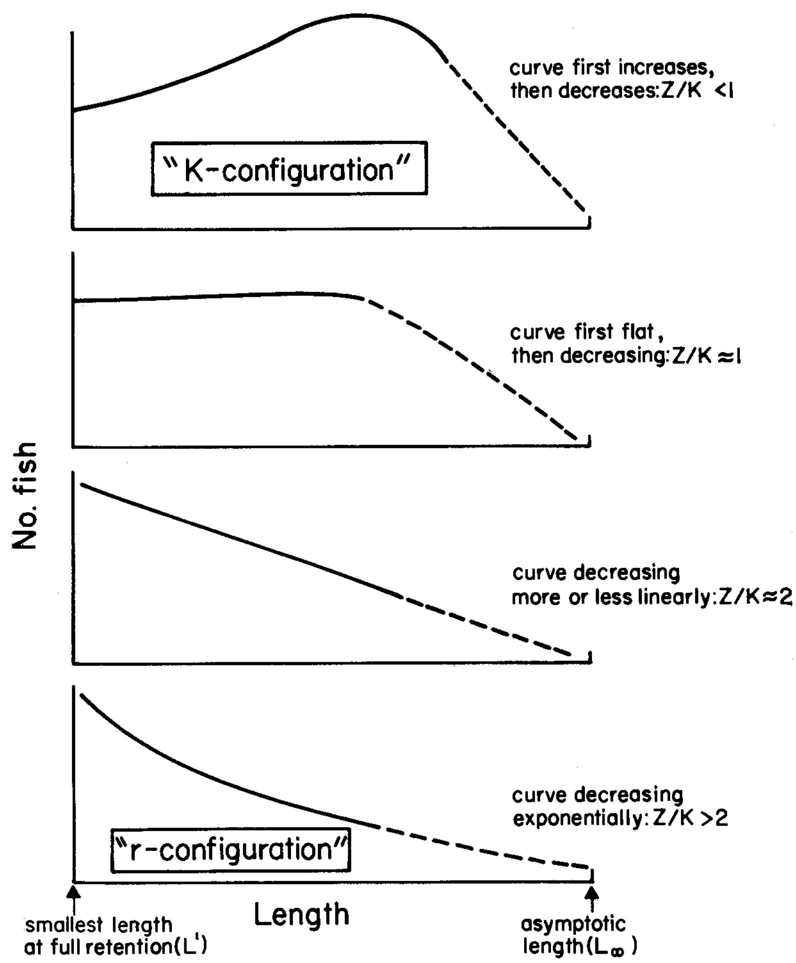

Fig. 5.13. Overall shapes of length-frequency plots, given different values of Z/K (special VBGF). Adapted from Powell (1979, Fig. 110) and Johnson (1981, Figs. 1 and 2). See text for definitions of r- and K-configurations.

For example, Fig. 5.13 shows that fish with very low mortalities and even slower growth, e.g., the whitefish of unexploited northern Canadian lakes (Johnson 1981), display such a considerable "pile-up effect" (see above for definition) that large fish are more numerous than fish of intermediate size, a phenomenon which Johnson calls "K-configuration", as opposed to the "r-configuration" occurring when fish numbers decrease exponentially with size (see Figs. 5.13 and 5.14).

Whether fishes with a clear "K-configuration" occur in the tropics is unclear; this would be surprising, however, given that the ratio M/K (and hence Z/K also) is generally higher in tropical fishes than in temperate fishes (see below). The ecology texts listed in Chapter 11 may be consulted, incidentally, for definitions of "r- and K-strategies", from which Johnson (1981) derived the concept of r- and K-configurations.

METHODS FOR SPLITTING Z INTO M AND F

Two methods will be presented here which allow division of estimates of Z into their constituent parts, M and F, while a third (the method of Csirke and Caddy) is discussed in Chapter 10.

These methods are (1) plotting different values of Z on their corresponding effort and (2) analysis of tag return data.

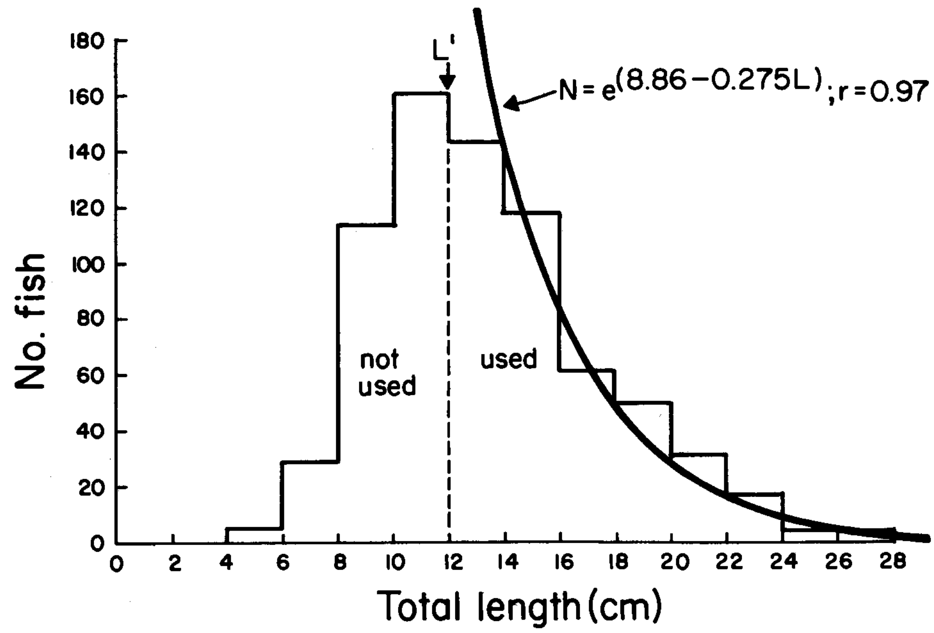

Fig. 5.14. Length-frequency data from Table 5.4, fitted with an exponential curve to demonstrate that Z/K for *Epinephelus sexfasciatus* is 2 or greater (see text, Fig. 5.13 and Example 5.11).

Plot of Z on effort

When two or more values of Z are available which pertain to different periods (years or groups of years) with different levels of fishing effort (f) (as for example in Table 5.9), a linear plot of Z on f will provide an estimate of M through the relationship

$$Z = M + qf \qquad \ldots 5.37)$$

Table 5.9. Data for estimating M and q for *Selaroides leptolepis* from the Gulf of Thailand.[a]

Year	Effort[b]	$\bar{L}$	Z[c]
1966	2.08	13.25	2.41
1967	2.08	13.01	2.69
1968	3.50	19.99	2.72
1969	3.60	13.07	2.62
1970	3.80	12.37	3.73
1972	7.19	12.30	3.88
1973	9.94	12.01	4.61
1974	6.06	12.60	3.30
$\bar{X}$	4.87	12.70	3.25

[a]Based on data in Boonyubol and Hongskul (1978).
[b]In millions of trawling hours.
[c]As estimated from $Z = K \cdot (L_\infty - \bar{L})/(\bar{L} - L')$, with $L_\infty = 20$ cm, $K = 1.16$ and $L' = 10$ cm.

where q is the "catchability coefficient", which relates effort to fishing mortality such that

$$F = q \cdot f \qquad \ldots 5.38)$$

Equation (5.38), it must be realized, applies only when f measures *effective* effort (as opposed to *nominal* effort, as expressed, e.g., by simple "number of boats") and provides a measure of effort which is indeed proportional to F (see Rothschild 1977, and contributions in Gulland 1964).

A program for estimating the values of M and q is superfluous here as equation (5.38) provides yet another linear regression with intercept equal to M and slope equal to q (see Example 5.13 and Fig. 5.15).

When only one value of Z is available, or when the available values of Z and f cover too small a range for reasonable values of M and q to be obtained, the catchability coefficient (q) may be estimated through

$$q = (\overline{Z} - M)/\overline{f} \qquad \ldots 5.39)$$

where $\overline{Z}$ is the mean of the available values of Z (or a single value of Z) and $\overline{f}$ is the mean of the values of f (or a single value of f), M being an independent estimate of natural mortality. (See Ricker 1975, p. 172-174, and Example 5.15.)

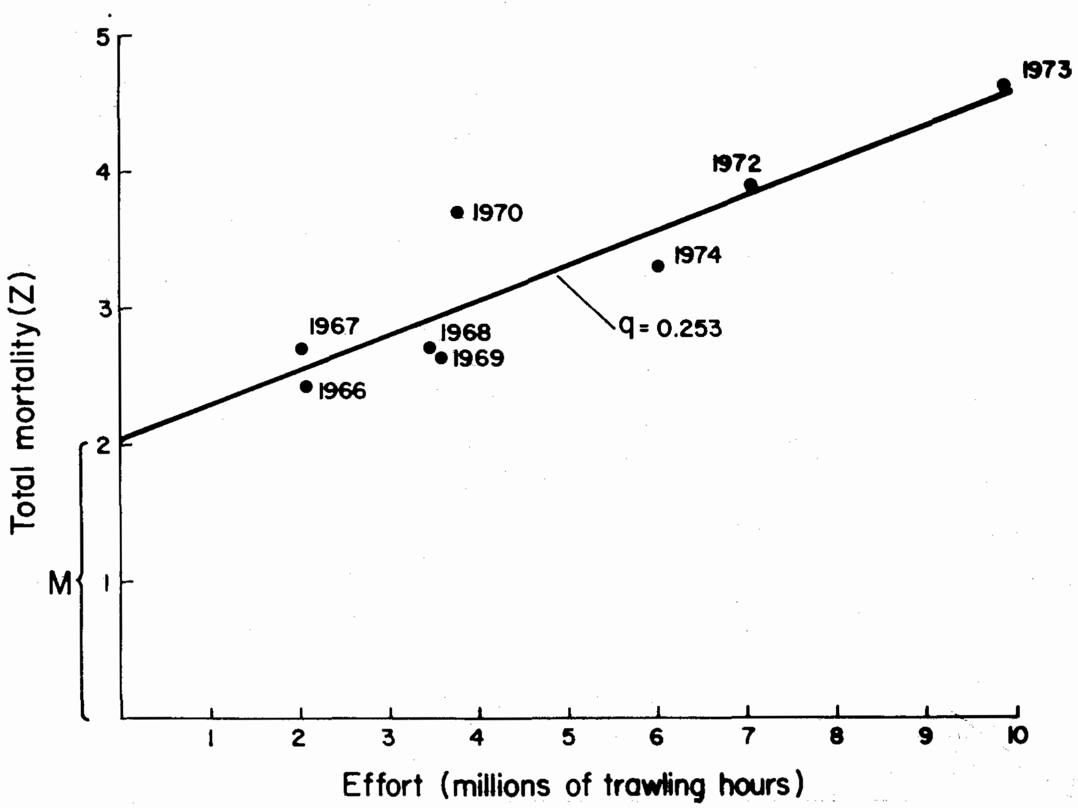

Fig. 5.15. Plot of total mortality (Z) on effort for the yellow striped trevally *(Selaroides leptolepis)* in the Gulf of Thailand trawl fishery, to obtain values of M and q (based on data in Table 5.9 and Example 5.13).

Analysis of tagging data

There is a very voluminous literature on methods to estimate mortalities by means of tagging studies. Reviews may be found in Jones (1977), Ricker (1975) and White et al. (1982). Only one case will be discussed here, namely that of tagging experiments in which all tagging is performed at one time (say over a period of a few days) and in which both fishing and natural mortality can be assumed constant during the period of the experiment.

In such cases, the analysis consists of simply plotting the natural logarithm of the number of recoveries, grouped by time intervals, on the number of the time intervals, or

$$\ln N_r = a + br' \qquad \ldots 5.40)$$

where $\ln N_r$ is the natural logarithm of the number of recoveries (N_r) per time interval and where r' is the time interval number (starting with 0, see Table 5.10). The slope of such a plot provides, with sign changed, an estimate of Z, while the intercept a can be used to estimate F through the relationship

$$F = \frac{e^a \cdot Z}{N_o\,(1 - e^{-Z})} \qquad \ldots 5.41)$$

where N_o is the total number of fish tagged and released (and provided there is no significant tag shedding, tag-induced mortality or non-recovery of tagged fish).

Table 5.10. Number of tagged and recovered chub mackerels *(Rastrelliger neglectus)*, grouped according to time spent at large after releasing.[a]

No. of month (r')[b]	No. of recoveries
0	1,052
1	748
2	165
3	46
4	8

[a]Area II, Gulf of Thailand, 1961 experiment. Total number released was N_o = 5,230. From Table XXI in Hongskul (1974).

[b]The first time period at large is coded 0, the following periods 1, 2, 3, etc.

Natural mortality is obtained by subtracting F from Z; then Z, F and M are converted to annual rates by multiplication by the number of times one of the time intervals is contained in a year (see Example 5.13).

Equations (5.40) and (5.41) are adapted from Gulland (1969, p. 76) whose chapter on tagging should be consulted for details on the method, particularly with regard to potential sources of errors.

It should be mentioned moreover, that tagging studies in other than well-monitored, single-species pelagic stocks (e.g., tuna and mackerels) are, in the tropics at least, generally very difficult to conduct successfully, particularly with regard to sufficient numbers of returns. Also, such studies are often too expensive to be cost-effective (Stephenson 1981; Pauly 1982a).

METHOD FOR OBTAINING INDEPENDENT ESTIMATES OF M

It has been demonstrated by various authors that the values of the parameter K of the VBGF are closely linked with longevity in fish (see e.g., Beverton and Holt 1959). This can be demonstrated on the basis of the observation that in nature the oldest fish of a stock generally grow to about 95% of their asymptotic length (Taylor 1958; Beverton 1963). This rule, which was derived from growth data used in conjunction with the special VBGF, does not strictly apply to large fish, such as tuna (see Pauly 1981). Still, in small fish at least, when

$$L_t = L_\infty\,(1 - e^{-K\,(t - t_o)}) \qquad \ldots 5.42)$$

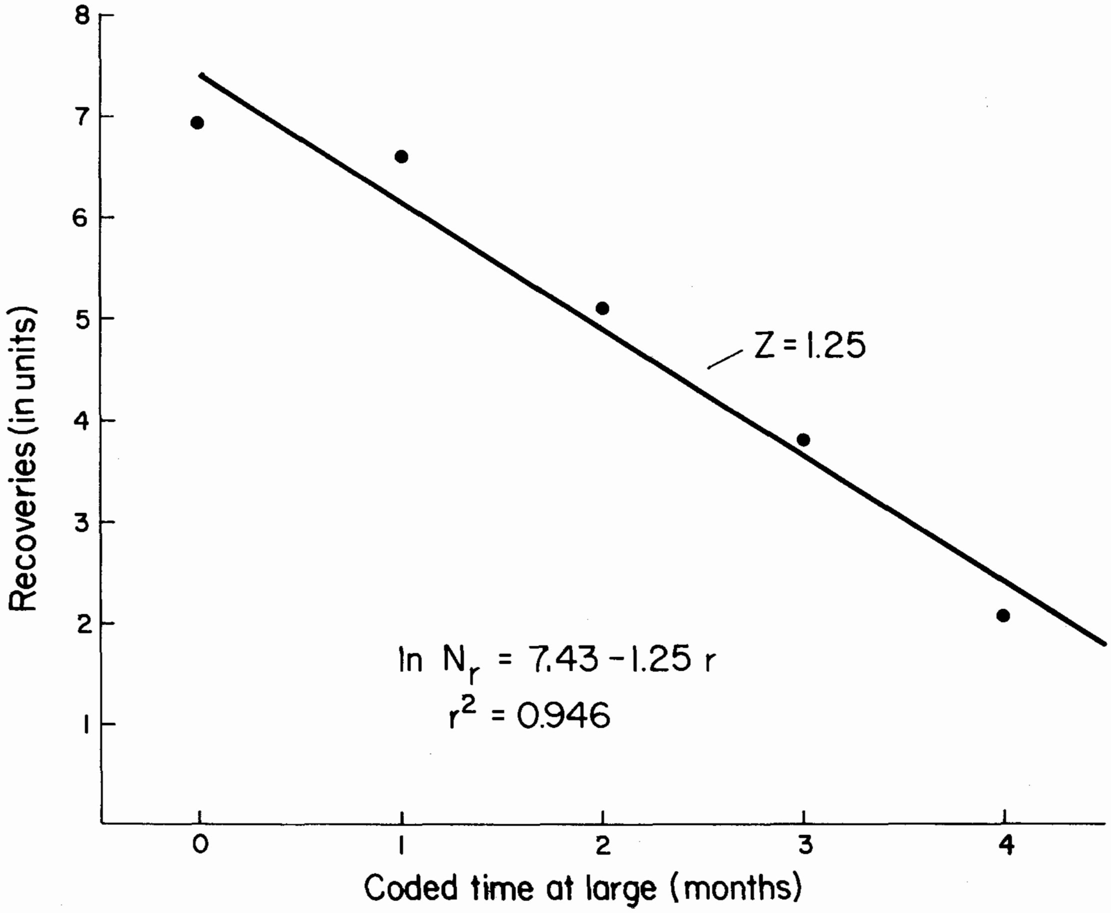

Fig. 5.16. Analysis of tag return data for chub mackerel *(Rastrelliger neglectus)* from the Gulf of Thailand (based on data in Table 5.10 and Example 5.13).

then

$$t - t_o = \frac{\ln(1 - (L_t/L_\infty))}{-K} \qquad \ldots 5.43)$$

or, inserting 95% of L_∞ for L_{max}

$$t_{max} - t_o = \frac{2.9957}{K} \qquad \ldots 5.44)$$

or, ignoring t_o

$$t_{max} \approx \frac{3}{K} \qquad \ldots 5.45)$$

where t_{max} is the longevity of the fish in question.

That natural mortality should, in fishes, be inversely correlated with longevity and hence be correlated with K, seems obvious (see also equation 5.5). Natural mortality should also inversely correlate with size, since large fish should have, as a rule, fewer predators than small fish.

Natural mortality can also be demonstrated to be correlated to mean environmental temperature in fishes, although the interpretation of this phenomenon is still open (Pauly 1980b).

These various interrelationships can be expressed for length growth data by the multiple regression

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.463 \log \overline{T} \qquad \ldots 5.46)$$

and for weight growth data by

$$\log M = -0.2107 - 0.0824 \log W_\infty + 0.6757 \log K + 0.4687 \log \overline{T} \qquad \ldots 5.47)$$

where M is the natural mortality in a given stock, L_∞ (total length, in cm) and W_∞ (live weight, in g) being the asymptotic size of that stock; K (as well as L_∞ and W_∞) refers to the special VBGF and is expressed on an annual basis; the value of $\overline{T}$ is the annual mean temperature (°C) of the water in which the stock in question lives. These equations are incorporated in Program FB 15. [Negative temperature values for polar fishes, down to −2°C may be used for input in Program FB 15, because an "effective physiological temperature" (Pauly 1980b), which happens to be always positive, is computed internally for all values of $T < 3.5°$ and $T \geqslant -2.0°C$.]

In general, the estimates of M provided by equations (5.46) and (5.47) are quite reasonable, especially because a very large number (175) of *independent* estimates of M have been used for their derivation. Also the fish considered covered an extremely wide range of sizes, taxa and habitats.

However, estimates of M obtained from these expressions may be biased upward in the case of strongly schooling fishes, such as the sardine-like fishes and downward in the case of polar fishes. Correction factors and a further discussion of equations (5.46) and (5.47) are given in Pauly (1980b), along with all data used in the derivation.

Equations (5.46) and (5.47) are incorporated into Program FB 15, which estimates M given the appropriate growth parameters of the special VBGF and an estimate of T, such as may be obtained from an oceanographic atlas (see Example 5.14).

EXPLOITATION RATES AND POTENTIAL YIELDS

Certain stock assessment methods, such as Beverton and Holt's relative yield-per-recruit assessment (Beverton and Holt 1966) and Jones' (1974) length cohort analysis (see following chapters) make exhaustive use of exploitation rates, which define the fraction (in numbers) of an age class which will be caught during the fished life span (or: E = number caught/number dying of all causes).

In terms of mortality rates, the exploitation rate is defined by

$$E = \frac{F}{F + M} = \frac{F}{Z} \qquad \ldots 5.48)$$

Another definition of E is given by

$$E = 1 - \frac{M/K}{Z/K} \qquad \ldots 5.49)$$

which implies that the exploitation rate of a stock can be assessed without their age or growth parameters being known (see Example 5.15).

When, on the other hand, only M and E are known, F can be estimated from

$$F = M \cdot E/(1 - E) \qquad \ldots 5.50)$$

Gulland (1971) suggested that in a stock that is optimally exploited, fishing mortality should be about equal to natural mortality, or

$$F_{opt} \approx M \qquad \ldots 5.51)$$

which corresponds to

$$E_{opt} \approx 0.5 \qquad \ldots 5.52)$$

and which also leads to the well-known equation

$$P_y \approx 0.5\,M\,B_o \qquad \ldots 5.53)$$

which states that the potential yield of a stock is about equal to half the virgin biomass (B_o) times the natural mortality prevailing in that stock (see Gulland 1971 p. x, xi for the two approaches that lead to this model).

Although widely used, equation (5.53) has been criticized by a number of authors, notably Francis (1974) and Caddy and Csirke (1983) who showed that the assumption $M \approx F_{opt}$ does not apply in a large number of stocks, notably in stocks of fish and shrimps low in the food chain.

Beddington and Cooke (1983) investigated equation (5.53) in great detail and concluded, on the basis of numerous simulations, that equation (5.53) generally overestimates potential yields by a factor which is itself a function of M. Thus, they showed that, for values of M ranging between 0.2 and 1, equation (5.53) overestimates potential yields by a factor of 2-3. For higher values of M—as often occurs in small tropical fish—equation (5.53) possibly overestimates potential yields by a factor of 3-4.

Thus, rather than $E_{opt} \approx 0.5$, it could well be that the optimum exploitation rate is—particularly in small fish with high recruitment variability—as low as 0.2 or, tentatively

$$P_y \approx 0.2\,M\,B_o \qquad \ldots 5.54)$$

Clearly, these results are very important and warrant further research on this topic. Also, they make it imperative to use approximations such as discussed here only in the last resort, and then very conservatively, e.g., by relying on (5.54) rather than (5.53).

Recommended reading: Although less abundant than the literature on growth, the literature on mortality is quite large. Some useful reviews are: Beverton and Holt (1956, 1959), Robson and Chapman (1961), Gulland (1969, 1971) and Ricker (1975).

Suggested research topics: Compare estimates of Z obtained from catch curves of commercially important fish with estimates obtained from mean sizes in the catch (using different equations to compute the latter). Attempt to estimate M from Z and effort data, and compare the estimate(s) of M with independent estimates obtained from expressions (5.46 and 5.47). Attempt to partition F into different fishing gears, and M into different predators. Investigate changes in F and in M.

EXAMPLE 5.1

Estimation of Z and its standard error from the maximum age of a fish sample.

Rodrigues (1968) aged 115 male specimens of the croaker *(Micropogon furnieri)* caught off Caera State, Brazil. The maximum age was 7 years. What is the total mortality in the stock from which the 115 fish were taken, if t_c is set at zero?

To obtain Z and its standard error, first read off the value of c_1 and c_2 corresponding to n = 115. These values, interpolated between the values for n = 110 and n = 120, are 0.198 and 0.049, respectively. Then perform

Keystrokes	Results	
197 ↑ .198 X ÷	0.72	Z
X^2 .049 X $\sqrt{x}$	0.16	$s.e._{(Z)}$

Other values of Z and $s.e._{(Z)}$ in Brazilian fishes are given in Table 5.3.

EXAMPLE 5.2

Estimation of Z from the mean weight of the catch (iterative solution).

If the following set of growth parameters of the special VBGF (corresponding to a small tuna are available) W_∞ = 10 kg, t_0 = −0.8, with t_c = 0.95 and the mean weight in the catch is equal to $\overline{\overline{W}}$ = 5 kg; what is the total mortality? The tolerated error of Z will be 0.001.

Computations:

1) Read sides 1 and 2 of Program FB 10.

2) Initialize

	Keystrokes	Results	
	10 ↑ .5 ↑ .95 ↑ .8 CHS f a 5 f b		
1st guess for Z = 4	.001 f e 4A	−2.47	[f(a)]
2nd guess for Z = 0.1	0.1B	3.34	[f(b)]
3) Estimate total mortality:	E	0.58	(Z)

Note: Depending on the values of f(a) and f(b), the iteration time can go beyond one minute.

Estimation of Z from the mean length of the catch.

Case I: Thompson and Munro (1978) give for the Jamaican grouper *(Epinephelus guttatus)* the parameter values $L_\infty = 52$ cm, $K = 0.28$ ($D = 1$), $L' = 34$ and $\bar{L} = 38.7$. What is the total mortality?

Keystrokes	Result	
.28 ↑ 52 ↑ 38.7–		
X 38.7 ↑ 34 – ÷	0.792	(Z)

Case II: Table 5.4 gives length-frequency data (averaged over one year to simulate equilibrium) for another grouper *(Epinephelus sexfasciatus)* from the Philippines. The data are used to illustrate the operation of the routine in Program FB 13 for the rapid computation of mean lengths and the effects of the omission of large fish on the estimated values of Z.

1) Load sides 1 and 2 of Program FB 13

2) Store L', ΔL and initialize; keystrokes: 12 ↑ 2 f b

3) Enter frequencies needed for computation of the mean length and its standard error

   Keystrokes: 143 A 118 A 61 A 50 A 32 A 17 A 4 A

4) Compute the mean length and its standard error

Keystroke	Results	
B	425	(n)
	15.951	($\bar{L}$)
	3.018	($s.d._{(L)}$)
	0.146	($s.e._{(\bar{L})}$)

5) Now recompute the mean length after adding the last frequency, which was omitted in step (3).

Keystroke	Results	
4 AB	429	(n)
	16.054	($\bar{L}$)
	3.186	($s.d._{(L)}$)
	0.154	($s.e._{(\bar{L})}$)

6) Finally, compute Z for the two values of $\bar{L}$ (15.951 and 16.054) using the same keystroke sequence as given in Case I of this Example.
   The results should be Z values equal to 1.868 when the last frequency is omitted, and 1.93 when it is included.

This Example illustrates that the values of Z obtained from mean lengths are quite sensitive to the inclusion of the few fish in the largest size classes (see text for a discussion of the problem that this represents). It will also be noted that an extraneous knowledge of L' is required by this method, as opposed to what occurs when semi-graphical methods are used (cumulative plots, length-converted catch curves).

EXAMPLE 5.4

Estimation of Z using Jones' method.

Data from Table 5.4

Computations

1) Read side 1 of Program FB 11.

2) Enter L_∞, D, ΔL, L_{max} and initialize

   Keystrokes: 30.9 ↑ 1 ↑ 2 ↑ 26

3) Enter all catches, starting with that corresponding to the largest fish

Keystrokes	Results	
4 A	1.589	In $(L_\infty^D - L_i^D)$
	1.386	In C (L_i, ∞)
4 A	1.932	...
	2.079	....
17 A	2.186	....
	3.219	....
etc.		

4) Plot the In $(L_\infty^D - L_i^D)$ and In C (L_i^D, ∞) data as in Fig. 5.2 and select points to be included in linear regression (see Fig. 5.2 for points selected).

5) Re-initialize, and re-enter data

   Keystrokes: 30.9 ↑ 1 ↑ 2 ↑ 26 f a 4 A 4 A R/S 17 A R/S 32 A R/S 50 A R/S 61 A R/S 118 A R/S 143 A R/S 161 A R/S

6) Compute parameters of linear regression and estimate Z/K.

Keystroke	Results	
E	0.998	(r^2)
	−5.235	(a)
	3.846	(b = Z/K)

7) Calculate Z through multiplication of Z/K with K.

Keystroke	Result	
.51 x	1.961	(Z)

As will be shown further below, this result (Z = 1.961) is very similar to those obtained using a number of different methods (i.e., various forms of the length-converted catch curve) if the same data points are included in the analysis.

EXAMPLE 5.5

Estimation of Z using Sparre's method.

Data from Table 5.4

Computations

1) Read side 1 of Program FB 11.

2) Enter L_∞, D, ΔL, L_{max} and initialize

   Keystrokes: 30.9 ↑ 1 D 26 f a

3) Enter K

   Keystrokes: 30.9 ↑ 1 ↑ 2 ↑ 26 fa

4) Enter all catches, starting with that corresponding to the largest fish

Keystrokes	Results	
4 B	3.611	t'_{L_i}
	1.386	ln C (L_i, ∞)
4 B	2.940	....
	2.079	....
17 B	2.441	....
	3.219	....
etc.		

5) Plot the t'_{L_i} and ln C (L_i, ∞) data as in Fig. 5.3 and select points to be included in the linear regression (see Fig. 5.3 for points selected).

6) Re-initialize and re-enter data

   Keystrokes: 30.9 ↑ 1 ↑ 2 ↑ 26 f a .51 STO 1 4 B 4 B R/S 17 B R/S 32 B R/S 50 B R/S 61 B R/S 118 B R/S 143 B R/S 161 B R/S

7) Compute parameters of linear regression and estimate Z

Keystroke	Results	
E	0.998	(r^2)
	7.959	(a)
	−1.961	(b = −Z)

It will be noted that the result (Z = 1.961) is exactly the same as that obtained using Jones' method.

EXAMPLE 5.6

Estimating Z from length-frequency data using a length-converted catch curve in which the "piling-up" effect is corrected for by the use of growth rates.

Data from Table 5.4.

1) Use Program FB 9 to compute the growth rate (dl/dt) and relative ages (t') corresponding to the class midpoints in Table 5.4; also compute ln N(dl/dt) for each class midpoint, and record results as shown here.

Class midpoint (cm)	N	dl/dt	ln N (dl/dt)	t'	Remarks
5	5	13.21	4.190	0.346	
7	29	12.19	5.868	0.504	not used, ascending
9	114	11.17	7.149	0.675	part of curve
11	161	10.15	7.399	0.863	
13	143	9.129	7.174	1.07	
15	118	8.109	6.864	1.30	
17	61	7.089	6.069	1.57	
19	50	6.069	5.715	1.87	used, descending
21	32	5.049	5.085	2.23	straight part of
23	17	4.029	4.227	2.67	catch curve
25	4	3.009	2.488	3.25	
27	4	1.989	2.074	4.06	

2) Plot these data as in Fig. 5.5 and select points to be included in regression.

3) Compute parameters of a length-converted catch curve using linear regression (standard Pac SDO 3A), using t' for the x-axis and ln N·(dl/dt) for the y-axis. When x- and y-values (see above) have been entered, compute parameters of catch curve:

Keystroke	Results	
C	0.974	(r^2)
	9.087	(a)
	−1.831	(b)

Thus Z is equal to 1.83, a value close to those estimated from the same data set using different methods (see Examples 5.3, 5.4 and 5.5).

It will also be noted that the plot in Fig. 5.4 gives no reason to delete the last point (that corresponding to $t' \approx 4$ years), which however, had to be deleted in Figs. 5.2 and 5.3.

EXAMPLE 5.7

Showing that not correcting for the "piling-up" effect leads to negatively biased estimates of Z.

Data from Example 5.6

1) Use the linear regression program (standard Pac SDO 3A) to estimate the parameters of a plot of ln N on t', using only the values of N and t' in Example 5.6 corresponding to fishes with class midpoints ranging from 13 to 27 cm. Read sides 1 and 2 of SDO 3A, enter data, with $x = t'$ and $y = \ln N$.

2) Estimate parameters of regression line

Keystroke	Results	
C	0.951	(r^2)
	6.331	(a)
	−1.322	(b)

3) Since the value of K in Table 5.4 was equal to 0.51 and D = 1, Z is obtained by adding 0.51 to the absolute value of the slope or

Keystrokes	Result	
CHS .51 +	1.832	(Z)

As might be seen from Example 5.6 Z = 1.83 is a value that was obtained when directly accounting for the "piling-up" effect. Thus, not accounting for this effect indeed leads to slopes with absolute values equal to Z − KD.

EXAMPLE 5.8

Estimation of Z from a length-converted catch curve (using N/Δt) with subsequent improvement using Sparre's method.

Data from Table 5.4

Computations

1) Read sides 1 and 2 of Program FB 12

2) Enter L_∞, ΔL, K, D and initialize

Keystrokes: 30.9 ↑ 2 ↑ .51 ↑ 1 f a

3) Enter class midlengths and frequencies

Keystrokes	Results	
5 ↑ 5A	3.497	(ln (N/Δt))
	0.346	(t')
7 ↑ 29A	5.174	(ln (N/Δt))
	0.504	(t')
etc.	. . .	

Continued

EXAMPLE 5.10

Estimation of K and Z in a stock of the white goby *(Glossogobius giurus)* using Ebert's method as improved by Saila and Lough (1981).

Data from Table 5.8

Computations

1) By inspection of the data in Table 5.8, the month of recruitment is set as August (1958); and the length at recruitment set at 8 cm (as the mean length in the two most abundant length classes in August).

2) Two sampling months, September (1958) and June (1959) are selected which, together with August as month of recruitment, provide, using Table 5.7, values of t_1 and t_2 equal to 0.091 and 0.909, respectively.

3) The mean lengths $\overline{\overline{L}}_1$ and $\overline{\overline{L}}_2$ are computed by combining the monthly means for August, September and October, and the means for May, June and July, respectively (see Table 5.8). (Combining the samples has the effect of reducing the effects of sampling variability on the estimates of $\overline{\overline{L}}_1$ and $\overline{\overline{L}}_2$).

4) $L_{(\infty)}$ is estimated from the largest fish in Table 5.8 as 26.5 cm.

5) Read sides 1 and 2 of Program FB 13 and enter parameters estimated above.

Keystrokes: 8 ↑ 9.5 ↑ 16.8 ↑ 1 f a .091 ↑ .909 ↑ 26.5 R/S

6) Enter initial guess of Z and iterate

	Keystroke	Results	
	1E	1	(Z_1)
		1.103	(Z_2)*
		.....	etc.
		0.686	(K)
value reached after 8 iterations		3.143	(Z final)

*When the second value of Z has a negative sign, this means that the initial guess of Z was much too high. In this case, press R/S, set STO 0 to 8 to zero, and start again with step 5.

EXAMPLE 5.11

Estimating Z/K from length-frequency data.

Case I

Thompson and Munro (1974) estimated $L_{(\infty)}$ from L_{max} in *Epinephelus striatus* as approximately 90 cm, while K could not be estimated reliably. The mean length at unexploited oceanic banks off Jamaica is 69 cm, with $L' = 60$ cm. What is the value of M/K (special VBGF)?

Computation

Keystrokes	Results	
90 ↑		
69 −		
69 ↑		
60 − ÷	2.33	(M/K)

Let's assume the mean length of *Epinephelus striatus* in a certain exploited area is 65 cm, with $L_{(\infty)} = 90$ cm and $L' = 60$. What is the value of Z/K?

Computation

Keystrokes	Results	
90 ↑		
65 −		
65 ↑		
60 − ÷	5.00	(Z/K)

Case II

The data in Table 5.4 and a value of $L' = 12$ cm are used to compute Z/K using equations (5.35) and (5.36). First the value of C^2 is computed, using parameter values computed with Program FB 13 (see Example 5.3 for computation of mean length (16.054) and $s.d._{(L)}$ (3.186) and equation (5.35):

Keystrokes	Results	
3.186 x^2		
16.054 ↑ 12		
− x^2 ÷	0.618	(C^2)

Then use value of C^2 to compute Z/K, using equation (5.31)

Keystrokes	Results	
.618 ↑		
2 x 1 ↑		
.618 − ÷	3.236	(Z/K)

This value of Z/K, when multiplied with the value of K given in Table 5.4 (0.51) leads to an estimate of Z = 1.65 which is lower than that obtained using other methods (see Examples 5.3 to 5.9)(see text).

Case III

The length-frequency data in Table 5.4 have been drawn in Fig. 5.14. It might be seen that, beyond L' the frequencies decline exponentially, a feature which is made more visible by the exponential curve superimposed on the data. Hence, using Fig. 5.14 as reference, we infer that Z/K is equal to or higher than 2, a fact substantiated by all previous analyses.

Table 6.1. Variants of equations (6.1) and (6.2) suggested by various authors. See also Program FB 16 and Example 6.1. Adapted from Jones (1977).

Reference	Type of sampling[a]	Estimates of population size (N)	Estimates of standard error of N
(A) Bailey (1951)	Direct	$N = \frac{T \cdot n}{m}$	$s.e._{(N)} = \left(\frac{T^2 n (n-m)}{m^3}\right)^{1/2}$
(B) Bailey (1952)	Direct	$N = \frac{T(n+1)}{m+1}$	$s.e._{(N)} = \left(\frac{T^2 (n+1)(n-m)}{(m+1)^2 (m+2)}\right)^{1/2}$
(C) Chapman (1951) Schaefer (1951)	Direct	$N = \frac{(T+1)(n+1)}{m+1} - 1$	$s.e._{(N)} = \left(N^2\left[\frac{N}{nT} + 2\left(\frac{N}{nT}^2\right) + 6\left(\frac{N}{nT}\right)^3\right]\right)^{1/2}$
(D) Bailey (1951)	Inverse	$N = \frac{n(T+1)}{m} - 1$	$s.e._{(N)} = \left(\frac{(T-m+1)(N+1)(N-T)}{m(T+2)}\right)^{1/2}$

[a]"Direct" sampling means that sampling is continued until a predetermined sample size (n) is obtained; "inverse" sampling means that sampling is carried out until a predetermined number of tagged animals (m) is obtained.

STANDING STOCK ESTIMATION WITH THE SWEPT-AREA METHOD

In areas where the bottom is smooth enough for trawling, the standing stock sizes of demersal fishes (B) can be obtained from the relationship

$$B = \frac{\overline{c}/f \cdot A}{a \cdot X_1} \qquad \ldots 6.3)$$

where $\overline{c}/f$ is the mean catch/effort obtained during a survey (or in a given stratum), A the total survey (or stratum) area and a the area swept by the trawl in one unit of effort (e.g., one hour), X_1 being the proportion of the fish in the path of the net which are actually retained by it ($1/X_1$ may be termed "escapement factor").

For trawlers such as those used in Southeast Asia, a value of $X_1 = 0.5$ is commonly used in survey work (Isarankura 1971; Saeger et al. 1976; SCSP 1978), and for the Gulf of Thailand at least, there is some evidence that this value is appropriate (Pauly 1980d).

For the western Indian Ocean south of the equator, it has been suggested, on the other hand, that all fish in the path of the trawl might be caught, which corresponds to $X_1 = 1$ (Gulland 1979, p. 3), a figure also suggested by Dickson (1974). The difference between these two values of X_1 (0.5 & 1) is difficult to resolve and attempts should be made, wherever possible, to substantiate the values of X_1 used in an assessment by as much corroborative evidence as possible, because the value of X_1 used in equation (6.3) has a very strong effect on standing stock estimates. Using $X_1 = 0.5$, for example instead of $X_1 = 1$ doubles the estimated value of B.

The surface swept by the gear in one unit of effort is computed from the expression

$$a = t \cdot V \cdot h \cdot X_2 \qquad \ldots 6.4)$$

where V is the speed of the trawler, over ground, when trawling, h is the length of the trawl's head rope (see Fig. 6.1), t is the time spent trawling and X_2 is a fraction equal to the effective width of the net divided by the length of the head rope.

In the Caribbean, a value of $X_2 = 0.6$ was used by Klima (1976), while in Southeast Asian waters values of X_2 ranging from 0.66 (Shindo 1973) to 0.4 (SCSP 1978) have been proposed, with 0.5 possibly being (for Southeast Asian waters at least) the best compromise (Pauly 1980d).

Gulland (1969) showed that

$$F = \frac{a \cdot f X_1}{A} \qquad \ldots 6.5)$$

i.e., that the fishing mortality exerted on a given stock is equal to the product of the area swept in a year by the combined activity of a fleet of trawlers ($a \cdot f$) times X_1, divided by the total area inhabited by the stock in question. The swept area method, thus, can be used both to estimate standing stocks and fishing mortality (Example 6.2). The method has been adapted, under certain assumptions pertaining to the behavior of fish, to line fishing over coral reefs (Wheeler and Ommaney 1953; Gulland 1979).

POPULATION SIZE FROM CATCH AND FISHING MORTALITY

Sekharan (1974), based on Beverton and Holt (1957) showed that:

$$\frac{Y}{F} = \bar{N} \cdot \bar{\bar{W}} \qquad \ldots 6.6)$$

from which one obtains

$$\frac{Y}{F} = \bar{B} \qquad \ldots 6.7)$$

where Y is the annual catch, in weight, F the instantaneous fishing mortality rate (on an annual basis), $\bar{N}$ the mean number of fish in the stock, $\bar{\bar{W}}$ their mean weight, and $\bar{B}$ the mean biomass in the course of a year.

This relationship, simple as it is, can also be used with great advantage, e.g., to estimate the standing stock of exploited coral reef fish, as suggested by Marshall (1980) on the basis of difficulties with the standard methods for estimating the biomass of coral reef fish (reviewed in Russel et al. 1978).

Equation (6.7) obviously can be rewritten

$$F = Y/\bar{B} \qquad \ldots 6.8)$$

which can be used to estimate fishing mortality from the catch and an independent estimate of $\bar{B}$, as obtained from the swept area method (see above) or by an acoustic survey. (See Example 6.3).

POPULATION SIZE AS ESTIMATED BY LESLIE'S METHOD

When the fish population of a body of water is fished down so rapidly that the effects of recruitment, immigration and natural mortality can be neglected, we have

$$c/f = qN_o - q\Sigma_t \qquad \ldots 6.9)$$

which expresses that catch per effort (c/f) in a given time period (t) plotted against the cumulative catch up to that period (Σ_t) gives a straight line, the slope of which is an estimate of the catchability coefficient (q) and whose intercept qN_o, divided by q provides an estimate of N_o, the population size prior to its reduction by fishing (Example 6.1, Case I, Table 6.2). When the special case applies that effort is constant for the period under consideration, the c/f values can be replaced by catch values, in which case F is estimated instead of q[a] (Example 6.4, Case II, Table 6.3).

Table 6.2. Successive sample sizes of reef eels *(Kaupichthys hyoproroides)* from an isolated Bahamian patch reef.[a]

Samples	No. of fish collected	Effort[b]
A	5	1
B	4	1
C	3	1
D + E	1	2

[a]Based on data in Smith (1973, Table 5, Station I).
[b]The unit of effort is "22 fluid ounces of emulsified rotenone applied from a plastic squeeze bottle".

Table 6.3. Successive sample sizes of bluehead wrasses *(Thalassoma bifasciatum)* from an isolated Bahamian patch reef.[a]

Samples	No. of fish collected	Effort[b]
A	8	1
B	5	1
C	4	1

[a]Based on data in Smith (1973, Table 6, Station X).
[b]The unit of effort is "22 fluid ounces of emulsified rotenone applied from a plastic squeeze bottle".

[a]This feature of the model was pointed out by E. Ursin (pers. comm.).

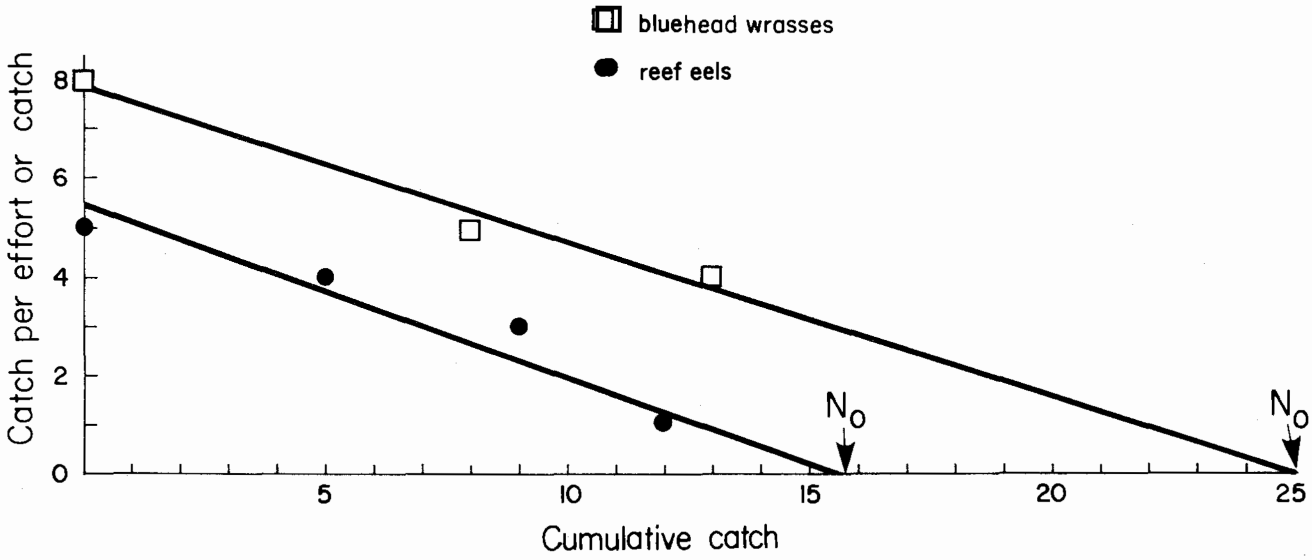

Fig. 6.1. Leslie plots for reef eels *(Kaupichthys hyoproroides)* and bluehead wrasses *(Thalassoma bifasciatum)* from an isolated Bahamian reef patch, with estimates of virgin population sizes (based on data in Tables 6.2, 6.3 and Example 6.4).

Recommended reading: For reviews of some of the voluminous literature on tagging see Ricker (1975) and Jones (1977). Kato and Yamada (1975) give application of a rather sophisticated method (Jolly-Seber) to a stock of seabreams in southern Japan, while Yap and Furtado (1980) give an application of various methods to a stock from a Malaysian river. The swept-area method is discussed in more detail in Gulland (1969). Ricker (1975) gives a discussion of Leslie's and related methods with several examples.

Suggested research topics: Use several methods to estimate population sizes on reefs, in enclosed or semi-enclosed water bodies, determine which methods give comparable results and why. Compare the population size of adjacent areas in relation to different fishing intensities.

EXAMPLE 6.1

Petersen population estimate of tigerfish *(Hydrocynus vittatus)* in the Sanyati Gorge, Lake Kariba, Zimbabwe.

Langerman (1980) conducted marking and tagging experiments on tigerfish *(Hydrocynus vittatus)* (Fam. Characinidae) in Sanyati Gorge, Lake Kariba, and concluded that under the conditions in and around that reservoir, tagging was superior to marketing with fluorescent dye. In an experiment conducted in 1979, T = 984 fish were tagged and released. Upon fishing one day later with a chartered vessel, 3,253 fish were caught, 68 of which bore tags. If the various assumptions involved in Petersen population estimates were met, what was the population size and its standard error?

Computation

1) Read sides 1 and 2 of Program FB 16

2) Enter data and initialize

Keystrokes 984 ↑ 3253 ↑ 68 f a

3) Calculate population size using different formulae (see Table 6.1)

Keystrokes	Results	
A	47,073	(N)
	5,648	$s.e._{(N)}$
B	46,405	(N)
	5,487	$s.e._{(N)}$
C	46,451	(N)
	5,680	$s.e._{(N)}$

Since sampling was direct, option D (inverse sampling) need not be considered. Note that the results using the three sets of equations give similar results; Langerman's paper also suggests that the assumptions involved in Petersen estimates were reasonably met. The population of tigerfish in the part of Sanyati Gorge for which the experiment was representative was about 46,600 ± 560.

EXAMPLE 6.2

Use of the swept-area method to estimate demersal standing stock size and fishing mortality in San Miguel Bay, Philippines.

A) Standing Stock

Vakily (1982) gives the following data for typical trawlers operating in San Miguel Bay, Philippines:

Trawling speed 2 knots (conversion knots to km/h : kn • 1.83 = km/h)
Length of headrope 17 m (headrope length/actual spread of net = 0.5 = X_2)
Fraction of fish in the part of the net that are retained by the gear (X_1) = 0.50 (assumed)
Mean catch per hour (in 1979-80): 33.5 kg
Total area of San Miguel Bay = 840 km^2

The estimation of the surface swept during one hour (a) is thus (according to equation 6.4):

Keystrokes	Results	
2 ↑ (knots)		
1.83 X (convers. to km/h)		
0.017 X (headrope, in km)		
.5 X (X_2)	0.031	(a, in km^2)

The standing stock (B) is then obtained via equation (6.3) and

0.0335 ↑ ($\overline{c}/f$, in tonnes)		
840 X (area of SM Bay)		
X ⇋ Y (put a in display)		
.5 X ÷ (use X_1 and finish)	1,809.065	(B, in tonnes)

B) Fishing mortality

Vakily (1982) gives 5,966 km^2 for the surface area swept annually by all trawlers in San Miguel Bay. The fishing mortality induced by trawlers according to equation (6.5) is thus

Keystrokes	Results	
5,966 ↑ (area swept annually)		
0.5 X (X_1)		
840 ÷ (area of bay)	3.551	(F)

EXAMPLE 6.3

Applications of the relationships linking catch, fishing mortality and mean standing stock size.

Case 1: Estimation of average standing stock

Sekharan (1974) gives for oil sardine *(Sardinella longiceps)* and for mackerel *(Rastrelliger kanagurta)* from southwestern Indian waters the following data (all on an annual basis):

	Z	M	F	Y (tonnes)
S. longiceps	1.66	1.12	0.54	210,000
R. kanagurta	2.05	0.90	1.15	65,000

What are the mean standing stock sizes?

Computation

Keystrokes	Results
210,000	
↑ .54 ÷	388,889 ($\bar{B}$)
	(or ≈ 390,000 tonnes)
65,000 ↑	
1.15 ÷	56,522 ($\bar{B}$)
	(or ≈ 57,000 tonnes)

Case 2: Estimation of fishing mortality

Anon. (1979b, Table 12, p. 161) gives for carangid spp. *(Trachurus* spp., *Caranx rhonchus)* for 1970 to 1976 a mean annual catch of 465,000 t. Acoustic surveys conducted in the region under consideration (West African Coast from Mauritania to Liberia) provided an average carangid standing stock estimate of 4,200,000 t. What is the fishing mortality inflicted on carangids?

Computation

Keystrokes	Results
465,000 ↑	
4,200,000 ÷	0.11 ($\bar{F}$)

As concluded in Anon. (1979b) "for fish of moderate longevity, this is a low but not insignificant value which suggests that stocks are lightly to moderately exploited."

EXAMPLE 6.4

Estimation of unfished population size (N_o) by means of Leslie's equation.

Case I: effort changing
Data from Table 6.2

Computation

1) Read side 1 of Program FB 17

2) Initialize and enter catch and effort data

Keystrokes: f a 5 ↑ 1 A 4 ↑ 1 A 3 ↑ 1 A 1 ↑ 2 A

3) Calculate r^2, q and N_o

Keystrokes	Results	
E	0.88	(r^2)
	5.39	($a = q\ N_o$)
	−0.35	($b = -q$)
	15.46	(N_o)

Case II: effort constant
Data from Table 6.3

Computation

1) Read side 1 of Program FB 17

2) Initialize and enter catch data

Keystrokes: f a 8 B 5 B 4 B

3) Calculate r^2, F and N_o

Keystrokes	Results	
E	0.98	(r^2)
	7.86	($a = F\ N_o$)
	−0.31	($b = -F$)
	25.05	(N_o)

Note the interesting result that the catchability (q) is similar with both fishes i.e., their susceptibility to rotenone is similar (see also Fig. 6.1).

7. Estimation of Past Population Sizes Using Virtual Population Analysis and Cohort Analysis

INTRODUCTION

The following four methods form an extremely powerful set of tools for the analysis of catch data from which reliable estimates of past population sizes (in numbers) and fishing mortality can be derived.

These four methods are:

— Virtual population analysis (VPA)
— Cohort analysis
— Length cohort analysis
— Length-structured VPA

Beverton and Holt (1957, p. 179) showed that the catch (C_i) from a population during a unit time period (i) is equal to the product of the population size at the beginning of the time period (N_i) times the fraction of the deaths caused by fishing, times the fraction of total deaths, or

$$C_i = \frac{F_i}{Z_i}(1 - e^{-Z_i})\ N_i \qquad \ldots 7.1)$$

where F_i is the fiching mortality in the ith period
M is the natural mortality, generally assumed constant for all periods
and $Z_i = F_i + M$

The version of Beverton and Holt's catch equation which has become most widely used for stock assessment purposes, however, is

$$\frac{N_{i+1}}{C_i} = \frac{Z_i \cdot e^{-Z_i}}{F_i\,(1-e^{-Z_i})} \qquad \ldots 7.2)$$

also written

$$\frac{C_i}{N_{i+1}} = \frac{F_i}{Z_i}(e^{Z_i} - 1) \qquad \ldots 7.2a)$$

which is the equation in Gulland's (1965) virtual population analysis and which can be derived from (7.1) by substituting for N_i the relationship

$$N_i = N_{i+1} \cdot e^{Z_i} \qquad \ldots 7.3)$$

Equation (7.2) is used with catch-at-age data from the whole of a fishery, and covering most of the life span of a given cohort* (thus VPA is used to estimate *retroactively* the size of *past* cohorts), an estimate of M and a (guessed) value of the fishing mortality that affected the oldest age group of a given cohort (terminal F, or F_t). The terminal fishing mortality (F_t) and the terminal catch (C_t) are used to estimate the size of the terminal population (N_t), either from

$$N_t = \frac{C_t \cdot Z_t}{F_t\,(1-e^{-Z_t})} \qquad \ldots 7.4)$$

or from

$$N_t = C_t \cdot Z_t / F_t \qquad \ldots 7.5)$$

---

*A cohort is a group of fish born at the same time, and exposed throughout their lives to the same mortalities.

Generally, equation (7.4) is used when the cohort is not extinct past N_t (and C_t), while equation (7.5) is used when C_t includes the last remnants of a cohort (Mesnil 1980). Then, using N_t as initial value of N_{i+1}, F_i and N_i values are estimated sequentially from older to younger age groups ("backward") by repeatedly solving equations (7.2) and (7.3), respectively.

Several authors have investigated the properties of equation (7.2) and its variants and their findings are summarized in Table 7.1.

Table 7.1. Review of work on the sensitivity of virtual population analysis and cohort analysis.

Equation No.	Author of equation	Sensitivity analysis by	Property investigated	Main result(s)
(7.1)	Beverton and Holt (1957) based on Baranov (1918)	Jones (1961)	Convergence of F-values toward true solution	"Backward" computation ensures convergence; forward computation leads to divergence
(7.1)	Beverton and Holt (1957) based on Baranov (1918)	Murphy (1965), Tomlinson (1970)	Convergence of F-values toward true solution	Confirmed Jones' result
(7.2)	Gulland (1965)	Pope (1972)	Errors due to erroneous F_t	Rapid convergence toward true F granted F_i's are high
			Sampling error of catches	Graph given to assess effects of sampling errors on F_i's
(7.2)	Gulland (1965)	Agger et al. (1971)	Sampling error of catches	"Relative error of F is about half the relative error of that found in the catches"
(7.2)	Gulland (1965)	Agger et al. (1973)	Erroneous M value	If M is overestimated, F is generally underestimated, and conversely
(7.2)	Gulland (1965)	Ulltang (1977)	M varying between years, and other properties	Stock sizes will be under- or overestimated, but relative changes will be approximately correct; see original paper for other properties
(7.2)	Gulland (1965)	Sims (1982)	Effects of seasonal fishing	Effects not severe unless M and/or F are not very high
(7.11)	Pope (1972)	Pope (1972)	Choice of M	Value of M > 0.3 for one time increment (generally 1 year) should not be used
(7.9)	Jones (1974)	Jones (1979)	Choice of L_∞ and M/K	Graphs given showing influence of L_∞ and M/K on results and "critical" value of M/K determined
(7.9)	Jones (1974)	Sparre (1979)	Choice of M exponential body growth* emigration* difference with VPA version	The same results were obtained independently: No limitation as to value of M; differs herein from cohort analysis; results highly sensitive to length increments: with large increments, F is overestimated and stock size is underestimated
(7.9)	Jones (1974)	Pauly (this chapter)	Choice of M difference with VPA version (effect of length class increment)	

*See Sparre (1979) for this part of his results.

DERIVATION OF A LENGTH-STRUCTURED VPA MODEL

Generalizing equation (7.2) for any time interval (Δt) gives

$$\frac{N_{i+\Delta t}}{C_i} = \frac{Z_i \cdot e^{-Z_i \cdot \Delta t}}{F_i\,(1-e^{-Z_i \cdot \Delta t})} \qquad \ldots 7.6)$$

or

$$C_i = N_{i+\Delta t} \frac{F_i}{Z_i} (e^{Z_i \Delta t} - 1) \quad \ldots 7.6a)$$

with all other parameters defined as in (7.2); these equations allow for structuring catch data in terms of length, rather than time intervals.

Converting length to age requires the use of a mathematical expression of fish growth. Used here is the generalized VBGF (see Chapter 4). Thus, any age t_1 pertaining to a length L_1 can be obtained from

$$t_1 = \frac{-\ln\left(1 - \frac{L_1{}^D}{L_\infty{}^D}\right)}{KD} + t_o \quad \ldots 7.7)$$

and similarly for age t_2, pertaining to L_2. From the length-age relationships for L_1 and L_2, Δt is obtained as the difference between t_2 and t_1, or after some rearrangement

$$\Delta t = \frac{\ln\left(\frac{L_\infty{}^D - L_1{}^D}{L_\infty{}^D - L_2{}^D}\right)}{KD} \quad \ldots 7.8)$$

which can be substituted for Δt in equation (7.6).

Thus, given catch-at-length data from a stock with stable age distribution, equation (7.6) can be used in a fashion similar to equation (7.2) to estimate, starting from a (guessed) terminal fishing mortality (affecting the largest length group) the number of fish in the smaller size classes and the fishing mortalities affecting them.

When equation (7.6) is used in conjunction with values of Δt that are not constant (i.e., when the Δt values are computed from length-converted ages), the results obtained will not apply to a specific cohort of fish, but rather pertain (for a given value of M) to the population sizes (per length class) that must have existed, on the average, for the observed catch to have been produced by the estimated values of F. The method is thus analogous to Jones' length cohort analysis (Jones 1974, 1979, 1981) which, in terms of the generalized VBGF is expressed by

$$N_1 \approx (N_2 \cdot X_L + C_{1,2}) X_L \quad \ldots 7.9)$$

where

$$X_L = \left(\frac{L_\infty{}^D - L_1{}^D}{L_\infty{}^D - L_2{}^D}\right)^{M/(2\,KD)} \quad \ldots 7.10)$$

where $C_{1,2}$ is the number of fish caught in a given time period with stable age distribution with length between L_1 and L_2 and where N_1 and N_2 represent the population size (in number) with length L_1 and L_2, respectively.

Jones' length cohort analysis is particularly helpful in that it requires, in addition to the value of D (see Chapter 4), a knowledge of only 2 parameters, L_∞ and the ratio M/K; the latter, as shown by Beverton and Holt (1959) tends to vary less between different groups of fish than either K or M alone (see also Chapter 5). However, a problem with Jones' method is that it is derived from the approximate "cohort analysis" of Pope (1972) i.e.,

$$N_i \approx N_{i+1} \cdot e^M + C_i \cdot e^{M/2} \quad \ldots 7.11)$$

through generalizing for any time interval i.e.,

$$N_i \approx N_{i+\Delta t}\, e^{M\Delta t} + C_i\, e^{M\Delta t/2} \qquad \ldots 7.12)$$

Since equation (7.6), which gives precise results and the approximation in (7.9) can both be used to obtain estimates of population size and fishing mortality from the same set of catch-at-length data, equation (7.6) can be used to assess the closeness of the approximation involved in (7.9). This is done in the example in Table 7.2. As might be seen in this table, the combination of parameter values used generates a mean difference between the results obtained with Jones' method and those obtained using equation (7.6) of only 0.7% for the population estimates and 2.2% for the fishing mortality estimates.

However, regrouping the catch data in Table 7.2 into larger and larger length class intervals produces increasing differences between the fishing mortality estimates (and population estimates) obtained by the two methods (Table 7.3, Fig. 7.1), suggesting that Jones' length cohort analysis may indeed be quite sensitive to coarse groupings of the catch data.

Varying the value of natural mortality used for the analysis produces, on the other hand, virtually no additional differences between the results of the two methods, i.e., the difference remained close to 2% for M = 0.1 to M = 1.0.

DISCUSSION OF THE LENGTH-STRUCTURED VPA MODEL

The main drawback of the length-structured VPA proposed here (equations 7.6 and 7.6a) and of length cohort analysis (equation 7.9) is the necessary assumption of a stable age distribution, which

Table 7.2. Comparison of results obtained using Jones' length cohort analysis and VPA using catch-at-length data on *Merluccius merluccius* off Senegal.

Length (cm)	Catch[a] ('000)	Population ('000) A	Population ('000) B	Population ('000) C (% diff.)	Fishing mortality (annual basis) A	Fishing mortality (annual basis) B	Fishing mortality (annual basis) C (% diff.)
6	1,823	98,919	98,238	−0.7	0.040	0.040	0.0
12	14,463	84,393	83,801	−0.7	0.386	0.392	1.3
18	25,227	59,476	59,010	−0.8	1.066	1.111	4.2
24	8,134	27,623	27,428	−0.7	0.647	0.661	2.2
30	3,889	15,968	15,849	−0.7	0.491	0.500	1.8
36	2,959	9,861	9,782	−0.8	0.592	0.605	2.4
42	1,871	5,501	5,455	−0.8	0.647	0.666	3.1
48	653	2,819	2,797	−0.8	0.385	0.392	1.8
54	322	1,691	1,678	−0.8	0.288	0.293	1.7
60	228	1,057	1,048	−0.9	0.307	0.313	1.6
66	181	621	616	−0.8	0.401	0.412	2.7
72	96	314	312	−0.6	0.389	0.399	2.6
78	16	149	148	0.0	0.110	0.111	0.9
84 (L_{ter})	46 (C_t)	92 (N_t)	92 (N_t)	–	0.280 (F_t)	0.280 (F_t)	–

[a]From Table 6 in Anon. (1978b) who also provided (for D = 1): L_∞ = 130 cm, K = 0.1 and M = 0.28.

A = Jones' length cohort analysis.
B = New method (VPA with length-at-age data).
C = (B/A − 1) · 100 = C (% diff.).

Table 7.3. Comparison of results using Jones' length cohort analysis (A) and length-structured VPA (B) (24-cm classes) (see also Table 7.2).

Length (cm)	Catch ('000)	Population size A	Population size B	Population size % diff.	Fishing mortality A	Fishing mortality B	Fishing mortality % diff.
12	51,713	93,010	84,379	−9.3	0.487	0.646	32.6
36	5,805	11,592	10,265	−11.4	0.357	0.482	35.0
60	521	1,236	1,087	−12.1	0.234	0.308	31.6
84	46 (L_{ter})	92 (N_t)	92 (N_t)	—	0.280 (F_t)	0.280 (F_t)	—
>84	—	—	—	—	—	—	$\bar{x}$ = 33.1

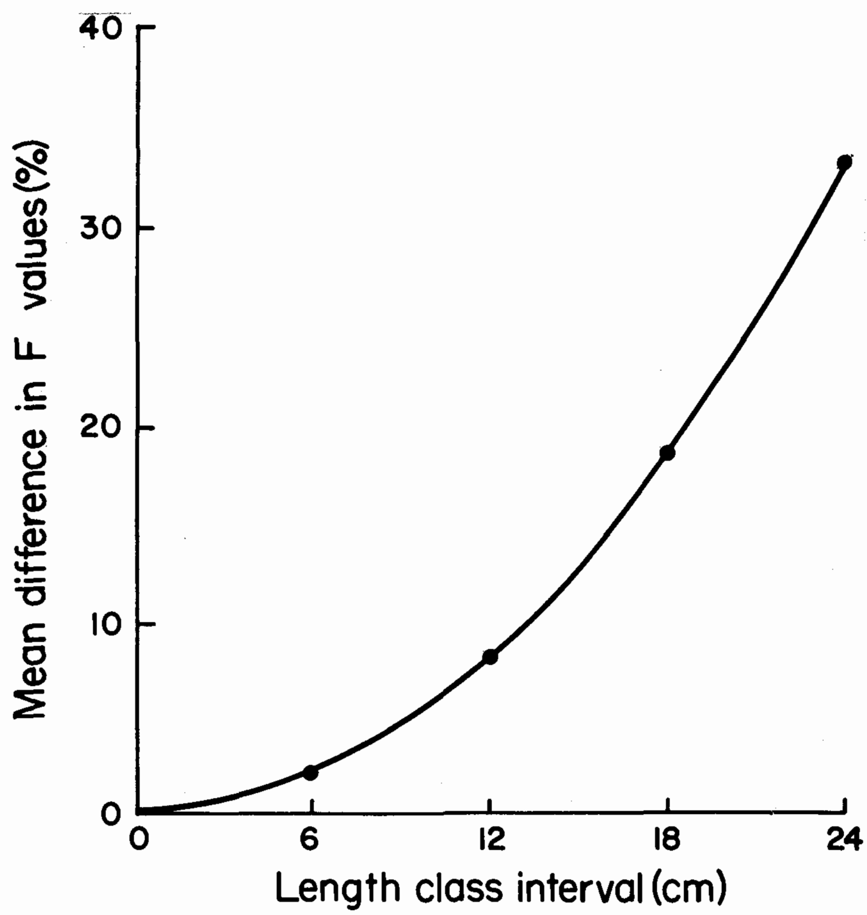

Fig. 7.1. Relationship between the length class interval in which catch data are grouped and the percentage difference between the results obtained using Jones' length cohort analysis and length-structured VPA. The calculation of the percentage difference is illustrated in Tables 7.2 and 7.3, which also document two of the four points plotted in this figure.

is not required in age-structured VPA. However, a number of methods have become widely accepted and used for stock assessment which rest on the same assumption of a stable age distribution, such as the estimation of total mortality from catch curves or from the mean length of fish in catch samples (see Chapter 5). As in the case of the procedure recommended for use with the above methods, a stable age distribution can be simulated in the case of length-structured VPA or length cohort analysis by averaging catch data for a length of time during which recruitment and fishing mortality can be assumed to have been constant.

Jones' length cohort analysis has the following advantages over the new method proposed here:

- it does not require separate estimates of K and M, but only of the ratio M/K, and
- it provides direct solutions, i.e., the solution does not need to be obtained iteratively, as in the case of solutions to (7.6)

On the other hand, Jones' method appears quite sensitive to coarse grouping of the catch data, a feature which may limit the applicability of the method where it may be most needed, e.g., when working with catch statistics of commercially graded penaeid shrimps (see Jones and Van Zalinge 1981).

APPLICATIONS OF AGE-STRUCTURED VPA AND COHORT ANALYSIS

Following are applications of the four methods in Table 7.4. Example 7.1, based on the data in Table 7.5, presents an application of VPA to Moroccan sardines (see also Fig. 7.2). Example 7.2, based on the data in Table 7.6, presents an application of cohort analysis to the Peruvian anchoveta. As might be seen from Table 7.6, the estimates of fishing mortality in young fish obtained by cohort analysis (and hence, by VPA) are virtually independent of the first guess of terminal mortality. This property is most useful, and is one of the main reasons why these methods have become so popular, at least around the North Atlantic.

Table 7.4. Some properties of four methods for the analysis of sequential catch data.

data requirement \ solution	iterative, but precise	direct, but approximate
catch-at-age data (single cohort)	VPA Murphy (1965) Gulland (1965)	Pope's cohort analysis (1972)
catch-at-length data (stable age distribution)	length-structured VPA	Jones' length cohort analysis (1974)

APPLICATION OF LENGTH COHORT ANALYSIS AND LENGTH-STRUCTURED VPA

Among the various methods presented in this manual, length cohort analysis and length-structured VPA may potentially be the most useful for tropical fisheries. However, to obtain population sizes and fishing mortalities based on these methods, it is necessary to have good catch-at-length data.

Converting catch in weight to catch-at-length data is rather straightforward, given length-frequency data representative of the catch, and the parameters of the length-weight relationship in the stock in question. A step-by-step approach to this conversion is given in Example 7.3. Once catch-at-length data are obtained, either length cohort analysis or length-structured VPA can be applied, as illustrated in Examples 7.4 and 7.5 and Table 7.7.

Table 7.5. Estimation by means of Gulland's virtual population analysis of the population (in numbers) and the fishing mortality (F) of a cohort of sardines *(Sardina pilchardus)* caught off Morocco.[a]

Year of capture	Trimester	Catch	Population	F (per trimester)	Annual F
1973	3	15,624	14,382,198	0.00	
	4	139,836	11,761,034	0.01	
1974	1	66,207	9,502,830	0.01	
	2	33,191	7,720,459	0.00	≈ 0.18 (1974)
	3	514,256	6,290,998	0.09	
	4	319,612	4,686,819	0.08	
1975	1	106,583	3,548,903	0.03	
	2	383,842	2,809,370	0.16	≈ 0.75 (1975)
	3	235,246	1,954,320	0.14	
	4	434,354	1,388,058	0.42	
1976	1	37,926	746,801	0.06	
	2	39,819	577,202	0.08	≈ 0.65 (1976)
	3	118,049	436,651	0.35	
	4	34,226	251,483	0.16	
1977	1	5,225	175,063	0.03	
	2	7,859	138,612	0.06	
	3	17,538 (C_t)	106,394 (N_t)	0.20 (F_t)	

[a]From Anon. (1978a, Table 1, p. 33) who also suggests values of M = 0.8 (per year, hence 0.2 per trimester) and of F_t = 0.8 (per year, hence 0.2 per trimester).

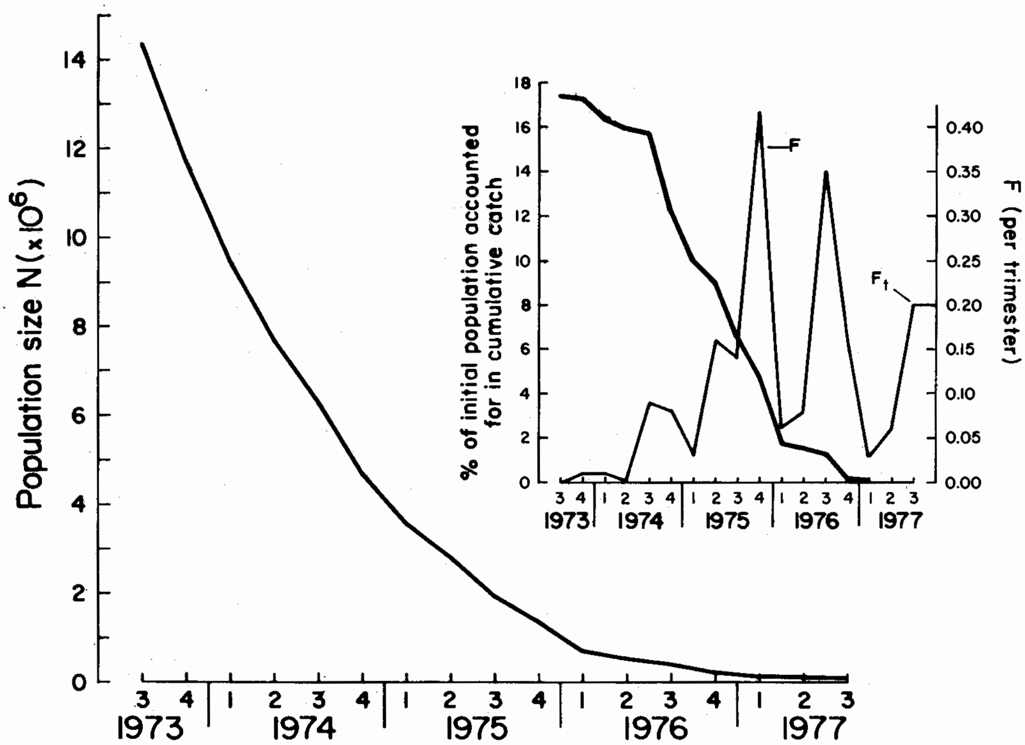

Fig. 7.2. Population sizes of a cohort of Moroccan sardines *(Sardina pilchardus)* as estimated by (age-structured) virtual population analysis (based on data in Table 7.5 and Example 7.1).

Table 7.6. Estimation of the population size in numbers (N) and fishing mortality (F) of a cohort of Peruvian anchovy *(Engraulis ringens)* by means of Pope's cohort analysis.

Time of capture Year	Months	Catch[a] (in millions of individuals)	N[b] (in millions)	F[c] (per 2 months)	F[d] (per 2 months)	F[e] (per 2 months)
1968	Nov-Dec	8,230	1,858,412	0.00	0.00	0.00
1969	Jan-Feb	120,060	1,514,092	0.09	0.09	0.09
	Mar-Apr	168,580	1,130,999	0.18	0.18	0.18
	May-June	21,380	773,446	0.03	0.03	0.03
	Jul-Aug	0	613,899	0.00	0.00	0.00
	Sep-Oct	21,860	502,618	0.05	0.05	0.05
	Nov-Dec	7,410	391,729	0.02	0.02	0.02
1970	Jan-Feb	7,390	314,016	0.03	0.03	0.03
	Mar-Apr	15,560	250,408	0.07	0.07	0.07
	May-June	6,420	190,937	0.04	0.04	0.04
	Jul-Aug	0	150,517	0.00	0.00	0.00
	Sep-Oct	43,310	123,233	0.49	0.47	0.50
	Nov-Dec	27,220	61,706	0.67	0.62	0.69
1971	Jan-Feb	0	25,891	0.00	0.00	0.00
	Mar-Apr	11,160	21,198	0.87	0.75	0.94
	May-June	1,290	7,257	0.22	0.17	0.25
	Jul-Aug	0	4,775	0.00	0.00	0.00
	Sep-Oct	1,020	3,909	0.34	0.25	0.41
	Nov-Dec	1,160	2,278	0.83	0.51	1.21
1972	Jan-Feb	0	815	0.00	0.00	0.00
	Mar-Apr	110 C_t	N_t = 667	F_t = 0.20	F_t = 0.10	F_t = 0.40

[a]Data adapted from Table 8.6 of Ricker (1975). Note that both F and M refer to a 2-month period and should be multiplied by 6 to obtain annual rates (e.g., M = 0.2 = 1.2/6).

[b]Rounded figures. Actual computation (based on F_t = 0.20) used 10 significant digits.

[c]Assuming F_t = 0.20 and M = 0.20, which provide, with equation (7.2) the estimate of N_t = 667.

[d]Assuming F_t = 0.10 and M = 0.20, population estimates omitted. Note convergence toward the F-values obtained by using F_t = 0.20.

[e]Assuming F_t = 0.40 and M = 0.20, population estimates omitted. Note convergence toward the F-values obtained by using F_t = 0.20 or F_t = 0.10.

Unfortunately, the catch and landing data-collection systems of most tropical countries are not geared toward collecting catch and landing data *and* length-frequency data representative of that catch, with the result that the methods outlined here generally cannot be applied to those fisheries. Yet these methods are extremely well-suited for use in tropical fisheries, where fishing is often conducted with a multitude of gears, the number and sampling properties of which are difficult to assess. Using such methods, it is thus possible to assess the impact on the fish themselves of all those gears in the form of values of F which can be used to state whether too many or not enough fish of certain sizes are being captured by the fishery as a whole or segments of it.

Finally, another important property of VPA and related methods is that the resulting population estimates of young (small) fish are estimates of absolute recruitment. Recruitment, as discussed in more detail in Chapter 9, is generally extremely difficult to estimate although it is an extremely important parameter.

It seems thus appropriate to stress here the need for fishery biologists working in tropical countries to help their fisheries department set up a catch reporting system which—at least for major fisheries—will allow for catch-at-length, and later catch-at-age data to emerge.

Table 7.7. Estimation of population size and exploitation rate for a West African stock of hake *(Merluccius merluccius)* based on Jones' length cohort analysis.[a]

Length (in cm)	Catch (in thousands)	Population (in thousands)	Exploitation rate (F/Z)	Annual Z	Annual F
6	1,823	98,919	0.13	0.32	0.04
12	14,463	84,393	0.58	0.67	0.39
18	25,227	59,476	0.79	1.35	1.07
24	8,134	27,623	0.70	0.93	0.65
30	3,889	15,968	0.64	0.77	0.49
36	2,959	9,861	0.68	0.87	0.59
42	1,871	5,501	0.70	0.93	0.65
48	653	2,819	0.58	0.67	0.39
54	322	1,691	0.51	0.57	0.29
60	228	1,057	0.52	0.59	0.31
66	181	621	0.59	0.68	0.40
72	96	314	0.58	0.67	0.39
78	16	149	0.28	0.39	0.11
84 (L_{ter})	46 (C_t)	92 (N_t)	0.50 (E_t)	(0.56)	(0.28)

[a]The catch-at-length data are from Anon. (1978b, Table 6, p. 78) from which (p. 17) the parameter values $L_\infty = 130$, $K = 0.10$, $M = 0.28$, $M/KD = 2.8$ and $D = 1$ also stem. The results (population estimates and E-values) presented here differ from those in Anon. (1978b) both because of the different E_t used, and because of various inconsistencies in the original analysis.

Recommended reading: The literature on VPA and cohort analysis is growing rapidly as far as applications are concerned. However, both Gulland (1965)* and Jones (1974) are technically unpublished papers which are rather hard to get, while Ricker's (1975) discussion of VPA and cohort analysis is rather opaque. Best is to get Pope (1972)* for both VPA and cohort analysis, and the recent manual of Jones (1981) or Jones and van Zalinge (1981) for length cohort analysis. For those who understand French, the best introduction to (age-structured) VPA and cohort analysis will be that of Mesnil (1980).

Suggested research topics: Convert catch data in weight to catch-at-length data using the method outlined in Example 7.3, and apply these data to either length cohort analysis or length-structured VPA. Then using the method of Jones (1979), assess the impact of a change in fishing mortality, mesh size or both. Use the results to assess the relative impact of several fisheries exploiting the same stock (e.g., a small-scale inshore fishery and a large-scale offshore fishery).

*Gulland (1965) and Pope (1972) have been reprinted and included in the reader recently edited by Cushing (1983).

EXAMPLE 7.1

Population sizes and fishing mortality of Moroccan sardines *(Sardina pilchardus)* as determined by Gulland's virtual population analysis.

Data: catch-at-age data of Table 7.5

Computation

1) Read sides 1 and 2 of Program FB 18.

2) Initialize, enter M, terminal fishing mortality and terminal catch.

   Keystrokes: .0001 STO O .2 ↑ .2 ↑ 17538 f a. This results in N_t = 106394.09

3) Enter the catch from the period immediately preceding that during which the terminal catch was made.

	Keystrokes	Results	
	7859 A	0.06	(F_i)
		138611.82	(N_i)
now enter the next earlier catch	5225 A	0.03	(F_i)
		175062.55	(N_i)
and so on	.....	....	
until you arrive at	15624 A	0.00	(F_i)
		14382197.51	(N_i)

The results of virtual population analysis (VPA) should be recorded in a manner similar to that used for Table 7.5.

EXAMPLE 7.2

Population sizes and fishing mortality of Peruvian anchoveta *(Engraulis ringens)* as determined by Pope's cohort analysis.

Data: Catch-at-age data of Table 7.6

Computation

1) Read sides 1 and 2 of Program FB 18.

2) Initialize, enter M and estimate the terminal population, with a terminal catch of 110 million fish and a terminal F of 0.2.

   Keystrokes: .0001 STO O .2 ↑ .2 ↑ 110 f a This results in N_t = 667.31.

3) Enter the catch from the period immediately preceding that during which the terminal catch was made.

	Keystrokes	Results	
	0 B	0.000	(F_i)
		815.51	(N_i)
now enter the next earlier catch	1160 B	0.83	(F_i)
		227.51	(N_i)
and so on	. . . . .		
until you arrive at	8230 B	0.00	(F_i)
		1858412.26	(N_i)

The cohort analysis, which should be recorded in a manner similar to Table 7.6 is now essentially complete. Its results (the F_i and N_i values) can be used to assess the stock directly (e.g., was the fishing mortality too high?) or may be used as input in other models (e.g., those requiring estimates of absolute recruitment). (Alternatively, F_i values considered more reasonable than the first F_t can be used as new F_t and the analysis run again.)

EXAMPLE 7.3

Conversion of length-frequency data to catch-at-length data, given data on bulk catch and a length-weight relationship.

Data from Table 5.8. We shall assume that the length-weight relationship of *Glossogobius giurus* is described by $W = 0.01\ L^3$, where W is expressed in g and L in cm.

Computation

1) Read sides 1 and 2 of Program FB 20.

2) Enter the parameters a and b of L/W relationship.

    Keystrokes: .01 ↑ 3 f b

3) Then enter lower limit of smallest length class considered, and width of length class (see Table 5.8, August sample).

    Keystrokes: 4 ↑ 2 f c

4) Now enter frequencies, successively

    Keystrokes: 1 C 138 C 153 C 49 C 9 C

    (The numbers appearing after each entry are the mean weights of the fish in each length class)

5) Compute total weight of sample

Keystroke	Results	
E	2530	(weight of sample)
	7.23	(mean fish weight)

6) Now assume 100 kg (= 100,000 g) of *Glossogobius giurus* had been caught in August. This would imply, given that the length-frequency sample is representative of the catch, that the equivalent of this sample has been caught 100,000/2,530 = *39.53 times;* thus each of the frequency in the length-frequency sample must be multiplied by the raising factor 39.53. The resulting numbers are catch-at-length data, as used in length-cohort analysis and length-structured VPA.

EXAMPLE 7.4

Population sizes and exploitation rate of West African hake *(Merluccius merluccius)* as determined by Jones' length cohort analysis.

Data: Catch-at-length data of Table 7.7

Computation

1) Read side 1 of Program FB 19.

2) Enter parameters needed, initialize and calculate N_t.

   Keystrokes: 130 STOA 2.8 ↑ 1 f b 84 ↑ 6 f c .5 ↑ 46 f d   Result: 92 (N_t)

3) Enter the catch for the length interval immediately preceding that to which C_t refers.

	Keystrokes	Results	
	16 A	148.68	(N_i)
		0.28	(E_i)
now enter the catch pertaining to the next smaller length class	96 A	313.71	(N_i)
		0.58	(E_i)
and so on	....	......	
until you arrive at	1823 A	98919.30	(N_i)
		0.13	(E_i)

Unless you have a value of M (rather than just a value of M/KD), the length cohort analysis is now completed.

4) If a value of M is available, values of Z and F (both on an annual basis) can be estimated by performing

	Keystrokes	Results	
store M	.28 STO2		
estimate Z	.5 B	0.56	(Z)
and F		0.28	(F)
corresponding to	.28 B	0.39	(Z)
the values of E		0.11	(F)
	etc. (see Table 7.3)		

It must be realized that as opposed to VPA and cohort analysis performed on catch-at-age data, length "cohort" analysis does not estimate population numbers pertaining to a specific cohort. Rather, the "population" estimates are the number needed to account for the catch at each size.

EXAMPLE 7.5

Population sizes and fishing mortality of West African hake as determined by length-structured VPA.

Data: catch-at-length data of Table 7.7 (the data are the same as those in Table 7.2, which also gives the source for $L_\infty = 130$ cm, K = 0.10, D = 1 and M = 0.28).

Computation

1) Read sides 1 and 2 of Program FB 20.

2) Enter parameters needed:

Keystrokes: 130 STO A .1 STO C 1 STO D .28 STO 2 84 STOI 6 STO E 10 ↑ 4 CHS Y^X STO O

3) Estimate terminal population:

		Keystrokes	Results	
enter F_t		.28 ↑		
and C_t		46 f a	92	(N_t)
4) Run VPA:		16 A	148.499	(F)
			0.111	(N)
		96 A	311.813	(F)
			0.399	(N)
		etc.		
	until	1823 A	98238. . .	(N)
			0.040	(F)

Note that the results are almost the same as those obtained with Jones' length cohort analysis. (See also Table 7.2.)

8. Yield-Per-Recruit Assessment

INTRODUCTION

This chapter contains some of the most horrible-looking equations used in fish population dynamics, and an attempt to explain how these equations are derived would certainly deter all but the most enthusiastic readers. Thus, rather than derive any of the equations included in this chapter, I will simply present them, and hope that they will gradually become familiar, especially after frequent use and consulting the original literature.

A new concept needs to be introduced at this stage, that of the "recruit". Although the definition may vary between authors, we may here visualize recruits as 1) fully metamorphosed young fish, 2) fish whose growth is described adequately by some form of the VBGF, 3) fish whose instantaneous rate of natural mortality is similar to that of the adults, and 4) fish which occur at (or swim into) the fishing ground(s). Such recruits have an average age t_r, an average length L_r and an average weight W_r. Upon reaching the age t_r, the recruits may be caught immediately, in which case the mean age at first capture (t_c) is equal to the age at recruitment ($t_c = t_r$). Alternatively, the recruits may be caught at a more advanced age (and a correspondingly larger size, L_c and W_c). In such case, the number of recruits actually entering the fishery (R_c) will be less than the initial number of recruits (R_r), or

$$R_c = R_r \cdot e^{-M\,(t_c - t_r)} \qquad \ldots 8.1)$$

Now, there is, for each combination of t_c and F values, a yield per recruit (Y/R = catch in weight, per recruit) the value of which can be estimated from various equations whose exact form depends on the model used to describe the growth of the fish. In the following paragraphs, equations for the estimation of Y/R will be given for various forms of the VBGF, i.e.,

Case I:

$$W_t = W_\infty\,(1 - e^{-K\,(t - t_o)})^3 \qquad \ldots 8.2)$$

or special VBGF, as based on conversion from length using the isometric length-weight relationship

$$W = (\text{c.f.}/100)L^3 \qquad \ldots 8.3)$$

Case II:

$$W_t = W_\infty\,(1 - e^{-K\,(t - t_o)})^b \qquad \ldots 8.4)$$

which is a form of the special VBGF where the exponent (b) of the length-weight relationship is allowed to take values other than 3, i.e.,

$$W = a \cdot L^b,\ b \neq 3 \qquad \ldots 8.5)$$

Case III:

$$W_t = W_\infty\,(1 - e^{-KD\,(3/b)\,(t - t_o)})^{b/D} \qquad \ldots 8.6)$$

the generalized VBGF for growth in weight.

ESTIMATION OF YIELD PER RECRUIT

Case I

Case I is that of Beverton and Holt (1957) for computing yield per recruit. The equation they proposed for this purpose is:

$$Y/R_r = F \cdot e^{-Mr_2} W_\infty \left\{ \frac{1 - e^{-Zr_3}}{Z} - \frac{3e^{-Kr_1}(1 - e^{-(Z+K)r_3})}{Z+K} + \frac{3e^{-2Kr_1}(1 - e^{-(Z+2K)r_3})}{Z+2K} - \frac{e^{-3Kr_1}(1 - e^{-(Z+3K)r_3})}{Z+3K} \right\} \qquad \ldots 8.7)$$

where
$Z = F + M$
$r_1 = t_c - t_o$
$r_2 = t_c - t_r$
$r_3 = t_{max} - t_c$

with W_∞, K and t_o being growth parameters, t_c the mean age at first capture, t_r the mean age at recruitment and t_{max} "the maximum age of significant contribution to the fishery" or more simply, the longevity of the fish in question (see Ricker 1975).

The effect of the exact value of t_{max} is generally very small, and equation (8.7) can be considerably simplified by setting $t_{max} = \infty$, in which case equation (8.7) becomes

$$Y/R_r = F \cdot e^{-Mr_2} W_\infty \left\{ \frac{1}{Z} - \frac{3e^{-Kr_1}}{Z+K} + \frac{3e^{-2Kr_1}}{Z+2K} - \frac{e^{-3Kr_1}}{Z+3K} \right\} \qquad \ldots 8.8)$$

in which all other parameters are defined as in equation (8.7).

Both equations (8.7) and (8.8) can be used to assess the effect of different values of t_c (corresponding, e.g., to a given mesh size) and values of F (corresponding to a certain amount of fishing effort) on the yield per recruit (Examples 8.1 and 8.2). The results of such computations are generally presented in the form of "yield curves", as in Fig. 8.1, from which the effect of increasing mesh size (e.g., from a size generating t_c = 0.2 yr to a size generating t_c = 0.3 yr) can be assessed.

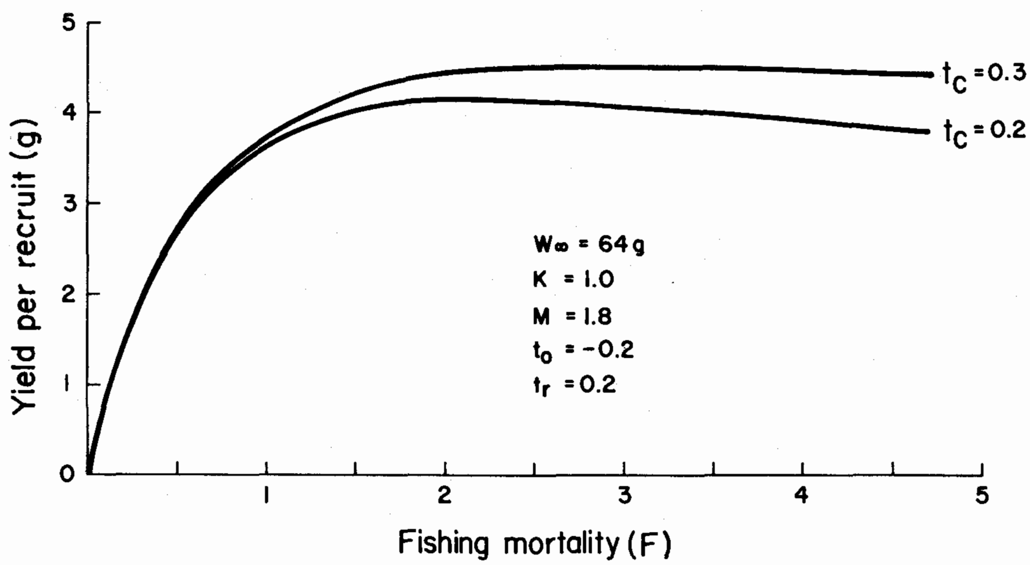

Fig. 8.1. Yield per recruit as a function of fishing mortality for the slipmouth *(Leiognathus splendens)* for two values of mean age at first capture (based on Example 8.1).

Another, more elaborate form of presenting the results of a yield-per-recruit analysis is the "yield-isopleth diagram", which shows the response of yield per recuit to both t_c and F over a wide range of both parameters, to allow the best selection of mesh size for given F, or a best F for a given mesh size (see Fig. 8.2). Program FB 21 can be used for this purpose.

Equation (8.7) requires the estimation of six constants (in addition to t_c and F which are used as variables) while equation (8.8) requires five constants.

In 1964, Beverton and Holt presented a modified version of their yield equation which requires only three input parameters, M/K, c (= L_c/L_∞) and E (= F/Z) and which has the form

$$Y'/R_r = E\,(1-c)^{M/K} \cdot \left\{ 1 - \frac{3(1-c)}{1+\frac{(1-E)}{(M/K)}} + \frac{3(1-c)^2}{1+\frac{2\,(1-E)}{(M/K)}} - \frac{(1-c)^3}{1+\frac{3\,(1-E)}{(M/K)}} \right\} \quad \ldots 8.9)$$

Here, however, it is not a yield per recruit in units of weight that is estimated, but something (Y'/R_r) proportional to it; this doesn't really matter because the absolute number of recruits (R_r) is not known anyway. Management advice is most often based on relative yield (see Example 8.3 and Fig. 8.3). Values of Y'/R_r have been tabulated by Beverton and Holt (1964) for a wide range of M/K, c and E values. Given appropriate inputs, program FB 21 provides the same values as those in Beverton and Holt (1964), whose paper, however, should still be consulted for more details.

[The relationship between ordinary Y/R_r (as given in Equation (8.8)) and Y'/R_r is given by $Y/R_r = (Y'/R_r) \cdot (W_\infty \cdot \exp - M\,(t_r - t_o))$].

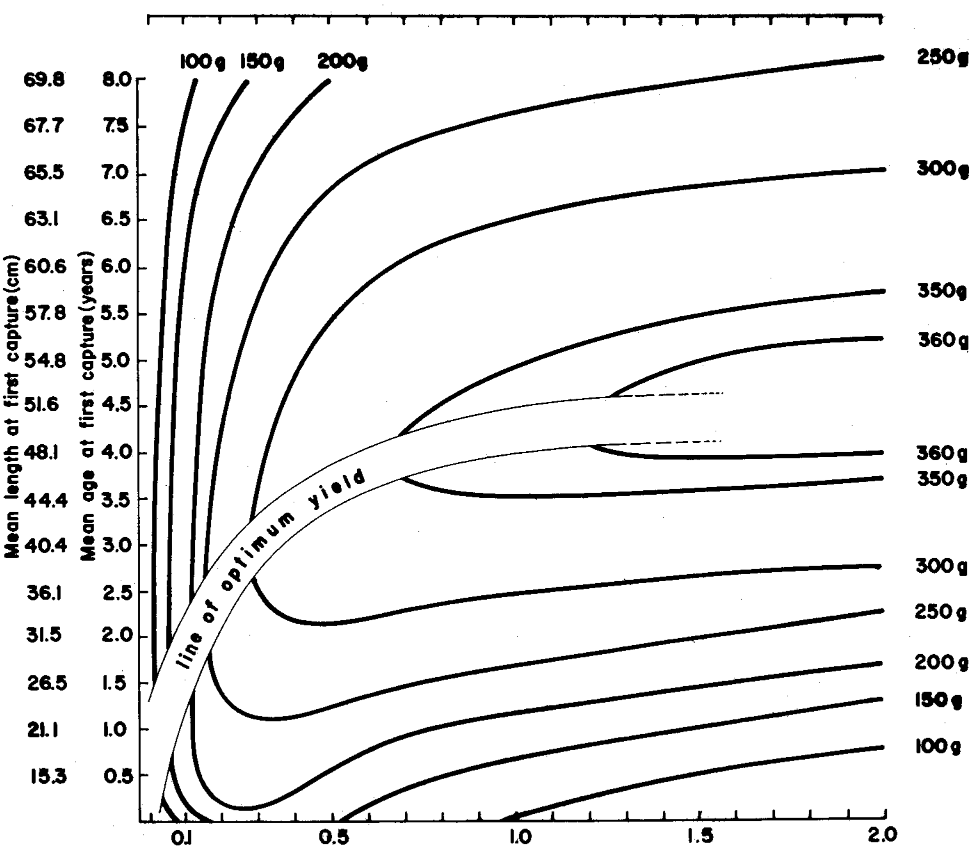

Fig. 8.2. Yield isopleth diagram for the snapper *(Lutjanus sanguineus)* of the South China Sea (from Pauly 1979b; see Example 8.2).

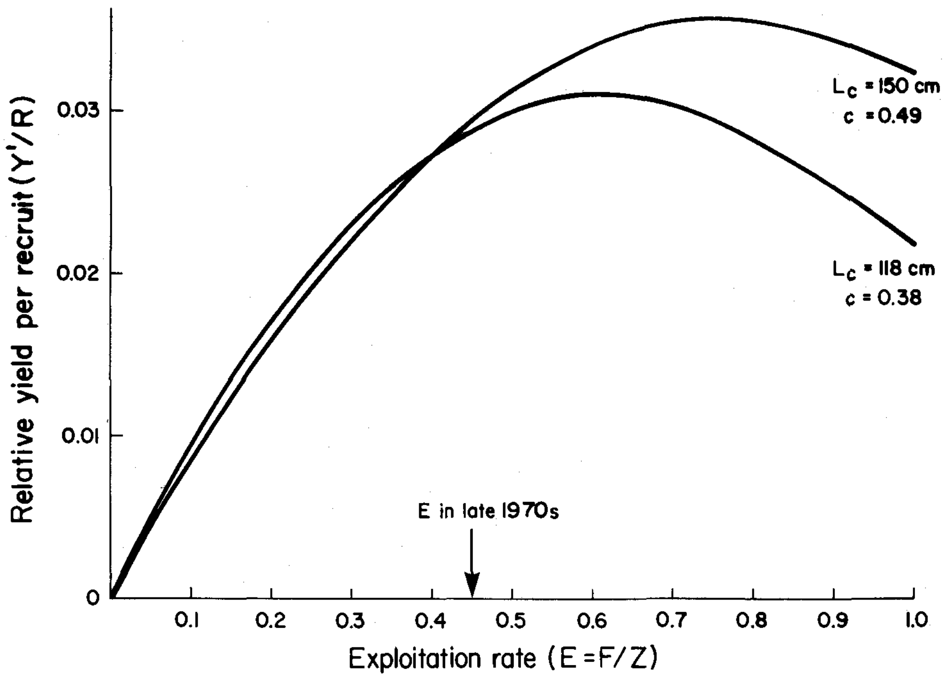

Fig. 8.3. Stock assessment of the swordfish *(Xiphias gladius)* off Florida, based on the relative yield-per-recruit concept (based on Example 8.3).

Case II

All three equations given above assume that growth in weight is isometric. This is often not the case and the value of b in the length-weight relationship generally ranges between 2.5 and 3.5 (see Chapter 2). The weight-at-age data of Table 8.1 were constructed to represent such a case, with b = 3.3.

Two methods are available to use the yield equations given above, even when growth is allometric.

The first of these methods simply consists of proceeding as if the length-weight relationship were isometric, i.e., of calculating a mean condition factor (which assumes b = 3) from the length-weight data at hand, then to use this mean condition factor to convert L_∞ to W_∞. This method stems from Beverton and Holt (1957).

[For the data of Table 8.1, a mean condition factor of 1.887 is obtained which can be used to convert the value of L_∞ = 186.5 cm obtained from a Ford-Walford Plot to a value of W_∞ = 122.6 kg

Table 8.1. Growth data of a hypothetical tuna reaching 146.5 cm (L_{max}) and 60 kg (W_{max}).[a]

Age (years)	FL (cm)	Weight (g)
1	35	648
2	55	2,879
3	75	8,011
4	90	14,622
5	105	24,318
6	115	32,833

[a]Adapted from the data in Table 4.4, using the length-weight relationship $W = 0.0052L^{3.3}$. Note that W_{max} = 60,000 g corresponds to a value of D = 0.47. The mean c.f. obtained from the length-weight data is 1.887. M is set at 0.3 and $t_{max} = \infty$.

(Table 8.2). The value of K is that provided by the same Ford-Walford plot, while the value of t_o is the mean of six estimates of t_o obtained by solving the growth equation for that parameter (by means of Program FB 9). Then the growth parameters are used to estimate t_c from W_c, t_c is set equal to t_r, and equation (8.8) is used to estimate Y/R_r (see Table 8.2 and Fig. 8.4).]

The second of these methods consists of calculating growth parameters directly from the weight data, and setting b = 3 (this can be done easily with the programs presented in Chapter 4). This results in values of K and t_o different from those that would have been obtained by computing the growth parameters from length data (see Table 8.2). However, once these parameter values have been derived from b = 3, any of the three equations given above can be used to estimate yield per recruit (see Table 8.2 and Fig. 8.4). This method was suggested by Paulik and Gales (1964).

Table 8.2. Parameter values of different growth equations based on the data of Table 8.1 for use in yield-per-recruit analysis. (W_∞ and K values stem from Ford-Walford plots.)

Method	D	W_∞ (kg)	K	t_o[a]	b	t_c[b]
Beverton and Holt (1957)	1	122.60	0.150	−0.535	3	2.28
Paulik and Gales (1964)	1	194.36	0.129	−0.265	3	2.45
Jones (1957)	1	162.25	0.150	−0.795	3.3	2.35
Generalized VBGF	0.47	85.95	0.582	−2.035	3.3	2.39

[a]Obtained by solving the VBGF with the empirical size and age values in Table 8.1 and the corresponding set of asymptotic size, K, b and D values and Program FB 9, then by taking the mean of the resulting 6 estimates of t_o.

[b]Based on a mean weight at first capture W_c = 5 kg.

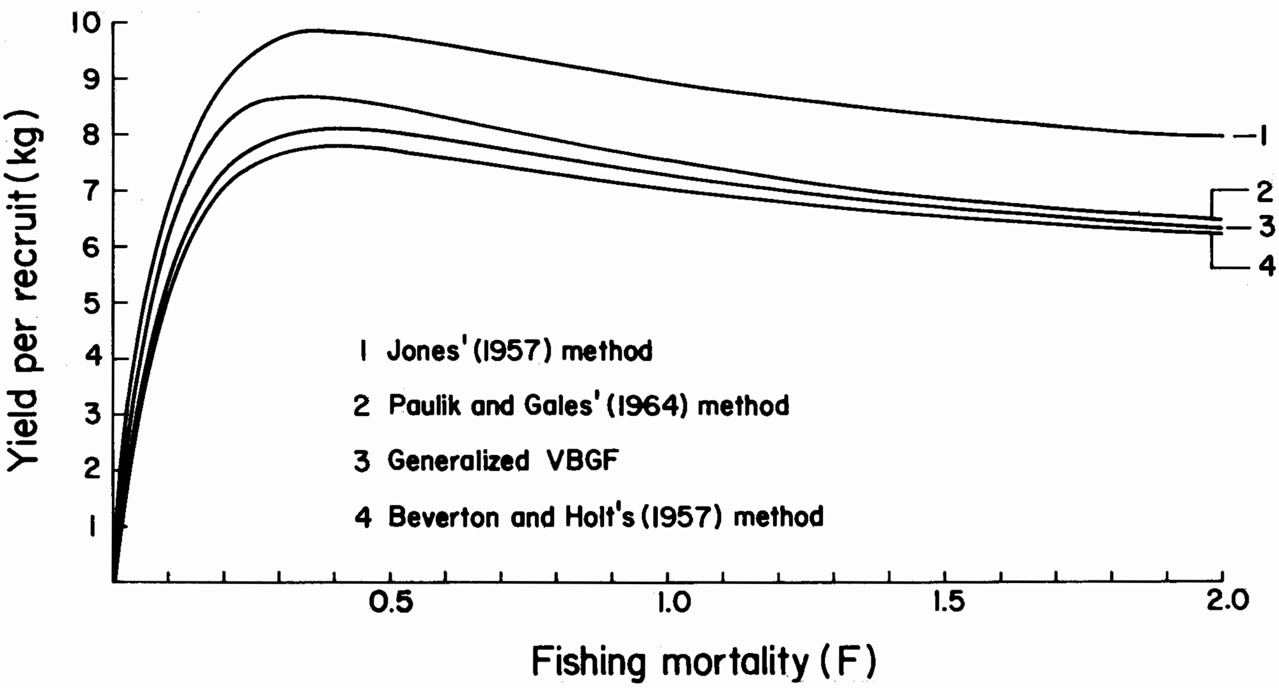

Fig. 8.4. Comparison of yield curves based on different methods to compensate for allometry when performing a yield-per-recruit analysis (see Table 8.2, Example 8.4 and text).

Another method for dealing with allometry in yield-per-recruit computations is the use of the incomplete β-function, as proposed by Jones (1957).

Here, the yield per recruit, when $t_{max} = \infty$, is given by

$$Y/R_r = F/K \cdot e^{Zr_1 - Mr_2} W_\infty \{\beta [X, P, Q]\} \qquad \ldots 8.10)$$

where $X = e^{-Kr_1}$
$P = Z/K$
$Q = b + 1$ (b being the length/weight exponent),
and β = being the symbol of the incomplete beta function
with $r_1 = t_c - t_o$
and $r_2 = t_c - t_r$

Tables of the incomplete β-function have been presented by Wilimovsky and Wicklund (1963); these tables are not needed here because Program FB 22 estimates the appropriate values of the incomplete β-function (see Example 8.4, Fig. 8.4 and text below).

Case III

The incomplete β-function, besides allowing for the integration of the special VBGF with $b \neq 3$, also allows for the integration of the generalized VBGF and its use in yield-per-recruit analysis. When the generalized VBGF is used, and $t_{max} = \infty$, we have

$$Y/R_r = \frac{F \cdot b}{3\,KD} \cdot e^{Zr_1 - Mr_2} W_\infty \{\beta [X, P, Q]\} \qquad \ldots 8.11)$$

where $X = e^{-3KDr_1/b}$
$P = Zb/3KD$
and $Q = (b/D) + 1$

with r_1 and r_2 being defined as above.

Thus, using the data of Table 8.1, first to estimate D (from W_{max} and Program FB 9) then to estimate W_∞ and K, with D = 0.47 and b = 3.3, it is possible to obtain growth parameters suitable for incorporation into equation (8.11) (see Table 8.2). Program FB 22 can then be used to estimate Y/R_r values for these, or any other combination of growth parameters (see Example 8.5).

COMPARISON OF VARIOUS EQUATIONS FOR YIELD-PER-RECRUIT ESTIMATION

Of the various equations available for the estimation of yield per recruit, the first [equation (8.7)] is the one which contains the most parameters. In fact, of the parameters used, one (t_{max}) is quite superfluous and may be set for most practical purposes equal to ∞, especially when Z is high (see Ricker 1975, p. 257).

Equation (8.8), on the other hand, is still widely used (when $b \approx 3$) and several examples are available of its application to tropical stocks (see recommended reading).

Equation (8.9) is particularly useful in situations where a detailed knowledge of the growth and mortality of the stock in question is not available. The results obtained from this equation are proportional to those obtained by means of equation (8.8) and allow a quick assessment of a fishery (Fig. 8.3).

Of the several methods available for compensating for allometry in yield-per-recruit analysis, that of Jones (1957) gave the results which differed most from those obtained using the generalized

VBGF, which serves as a benchmark (Fig. 8.4). The marked differences between the results obtained by Jones' method and the other methods are to a large extent due to growth beyond the ages considered in Table 8.1. This suggests that Jones' method is least robust with regard to violations of the assumption that $t_{max} = \infty$ in equation (8.10).

Paulik and Gales (1964) and Ricker (1975, p. 225) suggested that the "Chapman-Richards" curve (Richards 1959), which is essentially a form of the generalized VBGF, could be easily integrated by means of the incomplete β-function. Published examples have been wanting. This account (i.e., Case III) closes the gap.

THE USE OF THE YIELD-PER-RECRUIT MODEL: A WARNING

The yield-per-recruit model, although very elegant and still suited to the management of certain stocks (such as the North Sea plaice *(Pleuronectes platessa)*) should be used with caution.

Fishermen are not interested in an imaginary "yield per recruit"; they are interested in a physical *yield* of fish, and this yield is the product of the yield per recruit *times* the absolute number of recruits produced in the stock. Yield is directly proportional to yield per recruit over a wide range of fishing mortalities only if it can be assumed that there is no relationship—over a wide range of F values—between the size of the parental stock of fish and its progeny (see chapter on stock-recruitment relationships).

Where this assumption does not apply—and it does not seem to apply to more than a few stocks—the values of F and t_c needed to produce a maximum yield per recruit could well also generate an abysmally low yield, because the "best" value of F (the one maximizing yield per recruit) could also reduce the parental stock to a level at which virtually no recruits are produced.

Moreover, it must be realized that the finding of yield-per-recruit analyses apply to long-term or *equilibrium situations* only. In the short term, an increase of fishing mortality or a decrease in size at first capture always results in higher yields, even when the yield-per-recruit analysis predicts lower yields. Similarly, a decrease of fishing mortality or an increase in size at first capture always results in lower yields in the short term, although in the long run higher yields may be reached.

The duration of the transition period can be of several years in fish which have a high longevity and are subjected to exploitation over a number of years, as in a number of temperate stocks such as cod or halibut. In short-lived animals, the transition period will be much shorter; in the case of *very* short-lived animals, such as most penaeid shrimps, the distinction between "immediate" and "long-term" effect does not even apply, because the stocks are never in equilibrium. This and related problems are reviewed in Garcia and Le Reste (1981) who present a number of methods for the quantification of short- and long-term effects of changes in fishing mortality and mesh size (see also Jones 1981).

Another important feature of the yield-per-recruit model is that yield per recruit is maximized at low values of F only in the case of large, long-lived, low mortality fish, such as the swordfish *(Xiphias gladius)* (see Fig. 8.3). In small tropical fish, the values of F which maximize yield per recruit are generally extremely high (see Fig. 8.1). Thus, managing a tropical fishery based on a species of small fish (let alone a multispecies fishery based on such fish) using only yield-per-recruit analyses can be very misleading (see Pauly 1979b; Pauly and Martosubroto 1980).

It may be mentioned, finally, that in temperate waters, an (arbitrary) agreement has emerged to generally limit F (for assessment of stocks whose stock-recruitment relationships are unknown) to the value which corresponds to 1/10 of the rate of increase of yield per recruit that can be obtained by increasing F, at low levels of F (Gulland and Boerema 1973). This concept, called $F_{0.1}$ is illustrated in Fig. 8.5, Table 8.3 and Example 8.6. The $F_{0.1}$ concept may be viewed as a surrogate for MEY (Maximum Economic Yield, see Fig. 12.7), applicable in situations where economic data on the performance of a fishery are lacking. A concept analogous to $F_{0.1}$, but for use in conjunction with effort ($f_{0.1}$) is proposed in Chapter 12.

Table 8.3. Data for the computation of $F_{0.1}$ for *Nemipterus marginatus* from the South China Sea (see Example 8.6).

F	Y/R_r	Diff/10[a]	F	Y/R_r	Diff/10[a]
0.00	0.000				
0.01	0.030	$\boxed{3.00}$	1.0	1.215	
0.1	0.270	2.40	1.1	1.247	$\boxed{0.32}$
0.2	0.485	2.15	1.2	1.272	$\boxed{0.25}$
0.3	0.656	1.71	1.3	1.293	0.21
0.4	0.794	1.38	1.4	1.310	0.17
0.5	0.905	1.11	1.5	1.323	0.13
0.6	0.995	0.90	1.6	1.334	0.11
0.7	1.068	0.73	1.7	1.342	0.08
0.8	1.127	0.59	1.8	1.348	0.06
0.9	1.175	0.48	1.9	1.352	0.04
1.0	1.215	0.40	2.0	1.355	0.03

[a]The difference between two succeeding Y/R_r values, divided by ten is here used as approximation of the slope of the yield-per-recruit curve between the two values in question.

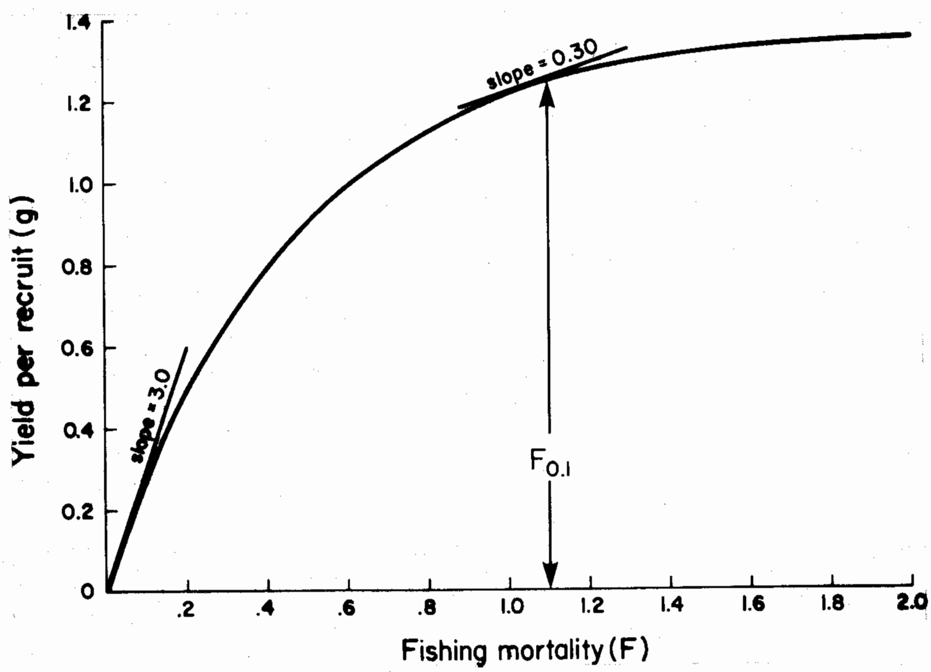

Fig. 8.5. Yield-per-recruit curve of the threadfin bream *(Nemipterus marginatus)* from the South China Sea, showing the position of $F_{0.1}$ (based on data in Table 8.3 and Example 8.6).

AN ALTERNATIVE USE OF BEVERTON AND HOLT'S YIELD EQUATION

An interesting property of the yield equation of Beverton and Holt (1957) is that it can be used in a given stock to estimate the proportion of fish above or below a certain size. Thus, when the special VBGF is used, the total standing stock (biomass) of fish above the size at first capture (t_c) is given, assuming $t_{max} = \infty$, by

$$B_c = R_c \cdot F \cdot W_\infty \left(\frac{1}{Z} - \frac{3e^{-Kr_1}}{Z+K} + \frac{3e^{-2Kr_1}}{Z+2K} - \frac{e^{-3Kr_1}}{Z+3K}\right) \qquad \ldots 8.12)$$

where R_c is the number of recruits of age t_c, and $r_1 = t_c - t_o$.

A factor (k) can be defined which relates the biomass of fish of and above a certain age (t_k) to the biomass of all fish of and above age t_c such that

$$B_k/k = B_c \qquad \ldots 8.13)$$

The value of k will depend on the value of Z, but not on W_∞, or R_c which are the same in both parts of the stock (B_c and B_k). Thus, the value of k, when $t_{max} = \infty$ can be estimated by the equation

$$k = \frac{\exp(-Zr_3) \cdot \left\{ \frac{1}{Z} - \frac{3\exp(-Kr_2)}{Z+K} + \frac{3\exp(-2Kr_2)}{Z+2K} - \frac{\exp(-3K_2)}{Z+3K} \right\}}{\frac{1}{Z} - \frac{3\exp(-Kr_1)}{Z+K} + \frac{3\exp(-2Kr_1)}{Z+2K} - \frac{\exp(-3Kr_1)}{Z+3K}} \qquad \ldots 8.14)$$

with $r_1 = t_c - t_o$; $r_2 = t_k - t_o$; and $r_3 = t_k - t_c$.

This equation can be used to estimate, e.g., the proportion of the total stock which consists of fish at or above the age at first maturity (t_m), by setting $t_m = t_k$, that is:

$$r_1 = t_c - t_o;\ r_2 = t_m - t_o;\ \text{and } r_3 = t_m - t_c.$$

This technique has been recently used to estimate the standing stock size of potentially mature fish in the Gulf of Thailand (Pauly 1980d) and can also be used to convert catch data obtained by a given mesh size to those that would have been obtained had another mesh size been used. This expression is based on an analogous equation presented by Hempel and Sarhage (1959) to estimate the expected proportion of undersized and discarded fish in a trawl fishery. Program FB 23 can be used to estimate values of k for any value of F given a value of M, and values of t_o, t_c and t_k (see Example 8.7).

Recommended reading: The book in which Beverton and Holt (1957) originally presented their model has been reprinted and still is a mine of good ideas—although it is often quite hard to follow. Ricker (1975) gives a review of the whole yield-per-recruit approach, including the earlier work of Baranov (1918) who was the pioneer in this field. Tropical applications of the yield-per-recruit approach are to be found, e.g., in Bayliff (1967), Le Guen (1971), Jones (1976b) and Sinoda et al. (1979).

Suggested research topics: Whenever growth data are available, reasonable estimates of M can be obtained (see Chapter 5); yield-per-recruit computations can then be performed. Attempts should be made to perform such assessments routinely and to suggest appropriate mesh sizes. In fisheries that have stabilized at a given level of effort and/or those consisting of short-lived fish, yield may be divided by Y/R_c to obtain estimates of recruitment, which may be compared with absolute recruitment estimates obtained from length cohort analysis.

EXAMPLE 8.1

Estimating the yield per recruit obtainable from the slipmouth *(Leiognathus splendens)* in western Indonesian waters.

Data: W_∞ = 64 g, K = 1.0, t_o = –0.2, t_c = 0.2, t_r = 0.2, M = 2, b = 3, D = 1 (adapted from Pauly 1980c).

Computation

1) Read sides 1 and 2 of Program FB 21

2) Enter parameters (except for b and D).

Keystrokes: 64 STO B1 STO1 2STO2.2 CHS STOO .2 STO D.2 STOI

3) Calculate Y/R_c and Y/R_r for F = 0.5 to F = 5 in steps of 0.5

Keystrokes	Results	
.5 B	2.247	(Y/R_c)
	2.247	(Y/R_r)
1 B	3.199	(Y/R_c)
	3.199	(Y/R_r)
etc.	. . . . .	
5 B	3.566	(Y/R_c)
	3.566	(Y/R_r)

4) Plot the values of Y/R_r onto a graph, and repeat with t_c = 0.3. A plot such as Fig. 8.1 will be obtained, which allows for the assessment that, for all values of fishing mortality considered, the mesh size which generates t_c = 0.3 will produce a greater yield than that which generates t_c = 0.2.

EXAMPLE 8.2

Estimating the yield per recruit obtainable from the snapper *(Lutjanus sanguineus)* in the South China Sea.

Data: W_∞ = 12226 g, K = 0.154, t_o = –0.67, D = 1, t_{max} = 10 years (assumed), M = 0.33, with $t_r = t_o$, and t_c = 2 years, b = 3 (adapted from Lai and Hsi 1974 and Pauly 1979b). Note that the age at recruitment is arbitrary.

Computation

1) Read sides 1 and 2 of Program FB 21

2) Enter parameters (b is assumed 3 and D is assumed 1 and need not be entered)

Keystrokes: 12226 STO B.154 STO1 .33 STO2 10 STO A .67 CHS STO0 2 STO D .67 CHS STO I

3) Calculate Y/R_c and Y/R_r for F = 1

Keystrokes	Results	
1 A	660.924	(Y/R_c)
	273.839	(Y/R_r)

4) Repeat with different value of F, e.g.

Keystrokes	Results	
.5 A	708.999	(Y/R_c)
	293.757	(Y/R_r)

5) Setting $t_{max} = \infty$ (i.e., using a very large number) and the same set of other parameters allows one to reproduce the yield isopleth diagram in Fig. 8.2.

EXAMPLE 8.3

Yield-per-recruit assessment of Atlantic swordfish *(Xiphias gladius)*.

Data: Berkeley and Houde (1980) give for swordfish caught off Florida: $L_\infty = 309$ (fork length, in cm; ♂ and ♀), $K = 0.0949$, $M = 0.18$ (hence $M/K = 1.9$), $L_c = 118$ (hence $c = L_c/L_\infty = 0.38$).

Computation

1) Read sides 1 and 2 of Program FB 21

2) Enter parameters needed

   Keystrokes: 1.9 STO 8 .38 STOC

3) Compute the relative yield per recruit for different values of E (= F/Z)

Keystrokes	Results	
.1 C	0.009	(Y'/R_r)
.2 C	0.017	(Y'/R_r)
etc.	.....	
1 C	0.022	(Y'/R_r)

4) Plot these values onto a graph, and repeat with a different value of c (e.g., 0.49). The result should look similar to Fig. 8.3 from which the assessment can be made that an increase of L_c from 118 to 150 cm would not result in a marked increase of yield per recruit under the present (late 1970s) exploitation rate, but would lead to an increased yield per recruit under higher exploitation rates.

EXAMPLE 8.4

Computation of yield per recruit in cases where weight growth is allometric (Jones' method).

Data: Growth and other parameters from Tables 8.1 and 8.2

Computation

1) Read sides 1 and 2 of Program FB 22

2) Enter parameters needed

Keystrokes: 162.25 STO B.15 STO A1STO D3.3 STO E.3 STO0 .795 CHS ↑ 2.35 f a 2.35 f c

3) Calculate yield per recruit for F = 0.1 to F = 2.0

Keystrokes	Results	
.1 A (and wait . . .)	0.018	(β)
	6.773	(Y/R_c)
	6.773	(Y/R_r)
etc.		
2 A (and wait . . .)	2.648. . .–06	(β)
	7.936	(Y/R_c)
	7.936	(Y/R_r)

4) Plot the Y/R_r values against the F-values. The graph that emerges should look as line 1 in Fig. 8.4 (but see text).

EXAMPLE 8.5

Computation of yield per recruit using the generalized VBGF.

Data: Growth and other parameters from Table 8.2

Computation

1) Read sides 1 and 2 of Program FB 22

2) Enter parameters needed

Keystrokes: 85.95 STOB .582STOA .47 STOD .3STO O 2.035 CHS ↑ 2.39 f a 2.39 f c

3) Calculate yield per recruit for F = 0.1 to F = 2

Keystrokes	Results	
.1 B	0.027	(β)
	5.444	(Y/R_c)
	5.444	(Y/R_r)
etc.	. . . . .	
2 B	3.490. . .–07	(β)
	6.347	(Y/R_c)
	6.347	(Y/R_r)

4) Plot the Y/R_r values against the F-values. The graph that emerges should look as line 3 in Fig. 8.4

EXAMPLE 8.6

Estimating $F_{0.1}$ for *Nemipterus marginatus* from the South China Sea.

Data: W_∞ = 210 g, K = 0.42, t_o = −0.41 (D = 1, b = 3), M = 1.73, t_c = 0.26, t_r = −0.41 (from Pauly and Martosubroto 1980).

Computation

1) Read sides 1 and 2 of Program FB 21

2) Enter parameters needed

   Keystrokes: 210 STO B .42 STO 1 1.73 STO2 .41 CHS STO0 .26STO D .41CHS STO I

3) Compute Y/R_r at a very low value of F, e.g., F = 0.01

	Keystrokes	Results
	.01 B	0.096 (Y/R_c)
		0.030 (Y/R_r)

Near the origin, Y/R_r increases from 0 to 0.03 when F increases from 0 to 0.01, thus the slope of the yield curve at the origin is close to 0.030/0.01 i.e.:

	Keystrokes	Results
	.01 ÷	2.999 (slope near origin)
increase per unit of F near origin:	DSP 2	3.00 (slope near origin)

4) Then compute Y/R_r for values of F ranging from 0.1 to 2, in steps of 0.1, record data and draw resulting graph (see Fig. 8.5 and Table 8.3).

5) Calculate increase in yield associated with each 0.1 increment of F, and divide this difference by 10 to obtain approximate slope (i.e., change in Y/R_r per unit change in F).

6) Locate slope value closest to 1/10 of value of slope near the origin (corresponding to $F_{0.1}$). This value is 0.32, corresponding to $F_{0.1}$ = 1.1 (see Table 8.3). The next closest value is 0.25, corresponding to F = 1.1-1.2. Thus, the best value, corresponding to 0.30 will be close to F = 1.1, which we may take as our estimate of $F_{0.1}$ (see Fig. 8.5).

EXAMPLE 8.7

Estimating the proportion (k) of adult slipmouth *(Leiognathus splendens)* in the total stock, under two different exploitation regimes.

Data: K = 1.0, t_o = –0.2, t_c = 0.2, M = 1.8 (see Fig. 8.1); to be estimated are values of k for F = 0 and F = 1, with t_k = 1 year.

Computation

1) Read side 1 of Program FB 23

2) Enter needed parameter values

Keystrokes: 1 STO1 .2 CHS STOO 1.8 STO2 .2 STOC 1 STOA

3) Calculate values of k for F = 0 and F = 1

Keystrokes	Results	
OA	0.55	(k_o)
1A	0.32	(k_1)

Thus, as expected, we find at F = 1 a smaller biomass of adults (32% of total stock) than at F = 0, where the adults contribute 55% of the total stock.

9. Stock-Recruitment Relationships

INTRODUCTION

Clearly, there can be no production of young fish (recruits) if no adult fish are left (by a fishery) to mature, spawn, and produce eggs which hatch and grow to become recruits (see Fig. 9.1A).

The females of most fish species are extremely fecund, producing during their adult lives several thousand eggs, sometimes millions. This fecundity has led many fishery biologists to believe that even a very limited parental biomass should be sufficient to allow a complete "restocking" after each spawning season. It was assumed that features of the abiotic environment (e.g., oceanographic conditions) mainly determine how many of the spawned eggs survive to become recruits, the size of the spawning stock, except for stock sizes very close to zero, being virtually irrelevant in determining recruit numbers. The situation in which the number of recruits in a given stock is determined mainly by factors other than parental biomass is called "lack of a stock-recruitment relationship". Early proponents of this view include Beverton and Holt (1957) (see also Beverton 1963).

However, work conducted in the 1960s and 1970s suggests that many fish stocks do display stock-recruitment relationships, as demonstrated in Parrish (1978) and Saville (1980). Also, it was shown for most of the stocks which collapsed in the last three decades that "recruitment overfishing" was the cause (Murphy 1966, 1977, 1980; Saville 1980).

However, stock-recruitment relationships generally cannot be established directly by plotting an index of recruitment on parental biomass. Rather, it is necessary to account simultaneously for a stock-recruitment relationship and the biotic and/or abiotic factor(s) which may affect that relationship. In tropical stocks, this approach has allowed e.g., Csirke (1980) to demonstrate a strong effect of oceanographic conditions on the recruitment of the Peruvian anchovy. Ricker (1975, p. 275-280), Bakun and Parrish (1980) and Bakun et al. (1982) have discussed methods to identify various factors affecting recruitment using multiple regression analysis (for which Program FB 7, with slight modifications, can be used).

To date four types of stock-recruitment relationships are commonly recognized:

1) Recruitment increasing rather steeply toward an asymptote (this model, paradoxically is the model generally used for illustrating *a lack* of stock-recruitment relationships, see Figs. 9.1B and 9.2).
2) Recruitment increasing in proportion to a power of parental biomass or of the number of eggs shed (Fig. 9.1C).
3) Recruitment increasing more or less steeply toward a maximum at an intermediate size of parental stock (P), then decreasing with increasing values of P (Fig. 9.1D and 9.3).
4) None of the above, but stock-recruitment *sensu stricto* conforming to 1, 2 or 3 *after* the simultaneous effects of environmental factors (biotic or abiotic) are removed, as in Csirke (1980).

Examples of relationships of types 1 and 3, the most commonly used, are illustrated here (Examples 9.1 and 9.2). These two examples must be taken with a grain of salt, however, because the first displays considerable scatter (as is typical of most such plots), while the second is based on points derived by a method which gives only approximate results.

At present, research in fish recruitment is in a state of flux, with a lot of new ideas and insufficient data to test them. Reviews covering what little is known of stock-recruitment relationships in tropical fish are given in Sharp (1980) for pelagics, by Sale (1980) for coral reef fish, Murphy (1982) for miscellaneous fish and Garcia (1983) for penaeid shrimps.

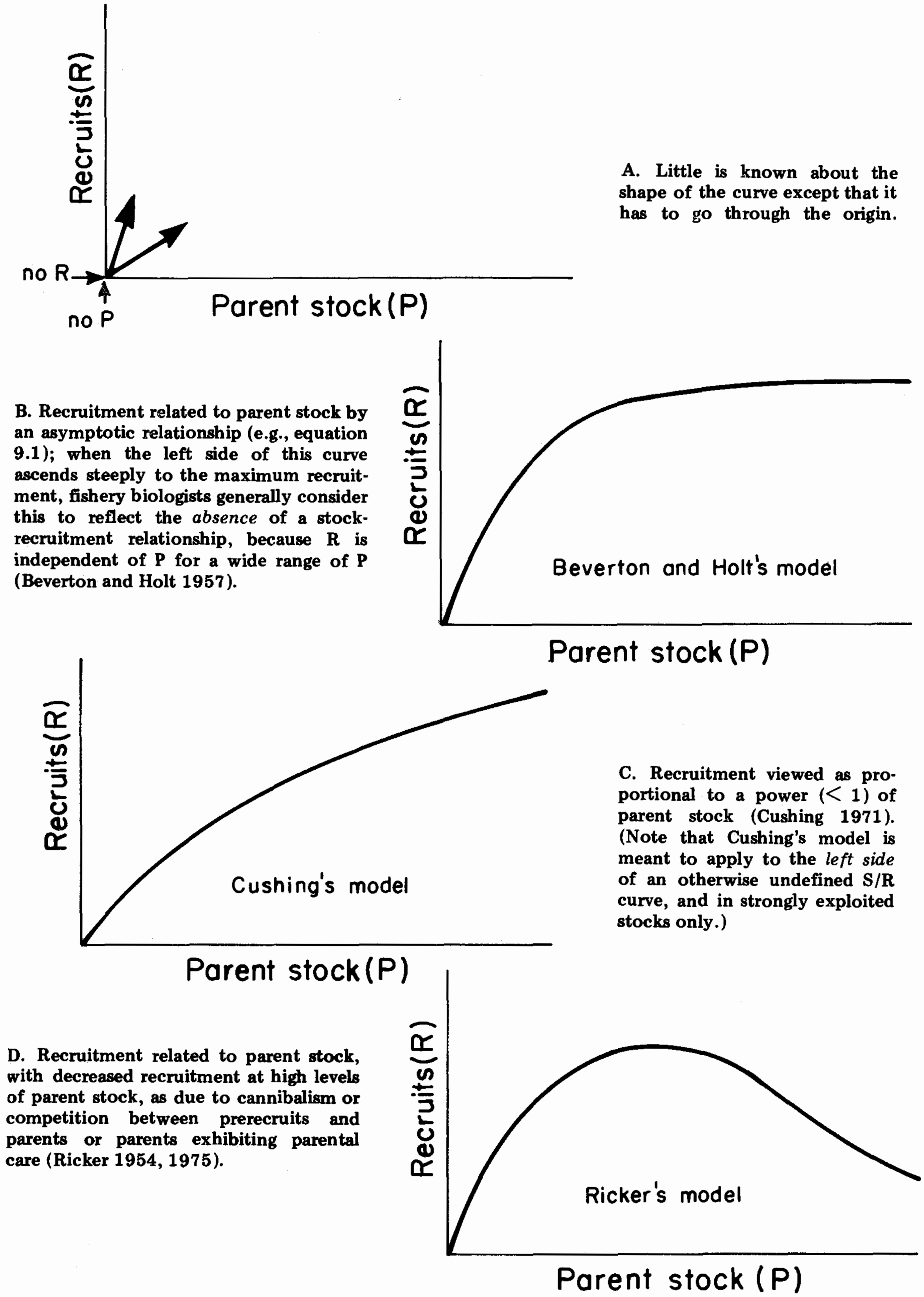

Fig. 9.1. Types of stock-recruitment relationships used in fishery research.

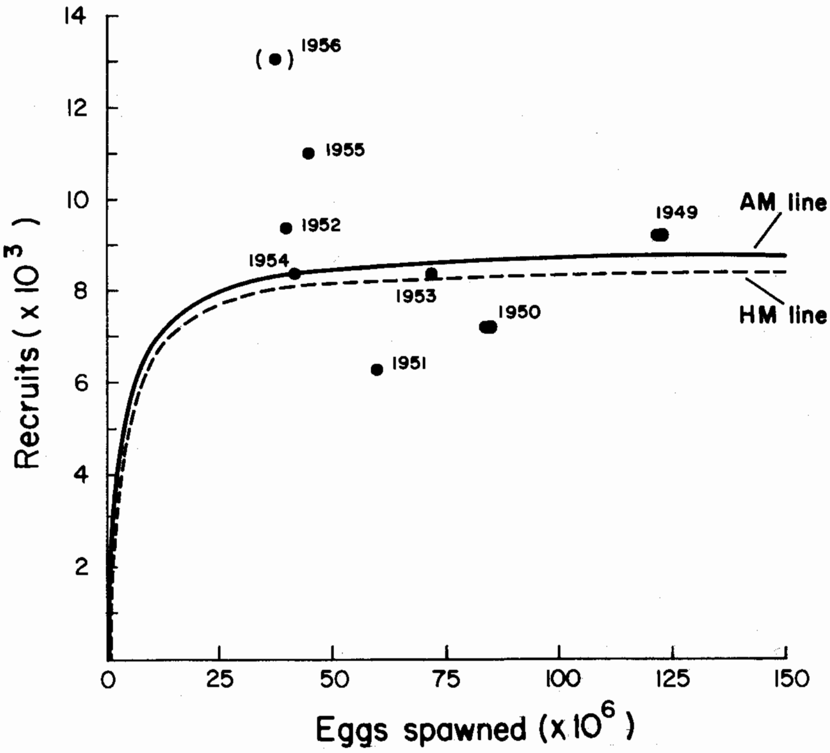

Fig. 9.2. Beverton and Holt type stock-recruitment relationship for the sea bream *(Taius tumifrons)* (East China Sea).

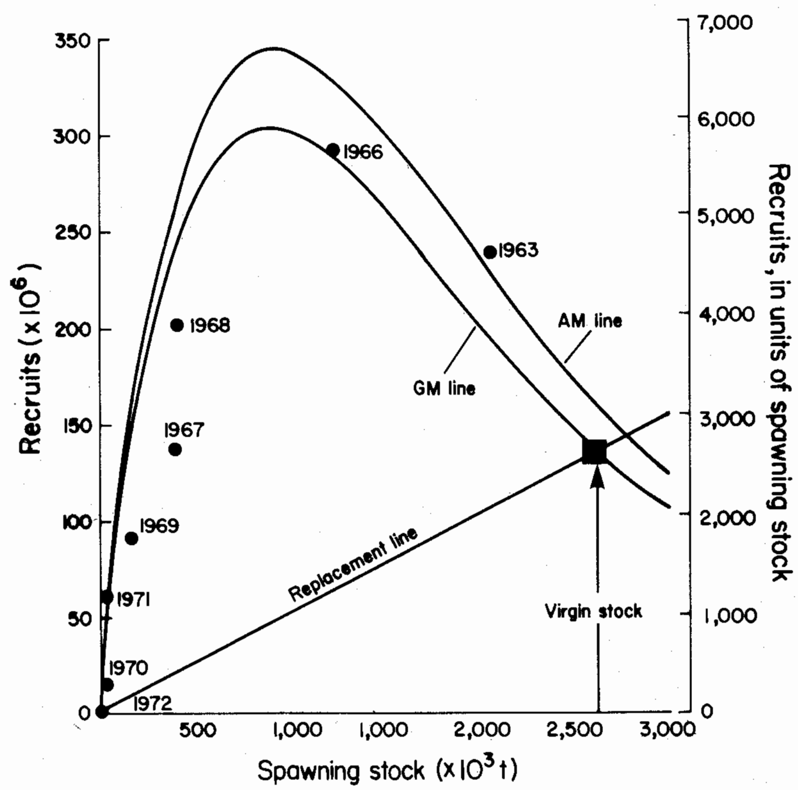

Fig. 9.3. Stock-recruitment data of false trevally *(Lactarius lactarius)* in the Gulf of Thailand, fitted with Ricker curves (GM and AM) (based on data in Table 9.2 and Example 9.3).

THE STOCK-RECRUITMENT RELATIONSHIP OF BEVERTON AND HOLT*

In this model, the relationship between the number of recruits (R) and the spawning stock size (P) is given by

$$R = \frac{1}{\alpha' + \beta'} \qquad \ldots 9.1)$$

Expression (9.1) can be expressed as a linear relationship of the form

$$\frac{P}{R} = \beta' + \alpha' P \qquad \ldots 9.2)$$

As this plot involves the use of inverses (e.g., $1/R$), the estimated values of α' and β' provide, for each value of P, estimated values of recruitment ($\hat{R}$) whose sum ($\Sigma \hat{R}$) is actually lower than the sum of the empirical values of R (ΣR). This is due to the fact that the use of inverse values implies the use of a harmonic mean (HM) in fitting equation (9.1) and to the fact that the harmonic mean of a series of values is always less than the arithmetic mean (AM) of these values.

An approximate conversion of the estimated recruitment values $\hat{R}_{HM}$ to the corresponding $\hat{R}_{AM}$ values can be obtained, however, by performing

$$C = \frac{\Sigma R \text{ (empirical values)}}{\Sigma R \text{ (harmonic mean values)}} \qquad \ldots 9.3)$$

and by multiplying the recruitment values of the HM line by the constant C (Ricker 1975).

An application of this model is given in Example 9.1, based on the data in Table 9.1.

Table 9.1. Data for the derivation of a Beverton and Holt type relationship for sea bream *(Taius tumifrons)* from the East China Sea. Figures derived from Murphy (1972, Fig. 3, based on Shindo 1960).

No.	Year	Eggs spawned No. x 10^6	Recruits No. x 10^3	P/R
1	1949	122	9.2	13.3
2	1950	84	7.2	11.7
3	1951	60	6.3	9.52
4	1952	40	9.4	4.26
5	1953	72	8.4	8.57
6	1954	42	8.3	5.06
7	1955	45	11.0	4.09
not used[a]	1956	(38)	(13.0)	(2.92)

[a]Use of the 1956 value generates a negative intercept in equation (9.2), and hence a negative value of β' in equation (9.1). See Users' Instruction for FB 24.

*Beverton and Holt (1957) actually presented *two* stock-recruitment models. Their second model, however, is in its form—if not in its derivation—similar to Ricker's model discussed further below.

RICKER'S STOCK-RECRUITMENT RELATIONSHIPS

First form of Ricker's curve

The stock-recruitment relationship proposed by Ricker (1954, 1975) can be written

$$R = \alpha P e^{-\beta P} \qquad \ldots 9.4)$$

where R is the number of recruits
P is the size of parental stock (in weight, in numbers, or as egg production)
α is an index of stock-independent mortality

and β is an index of stock-dependent mortality

Equation (9.4) can be rewritten

$$\ln R - \ln P = \ln a - bP \qquad \ldots 9.5)$$

which has the form of a linear regression $y = a + bx$, where $y = \ln R - \ln P$, $x = P$, $a = \ln\alpha$ and $b = \beta$.
Once α and β are estimated, maximum recruitment (R_m) is obtained by

$$R_m = \alpha/\beta e \qquad \ldots 9.6)$$

where e (= 2.1783) is the base of the natural logarithms. Also, the parental stock at maximum recruitment (P_m) can be estimated by the equation

$$P_m = 1/\beta \qquad \ldots 9.7)$$

The relationships between the parameters α and β in the first form of Ricker's curve to α' and β' in Beverton and Holt's curve are discussed in Chapter 11 (p. 156).
When P and R are expressed in the same units, a "level of replacement abundance" can be found where P = R. This replacement level (P_r) can be estimated through

$$P_r = \frac{\ln \alpha}{\beta} = R_r \qquad \ldots 9.8)$$

For most purposes, it is reasonable to assume that (the average size of) the virgin parental stock (P_v) should be equal to P_r, which allows, when an estimate of P_v is available, for the original units of recruitment to be converted to units of P through multiplication with P_v/P_r (see Table 9.2).
Program FB 25 can be used to estimate the parameters of the first type of Ricker curve (see Example 9.2).

Table 9.2. Data for the derivation of Ricker type stock-recruitment relationships for the false trevally *(Lactarius lactarius)* from the Gulf of Thailand.[a]

Year	P (in thousand tonnes)	R (in millions)	R (in units of P)[b]
virgin stock	2,660	—	(2,660)
1963	2,087	239	4,606.8
1966	1,277	292	5,628.4
1967	422	138	2,660.0
1968	444	202	3,893.6
1969	191	90.8	1,750.2
1970	29.8	15.5	298.77
1971	37.8	55.5	1,069.8
1972	4.0	8.9	171.55

[a]From Pauly (1980d); the values presented here should be considered tentative due to several approximations made for the estimation of the number of recruits.
[b]See Example 9.3.

Second form of Ricker's curve

When recruitment and parental stock are expressed in the same units, equation (9.4) can be rewritten in the form

$$R = Pe^{a(1 - P/P_r)} \qquad \ldots 9.9)$$

where P_r is the replacement abundance, and where a new parameter (a) is introduced, which is defined as

$$a = P_r\beta = \ln\alpha \qquad \ldots 9.10)$$

Thus, equation (9.9) can be rewritten

$$\ln R - \ln P = a - \frac{a}{P_r} P \qquad \ldots 9.11)$$

which has the form of a linear regression where $y = \ln R - \ln P$ and $x = P$, with the intercept of this regression providing an estimate of a and its slope an estimate of a/P_r.

Equation (9.9), as well as equation (9.4), incidentally, provide estimates of the geometric mean (GM) value of R at a given P; generally, GM values estimate the most probable values of recruitment for the observed P values, while the arithmetic mean (AM) curve estimates the long-term arithmetic average value of recruitment obtained at a given P (Ricker 1975, p. 283).

Thus, conversion of the GM curve to an AM curve is indicated especially when the R values are widely scattered about the stock-recruitment curve. Program FB 25 can be used for this conversion, which is performed according to the method given in Ricker (1975, p. 275 and 283-288) (see Example 9.2).

In temperate, single-species fisheries, the establishment of a stock-recruitment relationship of the type discussed here is sufficient for most purposes of fishery management, since the best strategy generally is to optimize the level of surplus recruitment (= the number of recruits produced in excess of replacement level, see Fig. 9.3).

This strategy also may be indicated in the case of tropical single-species fisheries, such as sardines, anchovies, chub mackerels or scads. In the case of multispecies fisheries, the establishment of a stock-recruitment relationship in one species is not sufficient—obviously—for deriving an optimum fishing strategy for the whole multispecies stock (see Chapter 12).

Recommended reading: The classic paper of Ricker (1954) is an excellent introduction to the field, which is also reviewed in Ricker (1975). Parrish (1978) edited a volume of papers on the subject of stock-recruitment relationships which contains many important contributions. Sharp (1980) presents an even more up-to-date review of the subject. Several contributions included in Pauly and Murphy (1982) are also of relevance to the topic, particularly as far as the tropics are concerned. Garcia (1983) discussed in detail the stock-recruitment relationships of tropical and subtropical shrimp and the numerous pitfalls (potential and realized) in the interpretation of such relationships. Shepherd (1982) recently proposed a versatile stock-recruitment model which has the Cushing, Beverton and Holt and Ricker models as special cases.

Suggested research topics: Every attempt should be made to estimate recruitment from stocks that are suitably well-documented, especially by using VPA and related methods. Attempts should be made to identify the factors which most strongly affect recruitment in a fishery and to derive from the properties of these factors the best strategy for the exploitation of the resource.

EXAMPLE 9.1

Estimating the parameters of a Beverton and Holt type stock-recruitment relationship (*Taius tumifrons*, East China Sea).

Data from Table 9.1

Computation

1) Read side 1 of Program FB 24

2) Enter P and R data

Keystrokes: f a 122 ↑ 9.2 A 84 ↑ 7.2 A 60 ↑ 6.3 A 40 ↑ 9.4 A 72 ↑ 8.4 A 42 ↑ 8.3 A 45 ↑ 11 A

3) Estimate parameters of curve

Keystroke	Results	
E	0.857	(r^2)
	0.116	(α')
	0.371	(β')

4) To obtain estimate of R_{HM} and R_{AM}, re-enter the P values

Keystrokes 122 D 84 D 60 D 40 D 72 D 42 D 45 D

5) Then estimate R_{HM} and R_{AM} for any given value of P

Keystroke	Results	
10C	6.541	R_{HM}
	6.827	R_{AM}
etc.	...	

The data can thus be plotted in the form of curves as in Fig. 9.2

EXAMPLE 9.2

Estimating the parameters of Ricker type recruitment curves (first and second forms).

Data from Table 9.2

Computation

1) Read sides 1 and 2 of Program FB 25

2) Enter P and R data (first form of curve)

Keystrokes: f a 2087 ↑ 239 A 1277 ↑ 292 A 422 ↑ 138 A 444 ↑ 202 A 191 ↑ 90.8 A 29.8 ↑ 15.5 A 37.8 ↑ 55.5 A 4 ↑ 8.9 A

3) Calculate parameters of stock recruitment curve (first form):

	Keystrokes	Results	
	E	0.694	(r^2)
		0.886	(α)
		0.001	(β)
		937.348	(P_m)
		305.516	(R_m)
4) Since β is not precise enough, do:	RCL B DSP 5	0.00107	(β)

5) Assuming that the value of P in the virgin stock (P_v) corresponds to P_r, estimate the ratio R_r/P_r

	Keystrokes	Results	
	2660 f d	0.05188	(R_r/P_r)

6) To convert the original values of R in units of P do:

Keystrokes	Results	
DSP 1		
239 ↑		
.05188 ÷	4606.8	($R_{(1963)}$)
292 ↑		
.05188 ÷	5628.4	($R_{(1966)}$)
etc.	...	
	(see Table 9.2)	

7) To obtain parameters of stock-recruitment curve (second form), first enter P and new R data:

Keystrokes: f a 2087 ↑ 4606.8 A 1277 ↑ 5628.4 A 422 ↑ 2660 A 444 ↑ 3893.6 A 191 ↑ 1750.2 A 29.8 ↑ 298.77 A 37.8 ↑ 1069.8 A 4 ↑ 171.55 A

(continued)

Example 9.2
(cont.)

(continued from p. 136)

8) To calculate parameters of new curve do:

Keystrokes	Results	
f e	0.694	(r^2)
	2.838	(P_r/P_m)
	2659.599	(P_r)

9) The parameter values obtained pertain to a GM curve; to obtain recruitment values corresponding to an AM curve, re-enter the P and R values:

Keystrokes: 2087 ↑ 4606.8 D 1277 ↑ 5628.4 D 422 ↑ 2660 D 444 ↑ 3893.6 D 191 ↑ 1750.2 D 29.8 ↑ 298.77 D 37.8 ↑ 1069.8 D 4 ↑ 171.55 D

10) When all P and new R values have been re-entered, the ratio between $R_{(AM)}$ and $R_{(GM)}$ values is obtained by:

Keystrokes	Results	
f c	1.13	(R_{AM}/R_{GM})

11) Which allows one to draw GM and RM curves by entering P values, and calculating the corresponding $R_{(GM)}$ and $R_{(AM)}$ values, i.e.,

10B	168.96	($R_{(GM)}$)
	190.84	($R_{(AM)}$)
100 B	1534.91	($R_{(GM)}$)
	1733.67	($R_{(AM)}$)
etc.	...	
	(see Fig. 9.4)	

10. Surplus-Yield Models

INTRODUCTION

Based on earlier work by Baranov (1927), Graham (1935) and others, Schaefer (1954, 1957) presented a model which, in its recent formulation (e.g., Ricker 1975 or Schnute 1977) can be used for stock assessment when a minimum of data is available (only catch-and-effort data are required) and which has been applied, with varying success, to a number of fisheries throughout the world.

The assumptions made for the derivation of this model are as follows:

1) Any fish population newly colonizing a given, finite ecosystem grows in weight until it approaches the maximum carrying capacity (most often in terms of available food) of this ecosystem, after which its increase in total weight gradually ceases as the stock size comes closer (asymptotically) to the carrying capacity of the environment (B_∞),
2) B_∞ more or less corresponds to the virgin stock (= unfished biomass, B_v),
3) the growth, in time, of the fish biomass toward B_∞ may be described by a logistic curve, the first derivative of which, dB/dt, has a maximum at $B_\infty/2$ and zero values at B_∞ and B = 0 (Fig. 10.1),

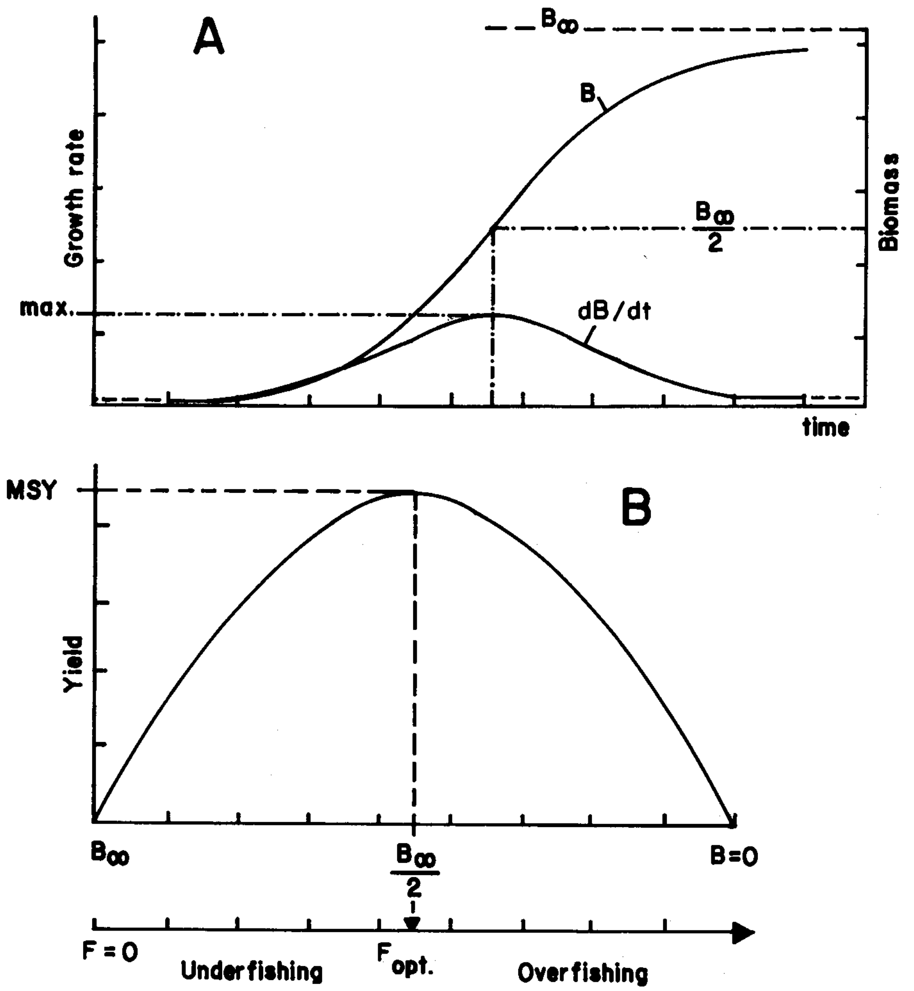

Fig. 10.1. The simple Schaefer model. A) the logistic curve and its first derivative. B) the yield-biomass and the yield-effort relationships.

4) the fishing effort which reduces B_∞ to half its original value will produce the highest net growth of the stock, that is the maximum *surplus yield* available to a fishery (Fig. 10.1),
5) the maximum surplus yield in (4) can be sustained indefinitely (hence, the term maximum sustainable yield), as long as the biomass of the exploited stock is maintained at $B_\infty/2$.

There is biological evidence to make these assumptions appear reasonable (Odum 1971; Silliman and Gutsell 1958). Some reasons for the low surplus production at stock size > $B_\infty/2$ are given here (from Ricker 1975):

"1) Near maximum stock density, efficiency of reproduction, and often 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 for growth.
3) An unfished stock tends to contain 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."

The main reason larger fish convert a smaller fraction of their food into new flesh, however, is due to the fact that oxygen is needed for synthesis of body substance, and the relative gill size (= gill surface/body weight) decreases sharply as fish get larger, down to a point where the body is so badly supplied with O_2 that most of it is used for maintenance, with very little left for synthesis of new body substance or surplus production (Pauly 1981).

From the assumptions listed above, two very important features of the Schaefer and related models follow, namely that the growth of a stock is a function of its size and of its size only—and that, therefore, a stock should respond by changes in its growth rate (dB/dt) instantaneously to any change of its size (e.g., by fishing). Thus, we have

$$\frac{dB}{dt} = \frac{r_m B\,(B_\infty - B)}{B_\infty} \qquad \ldots 10.1)$$

where B is the stock size, B_∞ is the carrying capacity of the environment, r_m is the intrinsic rate of growth of the stock in question.

Quite clearly, the assumption that a stock reacts instantaneously to change of its size is not realistic. Therefore, the concept of "equilibrium" is used here, and this refers to the situation which exists when a given fishing mortality (F_E) has been exerted long enough for a stock to have adjusted its size and rate of net growth such that the relationship expressed in equation (10.1) is fulfilled. The following series of equations, adapted from Ricker (1975) assumes equilibrium conditions, as expressed by the subscript "E". We start from

$$Y_E = \frac{dB}{dt} = F_E \cdot B_E \qquad \ldots 10.2)$$

where Y_E, the equilibrium yield (per unit of time) is equal to the net growth rate of the stock maintained by a fishing mortality F_E at the equilibrium level B_E.

Combining equations (10.2) and (10.1) and rearranging gives

$$Y_E = r_m\, B_E - \left(\frac{r_m}{B_\infty}\right) B_E^2 \qquad \ldots 10.3)$$

Expression (10.3) has the form of a parabola (Fig. 10.1B). The first derivative of (10.3) with respect to B_E can be equated to zero and solved for B_E, which gives the value of B_E (= B_{opt}) for which yield is maximum or

$$B_{opt} = \frac{B_\infty}{2} \qquad \ldots 10.4)$$

The maximum value of Y_E is commonly named *maximum sustainable yield* (MSY). Thus, substituting (10.4) into (10.3) gives

$$MSY = \frac{r_m \cdot B_\infty}{4} \qquad \ldots 10.5)$$

Also, substituting $F_{opt} \cdot B_{opt}$ for MSY in (10.5) and dividing both sides by expression (10.4) gives the fishing mortality at MSY (F_{opt}):

$$F_{opt} = \frac{r_m}{2} \qquad \ldots 10.6)$$

and, since fishing mortality is proportional to effort, we also have

$$f_{opt} = \frac{r_m}{2q} \qquad \ldots 10.7)$$

where f_{opt} is the fishing effort which brings about MSY and q is the catchability coefficient.
Since we have

$$B_E = B_\infty - \frac{F_E\, B_\infty}{r_m} \qquad \ldots 10.8)$$

equation (10.3) can be rewritten

$$Y_E = B_\infty\, F_E - \left(\frac{B_\infty}{r_m}\right) F_E^2 \qquad \ldots 10.9)$$

and, substituting qf_E for F_E gives

$$Y_E = af_E - bf_E^2 \qquad \ldots 10.10)$$

where $$a = qB_\infty \qquad \ldots 10.11)$$

and $$b = \frac{q^2\, B_\infty}{r_m} \qquad \ldots 10.12)$$

Thus, when the stock is in equilibrium, surplus yield is a parabolic function of stock size (B), or of fishing mortality (F) or of effort (f). Therefore, catch and effort data can be fitted easily by the linear regression

$$\frac{Y_E}{f_E} = a - bf_E \qquad \ldots 10.13)$$

The definition of f_{opt} in expression (10.7) and of a and b in (10.10) gives the following identities

$$f_{opt} = \frac{r_m}{2q} = \frac{q\, B_\infty \cdot r_m}{2\, q^2\, B_\infty} = \frac{a}{2b} \qquad \ldots 10.14)$$

[($f_{opt} = \frac{a}{2b}$), it will be noted, could also have been obtained by differentiating (10.10), equating to zero and solving for f_E.]

Thus, as Ricker (1975, p. 316) emphasizes "—maximum sustainable yield optimum rate of fishing [f_{opt}] can be estimated from the relation of equilibrium yield to equilibrium effort, without knowing the catchability (q) of the fish." This very important feature considerably simplifies the model originally proposed by Schaefer (1954, 1957), making it particularly well-suited to the investigation of tropical stocks.

THE "EQUILIBRIUM" PROBLEM

This leaves only one problem which remains associated with the model, namely the determination of what an "equilibrium situation" actually is.

Many authors, implicitly assuming that the stock reacts instantaneously to changes of its size simply plot the yield per effort of a given year against the effort of the corresponding year. This procedure is illustrated in Example 10.1 which is based on Table 10.1.

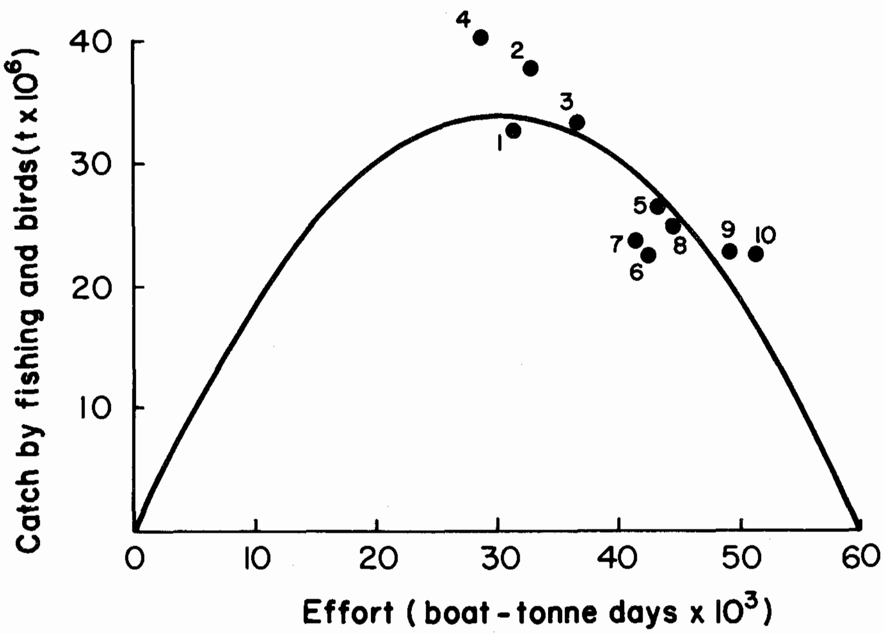

Fig. 10.2. Yield curve of Peruvian anchoveta *(Engraulis ringens)* off Peru, just prior to the collapse of the fishery (based on data in Table 10.1 and Example 10.1).

Table 10.1. Catch-and-effort data for anchoveta *(Engraulis ringens)* off Peru, prior to stock collapse (from Murphy 1972).

No.	Season	Total catch[a] ($t \times 10^6$)	Total effort[b]
1	1960-61	32.89	31.413
2	1961-62	37.78	32.999
3	1962-63	33.25	36.579
4	1963-64	28.86	40.367
5	1964-65	26.82	43.191
6	1965-66	22.26	42.716
7	1966-67	23.73	41.636
8	1967-68	25.04	44.634
9	1968-69	22.77	49.284
10	1969-70	22.64	52.048

[a]This "catch" accounts for the fish taken by the fishery, by guano birds and by fish predation.
[b]This "effort" accounts for both the fishery and the predatory animals (fish and birds) but is expressed in thousand of boat-tonnes per day.

Gulland (1969), on the other hand, suggested plotting the yield per effort of a given year against the mean effort ($\bar{f}$) of the present and preceding year(s), with the number of annual effort values to be included depending on the longevity and mortality of the fish under exploitation, i.e., on the number of year classes significantly contributing to the fishery. This technique, which is illustrated in Table 10.2 and Fig. 10.3, has been criticized by a number of authors (e.g., Roff and Fairbairn 1980; Walter 1975). The latter author also proposed an alternative, graphical method to simulate equilibrium condition.

Schnute (1977) presented a rigorous method for dealing with the problem caused by data drawn from a non-equilibrium situation. Only a simplified version of his model is presented here which has the form

$$\ln\left(\frac{U_i}{U_{i-1}}\right) = r_m - q \cdot \left(\frac{f_i+f_{i-1}}{2}\right) - \frac{r_m}{qB_\infty} \cdot \left(\frac{U_i+U_{i-1}}{2}\right) \qquad \ldots 10.15)$$

where U_i is the mean c/f prevailing in a given year i. This model has the form of a multiple regression whose intercept ($a = r_m$) and slopes ($b_1 = -q$; $b_2 = -\frac{r_m}{qB_\infty}$) lead to estimates of r_m and q and B_∞, respectively. This makes the model superior to the original formulation of Schaefer (1954) which, rather than providing estimates of q, required a knowledge of this parameter. Mohn (1980), however, suggests that the model is quite unstable when "noisy" catch-and-effort data are used (see also Example 10.2) and it would seem best to compare the results obtained by it with estimates e.g., of MSY obtained using another model (see Fig. 10.3).

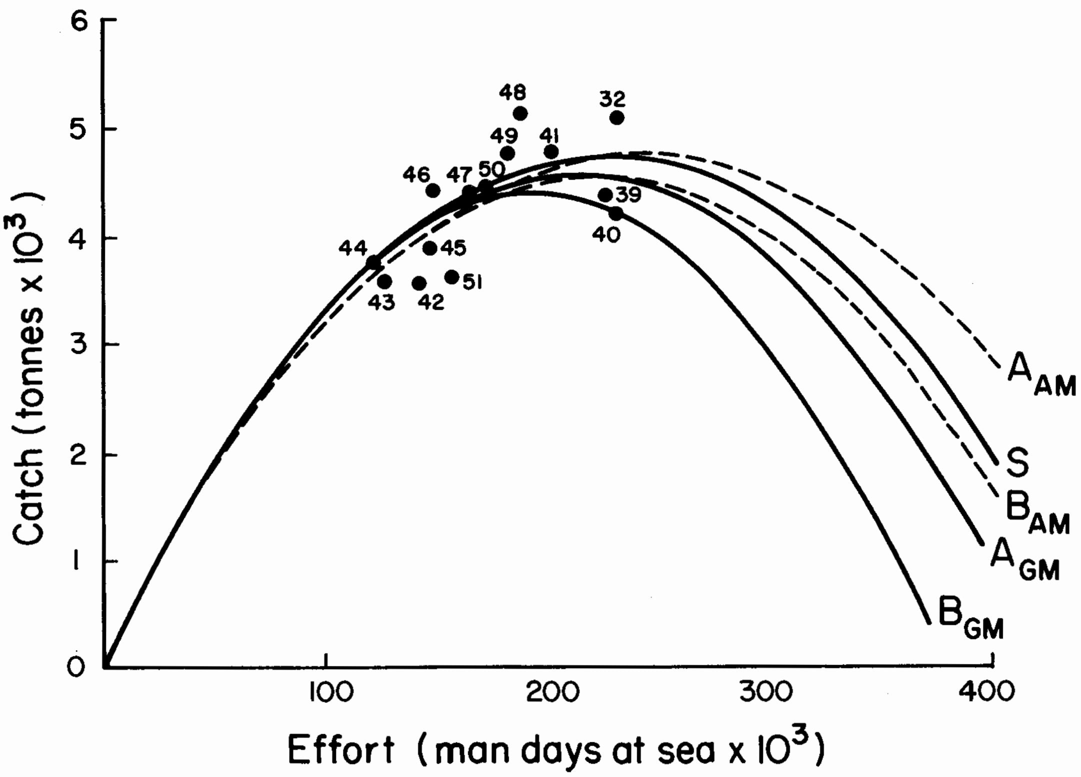

Fig. 10.3. Yield curves for the red snapper *(Lutjanus campecheanus)* fishery on the Bank of Campeche, Mexico. Note strong difference between curves obtained through arithmetic mean (AM) and those obtained through geometric mean regressions (GM); yield curve A_{AM} corresponds to that in Klima (1976, Fig. 3); the corresponding GM curve (A_{GM}), because of the scatter of the data points, suggests a lower value of f_{opt}. Similarly, the yield curves obtained by using only contemporary effort (A_{AM}, A_{GM}) differ from those obtained by also using the preceding years' effort (B_{AM}, B_{GM}). Curve S results from an application of Schute's model (but see Example 10.2).

Table 10.2. Catch-and-effort data for the red snapper fishery on Campeche Bank, Gulf of Mexico, illustrating Gulland's method to simulate equilibrium conditions. From Klima (1976, Table 8, Figs. 2 and 3).

No.	Year	Catch ($t \times 10^3$)	Contemporary effort (man-days at sea x 10^3)	Average effort I (contemp. + previous year)	Average effort II (contemp. + 2 preceding years)
1	1937	4.91	227	–	–
2	1938	5.02	224	225.5	–
3	1939	4.25	220	222.0	223.7
4	1940	4.14	227	223.5	223.7
5	1941	4.79	201	214.0	216.0
6	1942	3.46	141	171.0	189.7
7	1943	3.57	125	133.0	155.7
8	1944	3.77	123	124.0	129.7
9	1945	3.98	145	134.0	131.0
10	1946	4.37	149	147.0	135.0
11	1947	4.24	164	156.5	152.7
12	1948	5.06	182	173.0	165.0
13	1949	4.79	179	180.5	175.0
14	1950	4.38	166	172.5	175.7
15	1951	3.53	156	161.0	167.0

SOME MODIFICATIONS OF THE PARABOLIC MODEL

There are various modifications of the basic model in which curves are fitted which differ from a parabola (e.g., Fox 1970; Pella and Tomlinson 1969). Of these variants, only the model of Fox (1970) is presented here.

Put simply, this model consists of plotting the natural logarithm of yield per effort on effort or

$$\ln \frac{Y_E}{f_E} = a - bf_E \qquad \ldots 10.16)$$

instead of plotting yield per effort on effort, as in the case of expression (10.10). This provides the following set of relationships

$$f_{opt} = 1/b \qquad \ldots 10.17)$$

$$MSY = (e^a - 1)/b \qquad \ldots 10.18)$$

and

$$Y_E = fe^a \cdot e^{-bf_E} \qquad \ldots 10.19)$$

Other useful relationships may be found in Fox (1970) or Ricker (1975, p. 330-331). In this model, the value of B_{opt} is always 37% of B_∞, as opposed to 50% in the parabolic model [see expression (10.4)].

Program FB 26 can be used, given a set of yield (= catch in weight) and effort data, to assess the state of a fishery by using the Schaefer (parabolic) and the Fox (exponential) model, by one single entry of data. Values of MSY and f_{opt} are estimated; also values of r^2 for the regression equations (10.13) and (10.16) are given which allow comparison of the fit of each of the two models to a given set of data.

Here, the Schaefer and Fox models are fitted to data by means of a GM regression (see Chapter 4 for a definition), which has the effect of automatically accounting for uncertainty:

- when r^2 is low (that is when both catch and effort are estimated with large errors, and/or when the catch is strongly affected by environmental perturbations), the GM regression will provide lower (more conservative) estimates of optimum effort than an AM regression,
- when r^2 is high (that is when there is a tight relationship between the catch and effort data), the GM regression will have a slope and an intercept similar to those of an AM regression.

This feature, generally not considered when fitting surplus production models to data, seems particularly appropriate in light of the fact that costly investments are often based solely on the values of optimum effort generated by surplus production models.

An application of Fox's model is given in Example 10.3 (see also Fig. 10.4 and Table 10.3).

The models discussed above, although representing considerable simplifications or improvements of the model presented by Schaefer (1954, 1957), have a major drawback in that they require measures of effort, which are often unavailable and/or unreliable.

It is, however, not fishing effort itself which "generates" a surplus yield of an exploited stock, but fishing mortality. In an exploited fish stock, on the other hand, fishing mortality is often not directly measurable, because of the simultaneous effect of natural mortality.

To resolve this, Csirke and Caddy (1983) suggested to plot annual catch (Y) as a parabolic function of total mortality (Z), i.e.,

$$Y = a + b_1 Z + b_2 Z^2 \qquad \ldots 10.20)$$

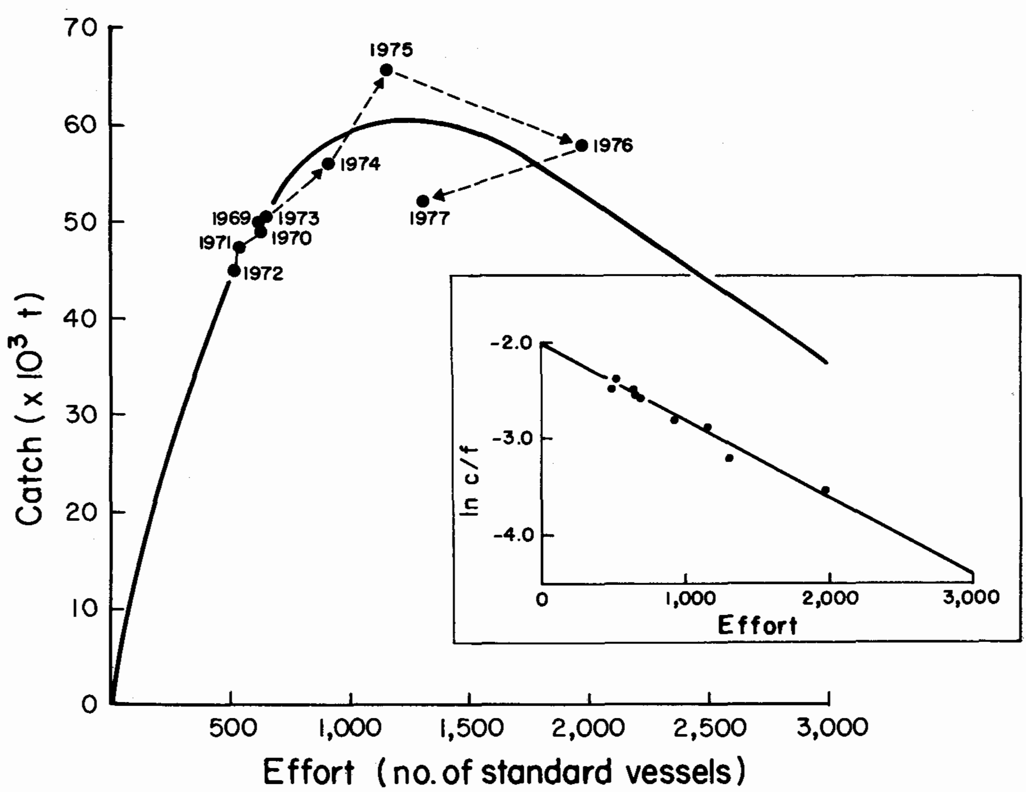

Fig. 10.4. Yield curve for the north Java coast trawl fishery (based on data in Table 10.3 and Example 10.3).

Table 10.3. Catch-and-effort data from the north Java demersal trawl fishery (all species aggregated) (from Dwiponggo 1979).

No.	Year	Catch t x 10^3	Effort No. of standard vessels
1	1969	50	623
2	1970	49	628
3	1971	47.5	520
4	1972	45	513
5	1973	51	661
6	1974	56	919
7	1975	66	1,158
8	1976	58	1,970
9	1977	52	1,317

where Z = F + M, from which the following parameters can be estimated.

$$M = \frac{-b_1 + \sqrt{b_1^2 - 4ab_2}}{2b_2} \qquad \ldots 10.21)$$

$$Z_{opt} = -\frac{b_1}{2b_2} \qquad \ldots 10.22)$$

$$F_{opt} = -\frac{b_1}{2b_2} - M \qquad \ldots 10.23)$$

$$r_m = 2F_{opt} \qquad \ldots 10.24)$$

$$MSY = a - (b_1^2/4b_2) \qquad \ldots 10.25)$$

and

$$B_\infty = \frac{MSY \cdot 4}{r_m} \qquad \ldots 10.26)$$

An application of this method is given in Example 10.4 (see also Fig. 10.5 and Table 10.4).

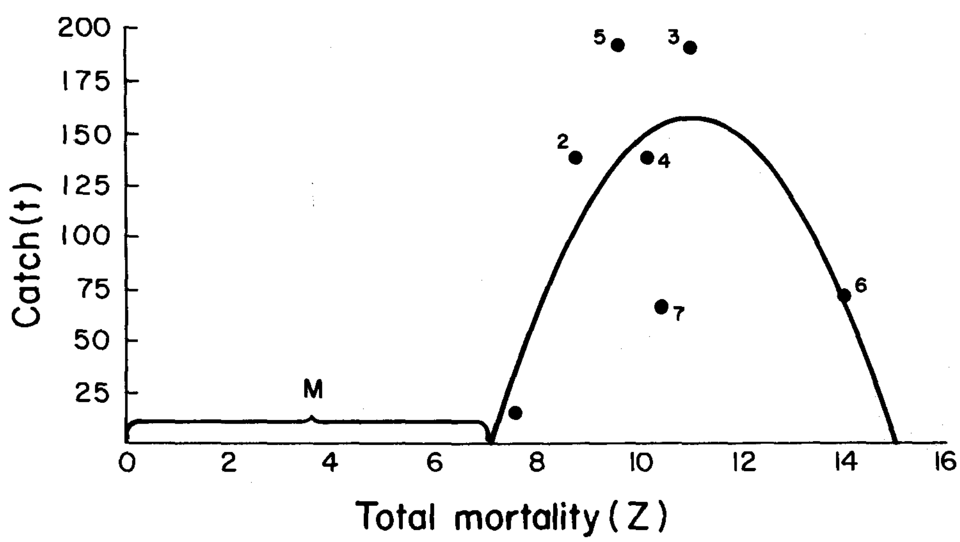

Fig. 10.5. Yield curve of shorthead anchovy *(Stolephorus heterolobus)* at Ysabel Passage, near New Hanover, Papua New Guinea. M = natural mortality. Numbers refer to those in Example 10.4.

A further property of the model of Csirke and Caddy is that Z in equation (10.20) above can be replaced by Z/K, the latter being a parameter which can be estimated from the average length composition of the fish catch and without an exact knowledge of the growth parameters of the fish in question (see Chapter 5). The modified model thus becomes

$$Y = a' + b_1' \, (Z/K) + b_2' \, (Z/K)^2 \qquad \ldots 10.27)$$

with

$$M/K = \frac{-b_1' + \sqrt{b_1'^{\,2} - 4a'b_2'}}{2b_2'} \qquad \ldots 10.28)$$

and

$$Z_{opt}/K = -b_1'/2a' \qquad \ldots 10.29)$$

The parameter Z_{opt}/K corresponds to an optimum mean length in the catch ($\bar{L}_{opt}$), the value of which may be estimated by trial and error, e.g., from

$$\frac{Z_{opt}}{K} = \frac{L_\infty - \bar{L}_{opt}}{\bar{L}_{opt} - L'} \qquad \ldots 10.30)$$

Finally, E = F/Z may be estimated for each value of Z/K from the equation

$$E = 1 - (M/K) \,/\, (Z/K) \qquad \ldots 10.31)$$

which can be used, along with the estimate of M/K, e.g., to estimate the relative yield per recruit obtained at each level of Z/K (see Chapter 8). See Chapter 5 for definitions of $\bar{L}$, L' and E.

All of these parameters, it should be mentioned are either solutions of, or are implicit in the Schaefer model. The point here is that they can all be derived from quantities (catch, total mortality) that can be estimated rather straightforwardly, e.g., using one of the various methods presented in Chapter 5.

When catch data are not available, catch-per-effort data (c/f = U) can be used in a linear regression of the form

$$U = a - bZ \qquad \ldots 10.32)$$

where

$$M = (a - U_\infty)/b \qquad \ldots 10.33)$$

and where U_∞ is the catch per effort corresponding to B_∞, i.e., to the unexploited biomass or virgin stock (assuming that $B_v \approx B_\infty$). Generally, when catch-per-effort data are available, it will be possible to estimate U_∞ by using the first two catch-per-effort values in a developing fishery (U_1, U_2) and defining

$$U_\infty \approx 2U_1 - U_2 \qquad \ldots 10.34)$$

(Obviously, data from biomass survey in an unexploited stock can be used to estimate both U_∞ and B_∞ directly). Using U_∞ and equation (10.32), it is then possible to estimate F_{opt} as

$$F_{opt} = U_\infty/(2b) \qquad \ldots 10.35)$$

while a knowledge of B_∞ can be used to estimate MSY from F_{opt}

$$MSY = 0.5B_\infty \cdot F_{opt} \qquad \ldots 10.36)$$

APPLYING SURPLUS-YIELD MODELS TO MULTISPECIES STOCKS

In demersal fisheries, especially in the tropics, the catch tends to consist of a multitude of species for which individual assessments are often impossible or inappropriate.

Table 10.4. Catch and total mortality estimates of shorthead anchovy *(Stolephorus heterolobus)* in Ysabel Passage, near New Hanover, Papua New Guinea. Data from Dalzell (1984); Z estimates based on mean lengths.

No.	Year	Catch (t)	Total mortality (Z)
1	1972	14	7.6
2	1973	138	8.8
3	1976	191	11.0
4	1977	138	10.2
not used	1978	(404)	(11.7)
5	1979	192	9.6
6	1980	72	14.0
7	1981	66	10.5

It has been a common practice to treat the various fish of tropical and other multispecies stocks as one single entity, applying the Schaefer or Fox model to the total multispecies catch of these fisheries (see Example 10.3 and FAO 1978). Pope (1979) recently provided a theoretical basis for this approach, while some of the problems associated with it were discussed in Pauly (1979b). See also Chapter 12.

Recommended reading: Ricker (1975) gives a good account of the historical development of surplus yield models, but it is best to read also some of the original papers on the topic, notably those by Graham (1943), Schaefer (1954, 1957), Silliman and Gutsell (1958), Schaefer and Beverton (1963), Gulland (1969) and Schnute (1977).

Suggested research topics: Crucial with surplus yield models is the availability of long time-series of catch-and-effort data (or, in the case of Csirke and Caddy's model, of catch and total mortality data); it is worthwhile to estimate these parameters reliably in an ongoing fishery. Where possible, one should also attempt to reconstruct time-series of total mortality (e.g., from length-frequency data) for use with available time series of catch.

EXAMPLE 10.1

Estimating MSY and optimum effort for a single-species pelagic fishery by means of the Schaefer model.

Data from Table 10.1

Computation

1) Read sides 1 and 2 of Program FB 26

2) Enter catch and effort data

Keystrokes: f a 32.89 ↑ 31.413 A 37.78 ↑ 32.999 A 33.25 ↑ 36.579 A 28.86 ↑ 40.367 A 26.82 ↑ 43.191 A 22.26 ↑ 42.716 A 23.73 ↑ 41.636 A 25.04 ↑ 44.634 A 22.77 ↑ 49.284 A 22.64 ↑ 52.048 A

3) Estimate parameters of plot of c/f on f, MSY and f_{opt}

Keystrokes	Results	
E	0.874	(r^2)
	2.285	(a)
	−0.038	(b)
D	29.879	(f_{opt})
	34.133	(MSY)

4) Use Program FB 26 to draw yield curve

	Keystrokes	Results	
enter f_1	10 C	19.024	(Y_1)
enter f_2	20 C	30.402	(Y_2)
etc.	....	....	

The result should look similar to Fig. 10.2 from which it appears that the fishery in the early 70s was in deep trouble. In fact, as Murphy (1972) pointed out "it shows that [. . .] a 20% increase in total effort [. . .] will drive the stock to extinction [and] it is not hard to imagine nature providing this increase or its equivalent, either through a negative perturbation of reproductive success, an increase in predation or some combination of these".

The negative perturbation came in the form of a strong "El Niño" and the stock collapsed.

EXAMPLE 10.2

Application of Schnute's model to the red snapper fishery on Campeche Bank, Mexico.

Data from Table 10.2

Computation

1) Read sides 1 and 2 of Program FB 27

2) Initialize and enter catch and effort data

Keystrokes: 4.91 ↑ 227 f a 5.02 ↑ 224 A 4.25 ↑ 220 A 4.14 ↑ 227 A 4.79 ↑ 201 A
3.46 ↑ 141 A 3.57 ↑ 125 A 3.77 ↑ 123 A 3.98 ↑ 145 A 4.37 ↑ 149 A
4.24 ↑ 164 A 5.06 ↑ 182 A 4.79 ↑ 179 A 4.38 ↑ 166 A 3.53 ↑ 156 A

3) Calculate parameters of regression

Keystrokes	Results	
E	0.006	(R^2)
	0.268	(a)
	–0.001	(b_1)
	–6.359	(b_2)

4) Estimate fishery-related parameters

f e	0.268	(r_m)
	0.001	(q)
	70.309	(B_∞)
	223.558	(f_{opt})
	4.712	(MSY)

As might be seen in Fig. 10.3, the yield curve based on Schnute's model (S) resembles quite closely the curve obtained by fitting the catch figures to the average of contemporary and the preceding year's effort (curve B_{AM}). Intuitively, this result makes sense since Schnute's model in fact uses the same averaged effort and is fitted with an AM multiple regression. The abysmally low value of R^2 (= 0.00635) sheds doubt on the reliability of the various parameter estimates, however.

EXAMPLE 10.3

Estimating MSY and optimum effort for a multispecies demersal trawl fishery by means of Fox's model.

Data from Table 10.3

Computation

1) Read sides 1 and 2 of Program FB 26

2) Enter catch and effort data

Keystrokes: f a 50 ↑ 623 A 49 ↑ 628 A 47.5 ↑ 520 A 45 ↑ 513 A 51 ↑ 661 A 56 ↑ 919 A 66 ↑ 1158 ↑ 1970 A 52 ↑ 1317 A

3) Estimate parameters of plot of in c/f on f, f_{opt} and MSY

Keystrokes	Results	
f e	0.966	(r^2)
	−2.027	(a)
	−0.001	(b)
DSP 6	−0.000799	(b)
DSP 2 f d	1251.99	(f_{opt})
	60.66	(MSY)

4) Use Program FB 26 to plot draw yield curve

Keystrokes	Results	
100 f c	12.16	(Y_1)
200 f c	22.45	(Y_2)
etc.	...	

This example and Fig. 10.4 suggest that the level of effort applied in 1975 and 1977 was near optimum. Furthermore, the plot shows very nicely the effect on a rapid increase of effort, as in 1975 and 1976 the points of which are *above* the curve, while the point for 1977 is *below* the curve, as would be expected following a rapid decrease of effort. When effort remains unchanged for several years the yield should, on the average come to lie *on* the curve. However, demersal trawling has been banned in Indonesia, so we may never know.

EXAMPLE 10.4

Estimation of MSY and Z_{opt} using Csirke and Caddy's model.

Data from Table 10.4

Computations

1) Read sides 1 and 2 of Program FB 28

2) Initialize and enter catch and mortality data

Keystrokes: f a 14 ↑ 7.6 A 138 ↑ 8.8 A 191 ↑ 11 A 138 ↑ 10.2 A 192 ↑ 9.6 A 72 ↑ 14 A 66 ↑ 10.5 A

3) Calculate parameters of multiple regression

Keystroke	Results	
E	0.495	(R^2)
	−1085.334	(a)
	225.316	(b_1)
	−10.211	(b_2)

4) Calculate parameters of yield curves

Keystroke	Results	
f e	7.104	(M)
	11.033	(Z_{opt})
	3.928	(F_{opt})
	7.857	(r_m)
	157.583	(MSY)
	80.228	(B_∞)

The results appear reasonable (particularly the value of M), but this was achieved by deleting one point (1978), which had a very high catch, such as might occur after an exceptionally good recruitment. Clearly, it would be appropriate here to assess the validity of the results, using another model.

11. The Intrinsic Rate of Population Increase

INTRODUCTION

In the preceding chapters, various models (= equations) were presented, each of which illustrated a different aspect of the dynamics of fish populations.

It is the purpose of this chapter to demonstrate the interrelationships between some of these models, to show that several of the equations presented here actually reflect different aspects of the same processes.

The concept most helpful to show interrelationships between different models used in fish population dynamics is, paradoxically, rarely used in this field. It is the intrinsic rate of increase (r_m) of a population, which may be defined as "the innate capacity of (a) species to increase when population growth is not slowed down by competition" (Pielou 1978).

The r_m concept is extremely important in quantitative ecology, and at least one chapter in every good ecology text is devoted to it (e.g., Odum 1971; Slobotkin 1980; Ricklefs 1979). In terms of Russel's Axiom (see Chapter 1), r_m can be defined as

$$r_m = \frac{R^* + G^* - M^*}{B} \qquad \ldots 11.1)$$

(when B is low) but this cannot be used for quantitative stock assessment purposes because Russel's axiom itself expresses things only qualitatively.

MAXIMUM SUSTAINABLE YIELDS AND r_m

The intrinsic rate of increase (r_m) can be defined quantitatively in terms of the Schaefer model, where r_m, MSY and B_∞, the carrying capacity of the environment are related such that:

$$MSY = \frac{r_m \cdot B_\infty}{4} \qquad \ldots 11.2)$$

As discussed in Chapter 10, the Schaefer model is based on the assumption that the growth of a fish population released into a new environment can be described by a logistic growth curve. This curve has the form

$$B_{\cdot} = \frac{B_\infty}{1 + e^{-r_m (t - t_i)}} \qquad \ldots 11.3)$$

where B_∞ is the carrying capacity of the environment in terms of weight, r_m the intrinsic rate of population increase, and t_i (=t at inflexion point) is a constant which adjusts the time scale to an origin such that $t - t_i = 0$ when $B_t = B_\infty/2$, B_t being the biomass at time t. B_∞ and B_t may be replaced by N_∞ and N_t when equation (11.3) refers to numbers. When equation (11.3) is used to fit data from a selection experiment, B_t is equivalent to the probability of capture, t to the length, and t_i to L_c. (Refer to Chapter 3.)

Aquarium experiments demonstrate the growth of fish populations can often be approximated by a logistic curve (Silliman and Gutsell 1958, Fig. 3). In nature, cases of fish populations "exploding" into a new environment are obviously difficult to document. Some data, however, are available for Red Sea lizardfish *(Saurida undosquamis)* which penetrated into the Mediterranean via the Suez Canal, and after a lag phase (of genetic adjustment?) experienced a rapid increase of population size, as documented by catch-per-effort data off the Israel coast (Table 11.1).

As might be seen from Fig. 11.1 and Table 11.1, the course of the population increase reflected in the catch-per-effort data roughly corresponds to a logistic curve, the r_m and t_i values of which may

Table 11.1. Data on the growth of a newly established Mediterranean population of *Saurida undosquamis*, a Red Sea immigrant. Data from Ben-Yami and Glaser (1974, Fig. 5B).

Code year	Catch/effort (kg/h)
1	1
2	2
3	3
4	75
5	78

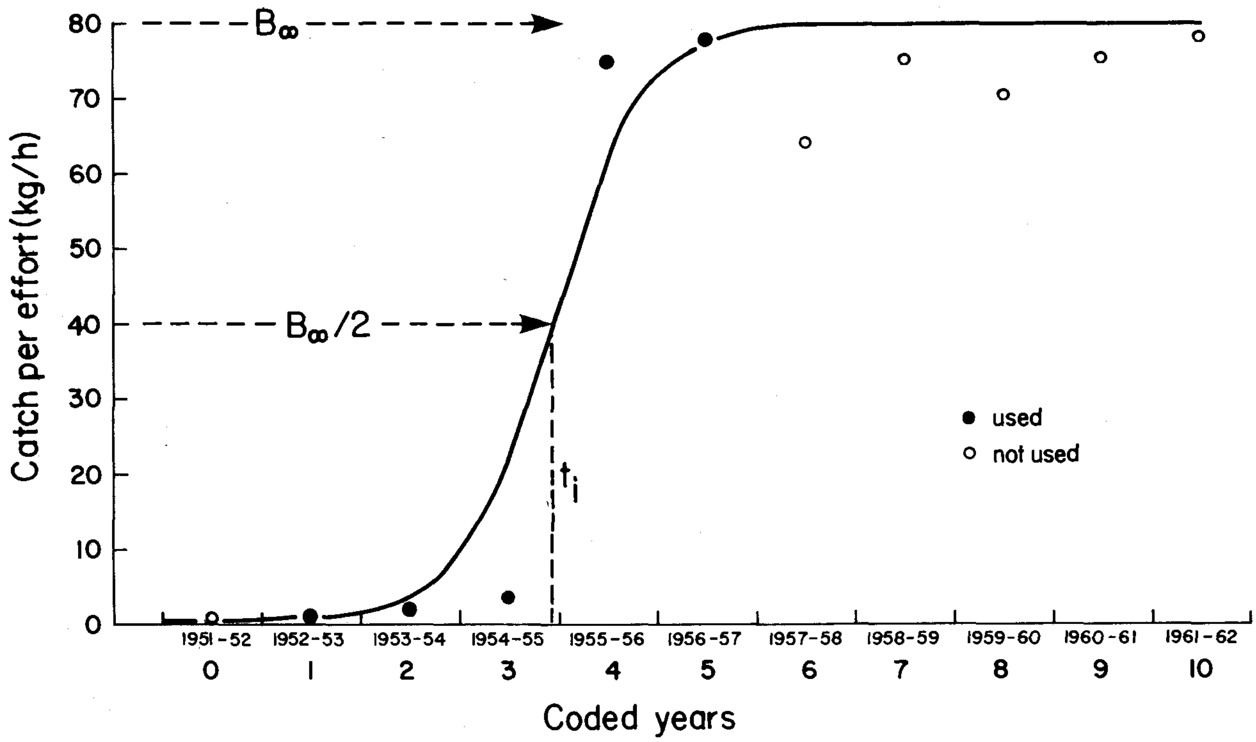

Fig. 11.1. Logistic growth curve fitted to catch-per-effort data on a newly established Mediterranean population of lizardfish *(Saurida undosquamis)* (based on data in Table 11.1, and see Example 11.1 for selection of points used in curve fitting).

be estimated by means of Program FB 28 (Example 11.1). MacCall (1980) presented data on a temperate fish *(Engraulis mordax)* suggesting a similar logistic increase of biomass.

Equation (11.2) suggests that when an estimate is available of the virgin biomass of a given population (B_v, or B_o in Gulland 1971) and when it is legitimate to set $B_\infty \approx B_v$ (it is *not* always the case, see Pauly 1979b, or May et al. 1979), all that is needed to obtain a preliminary estimate of (future) MSY (also called Potential Yield, P_y) is an estimate of r_m.

Several, rather elaborate methods are used by ecologists to estimate r_m. One of them is the calculation of r_m from so-called "life tables" (see Pielou 1978, Ricklefs 1979). This method has data requirements which fishery biologists will find quite hard to meet and only two studies have come to my attention which estimates r_m using this approach in fish (Murphy 1967, Pitcher and Hart 1982). Two HP 67/97 programs are available to estimate r_m from life tables. Demography I and Demography II, both in the HP Users' Library Solutions booklet devoted to "Biology".

Blueweiss et al. (1978) have shown that r_m in animals and various small organisms is inversely related to body weight and presented a double logarithmic plot of r_m on "mean adult body weight" ($\overline{W}$) spanning 22 orders of magnitude. I have added several values to the plot presented by Blueweiss et al. (1978) which pertain to fish and whales, the latter expanding the range covered by the plot to 24 orders of magnitude (Fig. 11.2).

Although the fit, particularly in organisms ranging from 10^{-6} to 10^{0} g is not particularly good, a clear relationship emerges which allows, when mean adult body weight is known, a rough estimate of r_m through the relationship

$$r_m \approx 9.13 \cdot \overline{W}^{-0.26} \qquad \ldots 11.4)$$

where r_m is expressed on a yearly basis and $\overline{W}$ is grams, and computed from $\overline{W} = (W_{max} + W_m)/2$; W_{max} is the maximum weight reached by the adults of a stock and W_m is their weight at first maturity (see Example 11.2).

Combining expression (11.4) with expression (11.2) gives

$$P_y \approx 2.3 \cdot \overline{W}^{-0.26} B_v \qquad \ldots 11.5)$$

which can be used to obtain first estimates of MSY, i.e., potential yield, when only virgin stock size and mean adult body weight are known.

The results obtained by means of this equation may thus be compared with those obtained using Gulland's (1971) well-known relationship

$$P_y \approx 1/2 \cdot M \cdot B_v \qquad \ldots 11.6)$$

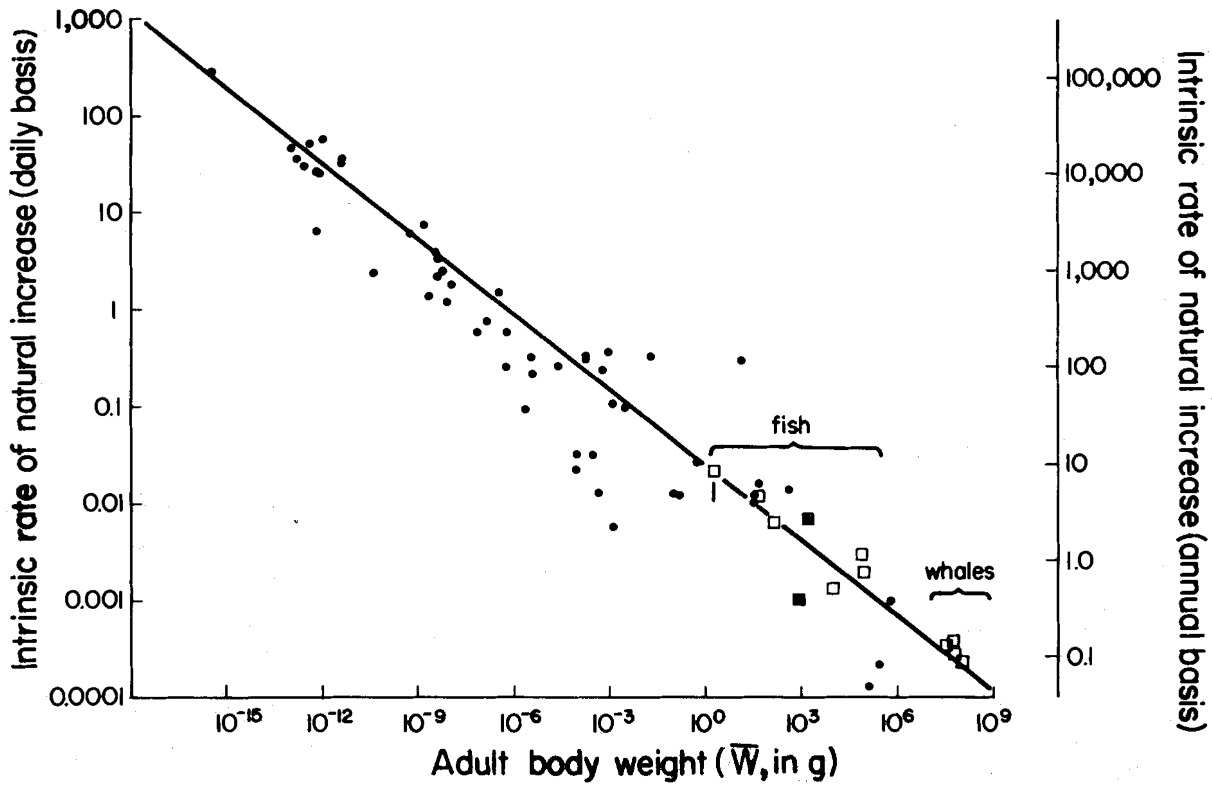

Fig. 11.2. Relationship between intrinsic rate of population increase (r_m) and adult body weight for various organisms. (The dots and the line are from Blueweiss et al. 1978; the open squares were added by Pauly 1982a.)

See also Example (11.3). Expressions (11.5) and (11.6) are rough approximations; with expression (11.5) the major problem is the fact that the built-in relationship between $\overline{W}$ and r_m is based on a linear regression whose scatter of data is not negligible, while the major drawback of expression (11.6) is that the resulting P_y estimates are directly proportional to and thus highly sensitive to, the value of M used. Also, the validity of (11.6) rests on the assumption that $F_{opt} = M$ which probably does not apply in most stocks (see p. 77).

STOCK-RECRUITMENT RELATIONSHIPS AND r_m

Another integrative property of r_m is that it can also be shown to be an implicit parameter of both Beverton and Holt and Ricker-type stock-recruitment curves. This property, which was discussed by Murphy (1967) and Eberhardt (1977) will be here touched upon only briefly because its various ramifications have not yet been fully investigated. Starting with the second form of Ricker's stock-recruitment curve (see Chapter 9), one can define

$$a = P_r/P_m \qquad \ldots 11.7)$$

where P_r is the replacement abundance of parent stock and P_m is the parent stock producing maximum recruitment (see Chapter 9 for details on these definitions). Subsitution into Ricker's second stock-recruitment curve gives:

$$R = P_e^{P_r/P_m - P/P_m} \qquad \ldots 11.8)$$

Now, it is obvious that as P approaches zero, the second term of the exponent (P/P_m) will also tend to approach zero.* Division of both sides of (11.8) with P, when P is very small, yields:

$$R/P = e^{P_r/P_m} \qquad \ldots 11.9)$$

Since the ratio R/P expresses the ratio between total births in two successive generations at very low population sizes there is an identity between (11.9) and the equation used in the ecological literature

$$N_T/N_o = e^{r_m \cdot T} \qquad \ldots 11.10)$$

where, at very low population sizes

N_o is the total number of animals in the population at the beginning of a generation
N_T is the number of animals at the end of that generation
T is the generation time

and where

r_m is the ubiquitous intrinsic rate of increase.

In view of this identity:

$$P_r/P_m = r_m \cdot T \qquad \ldots 11.11)$$

*In Murphy (1967) the word "zero" has been erroneously replaced by "unity."

which may be called "Murphy's identity". An application of this identity is given in the following paragraphs.

The generation time, T, of an animal is generally quite difficult to estimate (but see Slobotkin 1980, Fig. 5.2). However, it appears that a great number of the small fish caught in tropical waters have growth parameters suggesting a rather short life span (2-4 years) and an age at first maturity (t_m) of generally one year (Banerji and Krishnan 1973; Qasim 1973a, 1973b). High natural mortality and lack of substantial post-maturity growth will cause a mean generation time of about 1 year in such fish, or:

$$r_m \approx P_r/P_m \qquad \ldots 11.12)$$

Only one data set is readily available which can be used to test these conjectures. In Chapter 9, Example 9.4, a value of P_r/P_m was estimated for *Lactarius lactarius*, a fish with the characteristics given in the above paragraph and this value was 2.84.

The value of W_∞ used in Pauly (1980d) was 193 g, which may roughly correspond to W_{max}, while the value of W_m is 57.3 g. Hence, $\overline{W}$, as defined above, is (193 + 57)/2 = 125 g, from which r_m is estimated, via equation 11.4, to be 2.60. Conversely, T can be estimated from

$$T = 2.84/2.60 = 1.09 \qquad \ldots 11.13)$$

which is similar to the value assumed previously.

While Murphy (1967) investigated the second form of Ricker's curve, Eberhardt (1977) demonstrated a link between the first form of Ricker's curve and the logistic growth curve, which led to the identities

$$\alpha = e^{r_m} \qquad \ldots 11.14)$$

and

$$\beta = r_m/N_\infty \qquad \ldots 11.15)$$

while the link between Beverton and Holt's stock-recruitment curve and the logistic growth curve was established through the identities

$$\alpha' = (1 - e^{-r_m})/N_\infty \qquad \ldots 11.16)$$

and

$$\beta' = e^{-r_m} \qquad \ldots 11.17)$$

The parameters α' in Ricker's curve and β' in Beverton and Holt's curve are often called "density-independent terms"; given equations (11.15) and (11.17), their relationship is given by

$$\alpha = 1/\beta' \qquad \ldots 11.18)$$

The "density-dependent terms" (β in Ricker's curve, α' in Beverton and Holt's curve) are also closely related, and are approximately the same when r_m is small, diverging up to 20% when r_m is large; this is expressed by the approximations

$$\alpha' \approx \beta \approx (1 - e^{-r_m})/N_\infty \qquad \ldots 11.19)$$

which applies when r_m is small (Eberhardt 1977; Pitcher and Hart 1982).

The presentation of these interrelationships between different models and the example for *Lactarius lactarius* given above are not meant to suggest that values of r_m obtained say from equation (11.4) and from stock-recruitment relationships should necessarily coincide. Rather, the suggestion made earlier by Murphy (1967) is reiterated that there might be here a type of interrelationship worth pursuing further which might lead to a further integration of the various concepts used in fishery biology.

Indeed, as the following, last chapter should demonstrate, there is a great need for attempts to integrate concepts derived from fish population dynamics with some of those derived by theoretical ecologists, and thus to cross-pollinate the two disciplines.

Recommended reading: Since a good background in ecological theory should help the fishery biologist put her or his field into perspective, it may be appropriate to list here some ecological texts, all of which discuss, among other things, the intrinsic rate of increase of populations and related concepts, e.g., Slobotkin (1980), Odum (1971), Ricklefs (1979) and Pielou (1978). These books also contain most of the references needed to plunge into the ecological literature.

Suggested research topics: Since r_m is so closely related to yields, it would seem that attempts to estimate this parameter from life tables of commercial fish populations should represent worthwhile research projects (see Pitcher and Hart 1982 for data requirements and method). Such a study also would allow one to identify factors (such as temperature or fecundity) other than body weight which may help to predict values of r_m, or to improve estimates obtained from plots such as Fig. 11.2.

EXAMPLE 11.1

Estimating the intrinsic rate of increase for an "exploding" population of lizardfish *(Saurida undosquamis)*.

Data from Table 11.1 and Fig. 11.1. (Only the data points for the years 1952-53 to 1956-57 are used for the computation. The earlier points were too low to be precisely read off the original figure in Ben-Yami and Glaser (1974). The later points, on the other hand, probably indicate a drop in biomass occurring after the initial build-up.)

Computation

1) Read side 1 of Program FB 29

2) Enter set value of B_∞, and B_t and t data

Keystrokes: 80 f a 1 ↑ 1 A 2 ↑ 2 A 3 ↑ 75 ↑ 4 A 78 ↑ 5 A

3) Calculate r^2, r_m and t_i

Keystrokes	Results	
E	0.854	(r^2)
	2.244	(r_m)
	3.437	(t_i)

4) Confirm that t_i corresponds to $B_\infty/2$

C	40.000	($B_\infty/2$)

By entering other t values and pressing the C-Key, data points for a curve such as in Fig. 11.1 can be obtained. It must be realized, however, that the values of r_m and t_i obtained here depend critically on the choice of points included in the computation and of 80 kg/hr as the c/f figure corresponding to B_∞; the estimate of r_m is thus tentative.

EXAMPLE 11.2

Estimating r_m from the mean weight ($\overline{W}$) of the adults in a given stock.

1) Read side 1 of Program FB 29

Case I

2) Estimate $\overline{W}$: Thompson and Munro (1978) give data from which W_{max} in Jamaican *Epinephelus guttatus* can be estimated at 2,324 g, while W_m, the mean weight at first maturity is about 243 g. Thus, to obtain $\overline{W}$, we perform

	Keystrokes	Results
	2,324 ↑	
	243 + 2 ÷	1,283. 5 ($\overline{W}$)
3) Estimate r_m from $\overline{W}$	f e	1.42 (r_m)

Case II

4) Estimate $\overline{W}$: Pauly (1980d) gives a value of 193 g for W_∞ in *Lactarius lactarius* from the Gulf of Thailand. Using this as an estimate of W_{max} and using $W_m = W_{max} \cdot 0.3 = 57.9$, we obtain $\overline{W}$ from:

	Keystrokes	Results
	193 ↑	
	57.9 + 2 ÷	125.45 ($\overline{W}$)
5) Estimate r_m from $\overline{W}$	f e	2.60 (r_m)

It must be realized that these two estimates of r_m are rather crude and should not preclude attempts to estimate this important parameter independently.

EXAMPLE 11.3

Estimating potential yields when catch-and-effort data are not available.

1) Thompson and Munro (1978) give for the Caribbean grouper *Epinephelus guttatus* the following data: natural mortality = 0.68, TL_{max}, in cm = 53.7 cm (corresponding to W_{max} = 2,324), approximate weight at first maturity = 243. From these data, adult body weight ($\overline{W}$) is computed as 1,283.5 g (see Example 11.2).

2) Estimating potential yield (P_y) from Gulland's equation (11.6) assuming B_v = 1:

Keystrokes	Results	
.68 ↑ (M)		
.5 x	0.34	(P_y)

3) Estimating potential yield (P_y) from equation (11.5), also assuming B_v = 1:

Keystrokes	Results	
1,283.5 ↑ (w)		
.26 CHS		
y^x 2.3x	0.36	(P_y)

The estimates (0.34 and 0.36) are close enough to each other to feel confident that P_y is about 1/3 of the virgin biomass per year. Obviously, this is so because this example is in a manual; real-life data do not always behave so nicely. In fact, Beddington and Cooke (1983) argue, quite cogently, that Gulland's equation (and consequently any other equation which gives similar results) has an extremely strong upward bias (see p. 77).

12. Multispecies Fisheries

INTRODUCTION

With few exceptions, the models discussed in the previous chapters were developed for use in conjunction with single-species stocks and fisheries.

When using such models, an implicit assumption is that the stock under investigation has only negligible interaction with other species, except for those interactions accounted for by the catch-all interaction term "M", natural mortality (caused mainly by predation).

This approach may be justified in temperate waters, where some stocks (e.g., cod, pollock, herring, salmon) sustain "aimed" fisheries, in which the fish not belonging to the target species form only a minor part of the catch (the "bycatch").

In tropical fisheries, especially in demersal fisheries, no single species is aimed at, generally, and there is no "bycatch" when the definition above is used, except in shrimp fisheries where the fish caught (often 90% of the total catch by weight) are frequently thrown overboard. Table 12.1 reproduces the typical catch of a Southeast Asian trawler. The large number of species, none of which is dominant, will be noted.

Table 12.1. A typical trawler catch (45 min haul) from the Java Sea (06° 12'S, 108° 26'E, 34-35 m depth) made on 5 September 1976 by *R/V Mutiara IV* showing the diversity of tropical demersal multispecies stocks. (Asterisks refer to weight and number raised from a sorted sample of 1 out of 5 boxes. Invertebrates not included.)

No.	Family	Species	W (kg)	N
1	Ariidae	*Osteogeniosus militaris*	3.4	17
2	Balistidae	*Abalistes stellaris*	0.5	1
3	Carangidae	*Seriolina nigrofasciata*	0.32	1
4	Carangidae	*Scomberoides* sp.	0.15	5
5	Carangidae	*Alepes kalla*	5.0*	90*
6	Carangidae	*Alepes djedaba*	7.50*	290*
7	Carangidae	*Megalaspis cordyla*	8.5*	170*
8	Carangidae	*Selaroides leptolepis*	0.25*	10*
9	Carangidae	*Carangoides* spp.	6.10*	145*
10	Carangidae	*Atropus atropus*	1.75*	30*
11	Chirocentridae	*Chirocentrus dorab*	0.80*	5*
12	Clupeidae	*Anadontostoma chacunda*	0.15*	5*
13	Clupeidae	*Opisthopterus valenciennensis*	1.10*	15*
14	Clupeidae	*Dussumieria acuta*	1.70*	50*
15	Clupeidae	*Ilisha* sp.	5.60*	65*
16	Clupeidae	*Sardinella gibbosa*	0.30*	10*
17	Dasyatidae	not identified	2.65	1
18	Drepanidae	*Drepane longimana*	0.35*	5*
19	Engraulidae	*Stolephorus* spp.	21.0*	4,175*
20	Gerridae	*Pentaprion longimanus*	15.25*	1,165*
21	Fistulariidae	not identified	0.15*	10*
22	Formionidae	*Formio niger*	0.2	1
23	Lagocephalidae	not identified	4.0	95
24	Leiognathidae	*Leiognathus splendens*	10.0*	720*
25	Leiognathidae	*Leiognathus leuciscus*	4.20*	780*
26	Leiognathidae	*Leiognathus bindus*	1.20*	340*
27	Leiognathidae	*Secutor ruconius*	1.20*	380*

Continued

Table 12.1 continued

28	Leiognathidae	*Secutor insidiator*	2.80*	560*
29	Lutjanidae	*Lutjanus sanguineus*	4.0	1
30	Lutjanidae	*Lutjanus johni*	5.0*	10*
31	Lutjanidae	*Lutjanus lineolatus*	0.20*	10*
32	Lutjanidae	*Caesio erythrogaster*	0.10*	5*
33	Mullidae	*Upeneus sulphureus*	75.0*	6,075*
34	Nemipteridae	*Nemipterus japonicus*	3.0*	15*
35	Nemipteridae	*Nemipterus bathybius*	0.40*	15*
36	Pentapodidae	*Pentapodus setosus* (?)	0.25*	5*
37	Platycephalidae	not identified	0.25*	5*
38	Plectorhynchidae	*Plectorhynchus pictus*	0.40*	15*
39	Pomadasydae	*Pomadasys maculatus*	0.25*	5*
40	Pomadasydae	*Pomadasys* sp.	0.50*	35*
41	Priacanthidae	*Priacanthus macracanthus*	3.10*	80*
42	Scombridae	*Scomberomorus guttatus*	7.20*	65*
43	Scombridae	*Scomberomorus commerson*	2.6	14
44	Scombridae	*Rastrelliger brachysoma*	3.0*	50*
45	Stromateidae	*Pampus chinensis*	0.75	1
46	Stromateidae	*Pampus argenteus*	6.3*	30*
47	Synodontidae	*Saurida tumbil*	0.35	1
48	Synodontidae	*Saurida elongata*	3.75*	45*
49	Synodontidae	*Saurida longimana*	0.90*	105*
50	Sphyraenidae	*Sphyraena obtusata*	0.60*	10*
51	Scienidae	not identified	0.25*	5*
52	Theraponidae	*Therapon* sp.	3.75	100
53	Triacanthidae	not identified	1.0*	25*
54	Trichiuridae	*Trichiurus lepturus*	1.0*	55*
55	Trichiuridae	*Lepturacanthus savala*	2.0*	25*
Σ	29 families	43 genera and over 55 spp	231.02	15,939

The goal of fishery biologists studying a fishery is generally to obtain information upon which management measures (e.g., catch allocation, effort control) can be based. Most often, these management measures aim at one of the following items:

- to provide as high a sustained catch as possible
- to provide a reasonable income for as many people as possible
- to generate profits as high as possible for those who have invested in the fishery.

These items, it will be noted, are not necessarily compatible with each other and more often than not, they are mutually exclusive (Clark 1976).

When the policy is to maximize yields, three forms of overfishing must be prevented:

- growth overfishing, i.e., taking fish that are too small. (The methods used to detect and quantify growth overfishing are outlined in Chapter 8)
- recruitment overfishing, i.e., taking so many adult fish that recruitment of young fish to the fishery is affected. (The methods to detect and quantify recruitment overfishing are outlined in Chapter 9)
- ecosystem overfishing, i.e., inducing changes in stock composition through excessive fishing such that abundant species decline *without* the subsequent compensatory increase of another (group of) species.

Obviously, when exploiting with an unselective gear a community of widely different fish, some large and long-lived, others small and short-lived, it is not possible to prevent growth and recruitment overfishing of the most sensitive stocks. With increasing effort, some species will then gradually disappear resulting at high levels of exploitation in a complete alteration of the original food chains and catch compositions and in ecosystem overfishing as well. This, and related problems are reviewed in FAO (1978), Pope (1979), Pauly (1979b), and in several papers included in Pauly and Murphy (1982).

In the following, a brief discussion is given of approaches to modelling and managing multispecies systems.

MODELLING MULTISPECIES SYSTEMS

Two-species systems

Attempts by biologists to model quantitatively interacting species started, logically enough, with studying the two-species case. The pioneers in this field were Lotka (1925) and Volterra (1926), who suggested independently what are now known as the Lotka-Volterra equations,

$$\frac{dN_1}{dt} = [\, r_{m1} - m_1\,(c_1N_1 + c_2N_2)\,]N_1 \qquad \ldots 12.1a)$$

$$\frac{dN_2}{dt} = [\, r_{m2} - m_2\,(c_1N_1 + c_2N_2)\,]N_2 \qquad \ldots 12.1b)$$

which describe the rate of change, in numbers, of two competing species, where r_{m1} and r_{m2} are the intrinsic rates of increase of species 1 and species 2 respectively, m_1 and m_2 are positive proportionality constants, and C_1 and C_2 are interaction terms.

It can be shown (Gause 1934; von Bertalanffy 1951) that the systems represented by equations (12.1a and 12.1b) are stable only in the unlikely case that $r_{m1}/m_1 = r_{m2}/m_2$. In all other cases, one species (that with the highest r_m/m) will survive while the other will become extinct. This behavior, the "competitive exclusion principle" of Gause (1934) was demonstrated to occur in micro-habitats such as culture bottles and aquaria in a wide variety of animals, including tropical fish (Silliman 1975). A pair of Lotka-Volterra equations can also be formulated for a predator-prey system:

$$\frac{dN_1}{dt} = (r_m - c_1N_2)\,N_1 \qquad \ldots 12.2a)$$

$$\frac{dN_2}{dt} = (-g + c_2N_1)\,N_2 \qquad \ldots 12.2b)$$

where g is a coefficient of negative growth (decline) of the predators (N_2) in the absence of prey (N_1), while r_m is the intrinsic rate of increase of the prey population, c_1 and c_2 being interaction terms. An interesting property of these equations is that they generate oscillations over time, under certain circumstances, in the number of prey and predators that are independent of environmental fluctuations, and can be used to explain the oscillating behavior of at least some terrestrial predator-prey systems. Such oscillations have rarely been reported from tropical waters, one exception being possibly Munro (1967) who discussed the oscillatory behavior of a tilapia-tigerfish *(Hydrocyon)* system in Lake McIlwaine, Zimbabwe.

An HP 67/97 program incorporating the Lotka-Volterra equation ("fox and rabbit case") was submitted by J. van Thielen to the HP67/97 Users Library (# 02752D); the "fox and rabbit case" can also be simulated on the HP67/97 with the help of the keystroke sequences in Green and Lewis (1979).

The Lotka-Volterra equations, while providing insight into various aspects of the interactions between species, have been often criticized because of their extreme simplicity and lack of realism, e.g., by Beverton and Holt (1957) who proposed a much more elaborate two-species model.

However, bringing some realism into the Lotka-Volterra system of equations is relatively straightforward. Larkin (1966), who briefly reviewed some earlier variants, suggested the following set for predator-prey interactions:

$$\frac{dN_1}{dt} = (r_{m1} - a_1 N_1 - c_1 N_2) N_1 \qquad \ldots 12.3a)$$

$$\frac{dN_2}{dt} = (r_{m2} - a_2 N_2 - c_2 N_1) N_2 \qquad \ldots 12.3b)$$

where r_{m1} and r_{m2} are the intrinsic rates of increase of the preys (N_1) and the predators (N_2), a_1 and a_2 are coefficients of intraspecific competition, c_1 and c_2 are interaction terms, expressing decrease for the prey in the presence of predator and increase of the predator in the presence of prey. This system of equations, which is far more realistic than the original Lotka-Volterra formulation, has the following properties:

— the abundance of predator and prey are mutually dependent
— the abundance of prey has an upper limit in the absence of predators
— the abundance of predators has a lower limit in the absence of prey (i.e., they switch to another prey and don't become extinct)

Larkin (1966) presented a discussion of the behavior of the predator-prey system in expression (12.3) under exploitation by a fishery. As this behavior is similar to that of the model developed by Pope (1979), we shall now go directly to the latter model.

Pope (1979) presented an equation which is extremely helpful in making species interaction visible. The model has the form

$$Y_T = aF_P - bF_P^2 + c_1 F_P F_Q + dF_Q - eF_Q^2 + c_2 F_P F_Q \qquad \ldots 12.4)$$

or

$$Y_T = \qquad Y_P \qquad + \qquad Y_Q$$

where P and Q are interacting species, a, b, d and e are constants of parabolic yield curves, c_1 and c_2 interaction terms, Y_P and Y_Q yields from species P and Q, respectively, given the fishing mortalities F_P and F_Q and where Y_t is the total yield from the two-species system.

For example we could have

$$Y_T = 200F_P - 100F_P^2 - 25\, F_P F_Q + 100F_Q - 50F_Q^2 + 25\, F_P F_Q \qquad \ldots 12.5)$$

where P is an abundant prey, Q a less abundant predator and —25 and +25 are the interaction terms, positive for the predator whose yield increases in the presence of prey. (This example is illustrated in Fig. 12.2). Table 12.2 presents some combinations of values of a, b, d, e and c_1 and c_2 and indicates the type of interaction that these values suggest. Based on the values in Table 12.2 a series of four figures have been drawn (Figs. 12.1 to 12.4) as in Pope (1979) which demonstrate the effects of biological interactions on the combined yields of two interacting species.

In addition to illustrating biological interactions, Pope's model equation (12.4) also allows for a precise definition of what he calls "technological interactions", i.e., the fact that in a multispecies fishery (and in fact in "single" species fisheries also) catching a certain quantity of a given species necessarily implies catch of a certain quantity of other species. When the ratio of the fishing mortalities (F_P, F_Q) applied on species P and Q, respectively, remains constant for any level of F_P, a straight line is generated which starts at the origin and cuts through the yield isopleths (see lines

Table 12.2. Constants used for drawing Figs. 12.1 to 12.4.

Fig. no.	Constants of yield curve and interaction terms: a	b	d	e	c_1	c_2	System optimum: MSY	F_Q	F_P
12.1	200	100	200	100	−25	25	200	1.00	1.00
12.2	200	100	100	50	−25	25	150	1.00	1.00
12.3	100	50	50	25	10	25	146	2.25	1.79
12.4	100	50	50	25	5	10	94	1.36	1.20

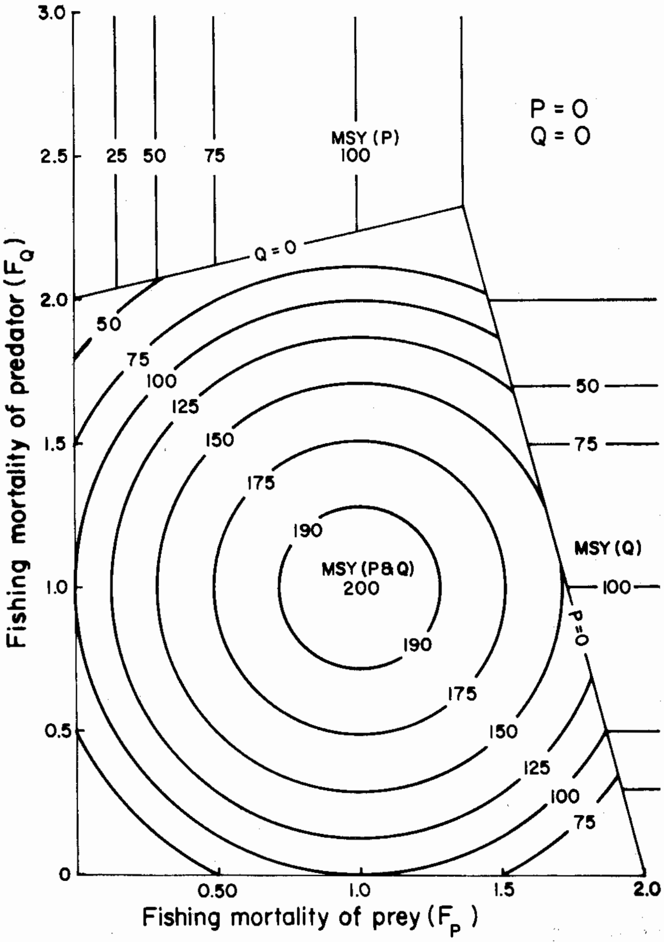

Fig. 12.1. Combined yield of two similar species, one preying to a small extent on the other (see constants of Table 12.2).

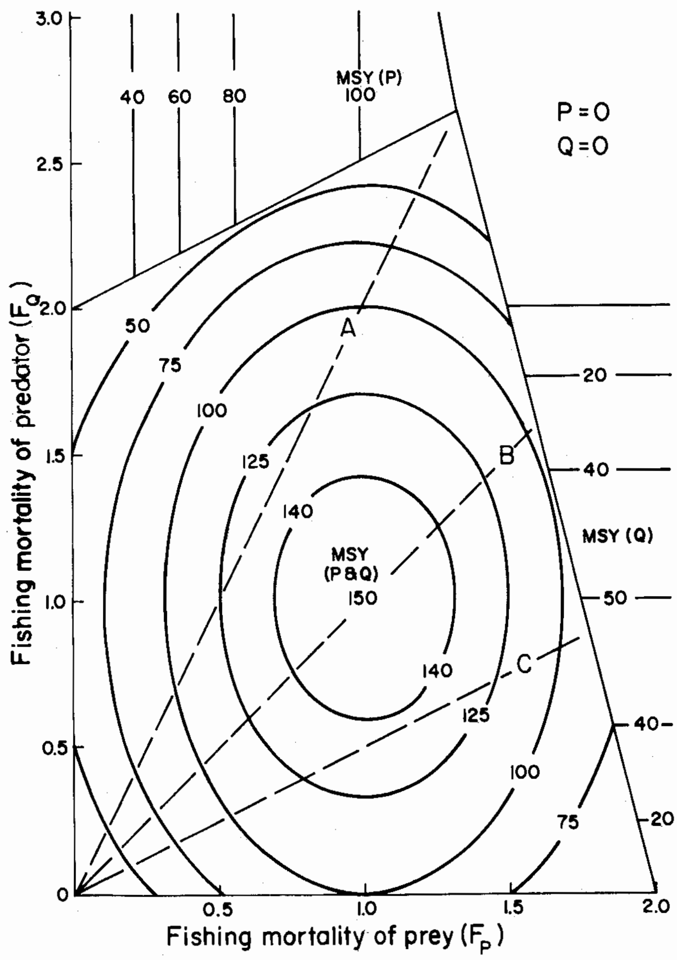

Fig. 12.2. Combined yield from a predator-prey system (see constants in Table 12.2). Lines A, B and C refer to three fixed F-ratios (see Fig. 12.5).

A, B, and C on Fig. 12.2). The interesting thing about such lines, however is that, while any F-ratio necessarily generates a parabolic yield curve (see Fig. 12.5 and Pope 1979 for a mathematical proof), this yield curve does not necessarily go through the maximum sustainable yield (MSY) of the whole system (see Figs. 12.1 and 12.5). As Pope (1979) demonstrated, the two-species system may be extended to any number of species with the overall conclusions remaining that

- For constant F-ratios, the total yield curve for any system composed of parabolic single species curves and linear interaction terms is itself a parabola.
- The F-ratio occurring in a given fishery does not necessarily generate the MSY, and the optimum F-ratios can be found only iteratively by changing F-ratios until MSY is reached.

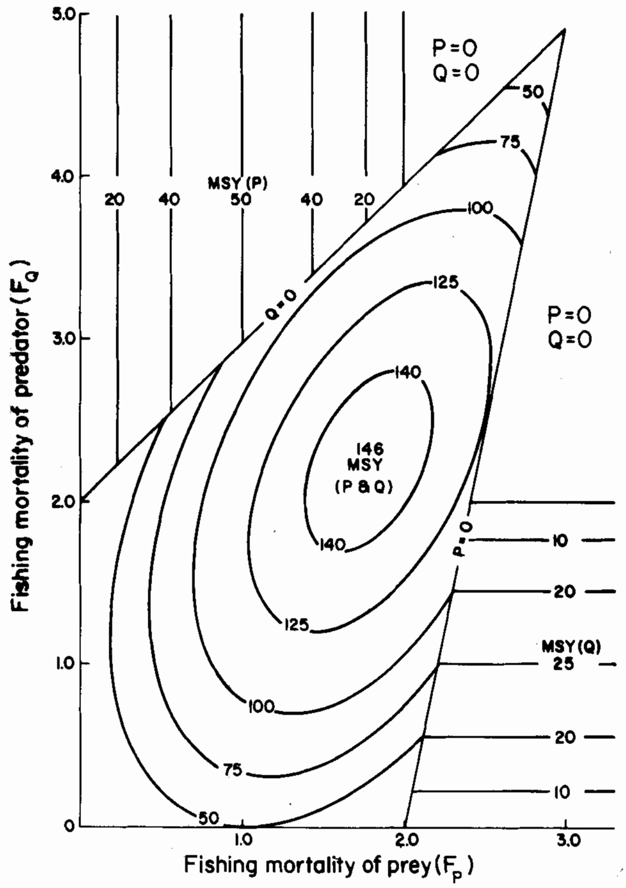

Fig. 12.3. Combined yield from a system in which each species strongly benefits from the presence of the other—mutualism (see constants in Table 12.2).

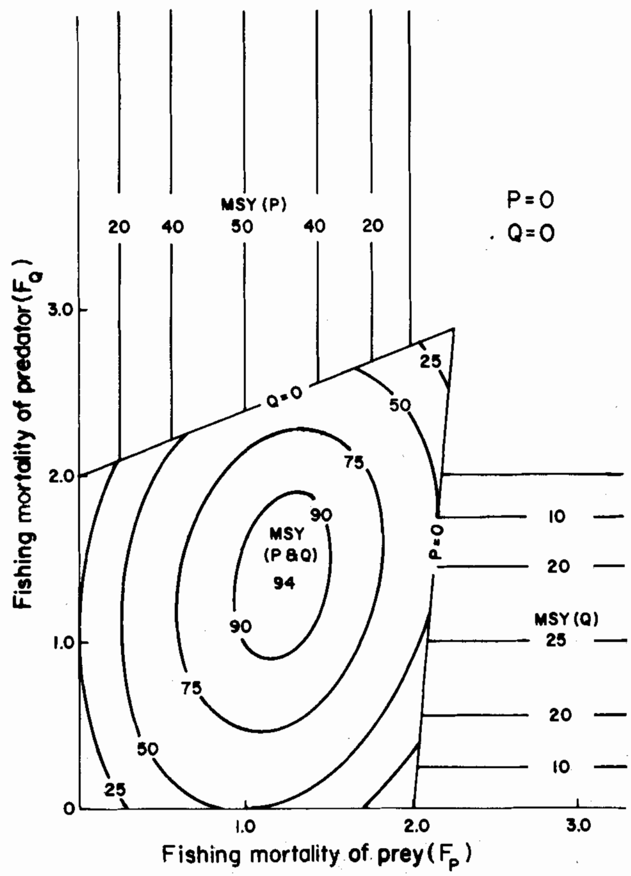

Fig. 12.4. Combined yield from a system in which each species, to a small extent, benefits from the presence of the other (see constants in Table 12.2).

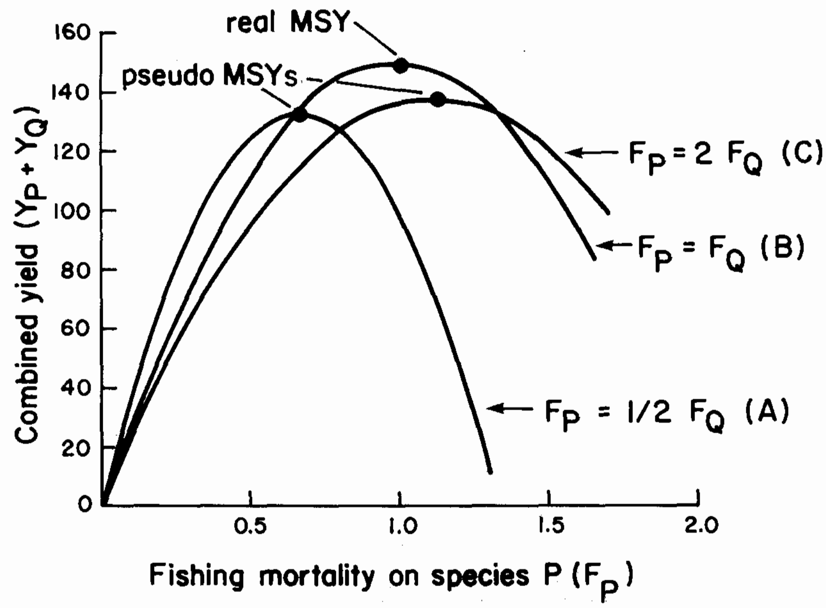

Fig. 12.5. Graph showing how the choice of a given constant ratio of fishing mortalities affects the shape and height of a yield curve; note that one optimum F-ratio leads to the real MSY of the two-species system (see also Fig. 12.2).

Pope's model is very useful in that it enables the user, at least in the two-species case—to literally *see* the interactions affecting the yields of the system. However, the constants (a, b, c, d, e) of the model cannot be estimated, for which reason it generally cannot be used directly for stock assessment purposes.

Concerning equation (12.4) it may finally be mentioned that the intrinsic rates of population increase (r_m) are implied in it, i.e.,

$$r_{mP} = 2F_{P\,(opt)} \qquad \ldots 12.6a)$$

and

$$r_{mQ} = 2F_{Q\,(opt)} \qquad \ldots 12.6b)$$

where $F_{P(opt)}$ and $F_{Q(opt)}$ are the fishing mortalities which generate MSY in species P and Q, respectively.

Program FB 30 is provided here to help the reader quickly calculate values of Y_T, Y_P and Y_Q for any set of constants as well as for finding the MSY and F_{opt} values of the two-species system. It is hoped that exercises using this program and combinations of constants such as exemplified in Table 12.2 will help visualize the nature and effects of both technological and biological interactions (see Example 12.1).

N-species systems

It is only since the advent of electronic computers that it has become possible to model systems containing more than two species realistically. Particularly, the availability of computers made it possible to depart from simplifying approaches such as represented by equations (12.1) to (12.4) and to incorporate into the models, as suggested earlier by Beverton and Holt (1957), more realistic representations of growth, mortality, predation and other processes. This approach is taken in the large and complex "North Sea model" of Andersen and Ursin (1977), and in the various models of "multispecies VPA" presented by Pope (1979), Helgason and Gislason (1979) and Sparre (1980).

However, smaller simulation models, involving only a few trophic groups and the transfers between them can be used to test and validate hypotheses concerning the interactions within an exploited multispecies stock. This approach is best exemplified by Larkin and Gazey (1982) who designed a simulation model of the Gulf of Thailand stocks and fisheries and used it for testing mechanisms suggested by Pope (1979) and Pauly (1979b) to explain the observed changes in catch rates of different species groups. Such models, as well as the box model discussed below can also help in identifying gaps in our understanding of a system.

METHOD FOR CONSTRUCTING QUANTITATIVE "BOX MODELS"

While the mathematical simulation of multispecies systems is generally so complex as to discourage all but very mathematically-oriented biologists, constructing "box" models of an ecosystem is rather straightforward. "Box" models are here defined as a class of models where emphasis is on the ***graphical*** representation of an ecosystem and where the taxa having similar ecological roles are grouped together in "boxes" (see Fig. 12.6).

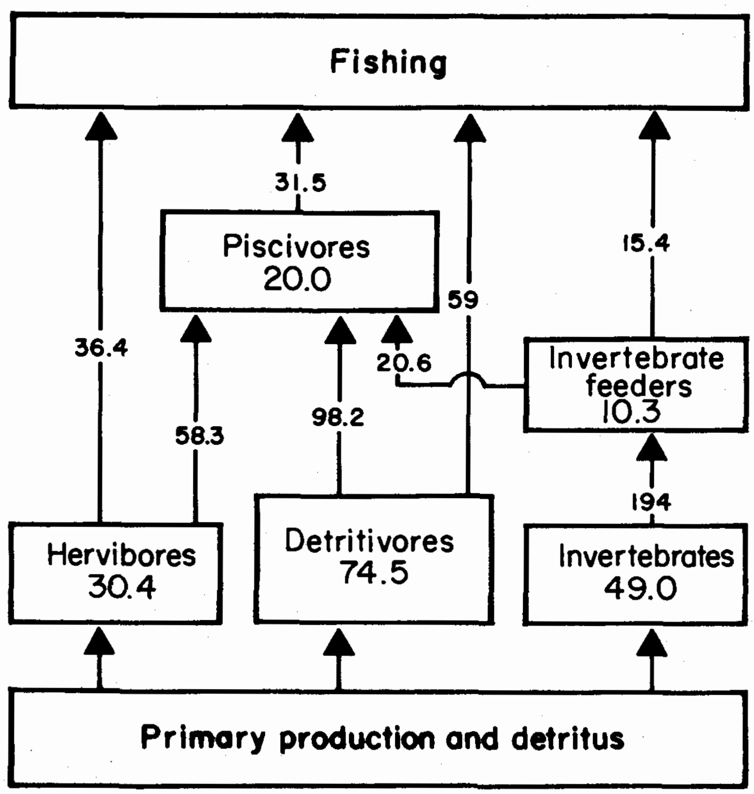

Fig. 12.6. Simplified trophic model of Bukit Merah Reservoir, Malaysia. The numbers in the boxes refer to annual mean standing stocks in tonnes, wet weight, while the numbers along the arrows express annual flows in tonnes (adapted from Yap 1983).

Box models can be either qualitative as in Pauly's (1975) model of a West-African lagoon, or quantitative as in Walsh's (1981) model of the Peruvian upwelling system.

Quantitative box models consist of four elements:

a) the taxa included in each box (see Table 12.3 for an example)
b) the biomass transfer between each box (i.e., the direction of the arrow linking the boxes with each other),

Table 12.3. Data for the construction of a quantitative box-model of Bukit Merah Reservoir, Malaysia. Adapted from Yap (1983).

Trophic group of fish	Annual catch (tonnes)	Representative species[a]	F	M
Detritivores	59.8	*Labiobarbus festiva*	0.58	2.22
Herbivores	36.4	*Osteochilus hasselti*	1.18	2.12
Piscivores	31.5	*Oxyeleotris marmorata*	2.61	1.68
Invertebrate feeders	15.4	—	1.5[b]	2.0[b]

[a]Species representative of their trophic group.
[b]Mean of 3 preceding values, taken in absence of other information.

c) the average biomass represented in each box, and
d) the average biomass transfer between boxes (i.e., the quantities represented by the arrows) (see Fig. 12.6).

Identifying the taxa to be included in the various boxes involves criteria relating to the size of the animals, to their distribution and to their feeding habits. Generally, it will be possible to identify groups separated by all three criteria, e.g.,

— large predators, e.g., sharks and groupers, which are large, tend to occur in deeper waters and feed on smaller fish,
— small, demersal, forage fish, e.g., slipmouths, which occur in relatively shallow waters and feed on zooplankton or zoobenthos, or
— small pelagics . . . etc.

Since food and feeding habits cannot be determined for all species concerned, exhaustive use should be made of the available extensive literature on food and feeding habits of fish and of generalizations relating the morphology of fishes to their feeding habits.

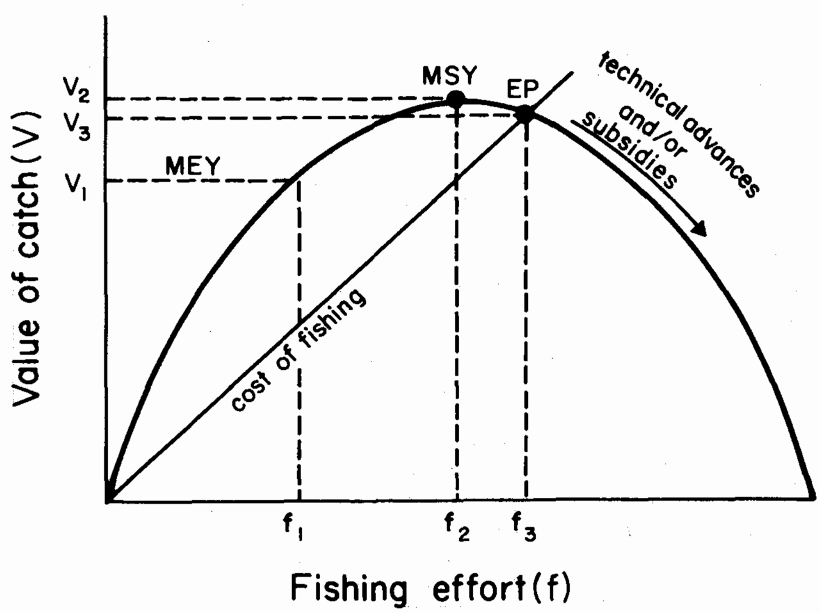

Fig. 12.7. A simple economic model of a fishery with fishing costs linearly proportional to effort. Note that MEY (maximum economic yield, i.e., the maximum difference between gross value of catch and cost of fishing) is achieved at a level of effort (f_1) lower than that needed (f_2) to obtain MSY (maximum sustainable yield). Under conditions of open access to fishing, fishing effort will increase until total costs equal the gross value of the catch (i.e., fishing reaches f_3, and the equilibrium point, EP) and at which profit for the average fishing unit is zero. Note also that lowering the cost line (e.g., by subsidizing the fishery) lowers the point at which equilibrium is reached, ***and thus lowers the catch*** **(Smith 1981).**

Examples of such generalizations are:
- large fish with strong, pointed teeth (sharks, conger eels, barracuda) are piscivorous (De Groot 1973)
- piscivorous fish tend to eat fish about one-quarter to one-fifth of their length (Ursin 1973; Cushing 1978)
- fish with long, coiled guts (longer than 3-4 times their body length) are generally detritivorous (Pauly 1975)
- fish with an extremely small mouth are generally zooplanktivorous
- generalist-type fish, such as snappers, are omnivorous
- the size of the spaces between the gill-rakers of pelagics gives a direct indication of the size of their favorite food, etc.

This list is not exhaustive but indicates some of the methods which can be used to group fish into feeding niches and hence into the various boxes of a model. Obviously, when detailed data are available on the food and feeding habits, ecological similarity (≈ niche overlap) indices can be computed to quantify objectively the similarity in the diet of different fish to assist grouping. One such index is:

$$c_{ab} = 1 - \tfrac{1}{2} \Sigma \mid p_{aj} - p_{bj} \mid \qquad \ldots 12.7)$$

where p_{aj} and p_{bj} are the percentages of a certain food item j in the food of fish species a and b, respectively, the index having a value of zero when the two fish species have no food item in common, and of unity when both fish species have the same food items in the same percentage composition (see Colwell and Futuyama 1971, and Pianka 1973 for another index).

Obviously, grouping fish and invertebrates into boxes on the basis of their food and feeding habits makes the drawing of the arrows which link the various boxes quite easy, such that task (b) above becomes part of task (a). Putting numbers into the boxes is a little more complicated.

The first step is to obtain the mean standing stock in each box (or at least in most of them). The most straightforward method to obtain standing stock estimates is to conduct a trawl survey in the case of demersal stocks, or an acoustic survey in the case of pelagic stocks. In both cases, tagging-recapture experiments can also be conducted from which biomass and a number of other important parameters can be estimated.

These methods, however, are rather expensive, and in the following a method to bypass the problem is shown—at least as a first approach.

First, estimate the annual yield, by species group that is extracted from the system. Then, using methods selected from Chapter 5, first estimate fishing and natural mortality for species representative of each (or most) of the boxes of the model. Then estimate mean standing stock from Equation (6.7) or by means of any of the other methods available to estimate standing stock in Chapters 6 and 7.

It will generally not be possible to obtain estimates of mean biomasses ($\overline{B}$) for all fish included in each box. As a first approximation, however, all the fish in a given box may be assumed to have the same fishing mortality (they will have similar sizes and occur at similar places, so it is not a completely unreasonable assumption) (see Table 10.3). Putting numbers along the arrows linking boxes with each other is now relatively simple:

- for the arrow linking fish with the fishery, use the yield data themselves, i.e.,

$$Y = F \cdot \overline{B} \qquad \ldots 12.8)$$

- for the arrows linking predators and their prey use, assuming that all natural mortality is due to predation

$$Q = M \cdot \overline{B} \qquad \ldots 12.9)$$

  where M is the natural mortality and Q is the wet weight of prey consumed by the predators. When a predation arrow goes to two or more predators, the value of Q is divided up in proportion of the biomass of each **predator** box (see Fig. 12.6).

From a box model such as in Fig. 12.6, the following quantities may be estimated:

a) food consumption per day and unit of weight of the animals in each box. Divide the amount (ΣQ) going into a box by $\overline{B}$, and then by 365, and
b) the food conversion rate within each box (or by trophic level if appropriate adjustments are made), calculated by dividing all matter leaving a box ($\Sigma[Y + Q]$) by all matter entering it.

The values of food consumption should generally fall between 3% and 6%/day, and those of food conversion rate, 5% to 25%. These ranges can also be used to complete empty boxes in the model, when values of Y and F are unobtainable, e.g., for zooplankton (see Fig. 12.6).

Quantitative box models, constructed along principles such as outlined here can serve the following purposes:

— summarizing the data available on a multispecies system
— allowing for an integration of a fishery with ecological data
— identifying those parts of the system where gaps in knowledge occur
— assessing the possible impact of exploiting one stock or the other.

Useful references that may be consulted when dealing with aquatic food chains and box models of exploited systems are Winberg (1971), Steele (1973), Boje and Tomczak (1978), Pauly (1979b), Jones (1982) and Polovina and Ow (1983).

MANAGING MULTISPECIES FISHERIES

Fortunately, finding out what is necessary to manage a multispecies fishery rationally is most often less complicated than trying to understand how the system works in biological terms.

Throughout much of the world, as a rule, once exploitation of a stock has begun, the fishery rapidly moves toward overfishing because, in the absence of effective regulations, the point of equilibrium of a fishery occurs when the costs of fishing becomes as high as the gross returns from the fishery as shown in Fig. 12.7 and in Clark (1976).

Thus, managing a fishery (as opposed to developing one) is for most purposes synonymous with attempting to reduce or redirect fishing effort, in order either to increase the catch and/or to reduce losses due to overcapitalization, i.e., increase the income of those remaining in the fishery (see Fig. 12.7 and Smith 1981).

Pope (1979) suggested that fitting a parabolic yield curve to time series of catch-and-effort data from a multispecies fishery, although it may underestimate MSY, may be an appropriate method to identify an optimum level of aggregate effort, and this is, in fact, what is generally done in practice when time series of catch-and-effort data are available. However, Larkin (1982) pointed out that, contrary to expectations, "there is little evidence that total catches have fallen in tropical fisheries due to overfishing. Though catches of individual species have dropped, these often have been made up by increases of other species."

For example, the catch-and-effort data of the Gulf of Thailand demersal trawl fishery (Table 12.4) have been fitted with a total biomass Schaefer model (SCSP 1978) and a Fox model (FAO 1978) although the data do not really suggest a downward trend of total *catch* at high levels of effort (although the *catch-per-effort* rate decreased dramatically). For this reason, a more or less flat-topped model would fit the data (see Fig. 12.8).

Such a model is, for example

$$Y = Y_\infty (1 - e^{-\alpha f}) \qquad \ldots 12.10)$$

where Y_∞ is the "asymptotic yield" while α is an empirical constant.

Obviously, when this model is used to reduce a set of catch-and-effort data, the need arises to somehow define an optimal level of effort (since infinite effort, giving Y_∞, would clearly be an unreasonable proposition), especially when economic data are not available from which the equilibrium point and maximum economic yield can be defined.

In analogy to the $F_{0.1}$ concept discussed in Chapter 8, a level of catch and effort may be defined at which the slope of the yield curve is one-tenth of the slope at the origin ($Y_{0.1}$, $f_{0.1}$) by first defining the slope of equation (12.10)

$$\frac{dY}{df} = Y_\infty \cdot \alpha \cdot e^{-\alpha f} \qquad \ldots 12.11)$$

which, when $f = 0$, reduces to $Y_\infty \cdot \alpha$.

Thus, $f_{0.1}$ can be obtained from

$$Y_\infty \cdot \alpha/10 = Y_\infty \cdot \alpha \cdot e^{-\alpha f_{0.1}} \qquad \ldots 12.12)$$

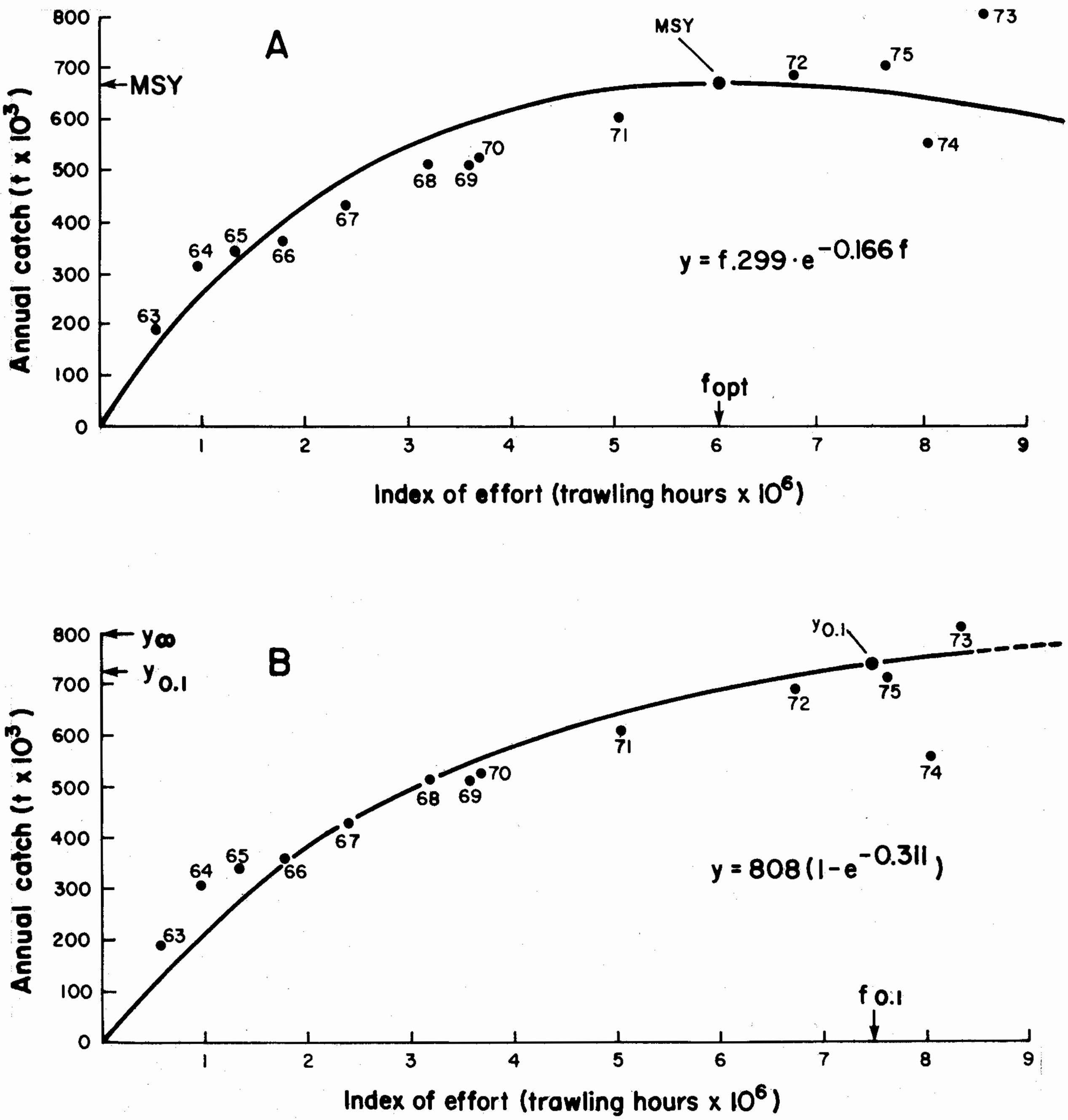

Fig. 12.8. Comparison of two yield models fitted to catch-and-effort data from a tropical multispecies fishery (the Gulf of Thailand trawl fishery). ***Upper:*** **Fox model;** ***lower:*** **asymptotic yield model. Note that both models suggest that effort should be reduced, and yields stabilized in the neighborhood of 700,000 tonnes. (Based on Table 12.4 and Example 12.2).**

or

$$\frac{\ln 10}{\alpha} = f_{0.1} \qquad \ldots 12.13)$$

while $Y_{0.1}$ is obtained from

$$Y_{0.1} = Y_{\infty} \cdot 0.9 \qquad \ldots 12.14)$$

Thus, paraphrasing Gulland and Boerema (1973) who introduced the $F_{0.1}$ concept, I wish to suggest that "the selection of 10% is arbitrary, but once the 10% figure is accepted, the corresponding catch can be calculated objectively. Thus it can be used to provide a commission or other management body objective guidance based on scientific grounds". An application of this model to a set of catch-and-effort data is given in Example 12.2 (see also Table 12.4) and Fig. 12.8.

To avoid misunderstandings, it is stressed here that equation (12.10) is not meant to describe the whole range of yield/effort relationships, which *must* exhibit a decline at very high levels of effort, but to help cope with a situation where the yield/effort relationship shows no maximum and where, therefore, a management goal different from MSY *must* be used.

Techniques on how to exploit a multispecies stock to obtain a desired species mix or avoid an undesired one are not available (Daan 1980). At least some of the following changes may be expected, however, given a steadily increasing level of effort on a demersal multispecies stock:

- a decline of the catch per effort (although not necessarily of the total catch as noted above)
- a rapid decrease and virtual extinction of very large fish (assuming that they are caught in the first place)
- a decrease in the average size of the fish caught
- an increase of the relative contributions of low-value, small-sized fish
- the unexpected increase of previously insignificant components of the system (e.g., squids or jellyfish).

I leave it to the reader to sort out these things in more detail.

Table 12.4. Nominal catch-and-effort data from the Gulf of Thailand Trawl Fishery. Data derived from Fig. 7 in Buzeta (1978).

#	Year	Catch $t \times 10^3$	Effort trawl-hours $\times 10^6$
1	1963	190	0.57
2	1964	310	0.98
3	1965	340	1.35
4	1966	360	1.8
5	1967	430	2.4
6	1968	510	3.2
7	1969	510	3.6
8	1970	520	3.7
9	1971	600	5.05
10	1972	680	6.75
11	1973	800	8.6
12	1974	550	8.05
13	1975	700	7.65

Recommended reading: The literature on tropical multispecies fisheries and on the modelling of such systems is rapidly growing. Useful contributions are FAO (1978), Pope (1979), Pauly (1979b), Saila and Roedel (1980), Munro (1983), Simpson (1982), Marten and Polovina (1982) and Larkin and Gazey (1982).

Suggested research topics: Evidently, it is difficult to define a research program that applies to all multispecies stocks. However, the following elements should be included in any basic fishery research program:

- monitoring total catch and catch per effort of the fishery
- monitoring catch per effort of various "indicator" species representing various groups of fish (e.g., large, medium- and small-sized)
- thorough study of the biology and population dynamics of the most abundant and of the most valuable species
- an attempt to construct a "box model" of the system in question
- an attempt to identify gear that would selectively remove certain groups of species (e.g., attempt to identify the best F-ratios in the system in question).

The various reviews included in Pauly and Murphy (1982) should be helpful in defining such a research program.

EXAMPLE 12.1

Yields from a two-species (predator-prey) system.

The yield-isopleths in Fig. 12.2 are meant to represent a predator-prey system and are based on the following set of assumed constants:

Prey (P)	Predator (Q)
a = 200	d = 100
b = 100	e = 50
c_1 = –25	c_2 = 25

Case I: Estimate Y_P and Y_Q for $F_P = 0.8$ and $F_Q = 0.8$ (i.e., using an F-ratio of 1:1):

1) Read sides 1 and 2 of Program FB 30

2) Enter constants:

Keystrokes: 200 STO A 100 STO B 25 CHS STO 2 100 STO D 50 STO E 25 STO 3 .8 STO 0

3) Estimate Y_P, Y_Q and Y_T for $F_P = 1$

Keystrokes	Results	
.8 A	80	(Y_P)
	64	(Y_Q)
	144	(Y_T)

Case II: Estimate "real" MSY, $F_{Q\ (opt)}$ and $F_{P\ (opt)}$ of the two-species system:

1) Read sides 1 and 2 of Program FB 30

2) Enter constants, including initial values F'_P and F'_Q (say, $F'_Q = 0.8$ and $F'_P = 1.2$).

Keystrokes: 200 STO A 100 STO B 25 CHS STO 2 100 STO D 50 STO E 25 STO 3.8 STO 0 1.2 STO 1

3) Enter ΔF, TOL and estimate $F_{Q\ (opt)}$, $F_{P\ (opt)}$ and MSY:

Keystrokes	Results	
.05 ↑		
0.001 f a	1.002	($F_{Q\ (opt)}$)
	0.998	($F_{P\ (opt)}$)
	150.000	(MSY)

Entering a smaller value of TOL (e.g., 0.0001) produces the exact values: $F_{Q\ (opt)} = 1.000$, $F_{P\ (opt)} = 1.000$ also with MSY = 150.000.

EXAMPLE 12.2

Fitting an asymptotic yield model to bulk catch-and-effort data from a multi-species fishery.

Data from Table 12.4

Computations

We take advantage of the fact that equation (12.10) has the same form as the special VBGF [see Chapter 4] (with $t_o = 0$) and use Program FB 3 (von Bertalanffy plot) to fit the data. Fitting the data is here viewed as finding the values of α and Y_∞ for equation 12.10 which generate a curve that goes through the intercept (i.e., for which $t_o = 0$); α and Y_∞ correspond to K and L_∞ of the VBGF, respectively.

1) Read sides 1 and 2 of Program FB 3.

2) Select an initial value of Y_∞ (Y_∞ must always be higher than the highest reported catch). Upon visual inspection of Table 12.4, we select 850 (x 10^3 tonnes) as an appropriate seed value. Thus

   Keystrokes: 850 ↑ 1 f a 190 ↑ .57 A 310 ↑ .98A 340 ↑ 1.35 A 360 ↑ 1.8 A 430 ↑ 2.4 A 510 ↑ 3.2 A 510 ↑ 3.6 A 520 ↑ 3.7 A 600 ↑ 5.05 A 680 ↑ 5.75 A 800 ↑ 8.6 A 550 ↑ 8.05 A 700 ↑ 7.65 A

3) Obtain value of r^2, α and "t_o" corresponding to $Y_\infty = 850$

Keystrokes	Results	
E	0.750	(r^2)
	0.211	(α)
	–0.854	("t_o")

4) Since equation (12.10) implies that "t_o" = 0, the seed value of $Y_\infty = 850$ is too high, it is reduced to 825, which provides, upon repeating step 3 a value of "t_o" = –0.470. Thus, Y_∞ must be lower, i.e., 810. This provides, upon repeating step 3 a value of "t_o" = –0.073. Clearly, we are on the right track. Further trials with 809 and 808 reveal that 808 gives a value of "t_o" very close to zero. Thus, for $Y_\infty = 808$ we have

Keystrokes	Results	
E	0.607	(r^2)
	0.311	(α)
	0.008	("t_o")

5) Using Program FB 9, and replacing age by effort and length by yield, we obtain values for drawing the yield curve, by first entering the values of α in STO1 and Y_∞ in store A (see Table 4.8) then entering the f values and pressing A.

6) Finally, $f_{0.1}$ and $Y_{0.1}$ are estimated from equations (12.13) and (12.14) by performing

	Keystrokes	Results	
	10 LN		
	.311 ÷	7.404	($f_{0.1}$)
and	808 ↑		
	.9 x	727.200	($Y_{0.1}$)

As might be seen in Fig. 12.8, $f_{0.1}$ and $Y_{0.1}$ are higher than f_{opt} and MSY as obtained by using the Fox model (Fig. 12.8, upper). This example was meant to illustrate the asymptotic yield model, and not to perform an assessment of the Gulf of Thailand trawl fishery. For such an assessment, the data of Table 12.4 are inadequate, since they probably include fish caught outside the Gulf (Simpson 1982).

Appendix I. Testing Models and Their Results: An Introduction to Sensitivity Analysis and the Jackknife

INTRODUCTION

Throughout the twelve chapters of this book, various models have been presented through equations all of which provide, given appropriate inputs (e.g., data points), some useful output (a "statistic"). As the astute reader will have noted, neither the accuracy, nor the precision of the estimated statistics is discussed at length for any of the models presented in these twelve chapters and in fact, equations for estimating standard errors of estimates are given in a few cases only.

The reasons for this are two-fold:

- for a number of models, equations for the estimation of standard errors are either lacking, or inordinately complex, and
- a simple method exists, called the "jackknife", which can be used to estimate standard errors for the output of any model, thus making specific equations for each model superfluous.

While the jackknife method, presented in detail below, can be used to assess for any model the precision associated with estimates of a given statistic (i.e., the width of the confidence interval about that statistic), another method must be used to assess the "sensitivity" of a model to its input parameters.

Only "ordinary sensitivity analysis" will be discussed here; it has as its main objective "the identification of input parameters which, when changed by a fixed percentage, produce either a strong or a weak effect on the model output" (Majkowski 1982).

SENSITIVITY ANALYSIS

In ordinary sensitivity analysis, only one parameter is changed at a time, usually by a fixed percentage (U %). The effect of the changes is expressed by a "D-measure"* which is used to express the changes in output caused by changes in the inputs. The D-measure relates the output values in the "perturbed" state (i.e., when the parameter values have been changed) to those in the "unperturbed" state (i.e., as occurs when the best available parameter estimates are used).

An example of a D-measure which can be used for a variety of purposes is

$$D = \frac{X - X^o}{X^o} \cdot 100 \qquad \ldots 1)$$

where X and X^o are perturbed and unperturbed outputs, respectively. Majkowski (1982), from whose paper this account is adapted, gave an application of ordinary sensitivity analysis to an equation commonly used in tropical fish stock assessment (equation 5.9). A summary of his analysis, based on the special VBGF and the parameter values $L_\infty = 28.9$ cm, K = 0.46, $\bar{L} = 16.4$ cm and L′ = 12 cm, (for *Nemipterus peronii* from the Gulf of Thailand) is reproduced here (Appendix Table I.1).

The analysis led to the conclusion that equation (5.9) is extremely sensitive to changes in the value of $\bar{L}$ and that, therefore, every effort must be made, when using this equation, to ensure that $\bar{L}$ is estimated as reliably as possible.

Similarly, Moreau (1980), who applied ordinary sensitivity analysis to Beverton and Holt's yield-per-recruit model (see Chapter 8), found that the parameter which most influences the results is natural mortality. He concluded that, when using the yield-per-recruit model, attention must be devoted to increasing the accuracy and precision of estimates of M (rather than, e.g., spend resources on better estimates of growth parameters).

*Not to be mistaken for the parameter D in the generalized VBGF (see Chapter 4).

Appendix Table I.1. Values of the D-measure (formula 1) for various perturbations in the input parameters. The perturbed parameter is indicated in the first column of the table and magnitude of the perturbation (U%) in the first row of the table (from Majkowski 1982).

U%	−40	−20	−10	−5	−1	1	5	10	20	40
K	−40.00	−20.00	−10.00	−5.00	−1.00	1.00	5.00	10.00	20.00	40.00
L_∞	−92.48	−46.24	−23.12	−11.56	−2.31	2.31	11.56	23.12	46.24	92.48
$\bar{L}$	−410.61	395.94	80.34	30.97	5.23	−4.86	−21.24	−36.71	−57.74	−80.92
L′	−52.17	−35.29	−21.43	−12.00	−2.65	2.80	15.79	37.50	120.00	−1,200.00

Two other forms of sensitivity analysis exist in addition to ordinary sensitivity analysis—extended deterministic sensitivity analysis and extended stochastic sensitivity analysis. They allow assessment of the impact of simultaneous changes of input parameters, for considering the effects of various types of error distributions in the input parameters, etc. (see Majkowski 1982). Ordinary sensitivity analysis as presented here, should suffice, however, for most models presented in this book.

THE JACKKNIFE METHOD

The underlying principle of Tukey's "jackknife" method is (1) that a given statistic A, computed via a given model from a certain number (n) of data points will take different values (A_{-i}), depending upon which subset of the available data points are used for computation, and (2) that the distribution of the A_{-i} values is related to the distribution of the statistic A itself (Miller 1974; Tukey 1977; Mosteller and Tukey 1977; Sokal and Rohlf 1981).

Computationally, the jackknife involves the following steps:

a) compute the value of the statistic A, using all available data points (n). This results in estimate $\hat{A}_1$ of the statistic in question,
b) then compute n new values of the statistic A, but omitting each time another of the n available data points. This results in n estimates of "A_{i-1}", each estimated by omitting a *single* data point (see Appendix Table I.2),
c) use the A_{i-1} values to compute "pseudovalues" of A, (ϕ_i), through the equation

$$\phi_i = (n \cdot \hat{A}_1) - [(n-1) \cdot A_i]$$

d) obtain a new estimate of A through

$$\hat{A}_2 = \frac{\Sigma\, \phi_i}{n} = \bar{\phi}$$

[In a perfect world, the two estimates of A ($\hat{A}_1$, $\hat{A}_2$) would be equal; in reality, they often are not. The standard error of A that is estimated by the jackknife (see below) pertains to $\hat{A}_2$, for which reason it may be more appropriate to stick to $\hat{A}_2$ as most useful estimator of A.]

e) the standard error of $\hat{A}_2$ is then computed from

$$s.e._{(A)} = \sqrt{(sd^2_\phi)/n}$$

where $sd_{(\phi)}$ is the standard deviation of the ϕ_i values.

The authors cited above give more detailed accounts of the jackknife, which is illustrated here—following a suggestion by S. Saila (pers. comm.)—by the computation of standard error for the output of a surplus production model (MSY and f_{opt} as defined in Chapter 10).

Appendix Table I.2, which is an extension of Table 10.3, gives the catch-and-effort values used and/or omitted for the computation of the A_{i-1} values (i.e., estimates of MSY_{i-1} and $f_{opt\ i-1}$) computed by omitting the data points (i) pertaining to the years 1969 to 1977.

As might be seen, the results suggest rather small standard errors for the MSY and f_{opt} values, which, multiplied with the appropriate $\hat{t}$ value (see Chapter 1), would yield a narrow confidence interval.

This application of the jackknife should have made the versatility of this method obvious. In principle, the method can be applied to all models presented in this book—except when the results are obtained through accumulation, where values cannot be omitted without distorting the final result entirely.

Table I.2. Application of the jackknife method to the surplus model (see also Chapter 10).

#	Year	Catch[a]	Effort[b]	A_{i-1} values		Pseudovalues (ϕ_i)	
				MSY_{i-1}	$f_{opt\ i-1}$	ϕ_{msy}	$\phi_{f_{opt}}$
1	1969	50	623	60.6	1,253	63.3	1,442
2	1970	49	628	60.8	1,246	62.4	1,496
3	1971	47.5	520	60.5	1,275	64.1	1,264
4	1972	45	513	60.6	1,253	63.3	1,436
5	1973	51	661	60.7	1,250	62.9	1,461
6	1974	56	919	60.9	1,253	60.9	1,442
7	1975	66	1,158	59.8	1,237	70.1	1,567
8	1976	58	1,970	57.4	1,087	89.0	2,767
9	1977	52	1,317	63.2	1,337	43.2	767
$\bar{X}$	=	52	923	60.5	1,244	64.2	1,509
s.d.	=	6.39	485	1.47	65.8	11.1	496
s.e.	=	2.13	162	0.491	21.9	3.70	165

[a] 10^3 tonnes (see Table 10.3).
[b] No. of standard vessels (see Table 10.3).

Appendix II. List of Programs and Program Listings

User Instructions

LENGTH - WEIGHT RELATIONSHIPS FB1

A	B	C	D	E
L, W	L, W, n	→ c.f.		→ r^2, a, b, $\hat{i}$

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS	OUTPUT DATA/UNITS
1	Initialize		f a	0.000
	DATA NOT WEIGHTED BY SAMPLE SIZE :			
2	Enter L-W data pairs	L	↑	L
		W	A	i
3	Remove erroneous data pairs	L	↑	L
		W	f b	i - 1
	DATA WEIGHTED BY SAMPLE SIZE :			
4	Enter L, W, n	L	↑	L
		W	↑	W
	(No correction routine provided here.	n	B	i
	In case of an erroneous data entry,			
	reinitialize and start again.)			
5	Calculate coefficients of L-W relationship		E	r^2
				a
	(If L-W conversions are to be performed with-			b
	out a, b, or c.f. having been estimated			$\hat{i}$
	internally, store "a" in A, "b" in B and "c.f."			
	in C.)			
6	Use "a" and "b" to estimate weight from length	L	D	W
7	Use "a" and "b" to estimate length from weight	W	f d	L
8	Calculate (mean) condition factor		C	c.f.
9	Use c.f. to estimate weight from length	L	f C	W
10	Use c.f. to estimate length from weight	W	f e	L

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	CLRG	16-53	
005	CLX	-51	
006	RTN	24	
007	*LBLA	21 11	
008	P⇄S	16-51	
009	ST+3	35-55 03	
010	LOG	16 32	
011	X⇄Y	-41	
012	ST+0	35-55 00	
013	P⇄S	16-51	
014	LOG	16 32	
015	Σ+	56	
016	RTN	24	
017	*LBLb	21 16 12	
018	P⇄S	16-51	
019	ST-3	35-45 03	
020	LOG	16 32	
021	X⇄Y	-41	
022	ST-0	35-45 00	
023	P⇄S	16-51	
024	LOG	16 32	
025	Σ-	16 56	
026	RTN	24	
027	*LBLB	21 12	
028	P⇄S	16-51	
029	STOE	35 15	
030	ST+9	35-55 09	
031	R↓	-31	
032	X⇄Y	-41	
033	ST+3	35-55 03	
034	LOG	16 32	
035	STO1	35 01	
036	R↓	-31	
037	ST+0	35-55 00	
038	LOG	16 32	
039	STO2	35 02	
040	RCL1	36 01	
041	x	-35	
042	RCLE	36 15	
043	x	-35	
044	ST+8	35-55 08	
045	RCL2	36 02	
046	X^2	53	
047	RCLE	36 15	
048	x	-35	
049	ST+7	35-55 07	
050	RCL2	36 02	
051	RCLE	36 15	
052	x	-35	
053	ST+6	35-55 06	
054	RCL1	36 01	
055	X^2	53	
056	RCLE	36 15	
057	x	-35	
058	ST+5	35-55 05	
059	RCL1	36 01	
060	RCLE	36 15	
061	x	-35	
062	ST+4	35-55 04	
063	ISZI	16 26 46	
064	RCLI	36 46	
065	P⇄S	16-51	
066	RTN	24	
067	*LBLE	21 15	
068	P⇄S	16-51	
069	SPC	16-11	
070	RCL8	36 08	
071	RCL4	36 04	
072	RCL6	36 06	
073	x	-35	
074	RCL9	36 09	
075	÷	-24	
076	-	-45	
077	ENT↑	-21	
078	ENT↑	-21	
079	RCL4	36 04	
080	X^2	53	
081	RCL9	36 09	
082	÷	-24	
083	RCL5	36 05	
084	X⇄Y	-41	
085	-	-45	
086	÷	-24	
087	STOB	35 12	
088	x	-35	
089	RCL6	36 06	
090	X^2	53	
091	RCL9	36 09	
092	÷	-24	
093	CHS	-22	
094	RCL7	36 07	
095	+	-55	
096	÷	-24	
097	PRTX	-14	
098	STOD	35 14	
099	RCL6	36 06	
100	RCL4	36 04	
101	RCLB	36 12	
102	x	-35	
103	-	-45	
104	RCL9	36 09	
105	÷	-24	
106	10^x	16 33	
107	STOA	35 11	
108	DSP9	-63 09	
109	PRTX	-14	
110	RCLB	36 12	
111	DSP3	-63 03	
112	PRTX	-14	

REGISTERS

0	1	2	3	4	5	6	7	8	9

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
used	used	used	used	Σx	Σx^2	Σy	Σy^2	Σxy	n

A	B	C	D	E	I
a	b	c.f.	r^2	used	i

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	P⇄S	16-51	
114	S	16 54	
115	P⇄S	16-51	
116	X⇄Y	-41	
117	÷	-24	
118	RCLB	36 12	
119	3	03	
120	-	-45	
121	ABS	16 31	
122	1	01	
123	RCLD	36 14	
124	-	-45	
125	√X	54	
126	÷	-24	
127	x	-35	
128	RCL9	36 09	
129	2	02	
130	-	-45	
131	√X	54	
132	x	-35	
133	PRTX	-14	
134	P⇄S	16-51	
135	0	00	
136	RTN	24	
137	*LBLD	21 14	
138	RCLB	36 12	
139	Y^x	31	
140	RCLA	36 11	
141	x	-35	
142	RTN	24	
143	*LBLd	21 16 14	
144	RCLA	36 11	
145	÷	-24	
146	RCLB	36 12	
147	1/X	52	
148	Y^x	31	
149	RTN	24	
150	*LBLC	21 13	
151	P⇄S	16-51	
152	RCL6	36 06	
153	RCL9	36 09	
154	÷	-24	
155	2	02	
156	+	-55	
157	RCL4	36 04	
158	RCL9	36 09	
159	÷	-24	
160	3	03	
161	x	-35	
162	-	-45	
163	10^x	16 33	
164	STOC	35 13	
165	SPC	16-11	
166	PRTX	-14	
167	P⇄S	16-51	
168	RTN	24	
169	*LBLc	21 16 13	
170	3	03	
171	Y^x	31	
172	RCLC	36 13	
173	x	-35	
174	1	01	
175	0	00	
176	0	00	
177	÷	-24	
178	RTN	24	
179	*LBLe	21 16 15	
180	1	01	
181	0	00	
182	0	00	
183	x	-35	
184	RCLC	36 13	
185	÷	-24	
186	3	03	
187	1/X	52	
188	Y^x	31	
189	RTN	24	

LABELS

A L,W →	B L,W,n →	C → c.f.	D L → W	E → r^2, a, b, $\hat{t}$
a initialize	b correct	c L → W	d W → L	e W → L
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3, 9	

Program Description

Program Title *Length – Weight Relationships*

Name *Daniel Pauly* Date *January, 1982*

Address *ICLARM, MCC P.O. Box 1501*
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. *This program fits data to a length – weight relationship of the form*

$$W = a \cdot L^b \qquad \ldots 1)$$

where W is the weight and L is the length of an animal. The fit is obtained by means of a linear regression of the form

$$\log_{10} W = \log_{10} a + b \log_{10} L \qquad \ldots 2)$$

whose goodness of fit is estimated by r^2.
Also, a condition factor (c.f.) is estimated by means of the expression

$$c.f. = W \cdot 100 / L^3 \qquad \ldots 3)$$

Both expression (1) and the condition factor can be used to perform length - to - weight and weight - to - length conversions.
When grams (live weight) and c.m. are used, the value of c.f. in most fishes will range between 0.5 and 1.5.

To test whether the values of b estimated via expression (2) differ significantly from (3) (isometric growth), a value of $\hat{t}$ is computed with each value of b which can be used in conjunction with a table of the t - distribution (d.f. = n-2).

$$\hat{t} = \frac{|b-3|}{\sqrt{1-r^2}} \cdot \frac{S_x}{S_y} \cdot \sqrt{n-2} \qquad \ldots 4)$$

as given in Sachs L. (1974, p. 339).

Operating Limits and Warnings *Values of b in equation (1) below 2.5 and 3.5 are questionable, and may reflect an error, or be based on too small a range of length and weight data.*
An error message will appear after computation of b if $r^2 = 1$, as may occur when n is very low (2 or 3).

User Instructions

GEAR SELECTION FB2

1 Trawl Selection: N-cover ↑ N-codend A | → L_c | correct

Gillnet Selection: Correct C_A, C_B, L → | → % retained (B) → % retained (A) | → a, b, r^2 → L_A, L_B, S^2 2

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	TRAWL SELECTION				
1	Enter lower class limit of smallest				
	length class (L_{min})	$L_{(min)}$	f	a	0.00
2	Enter, for each length class, the number	N cover	↑		
	of fish in cover and in cod end	N codend	A		i
3	Remove erroneous data pair	N cover	↑		
		N codend	B		$i-1$
4	Calculate L_c		f	b	L_c
	GILLNET SELECTION				
5	Set flag 1 for asymmetric selection		STF	1	
	curves (or clear it for symmetrical curves!)				
6	Enter smaller and larger mesh sizes and	A	↑		
	initialize	B	f	e	0.000
7	Enter (for each length class represented	C_A	↑		
	in catch of both nets) the catches and class	C_B	↑		
	midlength, i.e.	L_i	C		counter
	Set FLAG Ø to view data				
8	To remove erroneous entries, perform	C_A	↑		
		C_B	↑		
		L_i	f	c	counter -1
9	To estimate parameters of regression line				
	and mesh selection parameters, press		E		r^2
					a
					b
					L_A
					L_B
10	To obtain probabilities of capture, by length,				S.d.
	do for mesh size A	Length	D		frac. retained
	and similarly for B	Length	f	d	frac. retained

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	1	01	
004	-	-45	
005	STO2	35 02	
006	CLX	-51	
007	RTN	24	
008	*LBLA	21 11	
009	STO0	35 00	
010	+	-55	
011	RCL0	36 00	
012	X⇄Y	-41	
013	÷	-24	
014	ST+1	35-55 01	
015	1	01	
016	ST+2	35-55 02	
017	RCL2	36 02	
018	RTN	24	
019	*LBLB	21 12	
020	STO0	35 00	
021	+	-55	
022	RCL0	36 00	
023	X⇄Y	-41	
024	÷	-24	
025	ST-1	35-45 01	
026	1	01	
027	ST-2	35-45 02	
028	RCL2	36 02	
029	RTN	24	
030	*LBLb	21 16 12	
031	RCL2	36 02	
032	1	01	
033	+	-55	
034	RCL1	36 01	
035	-	-45	
036	RTN	24	
037	*LBLe	21 16 15	
038	CLRG	16-53	
039	P⇄S	16-51	
040	CLRG	16-53	
041	F1?	16 23 01	
042	LN	32	
043	STO1	35 01	
044	R↓	-31	
045	F1?	16 23 01	
046	LN	32	
047	STO0	35 00	
048	CLX	-51	
049	RTN	24	
050	*LBLC	21 13	
051	F1?	16 23 01	
052	LN	32	
053	R↓	-31	
054	X⇄Y	-41	
055	÷	-24	
056	LN	32	
057	R↑	16-31	
058	F0?	16 23 00	
059	PRTX	-14	
060	X⇄Y	-41	
061	F0?	16 23 00	
062	PRTX	-14	
063	X⇄Y	-41	
064	Σ+	56	
065	RTN	24	
066	*LBLc	21 16 13	
067	F1?	16 23 01	
068	LN	32	
069	R↓	-31	
070	X⇄Y	-41	
071	÷	-24	
072	LN	32	
073	R↑	16-31	
074	F0?	16 23 00	
075	PRTX	-14	
076	X⇄Y	-41	
077	F0?	16 23 00	
078	PRTX	-14	
079	X⇄Y	-41	
080	Σ-	16 56	
081	RTN	24	
082	*LBLE	21 15	
083	P⇄S	16-51	
084	SPC	16-11	
085	RCL8	36 08	
086	RCL4	36 04	
087	RCL6	36 06	
088	×	-35	
089	RCL9	36 09	
090	÷	-24	
091	-	-45	
092	ENT↑	-21	
093	ENT↑	-21	
094	RCL4	36 04	
095	X²	53	
096	RCL9	36 09	
097	÷	-24	
098	RCL5	36 05	
099	X⇄Y	-41	
100	-	-45	
101	÷	-24	
102	STOB	35 12	
103	×	-35	
104	RCL6	36 06	
105	X²	53	
106	RCL9	36 09	
107	÷	-24	
108	CHS	-22	
109	RCL7	36 07	
110	+	-55	
111	÷	-24	
112	PRTX	-14	

REGISTERS

0	1	2	3	4	5	6	7	8	9
Σ		L_A	L_B	S					

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
A	B			used	used	used	used	used	i

A	B	C	D	E	I
a	b	2a/A + B			

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCL6	36 06	
114	RCL4	36 04	
115	RCLB	36 12	
116	x	-35	
117	-	-45	
118	RCL9	36 09	
119	÷	-24	
120	STOA	35 11	
121	PRTX	-14	
122	RCLB	36 12	
123	PRTX	-14	
124	P⇄S	16-51	
125	RCLA	36 11	
126	2	02	
127	x	-35	
128	RCL0	36 00	
129	RCL1	36 01	
130	+	-55	
131	÷	-24	
132	STOC	35 13	
133	RCL0	36 00	
134	x	-35	
135	RCLB	36 12	
136	÷	-24	
137	CHS	-22	
138	F1?	16 23 01	
139	e^x	33	
140	PRTX	-14	
141	F1?	16 23 01	
142	LN	32	
143	STO2	35 02	
144	RCLC	36 13	
145	RCL1	36 01	
146	x	-35	
147	CHS	-22	
148	RCLB	36 12	
149	÷	-24	
150	F1?	16 23 01	
151	e^x	33	
152	PRTX	-14	
153	F1?	16 23 01	
154	LN	32	
155	STO3	35 03	
156	RCLC	36 13	
157	RCL0	36 00	
158	RCL1	36 01	
159	-	-45	
160	x	-35	
161	RCLB	36 12	
162	X^2	53	
163	÷	-24	
164	√X	54	
165	PRTX	-14	
166	STO4	35 04	
167	RTN	24	
168	*LBL0	21 14	
169	F1?	16 23 01	
170	LN	32	
171	RCL2	36 02	
172	-	-45	
173	X^2	53	
174	RCL4	36 04	
175	X^2	53	
176	2	02	
177	x	-35	
178	÷	-24	
179	CHS	-22	
180	e^x	33	
181	RTN	24	
182	*LBLd	21 16 14	
183	F1?	16 23 01	
184	LN	32	
185	RCL3	36 03	
186	-	-45	
187	X^2	53	
188	RCL4	36 04	
189	X^2	53	
190	2	02	
191	x	-35	
192	÷	-24	
193	CHS	-22	
194	e^x	33	
195	RTN	24	

LABELS

A Enter trawl data	B correct trawl data	C → L_c	D Enter gill-net data	E → gillnet selection
a → L_c	b → frac. retained	c store L_{min}	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	display of ln C_n/C_a
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☒	☒	DEG	☒	FIX	☒
1	☒	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	STEP	KEY ENTRY	KEY CODE
001	*LBLa	21 16 11	057	RCL3	36 03
002	CLRG	16-53	058	÷	-24
003	STOD	35 14	059	PRTX	-14
004	R↓	-31	060	RTN	24
005	STOA	35 11	061	*LBLc	21 16 13
006	CLX	-51	062	SPC	16-11
007	RTN	24	063	RCL4	36 04
008	*LBLC	21 13	064	RCL6	36 06
009	STOC	35 13	065	×	-35
010	ST+9	35-55 09	066	RCL9	36 09
011	R↓	-31	067	÷	-24
012	STO1	35 01	068	CHS	-22
013	R↓	-31	069	RCL8	36 08
014	RCLD	36 14	070	+	-55
015	Y^x	31	071	STO0	35 00
016	RCLA	36 11	072	RCL6	36 06
017	RCLD	36 14	073	X^2	53
018	Y^x	31	074	RCL9	36 09
019	-	-45	075	÷	-24
020	CHS	-22	076	CHS	-22
021	LN	32	077	RCL7	36 07
022	STO2	35 02	078	+	-55
023	RCL1	36 01	079	P⇄S	16-51
024	×	-35	080	STO1	35 01
025	RCLC	36 13	081	P⇄S	16-51
026	×	-35	082	RCL4	36 04
027	ST+8	35-55 08	083	X^2	53
028	RCL2	36 02	084	RCL9	36 09
029	X^2	53	085	÷	-24
030	RCLC	36 13	086	CHS	-22
031	×	-35	087	RCL5	36 05
032	ST+7	35-55 07	088	+	-55
033	RCL2	36 02	089	P⇄S	16-51
034	RCLC	36 13	090	STO0	35 00
035	×	-35	091	RCL1	36 01
036	ST+6	35-55 06	092	P⇄S	16-51
037	RCL1	36 01	093	×	-35
038	X^2	53	094	STO3	35 03
039	RCLC	36 13	095	RCL0	36 00
040	×	-35	096	X^2	53
041	ST+5	35-55 05	097	RCL3	36 03
042	RCL1	36 01	098	÷	-24
043	RCLC	36 13	099	PRTX	-14
044	×	-35	100	RCL0	36 00
045	ST+4	35-55 04	101	P⇄S	16-51
046	ISZI	16 26 46	102	RCL0	36 00
047	RCLI	36 46	103	P⇄S	16-51
048	RTN	24	104	÷	-24
049	*LBLE	21 15	105	STO3	35 03
050	GSBc	23 16 13	106	CHS	-22
051	RCLA	36 11	107	RCLD	36 14
052	RCLD	36 14	108	÷	-24
053	Y^x	31	109	PRTX	-14
054	LN	32	110	RCL4	36 04
055	X⇄Y	-41	111	RCL9	36 09
056	-	-45	112	÷	-24

REGISTERS

0	1	2	3	4	5	6	7	8	9
used	used	used	used	Σx	Σx^2	Σy	Σy^2	Σxy	Σn

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
used	used								

A	B	C	D	E	I
$L(\infty)$	$W(\infty)$	used	D	b	i

Program Listing (113 to end)

STEP		KEY ENTRY	KEY CODE	COMMENTS
	113	RCL3	36 03	
	114	×	-35	
	115	CHS	-22	
	116	RCL6	36 06	
	117	RCL9	36 09	
	118	÷	-24	
	119	+	-55	
120	120	RTN	24	
	121	*LBLb	21 16 12	
	122	CLRG	16-53	
	123	STOE	35 15	
	124	R↓	-31	
	125	STOD	35 14	
	126	R↓	-31	
	127	STOB	35 12	
	128	CLX	-51	
	129	RTN	24	
130	130	*LBLD	21 14	
	131	STOC	35 13	
	132	ST+9	35-55 09	
	133	R↓	-31	
	134	STO1	35 01	
	135	R↓	-31	
	136	RCLE	36 15	
	137	1/X	52	
	138	Y^X	31	
	139	RCLD	36 14	
140	140	Y^X	31	
	141	RCLB	36 12	
	142	RCLE	36 15	
	143	1/X	52	
	144	Y^X	31	
	145	RCLD	36 14	
	146	Y^X	31	
	147	-	-45	
	148	CHS	-22	
	149	LN	32	
150	150	STO2	35 02	
	151	RCL1	36 01	
	152	×	-35	
	153	RCLC	36 13	
	154	×	-35	
	155	ST+8	35-55 08	
	156	RCL2	36 02	
	157	X^2	53	
	158	RCLC	36 13	
	159	×	-35	
160	160	ST+7	35-55 07	
	161	RCL2	36 02	
	162	RCLC	36 13	
	163	×	-35	
	164	ST+6	35-55 06	
	165	RCL1	36 01	
	166	X^2	53	
	167	RCLC	36 13	
	168	×	-35	
	169	ST+5	35-55 05	
170	170	RCL1	36 01	
	171	RCLC	36 13	
	172	×	-35	
	173	ST+4	35-55 04	
	174	ISZI	16 26 46	
	175	RCLI	36 46	
	176	RTN	24	
	177	*LBLe	21 16 15	
	178	GSBc	23 16 13	
	179	RCLB	36 12	
180	180	RCLE	36 15	
	181	1/X	52	
	182	Y^X	31	
	183	RCLD	36 14	
	184	Y^X	31	
	185	LN	32	
	186	X⇄Y	-41	
	187	-	-45	
	188	RCL3	36 03	
	189	÷	-24	
190	190	PRTX	-14	
	191	RTN	24	
	192	*LBLA	21 11	
	193	1	01	
	194	GSBC	23 13	
	195	RTN	24	
	196	*LBLB	21 12	
	197	1	01	
	198	GSBD	23 14	
	199	RTN	24	
200				
210				
220				

LABELS

A L_t, t →	B L_t, t, n →	C W_t, t →	D W_t, t, n →	E → r^2, K, t_0, (L)
a initialize (L)	b initialize (W)	c used	d	e → r^2, K, t_0, (W)
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Description

Program Title Von Bertalanffy Plot

Name Daniel Pauly **Date** August, 1980

Address ICLARM, MCC P.O. Box 1601
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. The generalized Von Bertalanffy Growth Formula has for length the form

$$L_t = L_{(\infty)}\left(1 - e^{-KD(t-t_0)}\right)^{1/D} \quad \ldots 1)$$

and for weight the form

$$W_t = W_{(\infty)}\left(1 - e^{-KD\frac{3}{b}(t-t_0)}\right)^{b/D} \quad \ldots 2)$$

where b is the exponent of the length–weight relationship. Equation (1) can be rewritten as

$$\ln\left(1 - \left(\frac{L_t}{L_\infty}\right)^D\right) = KDt_0 - KDt \quad \ldots 3)$$

which has the form of a linear regression, where $\ln\left(1-\left(\frac{L_t}{L_\infty}\right)^D\right) = y$, $t = x$ and $KDt_0 = a$. Thus, given a preliminary estimate of L_∞ (which is here coded $L(\infty)$) and a value of D, the values of K and t_0 can be easily estimated and the preliminary value of $L(\infty)$ improved iteratively, until a maximum value of r^2 is reached. The method is similar for weight growth, except that values of $W^{1/b}$ are used instead of the weights themselves.

Weighting factors other than n may be used; the inverse ($1/x$) of the standard error of the mean size in each age group is, for example, a very appropriate weighting factor.

Operating Limits and Warnings 1) The values of $L(\infty)$ and $W(\infty)$ must always be higher than the size-at-age data. 2) A value of D must always be entered (e.g. D = 1 in the case of the normal, or "special" von Bertalanffy Growth Formula). 3) The value of t_0 can be used only when the ages entered are absolute ages.

User Instructions

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	LENGTH GROWTH				
1	Enter first length-at-age value and D	L_t	f		L_t
		D	f	a	0.000
2	Enter remaining length-at-age values	L_t	A		i
3	Calculate r^2, K and L_∞		E		r^2
					K
					L_∞
	WEIGHT GROWTH				
1	Enter first weight-at-age value, D and b	W_t	f		W_t
		D	f		D
		b	f	b	0.000
2	Enter remaining weight-at-age values	W_t	B		i
3	Calculate r^2, K and W_∞		E		r^2
					K
					W_∞

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	CLRG	16-53	
005	STO0	35 14	
006	R↓	-31	
007	STOA	35 11	
008	CLX	-51	
009	RTN	24	
010	*LBLb	21 16 12	
011	CLRG	16-53	
012	P⇄S	16-51	
013	CLRG	16-53	
014	STOE	35 15	
015	R↓	-31	
016	STOD	35 14	
017	R↓	-31	
018	STOB	35 12	
019	CLX	-51	
020	RTN	24	
021	*LBLA	21 11	
022	RCLD	36 14	
023	Y^x	31	
024	STOB	35 12	
025	RCLA	36 11	
026	RCLD	36 14	
027	Y^x	31	
028	STOC	35 13	
029	RCLB	36 12	
030	RCLD	36 14	
031	1/X	52	
032	Y^x	31	
033	STOA	35 11	
034	RCLC	36 13	
035	RCLB	36 12	
036	Σ+	56	
037	RTN	24	
038	*LBLE	21 15	
039	P⇄S	16-51	
040	SPC	16-11	
041	RCL8	36 08	
042	RCL4	36 04	
043	RCL6	36 06	
044	×	-35	
045	RCL9	36 09	
046	÷	-24	
047	−	-45	
048	ENT↑	-21	
049	ENT↑	-21	
050	RCL4	36 04	
051	X^2	53	
052	RCL9	36 09	
053	÷	-24	
054	RCL5	36 05	
055	X⇄Y	-41	
056	−	-45	
057	÷	-24	
058	STO3	35 03	
059	×	-35	
060	RCL6	36 06	
061	X^2	53	
062	RCL9	36 09	
063	÷	-24	
064	CHS	-22	
065	RCL7	36 07	
066	+	-55	
067	÷	-24	
068	PRTX	-14	
069	√X	54	
070	RCL3	36 03	
071	X⇄Y	-41	
072	÷	-24	
073	STO3	35 03	
074	LN	32	
075	RCLD	36 14	
076	÷	-24	
077	PRTX	-14	
078	RCL6	36 06	
079	RCL4	36 04	
080	RCL3	36 03	
081	×	-35	
082	−	-45	
083	RCL9	36 09	
084	÷	-24	
085	RCL3	36 03	
086	CHS	-22	
087	1	01	
088	+	-55	
089	÷	-24	
090	P⇄S	16-51	
091	RCLD	36 14	
092	1/X	52	
093	Y^x	31	
094	F2?	16 23 02	
095	GTOC	22 13	
096	PRTX	-14	
097	RTN	24	
098	*LBLB	21 12	
099	RCLE	36 15	
100	1/X	52	
101	Y^x	31	
102	RCLD	36 14	
103	Y^x	31	
104	STOA	35 11	
105	RCLB	36 12	
106	RCLE	36 15	
107	1/X	52	
108	Y^x	31	
109	RCLD	36 14	
110	Y^x	31	
111	STOC	35 13	
112	RCLA	36 11	

REGISTERS

0	1	2	3	4	5	6	7	8	9

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
used	used	used	used	Σx	Σx^2	Σy	Σy^2	Σxy	i

A	B	C	D	E	I
L_1 / used	W_1 / used	used	D	b	

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCLD	36 14	
114	1/X	52	
115	Y^x	31	
116	RCLE	36 15	
117	Y^x	31	
118	STOB	35 12	
119	RCLC	36 13	
120	RCLA	36 11	
121	Σ+	56	
122	RTN	24	
123	*LBLe	21 16 15	
124	SF2	16 21 02	
125	GTOE	22 15	
126	*LBLC	21 13	
127	RCLE	36 15	
128	Y^x	31	
129	PRTX	-14	
130	RTN	24	

LABELS

A $L \rightarrow$	B $W \rightarrow$	C	D	E $\rightarrow r^2, K, L_\infty$
a $L_t, D \rightarrow$	b $W_t, D, b \rightarrow$	c	d	e $\rightarrow r^2, K, W_\infty$
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	Weight ?
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☐
1	☐	☐
2	☒	☒
3	☐	☐

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

Program Description

Program Title Ford - Walford Plot (GM)

Name Daniel Pauly **Date** August 1980

Address I C L A R M , MCC P.O. Box 1501
Makati , Metro Manila , Philippines

Program Description, Equations, Variables, etc. When size - at - age data at equal time interval (year , month , week) are available , 2 parameters of the VBGF can be estimated from

$$L_{t+1}^{D} = a + bL_t^{D} \quad \ldots \; 1)$$

where

$$L_\infty = \left(\frac{a}{(1-b)}\right)^{1/D} \quad \ldots \; 2)$$

and

$$K = \ln b / D \quad \ldots \; 3)$$

However , since both L_t and L_{t+1} are measured with the same error, a geometric mean , or type II regression is used . For this purpose the parameters a & b of an arithmetic mean or type I regression are first calculated, then used in conjunction with the correlation coefficient (r) estimated along with a & b to obtain the slope and intercept of the GM regression through the relationships

$$b' = b/r \quad \ldots \; 4)$$

and

$$a' = \bar{Y} - (b'\bar{X}) \quad \ldots \; 5)$$

where $\bar{Y}$ and $\bar{X}$ are the means of the L_{t+1} and L_t values. a', b' are parameters of the GM regression , respectively (Ricker, 1975).

Operating Limits and Warnings Size - at - age data must be equidistant , and there must be at least 2 pairs of L_{t+1}, L_t values . When weight - at - age data are used, the exponent (b) of the length / weight relationship must be entered (e.g. b=3).
A value of D must be entered ; when using the normal , or "special" VBGF , enter D = 1.

User Instructions

GULLAND AND HOLT PLOT — FB 5

1 | Initialize Length | Weight | Print | Exec. W / Exec. L | 2

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS	OUTPUT DATA/UNITS
1	Initialize, enter D (and enter b in case of	D	f a	
	weight growth)	b	STO E	0.000
2	For print option, press		C	0.000
	To clear print option, perform		CLF 0	0.000
3	For length growth, perform	L_1	↑	L_1
		L_2	↑	L_2
		Δt	A	i
4	To calculate r^2, K, and L_∞, press		E	r^2
				K
				L_∞
5	IF a set value of $L_{(\infty)}$ is to be used,			
	perform step 3, enter $L_{(\infty)}$ and perform	$L_{(\infty)}$	f c	K
6	For weight growth, perform	W_1	↑	W_1
		W_2	↑	W_2
		Δt	B	i
7	To calculate r^2, K and W_∞, press		f e	r^2
				K
				W_∞
8	IF a set value of $W_{(\infty)}$ is to be used,			
	perform step 6, Enter $W_{(\infty)}$, and perform	$W_{(\infty)}$	f b	K

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	CLRG	16-53	
005	STOD	35 14	
006	CLX	-51	
007	RTN	24	
008	*LBLA	21 11	
009	STO0	35 00	
010	R↓	-31	
011	RCLD	36 14	
012	Y^x	31	
013	STO1	35 01	
014	X⇄Y	-41	
015	RCLD	36 14	
016	Y^x	31	
017	STO2	35 02	
018	RCL1	36 01	
019	-	-45	
020	RCL0	36 00	
021	÷	-24	
022	RCL1	36 01	
023	RCL2	36 02	
024	+	-55	
025	2	02	
026	÷	-24	
027	F0?	16 23 00	
028	PRTX	-14	
029	X⇄Y	-41	
030	CHS	-22	
031	F0?	16 23 00	
032	PRTX	-14	
033	CHS	-22	
034	Σ+	56	
035	F0?	16 23 00	
036	PRTX	-14	
037	RTN	24	
038	*LBLE	21 15	
039	P⇄S	16-51	
040	RCL4	36 04	
041	RCL6	36 06	
042	x	-35	
043	RCL9	36 09	
044	÷	-24	
045	CHS	-22	
046	RCL8	36 08	
047	+	-55	
048	STO0	35 00	
049	RCL4	36 04	
050	X^2	53	
051	RCL9	36 09	
052	÷	-24	
053	CHS	-22	
054	RCL5	36 05	
055	+	-55	
056	STO2	35 02	
057	RCL6	36 06	
058	X^2	53	
059	RCL9	36 09	
060	÷	-24	
061	CHS	-22	
062	RCL7	36 07	
063	+	-55	
064	STO1	35 01	
065	RCL2	36 02	
066	x	-35	
067	STO3	35 03	
068	RCL0	36 00	
069	X^2	53	
070	RCL3	36 03	
071	÷	-24	
072	SPC	16-11	
073	PRTX	-14	
074	RCL0	36 00	
075	RCL1	36 01	
076	÷	-24	
077	STO3	35 03	
078	RCLD	36 14	
079	÷	-24	
080	PRTX	-14	
081	RCL6	36 06	
082	RCL9	36 09	
083	÷	-24	
084	RCL3	36 03	
085	x	-35	
086	CHS	-22	
087	RCL4	36 04	
088	RCL9	36 09	
089	÷	-24	
090	+	-55	
091	RCL3	36 03	
092	÷	-24	
093	CHS	-22	
094	P⇄S	16-51	
095	RCLD	36 14	
096	1/X	52	
097	Y^x	31	
098	F2?	16 23 02	
099	GTOd	22 16 14	
100	PRTX	-14	
101	RTN	24	
102	*LBLB	21 12	
103	STO0	35 00	
104	R↓	-31	
105	RCLE	36 15	
106	1/X	52	
107	Y^x	31	
108	RCLD	36 14	
109	Y^x	31	
110	STO1	35 01	
111	X⇄Y	-41	
112	RCLE	36 15	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used	used	used							

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
used	used	used	used	Σx	Σx^2	Σy	Σy^2	Σxy	i

A	B	C	D	E	I
a	$b = -k$		D	b	

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	1/X	52	
114	Y^X	31	
115	RCLD	36 14	
116	Y^X	31	
117	STO2	35 02	
118	RCL1	36 01	
119	-	-45	
120	RCL0	36 00	
121	÷	-24	
122	RCL1	36 01	
123	RCL2	36 02	
124	+	-55	
125	2	02	
126	÷	-24	
127	F0?	16 23 00	
128	PRTX	-14	
129	X⇄Y	-41	
130	CHS	-22	
131	F0?	16 23 00	
132	PRTX	-14	
133	CHS	-22	
134	Σ+	56	
135	F0?	16 23 00	
136	PRTX	-14	
137	RTN	24	
138	*LBLb	21 16 12	
139	RCLE	36 15	
140	1/X	52	
141	Y^X	31	
142	GTOc	22 16 13	
143	*LBLd	21 16 14	
144	RCLE	36 15	
145	Y^X	31	
146	PRTX	-14	
147	RTN	24	
148	*LBLc	21 16 13	
149	RCLD	36 14	
150	Y^X	31	
151	STOB	35 12	
152	$\bar{x}$	16 53	
153	X⇄Y	-41	
154	RCLB	36 12	
155	-	-45	
156	STOB	35 12	
157	$\bar{x}$	16 53	
158	RCLB	36 12	
159	÷	-24	
160	PRTX	-14	
161	RTN	24	
162	*LBLe	21 16 15	
163	SF2	16 21 02	
164	GTOE	22 15	
165	*LBLC	21 13	
166	SF0	16 21 00	
167	RTN	24	

LABELS

A	B	C	D	E
enter L's	enter W's	Print	$\rightarrow r^2, K, L_\infty$	
a initialize	b $W_{(\infty)} \rightarrow K$	c $L_{(\infty)} \rightarrow K$	d $\rightarrow r^2, K, W_\infty$	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	Print ?
1	
2	Weight ?
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☒	☒	DEG	☒	FIX	☒
1	☐	☐	GRAD	☐	SCI	☐
2	☒	☒	RAD	☐	ENG	☐
3	☐	☐			n = 3	

Program Description

Program Title Gulland and Holt Plot
Name Daniel Pauly **Date** Sept., 1980
Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Gulland and Holt (1959) demonstrated that estimates of K and L_∞ can be obtained by means of the relationship

$$\underbrace{\frac{L_2 - L_1}{t_2 - t_1}}_{Y} \approx a + b \underbrace{\frac{L_1 + L_2}{2}}_{X} \qquad \ldots \; 1)$$

where L_1 and L_2 are the length of fishes at time t_1 and t_2, respectively. When the period Δt $(= t_2 - t_1)$ is short relative to the total life span of the fish, the equation yields an estimate of K through

$$K \approx -b \qquad \ldots \; 2)$$

while L_∞ is estimated through

$$L_\infty \approx \frac{a}{b} \qquad \ldots \; 3)$$

These equations can be easily expanded to cases pertaining to growth in weight by using values of $W^{1/b}$ instead of the length values, and to the generalized VBGF by replacing the length values by L^D values. A set of value for the asymptotic size $(L_{(\infty)})$ may be used in which case a "forced" Gulland and Holt Plot results, i.e.:

$$K \approx \frac{\bar{Y}}{L_{(\infty)} - \bar{X}} \qquad \ldots \; 4)$$

which can be easily expanded to weight growth and to the generalized VBGF.

Operating Limits and Warnings 1) A value of D must be entered, i.e. $D = 1$, in the case of the special VBGF and $D < 1$ in the case of the generalized VBGF.
2) The original paper by Gulland and Holt (1959) should be consulted for a method (and table) to estimate the error involved in using the approximations in equations (2) and (3). When the print option is used with weights, the output are $\bar{W}^{1/b}$ and $\Delta W^{1/b}/\Delta t$ values.

User Instructions

1	MUNRO PLOT			FB 6	2
initialize enter L	initialize enter W	Print K's	delete W delete L	→ $\bar{K}$, C.V.	

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	GROWTH IN LENGTH				
1	Enter $L_{(\infty)}$, D and initialize	$L_{(\infty)}$	↑		$L_{(\infty)}$
		D	f	a	0.000
2	Enter data triplets	L_1	↑		L_1
		L_2	↑		L_2
		Δt	A		i
3	Remove erroneous data triplet	L_1	↑		L_1
		L_2	↑		L_2
		Δt	D		i − 1
4	Calculate mean value of K and its C.V.		E		$\bar{K}$
					C.V.
	GROWTH IN WEIGHT				
5	Enter $W_{(\infty)}$, D, b and initialize	$W_{(\infty)}$	↑		$W_{(\infty)}$
		D	↑		D
		b	f	b	0.000
6	Enter data triplets	W_1	↑		W_1
		W_2	↑		W_2
		Δt	B		i
7	Remove erroneous data triplet	W_1	↑		W_1
		W_2	↑		W_2
		Δt	f	d	i − 1
8	Calculate mean value of K and its C.V.		E		$\bar{K}$
					C.V.
	NOTES : The Δt should be expressed				
	in days. The K values are annual values.				
	For print option, press		STF	0	
	To clear print option, perform		CLF	0	

Program Listing

STEP	KEY ENTRY	KEY CODE
001	001 *LBLa	21 16 11
	002 CLRG	16-53
	003 P⇄S	16-51
	004 CLRG	16-53
	005 STOD	35 14
	006 y^x	31
	007 STOA	35 11
	008 CLX	-51
	009 RTN	24
010	010 *LBLA	21 11
	011 STOC	35 13
	012 R↓	-31
	013 RCLD	36 14
	014 y^x	31
	015 CHS	-22
	016 RCLA	36 11
	017 +	-55
	018 LN	32
	019 X⇄Y	-41
020	020 RCLD	36 14
	021 y^x	31
	022 CHS	-22
	023 RCLA	36 11
	024 +	-55
	025 LN	32
	026 X⇄Y	-41
	027 -	-45
	028 RCLC	36 13
	029 ÷	-24
030	030 3	03
	031 6	06
	032 5	05
	033 ×	-35
	034 F0?	16 23 00
	035 PRTX	-14
	036 F2?	16 23 02
	037 RTN	24
	038 Σ+	56
	039 RTN	24
040	040 *LBLE	21 15
	041 SPC	16-11
	042 $\bar{x}$	16 53
	043 PRTX	-14
	044 STO0	35 00
	045 s	16 54
	046 RCL0	36 00
	047 ÷	-24
	048 PRTX	-14
	049 RTN	24
050	050 R/S	51
	051 *LBLb	21 16 12
	052 CLRG	16-53
	053 P⇄S	16-51
	054 CLRG	16-53
	055 STOE	35 15
	056 X⇄Y	-41
	057 STOD	35 14
	058 X⇄Y	-41
	059 ÷	-24
060	060 y^x	31
	061 STOB	35 12
	062 CLX	-51
	063 RTN	24
	064 *LBLB	21 12
	065 STOC	35 13
	066 R↓	-31
	067 RCLD	36 14
	068 RCLE	36 15
	069 ÷	-24
070	070 y^x	31
	071 CHS	-22
	072 RCLB	36 12
	073 +	-55
	074 LN	32
	075 X⇄Y	-41
	076 RCLD	36 14
	077 RCLE	36 15
	078 ÷	-24
	079 y^x	31
080	080 CHS	-22
	081 RCLB	36 12
	082 +	-55
	083 LN	32
	084 X⇄Y	-41
	085 -	-45
	086 RCLC	36 13
	087 ÷	-24
	088 3	03
	089 6	06
090	090 5	05
	091 ×	-35
	092 F0?	16 23 00
	093 PRTX	-14
	094 F2?	16 23 02
	095 RTN	24
	096 Σ+	56
	097 RTN	24
	098 R/S	51
	099 *LBLD	21 14
100	100 SF2	16 21 02
	101 GSBA	23 11
	102 Σ-	16 56
	103 RTN	24
	104 *LBLd	21 16 14
	105 SF2	16 21 02
	106 GSBB	23 12
	107 Σ-	16 56
	108 RTN	24
110		

LABELS					FLAGS
A enter L	B enter W	C print	D corr. L	E → $\bar{R}$, c.v.	0 print option
a initialize L	b initialize W	c	d corr. W	e	1
0	1	2	3	4	2 corrections
5	6	7	8	9	3

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☒	☒	DEG	☒	FIX	☒
1	☐	☐	GRAD	☐	SCI	☐
2	☒	☒	RAD	☐	ENG	☐
3	☐	☐			n= 3	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used									

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
				Σx	used	used	used	used	i

A	B	C	D	E	I
$L^{D}_{(\infty)}$	$W^{\%}_{(\infty)}$	used	D	b	

Program Description

Program Title Munro Plot
Name Daniel Pauly **Date** Sept., 1980
Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc.

Munro (1982) suggested that

$$\log_e (L_\infty - L_a) - \log_e (L_\infty - L_b) = K(b - a) \quad \ldots 1)$$

which becomes, in terms of the generalized VBGF and using a different notation

$$\ln (L_{(\infty)}^D - L_1^D) - \ln (L_{(\infty)}^D - L_2^D) = KD(t_2 - t_1) \quad \ldots 2)$$

Given a value of D and a first value of $L_{(\infty)}$, equation (2) can be used to obtain single values of K (one for each triplet of L_1, L_2 and Δt ($= t_2 - t_1$) values). The calculated values of K have the property of being close to each other when an optimal value of $L_{(\infty)}$ has been selected, and to differ widely from others when the selected value of $L_{(\infty)}$ is too high or too low. Thus, by calculating, for a given value of $L_{(\infty)}$ the coefficient of variation of the K-values (C.V. of $\bar{K}$ = s.d. of K-values / $\bar{K}$), one may select by trial and error the value of $L_{(\infty)}$ which produces the lowest C.V. in the K-values and which thus corresponds to L_∞ (= best $L_{(\infty)}$). The method resembles the "forced" Gulland and Holt Plot in that data at unequal time interval can be used. It has, however, the advantage of providing exact solutions (= K-values) irrespective of the value of Δt.

Operating Limits and Warnings

1) $L_{(\infty)}$ must be higher than any L_2 value.
2) Δt must be expressed in days.
3) The K-values are put on an annual basis automatically.
4) A value of D must be entered; set D = 1 when using the normal or "special" VBGF.

User Instructions

FB 7a

FITTING SEASONALLY OSCILLATING GROWTH DATA I

initialize input

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Read sides 1 and 2 of card I and initialize	10	10	↑	10.00
		5	5	y^x	100000.00
			f	a	100000.00
2	Enter data	t	↑		t
		L_t^D	↑		L_t^D
		$L_{(\infty)}^D$	A		i
3	Read sides 1 and 2 of card II, and go to Users Instructions, Part II.				

NOTES :

1) Input routine takes about 15 seconds per data triplet.

2) $L_{(\infty)}^D$ is entered with each set of length-at-age values.

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE
001	*LBLa	21 16 11
002	CLRG	16-53
003	STO0	35 00
004	STO4	35 04
005	STO7	35 07
006	STO9	35 09
007	P⇄S	16-51
008	CLRG	16-53
009	RAD	16-22
010	RTN	24
011	*LBLA	21 11
012	STOD	35 14
013	÷	-24
014	CHS	-22
015	1	01
016	+	-55
017	LN	32
018	STOD	35 14
019	X⇄Y	-41
020	STOC	35 13
021	2	02
022	×	-35
023	Pi	16-24
024	×	-35
025	SIN	41
026	RCLC	36 13
027	X⇄Y	-41
028	RCLC	36 13
029	2	02
030	×	-35
031	Pi	16-24
032	×	-35
033	COS	42
034	RCLD	36 14
035	ST+8	35-55 08
036	X²	53
037	ST+9	35-55 09
038	R↓	-31
039	GSBD	23 14
040	-	-45
041	STOE	35 15
042	P⇄S	16-51
043	RCL3	36 03
044	RCLC	36 13
045	×	-35
046	RCL2	36 02
047	RCLB	36 12
048	×	-35
049	+	-55
050	RCL1	36 01
051	RCLA	36 11
052	×	-35
053	+	-55
054	RCL0	36 00
055	+	-55
056	RCL6	36 06
057	RCLC	36 13
058	×	-35
059	RCL5	36 05
060	RCLB	36 12
061	×	-35
062	+	-55
063	RCL4	36 04
064	RCLA	36 11
065	×	-35
066	+	-55
067	RCL1	36 01
068	+	-55
069	P⇄S	16-51
070	STO5	35 05
071	RCLA	36 11
072	×	-35
073	X⇄Y	-41
074	STO4	35 04
075	+	-55
076	STOD	35 14
077	P⇄S	16-51
078	RCL8	36 08
079	RCLC	36 13
080	×	-35
081	RCL7	36 07
082	RCLB	36 12
083	×	-35
084	+	-55
085	RCL5	36 05
086	RCLA	36 11
087	×	-35
088	+	-55
089	RCL2	36 02
090	+	-55
091	RCL9	36 09
092	RCLC	36 13
093	×	-35
094	RCL8	36 08
095	RCLB	36 12
096	×	-35
097	+	-55
098	RCL6	36 06
099	RCLA	36 11
100	×	-35
101	+	-55
102	RCL3	36 03
103	+	-55
104	P⇄S	16-51
105	STO7	35 07
106	RCLC	36 13
107	×	-35
108	X⇄Y	-41
109	STO6	35 06
110	RCLB	36 12
111	×	-35
112	+	-55

COMMENTS (steps 012–035): These steps (and also step 009) may be deleted and the program may then be used for multiple linear regression analysis. 24 steps are available for linearizing transformations (e.g. taking log).

REGISTERS

0	1	2	3	4	5	6	7	8	9
a	b_1	b_2	b_3	used	used	used	used	used	used

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
c_0	c_1	c_2	c_3	c_4	c_5	c_6	c_7	c_8	c_9

A	B	C	D	E	I
used	used	used	used	used	counter

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCL0	36 14	
114	+	-55	
115	1	01	
116	+	-55	
117	1/X	52	
118	STOD	35 14	
119	RCLE	36 15	
120	×	-35	
121	STOE	35 15	
122	RCL7	36 07	
123	×	-35	
124	ST+3	35-55 03	
125	RCLE	36 15	
126	RCL6	36 06	
127	×	-35	
128	ST+2	35-55 02	
129	RCLE	36 15	
130	RCL5	36 05	
131	×	-35	
132	ST+1	35-55 01	
133	RCLE	36 15	
134	RCL4	36 04	
135	×	-35	
136	ST+0	35-55 00	
137	RCLD	36 14	
138	RCL4	36 04	
139	×	-35	
140	STOE	35 15	
141	RCL4	36 04	
142	×	-35	
143	RCLE	36 15	
144	RCL5	36 05	
145	×	-35	
146	RCLE	36 15	
147	RCL6	36 06	
148	×	-35	
149	RCL7	36 07	
150	P⇄S	16-51	
151	R↓	-31	
152	ST-2	35-45 02	
153	R↓	-31	
154	ST-1	35-45 01	
155	R↓	-31	
156	ST-0	35-45 00	
157	R↓	-31	
158	RCLE	36 15	
159	×	-35	
160	ST-3	35-45 03	
161	P⇄S	16-51	
162	RCLD	36 14	
163	RCL5	36 05	
164	×	-35	
165	STOE	35 15	
166	RCL5	36 05	
167	×	-35	
168	RCLE	36 15	
169	RCL6	36 06	
170	×	-35	
171	RCLE	36 15	
172	RCL7	36 07	
173	×	-35	
174	P⇄S	16-51	
175	ST-6	35-45 06	
176	R↓	-31	
177	ST-5	35-45 05	
178	R↓	-31	
179	ST-4	35-45 04	
180	P⇄S	16-51	
181	RCLD	36 14	
182	RCL6	36 06	
183	×	-35	
184	STOE	35 15	
185	RCL6	36 06	
186	×	-35	
187	RCLE	36 15	
188	RCL7	36 07	
189	×	-35	
190	RCLD	36 14	
191	RCL7	36 07	
192	X²	53	
193	×	-35	
194	P⇄S	16-51	
195	ST-9	35-45 09	
196	R↓	-31	
197	ST-8	35-45 08	
198	R↓	-31	
199	ST-7	35-45 07	
200	P⇄S	16-51	
201	ISZI	16 26 46	
202	RCLI	36 46	
203	RTN	24	
204	*LBLD	21 14	
205	STOC	35 13	
206	R↓	-31	
207	STOB	35 12	
208	R↓	-31	
209	STOA	35 11	
210	RCLD	36 14	
211	RCL0	36 00	
212	RCL1	36 01	
213	RCLA	36 11	
214	×	-35	
215	+	-55	
216	RCL2	36 02	
217	RCLB	36 12	
218	×	-35	
219	+	-55	
220	RCL3	36 03	
221	RCLC	36 13	
222	×	-35	
223	+	-55	
224	RTN	24	

LABELS

A enter data	B	C	D used	E
a initialize	b	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☐	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☒	ENG	☐
3	☐	☒			n = 2	

Program Description I

Program Title Fitting seasonally oscillating Growth data I

Name D. Pauly and G. Gaschütz Date July, 1979

*Address ICLARM, MCC P.O. Box 1501

Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. 1) Given a preliminary value of $L_{(\infty)}$, a value of D and length-at-age data, the program (Part I and II) estimates the values of the parameters K, t_0, t_s and C of the equation

$$L_t^D = L_\infty^D \left(1 - e^{-KD(t-t_0) + C \cdot \frac{KD}{2\pi} \cdot \sin 2\pi \cdot (t-t_s)}\right) \quad \ldots (1)$$

which is a version of the generalized VBGF suitable to describe seasonally oscillating length growth of animals, e.g. of fishes.

2) The parameter estimation is based on multiple regression analysis; the calculation of the regression coefficients is based on the program "Multiple Regression Analysis" No. 50584, HP 67/97 Users' Library (Europe) by Tapio Westerlund. By deleting step 009, and steps 012 to 034, the present program can also be used for solving multiple regression problems involving 3 independent variables (see Program Listing). In such cases, the second part of this program may be used for estimating R^2. (The regression coefficients (a, b_1, b_2, and b_3) are stored in STO 0 to STO 3).

3) The large number (10^5) used when initializing may be replaced by any large number of similar magnitude.

4) The program accepts only the year as time (age) unit. The appropriate conversions may be performed when entering the data.

Operating Limits and Warnings 1) $L_{(\infty)}^D - L_t^D$ must always be a positive number.

2) The values of time (age) must always be expressed in years or fractions thereof.

User Instructions

FB 7b

1 FITTING SEASONALLY OSCILLATING GROWTH DATA II 2

→ R^2 | → L_t^D | → K, t_o, t_s, C

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS	OUTPUT DATA/UNITS
3	You have already read in sides 1 and 2 of this			
	program card, if not, do it now.			0.000
4	Calculate R^2		A	R^2
5	Calculate KD, t_o, t_s and C		E	KD
				t_o
				t_s
				C
6	To estimate the length corresponding to a given			
	t value, perform	$L^D_{(\infty)}$	STO A	$L^D_{(\infty)}$
7a	Then calculate value of L_t	t	C	L_t^D
7b	Step 7 may be repeated at will, e.g. in order to	D	1/x y^x	L_t
	draw a seasonally oscillating growth curve.			
8	If L_t values are to be calculated without the			
	parameters having been estimated internally,			
	perform RAD, then	$L^D_{(\infty)}$	STO A	$L^D_{(\infty)}$
		KD	STO 4	KD
		t_o	STO 5	t_o
		t_s	STO 6	t_s
		C	STO 7	C
	and go to step 7.			

NOTES :

1) When C output is negative, transform C and t_s according to instructions in Program Description II.

2) Setting C = 0 in step 8 estimates values of L_t for the unseasonalized VBGF.

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS	STEP	KEY ENTRY	KEY CODE	COMMENTS
001	001 *LBLA	21 11			057 RCLA	36 11	
	002 3	03			058 x	-35	
	003 STO4	35 04			059 RCLD	36 14	
	004 P⇄S	16-51		060	060 RCL5	36 05	
	005 RCL7	36 07			061 x	-35	
	006 RCL4	36 04			062 RCLE	36 15	
	007 x	-35			063 -	-45	
	008 RCL5	36 05			064 RCLB	36 12	
	009 RCL5	36 05			065 x	-35	
010	010 x	-35			066 -	-45	
	011 -	-45			067 RCLC	36 13	
	012 STOA	35 11			068 RCLA	36 11	
	013 RCL8	36 08			069 x	-35	
	014 RCL4	36 04		070	070 RCLB	36 12	
	015 x	-35			071 RCLB	36 12	
	016 RCL6	36 06			072 x	-35	
	017 RCL5	36 05			073 -	-45	
	018 x	-35			074 ÷	-24	
	019 -	-45			075 P⇄S	16-51	
020	020 STOB	35 12			076 STO5	35 05	
	021 RCL9	36 09			077 P⇄S	16-51	
	022 RCL4	36 04			078 RCLD	36 14	
	023 x	-35			079 RCL5	36 05	
	024 RCL6	36 06		080	080 x	-35	
	025 RCL6	36 06			081 RCLE	36 15	
	026 x	-35			082 -	-45	
	027 -	-45			083 X⇄Y	-41	
	028 STOC	35 13			084 RCLB	36 12	
	029 RCL4	36 04			085 x	-35	
030	030 RCL2	36 02			086 -	-45	
	031 RCL1	36 01			087 RCLA	36 11	
	032 P⇄S	16-51			088 ÷	-24	
	033 RCL8	36 08			089 P⇄S	16-51	
	034 x	-35		090	090 STO6	35 06	
	035 RCL1	36 01			091 RCL5	36 05	
	036 -	-45			092 P⇄S	16-51	
	037 STOD	35 14			093 RCL6	36 06	
	038 R↓	-31			094 x	-35	
	039 RCL8	36 08			095 X⇄Y	-41	
040	040 x	-35			096 RCL5	36 05	
	041 RCL2	36 02			097 x	-35	
	042 -	-45			098 +	-55	
	043 x	-35			099 RCLD	36 14	
	044 STOE	35 15		100	100 +	-55	
	045 RCL3	36 03			101 RCL4	36 04	
	046 RCL8	36 08			102 ÷	-24	
	047 P⇄S	16-51			103 CHS	-22	
	048 RCL3	36 03			104 P⇄S	16-51	
	049 x	-35			105 STO7	35 07	
050	050 -	-45			106 RCLI	36 46	
	051 RCL4	36 04			107 RCL4	36 04	
	052 x	-35			108 -	-45	
	053 RCLD	36 14			109 1	01	
	054 RCL6	36 06		110	110 -	-45	
	055 x	-35			111 STOA	35 11	
	056 +	-55			112 RCLD	36 00	

REGISTERS

0	1	2	3	4	5	6	7	8	9
a	b_1	b_2	b_3	used/K	used/t_0	used/t_s	used/c	used	used
S0	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**
C_0	C_1	C_2	C_3	C_4	C_5	C_6	C_7	C_8	C_9

A	B	C	D	E	I
used	used	used	used	used	n

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCL8	36 08	
114	x	-35	
115	RCL7	36 07	
116	RCL1	36 01	
117	x	-35	
118	+	-55	
119	RCL6	36 06	
120	RCL2	36 02	
121	x	-35	
122	+	-55	
123	RCL5	36 05	
124	RCL3	36 03	
125	x	-35	
126	+	-55	
127	RCL8	36 08	
128	X^2	53	
129	RCLI	36 46	
130	÷	-24	
131	STOE	35 15	
132	-	-45	
133	STOD	35 14	
134	RCL9	36 09	
135	RCLE	36 15	
136	-	-45	
137	STOE	35 15	
138	÷	-24	
139	STOB	35 12	
140	RCLE	36 15	
141	RCLD	36 14	
142	-	-45	
143	RCLA	36 11	
144	÷	-24	
145	STOC	35 13	
146	RCLD	36 14	
147	RCL4	36 04	
148	÷	-24	
149	RCLC	36 13	
150	÷	-24	
151	STOD	35 14	
152	RCLB	36 12	
153	RTN	24	
154	*LBLE	21 15	
155	RAD	16-22	
156	RCL1	36 01	
157	CHS	-22	
158	PRTX	-14	
159	STO4	35 04	
160	CHS	-22	
161	RCL0	36 00	
162	X⇄Y	-41	
163	÷	-24	
164	CHS	-22	
165	STO5	35 05	
166	PRTX	-14	
167	RCL3	36 03	
168	RCL2	36 02	
169	÷	-24	
170	CHS	-22	
171	TAN^{-1}	16 43	
172	Pi	16-24	
173	÷	-24	
174	2	02	
175	÷	-24	
176	PRTX	-14	
177	STO6	35 06	
178	GSBa	23 16 11	
179	SIN	41	
180	RCL4	36 04	
181	x	-35	
182	RCL3	36 03	
183	GSBa	23 16 11	
184	÷	-24	
185	1/X	52	
186	PRTX	-14	
187	STO7	35 07	
188	RTN	24	
189	*LBLC	21 13	
190	STOB	35 12	
191	RCL6	36 06	
192	-	-45	
193	GSBa	23 16 11	
194	SIN	41	
195	RCL7	36 07	
196	x	-35	
197	Pi	16-24	
198	÷	-24	
199	2	02	
200	÷	-24	
201	RCL4	36 04	
202	x	-35	
203	RCLB	36 12	
204	RCL5	36 05	
205	-	-45	
206	RCL4	36 04	
207	x	-35	
208	+	-55	
209	CHS	-22	
210	e^x	33	
211	CHS	-22	
212	1	01	
213	+	-55	
214	RCLA	36 11	
215	x	-35	
216	RTN	24	
217	*LBLa	21 16 11	
218	Pi	16-24	
219	x	-35	
220	2	02	
221	x	-35	
222	RTN	24	

LABELS

A → R^2	B	C → L_t	D	E → K, t_p, t_s, C
a → π × 2 ×	b → π ÷ 2 ÷	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☐	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☒	ENG	☐
3	☐	☒			n = 3	

Program Description II

Program Title Fitting Seasonally Oscillating Growth Data II

Name D. Pauly and G. Gaschütz **Date** July, 1979
***Address** ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. (See also Program Description I)

5) The routine for the estimation of R^2 is taken from "Statistics for Multiple Regression Analysis" No. 50585, HP 67/97 Users' Library (Europe) by Tapio Westerlund.

6) Due to size limitation, the program may not always produce positive values of C. If a negative value of C is encountered, the following transformations should be applied

a) change −C to +C

and b) add 0.5 to the value of t_s.

Although the two sets of C and t_s values (original and transformed) are equivalent in their effects on a growth curve, the use of the transformed values agrees better with the definition of C given in the text.

7) Program No. 50585 (see 5) above) may be used subsequently to this program to obtain additional statistics for the multiple linear regression (e.g., to obtain standard errors and F-values for the regression coefficients).

Operating Limits and Warnings 1) The values of time (age) must always be expressed in years or fractions thereof.

2) Do not forget, when applicable, the transformations recommended in 6).

3) Steps 6, 7 and 8 must follow step 5.

User Instructions

FB8

1 SEASONAL GROWTH FROM TAGGING DATA 2

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter D and initialize	D	f	a	0.000
2	Enter data	L_1	↑		L_1
		L_2	↑		L_2
		Δt	↑		Δt
		T (°C)	A		i
3	Estimate a, b_1, b_2 and R^2		E		R^2
					a
					b_1
					b_2
4	To estimate value of L_∞ and K, enter $\bar{T}$ *	$\bar{T}$	C		L_∞
	N.B. K will be expressed in the units				K
	of time selected for Δt.				
5	To estimate value of C, enter T_s, T_W and $\bar{T}$ *	T_s	↑		
		T_W	↑		
		$\bar{T}$	f	c	C
6	To estimate value of K based on a forcing				
	value of $L_{(\infty)}$, do	$L_{(\infty)}$	↑		
		$\bar{T}$	f	e	K

NOTES:

* T_s : highest mean monthly temperature in a year

T_W : lowest mean monthly temperature in a year

$\bar{T}$: mean annual temperature

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	STO0	35 00	
005	P⇄S	16-51	
006	CLX	-51	
007	RTN	24	
008	*LBLA	21 11	
009	P⇄S	16-51	
010	STO4	35 04	
011	R↓	-31	
012	STO3	35 03	
013	R↓	-31	
014	RCL0	36 00	
015	Y^x	31	
016	STO2	35 02	
017	R↓	-31	
018	RCL0	36 00	
019	Y^x	31	
020	STO1	35 01	
021	RCL2	36 02	
022	+	-55	
023	2	02	
024	÷	-24	
025	RCL4	36 04	
026	RCL2	36 02	
027	RCL1	36 01	
028	-	-45	
029	RCL3	36 03	
030	÷	-24	
031	P⇄S	16-51	
032	STOC	35 13	
033	R↓	-31	
034	STOB	35 12	
035	R↓	-31	
036	STOA	35 11	
037	7	07	
038	STOI	35 46	
039	R↓	-31	
040	GSB1	23 01	
041	8	08	
042	STOI	35 46	
043	RCLB	36 12	
044	GSB1	23 01	
045	9	09	
046	STOI	35 46	
047	RCLC	36 13	
048	GSB1	23 01	
049	RCLA	36 11	
050	RCLB	36 12	
051	x	-35	
052	ST+1	35-55 01	
053	RCLA	36 11	
054	RCLC	36 13	
055	x	-35	
056	ST+2	35-55 02	
057	RCLB	36 12	
058	RCLC	36 13	
059	x	-35	
060	ST+3	35-55 03	
061	1	01	
062	ST+0	35-55 00	
063	RCL0	36 00	
064	RTN	24	
065	*LBL1	21 01	
066	ST+i	35-55 45	
067	RCLI	36 46	
068	3	03	
069	-	-45	
070	STOI	35 46	
071	R↓	-31	
072	X²	53	
073	ST+i	35-55 45	
074	RTN	24	
075	*LBLE	21 15	
076	RCL0	36 00	
077	RCL4	36 04	
078	x	-35	
079	RCL7	36 07	
080	X²	53	
081	-	-45	
082	STOD	35 14	
083	RCL0	36 00	
084	RCL3	36 03	
085	x	-35	
086	RCL8	36 08	
087	RCL9	36 09	
088	x	-35	
089	-	-45	
090	x	-35	
091	STOC	35 13	
092	RCL0	36 00	
093	RCL1	36 01	
094	x	-35	
095	RCL7	36 07	
096	RCL8	36 08	
097	x	-35	
098	-	-45	
099	STOA	35 11	
100	RCL0	36 00	
101	RCL2	36 02	
102	x	-35	
103	RCL7	36 07	
104	RCL9	36 09	
105	x	-35	
106	-	-45	
107	STOB	35 12	
108	x	-35	
109	RCLC	36 13	
110	X⇄Y	-41	
111	-	-45	
112	RCLD	36 14	

REGISTERS

0	1	2	3	4	5	6	7	8	9
n	Σxy	Σx_2	Σy_2	Σx^2	Σy^2	Σz^2	Σx	Σy	Σz

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
D	L_1^D	L_2^D	Δt	$T(°C)$					

A	B	C	D	E	I
a	b	c	used	used	used

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCL0	36 00	
114	RCL5	36 05	
115	×	-35	
116	RCL8	36 08	
117	X^2	53	
118	-	-45	
119	×	-35	
120	RCLA	36 11	
121	X^2	53	
122	-	-45	
123	÷	-24	
124	STOC	35 13	
125	RCLB	36 12	
126	RCLA	36 11	
127	RCLC	36 13	
128	×	-35	
129	-	-45	
130	RCLD	36 14	
131	÷	-24	
132	STOB	35 12	
133	RCL9	36 09	
134	RCLC	36 13	
135	RCL8	36 08	
136	×	-35	
137	-	-45	
138	RCLB	36 12	
139	RCL7	36 07	
140	×	-35	
141	-	-45	
142	RCL0	36 00	
143	÷	-24	
144	STOA	35 11	
145	RCL9	36 09	
146	×	-35	
147	RCLB	36 12	
148	RCL2	36 02	
149	×	-35	
150	+	-55	
151	RCLC	36 13	
152	RCL3	36 03	
153	×	-35	
154	+	-55	
155	RCL9	36 09	
156	X^2	53	
157	RCL0	36 00	
158	÷	-24	
159	-	-45	
160	RCL6	36 06	
161	RCL9	36 09	
162	X^2	53	
163	RCL0	36 00	
164	÷	-24	
165	-	-45	
166	÷	-24	
167	PRTX	-14	
168	RCLA	36 11	
169	PRTX	-14	
170	RCLB	36 12	
171	PRTX	-14	
172	RCLC	36 13	
173	PRTX	-14	
174	RTN	24	
175	*LBLC	21 13	
176	RCLC	36 13	
177	×	-35	
178	RCLA	36 11	
179	+	-55	
180	RCLB	36 12	
181	÷	-24	
182	P⇄S	16-51	
183	RCL0	36 00	
184	1/X	52	
185	Y^x	31	
186	CHS	-22	
187	PRTX	-14	
188	RCLB	36 12	
189	RCL0	36 00	
190	÷	-24	
191	CHS	-22	
192	P⇄S	16-51	
193	RTN	24	
194	*LBLc	21 16 13	
195	STOI	35 46	
196	R↓	-31	
197	-	-45	
198	RCLC	36 13	
199	×	-35	
200	RCLI	36 46	
201	RCLC	36 13	
202	×	-35	
203	RCLA	36 11	
204	+	-55	
205	2	02	
206	×	-35	
207	÷	-24	
208	PRTX	-14	
209	RTN	24	
210	*LBLe	21 16 15	
211	RCLC	36 13	
212	×	-35	
213	RCLA	36 11	
214	+	-55	
215	X⇄Y	-41	
216	÷	-24	
217	P⇄S	16-51	
218	RCL0	36 00	
219	P⇄S	16-51	
220	1/X	52	
221	Y^x	31	
222	RTN	24	

LABELS

A	B	C	D	E
→ enter data		$\bar{T} \to L_0, K$		$\to R^2, a, b, c$
a: initialize	b	c: $T_s, \bar{T}, T_N \to C$	d	e: $L_{(o)}, \bar{T} \to K$
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Description

Program Title Seasonal Growth from Tagging Data

Name Daniel Pauly **Date** January, 1987

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. A multiple regression of the form

$$Y = a + b_1 X_1 + b_2 X_2 \qquad \ldots 1)$$

is used to estimate the parameters L_∞ and K of the VBGF. The following definitions apply

$$Y = L_2^D - L_1^D / t_2 - t_1 \quad \text{and} \quad X_1 = L_1^D + L_2^D / 2$$

, where L_1 and L_2 are the length at tagging and at recapture, respectively, corresponding to the times t_1 and t_2, while X_2 is the mean water temperature when a given fish was at large (T). Thus, given a series of L_1 and L_2 data, of the times at large and their corresponding temperatures, the growth parameters can be estimated from

$$L_\infty = \left(\frac{a + (b_2 \bar{T})}{-b_1}\right)^{1/D} \qquad \ldots 2)$$

and

$$K = -b/D \qquad \ldots 3)$$

and

$$C = (b_2 (T_S - T_W)) / 2 (a + (b_2 \bar{T})) \qquad \ldots 4)$$

where T_S is the highest (summer) and T_W the lowest (winter) mean monthly temperatures in the water body in question, while $\bar{T}$ is the mean annual temperature.

In analogy to the "forced Gulland and Holt Plot" (see Program FB5), forcing value of L_∞) can be used in conjunction with equation 2), which allows for K to be estimated even when the fish used represented a narrow range of lengths only.

Operating Limits and Warnings 1) a value of D must be entered, i.e., $D = 1$ when the special VBGF is used, and $D < 1$ when the generalized VBGF is used.

2) the values of L_∞, K and C obtained by this method are approximate and should be confirmed whenever possible, using other methods.

User Instructions

1 GENERALIZED VBGF AND DERIVATIVES : SOLUTIONS FB92

$\to L_i$ / $t \to L_t$	$\to W_i$ / $t \to W_t$	$W_t \to t$ / $L_t \to t$	$W_t \to d_w/d_t$ / $L_t \to d_l/d_t$	$W_t, t \to t_0$ / $L_t, t \to t_0$

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter, in any order, the required constants				
		L_∞	STO	A	L_∞
		W_∞	STO	B	W_∞
		K	STO	1	K
		t_0	STO	0	t_0
		D	STO	D	D
		b^*	STO	E	b
2	Find solutions :				
2.0	length at a given age	t	A		L_t
2.1	weight at a given age	t	B		W_t
2.2	age at a given length	L_t	C		t
2.3	age at a given weight	W_t	f	c	t
2.4	t_0 for a given length and age	L_t	↑		L_t
		t	E		t_0
2.5	t_0 for a given weight and age	W_t	↑		W_t
		t	f	e	t_0
2.6	length at inflection point of curve **		f	a	L_i
2.7	weight at inflection point of curve		f	b	W_i
2.8	growth rate at a given length	L_t	D		d_l/d_t
2.9	growth rate at a given weight	W_t	f	d	d_w/d_t
3	Estimate d and D from W_{max} (in grams).				
	Enter W_{max}	W_{max}	GTO	7	
			R/S		d
					D

NOTES:

* Exponent of length-weight relationship.

** Step 2.6 can be performed only when $D < 1$.

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBL2	21 02	
002	RCLD	36 14	
003	1/X	52	
004	Y^x	31	
005	RTN	24	
006	*LBL3	21 03	
007	RCLD	36 14	
008	RCLE	36 15	
009	÷	-24	
010	Y^x	31	
011	RTN	24	
012	*LBL4	21 04	
013	RCL1	36 01	
014	RCLD	36 14	
015	×	-35	
016	×	-35	
017	RTN	24	
018	*LBL5	21 05	
019	3	03	
020	RCLE	36 15	
021	÷	-24	
022	×	-35	
023	RTN	24	
024	*LBL6	21 06	
025	RCL1	36 01	
026	RCLD	36 14	
027	×	-35	
028	×	-35	
029	CHS	-22	
030	e^x	33	
031	RTN	24	
032	*LBLA	21 11	
033	RCL0	36 00	
034	-	-45	
035	GSB6	23 06	
036	CHS	-22	
037	1	01	
038	+	-55	
039	GSB2	23 02	
040	RCLA	36 11	
041	×	-35	
042	RTN	24	
043	*LBLB	21 12	
044	RCL0	36 00	
045	-	-45	
046	GSB5	23 05	
047	GSB6	23 06	
048	CHS	-22	
049	1	01	
050	+	-55	
051	RCLE	36 15	
052	RCLD	36 14	
053	÷	-24	
054	Y^x	31	
055	RCLB	36 12	
056	×	-35	
057	RTN	24	
058	*LBLC	21 13	
059	GSB1	23 01	
060	RCL0	36 00	
061	+	-55	
062	RTN	24	
063	*LBL1	21 01	
064	RCLA	36 11	
065	÷	-24	
066	RCLD	36 14	
067	Y^x	31	
068	CHS	-22	
069	1	01	
070	+	-55	
071	LN	32	
072	CHS	-22	
073	RCL1	36 01	
074	RCLD	36 14	
075	×	-35	
076	÷	-24	
077	RTN	24	
078	*LBLc	21 16 13	
079	GSB0	23 00	
080	RCL0	36 00	
081	+	-55	
082	RTN	24	
083	*LBL0	21 00	
084	RCLB	36 12	
085	÷	-24	
086	RCLD	36 14	
087	RCLE	36 15	
088	÷	-24	
089	Y^x	31	
090	CHS	-22	
091	1	01	
092	+	-55	
093	LN	32	
094	CHS	-22	
095	RCL1	36 01	
096	GSB5	23 05	
097	RCLD	36 14	
098	×	-35	
099	÷	-24	
100	RTN	24	
101	*LBLE	21 15	
102	STO2	35 02	
103	X⇄Y	-41	
104	GSB1	23 01	
105	RCL2	36 02	
106	-	-45	
107	CHS	-22	
108	RTN	24	
109	*LBLe	21 16 15	
110	STO2	35 02	
111	X⇄Y	-41	
112	GSB0	23 00	

REGISTERS

0	1	2	3	4	5	6	7	8	9
t_0	K	used							

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I
L_∞	W_∞		D	b	

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCL2	36 02	
114	-	-45	
115	CHS	-22	
116	RTN	24	
117	*LBLa	21 16 11	
118	RCLD	36 14	
119	LN	32	
120	e^x	33	
121	CHS	-22	
122	1	01	
123	+	-55	
124	GSB2	23 02	
125	RCLA	36 11	
126	x	-35	
127	RTN	24	
128	*LBLb	21 16 12	
129	RCLE	36 15	
130	RCLD	36 14	
131	-	-45	
132	RCLE	36 15	
133	÷	-24	
134	RCLE	36 15	
135	RCLD	36 14	
136	÷	-24	
137	Y^x	31	
138	RCLB	36 12	
139	x	-35	
140	RTN	24	
141	*LBLD	21 14	
142	GSBC	23 13	
143	STO2	35 02	
144	RCL0	36 00	
145	-	-45	
146	GSB6	23 06	
147	CHS	-22	
148	1	01	
149	+	-55	
150	RCLD	36 14	
151	1/X	52	
152	1	01	
153	-	-45	
154	Y^x	31	
155	RCLA	36 11	
156	RCLD	36 14	
157	÷	-24	
158	x	-35	
159	RCL1	36 01	
160	x	-35	
161	RCLD	36 14	
162	x	-35	
163	RCL2	36 02	
164	RCL0	36 00	
165	-	-45	
166	GSB6	23 06	
167	x	-35	
168	RTN	24	
169	*LBLd	21 16 14	
170	STO2	35 02	
171	RCLB	36 12	
172	X⇄Y	-41	
173	÷	-24	
174	RCLD	36 14	
175	RCLE	36 15	
176	÷	-24	
177	Y^x	31	
178	1	01	
179	-	-45	
180	RCL2	36 02	
181	x	-35	
182	RCL1	36 01	
183	x	-35	
184	3	03	
185	x	-35	
186	RTN	24	
187	*LBL7	21 07	
188	SPC	16-11	
189	LOG	16 32	
190	.	-62	
191	0	00	
192	3	03	
193	5	05	
194	7	07	
195	4	04	
196	x	-35	
197	.	-62	
198	6	06	
199	7	07	
200	4	04	
201	2	02	
202	+	-55	
203	PRTX	-14	
204	3	03	
205	x	-35	
206	CHS	-22	
207	3	03	
208	+	-55	
209	STOD	35 14	
210	PRTX	-14	
211	RTN	24	

LABELS

A $t \to L_t$	B $t \to W_t$	C $L_t \to t$	D $L_t \to dL/dt$	E $L_t, t \to t_o$
a $\to L_i$	b $\to W_i$	c $W_t \to t$	d $W_t \to dW/dt$	e $W_t, t \to t_o$
0 used	1 used	2 used	3 used	4 used
5 used	6 used	7 $\to d, D$	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Description

Program Title Generalized VBGF and Derivatives : Solutions

Name Daniel Pauly **Date** Dec., 1981

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Program Description, Equations, Variables, etc. The generalized von Bertalanffy Growth Formula (VBGF) has for length the form

$$L_t = L_\infty \left(1 - e^{-KD(t-t_0)}\right)^{1/D} \qquad \ldots 1)$$

and its derivative is

$$dl/dt = \frac{L_\infty}{D}\left(1 - e^{-KD(t-t_0)}\right)^{1/D-1} \cdot KD \cdot e^{-KD(t-t_0)} \qquad \ldots 2)$$

when $D < 1$, there is an inflexion point at time

$$t_i = t_0 - \frac{\ln D}{KD} \qquad \ldots 3)$$

and at length

$$L_i = L_\infty \left(1 - e^{(\ln D)}\right)^{1/D} \qquad \ldots 4)$$

the generalized VBGF for weight is

$$W_t = W_\infty \left(1 - e^{-KD\frac{3}{b}(t-t_0)}\right)^{3/D} \qquad \ldots 5)$$

the first derivative of which is

$$dw/dt = W_\infty 3K \left(1 - e^{-KD\frac{3}{b}(t-t_0)}\right)^{\frac{b}{D}-1} \cdot e^{-KD\frac{3}{b}(t-t_0)} \qquad \ldots 6)$$

the weight at the inflexion point being given by

$$W_i = W_\infty \left(\frac{b-D}{b}\right)^{b/D} \qquad \ldots 7)$$

Equations 1) and 5) correspond to the normal, or "special" VBGF when $D = 1$ and $b = 3$. D and d are estimated from equations 26) and 27) in Pauly (1981).

Operating Limits and Warnings 1) Equations 3) and 4) have no solutions when $D = 1$.

2) L_t and W_t must always be lower than L_∞ and W_∞, respectively.

User Instructions

FB10

TOTAL MORTALITY FROM MEAN WEIGHT

$\rightarrow f(a)$ | $\rightarrow f(b)$ | | | $\rightarrow Z$

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter W_∞, K, t_c and t_o	W_∞	↑		
		K	↑		
		t_c	↑		
		t_o	f	a	0.000
2	Enter $\bar{\bar{W}}$	$\bar{\bar{W}}$	f	b	$\bar{\bar{W}}$
3	Enter TOL (tolerated error, e.g. 0.001)	TOL	f	e	TOL
4	Calculate $f(a)$ and $f(b)$:				
	enter a high Z-value	Z (a)	A		$f(a)$
	enter a low Z-value	Z (b)	B		$f(b)$
	Note: $f(a)$ must be negative, $f(b)$ positive; if this is not the case, enter new values of Z(a) and/or Z(b).				
5	Iterate for Z		E		Z

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	-	-45	
003	X⇄Y	-41	
004	STO1	35 01	
005	×	-35	
006	STO5	35 05	
007	X⇄Y	-41	
008	STO4	35 04	
009	CLX	-51	
010	RTN	24	
011	*LBLe	21 16 15	
012	STOE	35 15	
013	RTN	24	
014	*LBLb	21 16 12	
015	STO6	35 06	
016	RTN	24	
017	*LBLA	21 11	
018	STOB	35 12	
019	GSBD	23 14	
020	STO8	35 08	
021	RTN	24	
022	*LBLB	21 12	
023	STOA	35 11	
024	STOC	35 13	
025	GSBD	23 14	
026	STO7	35 07	
027	STO9	35 09	
028	RTN	24	
029	*LBLE	21 15	
030	RCL8	36 08	
031	X=0?	16-43	
032	GTO5	22 05	
033	RCLB	36 12	
034	RCLC	36 13	
035	-	-45	
036	ABS	16 31	
037	RCLE	36 15	
038	X>Y?	16-34	
039	GTO5	22 05	
040	2	02	
041	÷	-24	
042	EEX	-23	
043	CHS	-22	
044	9	09	
045	RCLB	36 12	
046	×	-35	
047	+	-55	
048	STOI	35 46	
049	RCL8	36 08	
050	RCL7	36 07	
051	RCL8	36 08	
052	-	-45	
053	RCLA	36 11	
054	RCLB	36 12	
055	-	-45	
056	÷	-24	
057	÷	-24	
058	RCLB	36 12	
059	X⇄Y	-41	
060	-	-45	
061	STOD	35 14	
062	RCLB	36 12	
063	-	-45	
064	RCLC	36 13	
065	RCLB	36 12	
066	-	-45	
067	÷	-24	
068	X<0?	16-45	
069	GTO1	22 01	
070	1	01	
071	X≤Y?	16-35	
072	GTO1	22 01	
073	RCLB	36 12	
074	RCLC	36 13	
075	-	-45	
076	ABS	16 31	
077	4	04	
078	÷	-24	
079	RCLD	36 14	
080	RCLC	36 13	
081	-	-45	
082	ABS	16 31	
083	X≤Y?	16-35	
084	GTO1	22 01	
085	RCLI	36 46	
086	RCLD	36 14	
087	RCLB	36 12	
088	-	-45	
089	ABS	16 31	
090	X>Y?	16-34	
091	GTO2	22 02	
092	X⇄Y	-41	
093	RCLC	36 13	
094	RCLB	36 12	
095	-	-45	
096	ENT↑	-21	
097	ABS	16 31	
098	÷	-24	
099	×	-35	
100	RCLB	36 12	
101	+	-55	
102	STOD	35 14	
103	GTO2	22 02	
104	*LBL1	21 01	
105	RCLB	36 12	
106	RCLC	36 13	
107	+	-55	
108	2	02	
109	÷	-24	
110	STOD	35 14	
111	*LBL2	21 02	
112	RCLB	36 12	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used	K		Z	W_0	$K(t_c-t_0)$	$\bar{W}$	used	used	used

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I
used	used	used	used	TOL	

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	STOA	35 11	
114	RCL8	36 08	
115	STO7	35 07	
116	RCLD	36 14	
117	STOB	35 12	
118	GSBD	23 14	
119	STO8	35 08	
120	RCL9	36 09	
121	x	-35	
122	X<0?	16-45	
123	GTO3	22 03	
124	RCLA	36 11	
125	STOC	35 13	
126	RCL7	36 07	
127	STO9	35 09	
128	*LBL3	21 03	
129	RCL9	36 09	
130	ABS	16 31	
131	RCL8	36 08	
132	ABS	16 31	
133	X≤Y?	16-35	
134	GTOE	22 15	
135	RCLB	36 12	
136	RCLC	36 13	
137	STOB	35 12	
138	X⇄Y	-41	
139	STOC	35 13	
140	STOA	35 11	
141	RCL8	36 08	
142	RCL9	36 09	
143	STO8	35 08	
144	X⇄Y	-41	
145	STO9	35 09	
146	STO7	35 07	
147	GTOE	22 15	
148	*LBL5	21 05	
149	RCLB	36 12	
150	RTN	24	
151	*LBLD	21 14	
152	STO3	35 03	
153	RCL5	36 05	
154	2	02	
155	x	-35	
156	CHS	-22	
157	e^x	33	
158	x	-35	
159	3	03	
160	x	-35	
161	RCL1	36 01	
162	2	02	
163	x	-35	
164	RCL3	36 03	
165	+	-55	
166	÷	-24	
167	RCL5	36 05	
168	CHS	-22	
169	e^x	33	
170	RCL3	36 03	
171	x	-35	
172	3	03	
173	x	-35	
174	RCL1	36 01	
175	RCL3	36 03	
176	+	-55	
177	÷	-24	
178	-	-45	
179	RCL5	36 05	
180	3	03	
181	x	-35	
182	CHS	-22	
183	e^x	33	
184	RCL3	36 03	
185	x	-35	
186	RCL1	36 01	
187	3	03	
188	x	-35	
189	RCL3	36 03	
190	+	-55	
191	÷	-24	
192	-	-45	
193	1	01	
194	+	-55	
195	RCL4	36 04	
196	x	-35	
197	RCL6	36 06	
198	-	-45	
199	RTN	24	

LABELS

A → $f(a)$	B → $f(b)$	C	D	E → Z
a enter constants	b enter $\bar{w}$	c used	d	e enter TOL
0	1 used	2 used	3 used	4
5 used	6	7	8	9

FLAGS

0
1
2
3

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Description

Program Title Total Mortality from Mean Weight

Name Daniel Pauly

Date Sept. 1980

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Program Description, Equations, Variables, etc. Total mortality (Z) can be estimated iteratively from the equation

$$\bar{W} = W_\infty \left\{ 1 - \frac{3Z \exp(-a)}{Z+K} + \frac{3Z \exp(-2a)}{Z+2K} - \frac{Z \exp(-3a)}{Z+3K} \right\} \quad \ldots 1)$$

where $a = K(t_c - t_0)$, W_∞, K and t_0 being parameters of the special von Bertalanffy Growth Formula. Where t_c is the mean age at first capture obtained by a given gear and where $\bar{W}$ is the mean weight of the fishes in the catch (Gulland, 1969). "Knife-edge" selection (at t_c) is assumed.

The method of iteration used here is the "regula falsi" as incorporated in HP 67/97 program "solution to $f(x) = 0$" (HP 67/97 MA1 08A, Math Pac).

Operating Limits and Warnings The iteration time in (1) can be quite long (≈ 1 min.) and depends on the values $f(a)$ and $f(b)$, which should be both close to zero, and on TOL, with low TOL values increasing iteration time.

User Instructions

FB11

Z USING JONES' OR SPARRE'S METHOD

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	<u>Jones' Method</u>				
1	Enter L_∞, D, ΔL and L_{max} *	$L_\infty, D, \Delta L, L_{max}$	f	a	0.000
2	Enter successive catches, starting with the catch in highest length class with non-zero catch	C	A		$\ln(L_\infty - L_1)$
					$\ln C(L_{1,\infty})$
3	If the values obtained in step 2 are to be used for estimation of Z/KD, press R/S		R/S		i
4	When all catch values have been entered, do		E		r^2
					a
					b = Z/KD
5	To obtain value of Z, multiply by K·D	K·D	×		Z
	<u>Sparre's Method</u>				
6	same as step 1 above				
7	Enter K·D; if not available, enter 1	K·D	STO	1	
8	Enter successive catches, starting with the catch in highest length class with non-zero catch	C	B		(rel.) age
					$\ln C(L_{1,\infty})$
9	If values obtained in step 8 are to be used for estimation of Z/KD, press R/S		R/S		i
10	When all catch values have been entered, do (and multiply Z/KD with KD if K is available)		E		r^2
					a
					or −Z/KD

* Note: Value of $L_{max} + \Delta L$ (class interval) must be < L_∞;
also: L_{max} is the lower limit of its class.

Program Listing

STEP	KEY ENTRY	KEY CODE
001	*LBLa	21 16 11
002	CLRG	16-53
003	P⇄S	16-51
004	CLRG	16-53
005	STO2	35 02
006	R↓	-31
007	STOI	35 46
008	R↓	-31
009	STOD	35 14
010	R↓	-31
011	STO0	35 00
012	CLX	-51
013	RTN	24
014	*LBLA	21 11
015	SPC	16-11
016	ST+3	35-55 03
017	RCL0	36 00
018	RCLD	36 14
019	Y^x	31
020	RCL2	36 02
021	RCLD	36 14
022	Y^x	31
023	-	-45
024	LN	32
025	PRTX	-14
026	RCL3	36 03
027	LN	32
028	PRTX	-14
029	RCL2	36 02
030	RCLI	36 46
031	-	-45
032	STO2	35 02
033	R↓	-31
034	R/S	51
035	X⇄Y	-41
036	Σ+	56
037	RTN	24
038	*LBLB	21 12
039	SPC	16-11
040	ST+3	35-55 03
041	RCL0	36 00
042	RCLD	36 14
043	Y^x	31
044	RCL2	36 02
045	RCLD	36 14
046	Y^x	31
047	-	-45
048	RCLD	36 00
049	RCLD	36 14
050	Y^x	31
051	÷	-24
052	LN	32
053	CHS	-22
054	RCL1	36 01
055	÷	-24
056	PRTX	-14
057	RCL3	36 03
058	LN	32
059	PRTX	-14
060	RCL2	36 02
061	RCLI	36 46
062	-	-45
063	STO2	35 02
064	R↓	-31
065	R/S	51
066	X⇄Y	-41
067	Σ+	56
068	RTN	24
069	*LBLE	21 15
070	P⇄S	16-51
071	RCL8	36 08
072	RCL4	36 04
073	RCL6	36 06
074	x	-35
075	RCL9	36 09
076	÷	-24
077	-	-45
078	ENT↑	-21
079	ENT↑	-21
080	RCL4	36 04
081	X^2	53
082	RCL9	36 09
083	÷	-24
084	RCL5	36 05
085	X⇄Y	-41
086	-	-45
087	÷	-24
088	STOB	35 12
089	x	-35
090	RCL6	36 06
091	X^2	53
092	RCL9	36 09
093	÷	-24
094	CHS	-22
095	RCL7	36 07
096	+	-55
097	÷	-24
098	SPC	16-11
099	PRTX	-14
100	RCL6	36 06
101	RCL4	36 04
102	RCLB	36 12
103	x	-35
104	-	-45
105	RCL9	36 09
106	÷	-24
107	STOA	35 11
108	PRTX	-14
109	RCLB	36 12
110	PRTX	-14
111	P⇄S	16-51
112	RTN	24

LABELS

A	B	C	D	E
a	b	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☐	DEG	☐	FIX	☐
1	☐	☐	GRAD	☐	SCI	☐
2	☐	☐	RAD	☐	ENG	☐
3	☐	☐			n=	

REGISTERS

0	1	2	3	4	5	6	7	8	9
L_∞	K	L'_{max}	ΣC						

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
				Σx	Σx^2	Σy	Σy^2	Σxy	Σn

A	B	C	D	E	I
intercept	slope		D		ΔL

Program Description

Program Title Z Using Jones' or Sparre's Method

Name Daniel Pauly

Date Sept. 1983

Address ICLARM, MCC P.O. Box 1501, Makati
Metro Manila, Philippines

Program Description, Equations, Variables, etc.

Jones (1981) showed that Z/K is equal to the slope of the straight part of a plot ln C on ln ($L_\infty - L_1$), where C is the cumulative catch (starting from the highest length class) corresponding to a given length class of which L_1 is the lower class limit.

The method has been modified by Sparre (MS) who showed that K can be estimated from the slope of the straight part of a plot of ln C on the age corresponding to L_1, where both ln C and L_1 are defined as above. When K is not known, using 1 instead of K for the transformation of length to age makes the slope of the plot equal to Z/K.

Both methods were here modified for use with the generalized VBGF, by addition of the parameter D where appropriate. Also, the ages in Sparre's method are replaced by relative ages.

Operating Limits and Warnings (1) Proper selection of the x and y values to be included in the computation of Z or Z/K requires that a graph be made from which the point belonging to the straight section are selected.

(2) Do not use the method with data obtained from a gear that selects for or against larger sizes.

User Instructions

LENGTH-CONVERTED CATCH CURVES FB12

initial Z $L, N \rightarrow$ | improved Z $L, N \rightarrow$ | | | $\rightarrow r^2, a, Z$

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	Preliminary estimation of Z or Z/K				
1	Enter L_∞, ΔL, K, D and initialize	L_∞	↑		
	(if K is unknown, enter 1 instead)	ΔL	↑		
		K	↑		
		D	f	a	0.000
2	Enter class midpoint and frequency	L	↑		
		N	A		$\ln(N/\Delta t)$
					t'_i
3	If data pair is to be included in linear regression, do		$\Sigma+$		i
	(do $\Sigma-$ instead of $\Sigma+$ to remove erroneous entries)				
4	When all values to be included have been entered, press		E		r^2
					a
	Iteration for improving estimate of Z or Z/K				Z or Z/K
5	Enter preliminary value of Z (or Z/K) and re-initialize		f	b	Z or Z/K
6	Enter class midpoint and frequency	L	↑		
		N	B		$\ln(N/1-e^{-Z\Delta t})$
					t'_{i_2}
7	If data pair is to be included in regression, do		$\Sigma+$		i
	(do $\Sigma-$ instead of $\Sigma+$ to remove erroneous entries)				
8	When all values to be included have been entered, press		E		r^2
					a
9	Stop if new value of Z or Z/K is close to initial value. If not repeat steps 6-9 using last value of Z or Z/K as input in step 6. Repeat until convergence is achieved.				Z or Z/K

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	001 *LBLa	21 16 11	
	002 P⇄S	16-51	
	003 CLRG	16-53	
	004 P⇄S	16-51	
	005 STOD	35 14	
	006 R↓	-31	
	007 STO1	35 01	
	008 R↓	-31	
	009 2	02	
010	010 ÷	-24	
	011 STOC	35 13	
	012 X⇄Y	-41	
	013 STO5	35 05	
	014 CLX	-51	
	015 RTN	24	
	016 *LBLb	21 16 12	
	017 STO4	35 04	
	018 P⇄S	16-51	
	019 0	00	
020	020 STO4	35 04	
	021 STO5	35 05	
	022 STO6	35 06	
	023 STO7	35 07	
	024 STO8	35 08	
	025 STO9	35 09	
	026 P⇄S	16-51	
	027 CLX	-51	
	028 RTN	24	
	029 *LBLA	21 11	
030	030 STO0	35 00	
	031 R↓	-31	
	032 STO8	35 08	
	033 GSB0	23 00	
	034 STO7	35 07	
	035 RCL8	36 08	
	036 GSB1	23 01	
	037 RCL0	36 00	
	038 RCL7	36 07	
	039 ÷	-24	
040	040 LN	32	
	041 SPC	16-11	
	042 PRTX	-14	
	043 X⇄Y	-41	
	044 PRTX	-14	
	045 RTN	24	
	046 *LBLB	21 12	
	047 STO0	35 00	
	048 R↓	-31	
	049 STO8	35 08	
050	050 GSB0	23 00	
	051 RCL4	36 04	
	052 ×	-35	
	053 CHS	-22	
	054 e^x	33	
	055 CHS	-22	
	056 1	01	
	057 +	-55	
	058 1/X	52	
	059 RCL0	36 00	
060	060 ×	-35	
	061 LN	32	
	062 SPC	16-11	
	063 PRTX	-14	
	064 RCL8	36 08	
	065 RCLC	36 13	
	066 -	-45	
	067 GSB1	23 01	
	068 PRTX	-14	
	069 RTN	24	
070	070 *LBL0	21 00	
	071 RCLC	36 13	
	072 +	-55	
	073 GSB1	23 01	
	074 RCL8	36 08	
	075 RCLC	36 13	
	076 -	-45	
	077 GSB1	23 01	
	078 -	-45	
	079 RTN	24	
080	080 *LBL1	21 01	
	081 RCL5	36 05	
	082 ÷	-24	
	083 RCLD	36 14	
	084 Y^x	31	
	085 CHS	-22	
	086 1	01	
	087 +	-55	
	088 LN	32	
	089 CHS	-22	
090	090 RCL1	36 01	
	091 ÷	-24	
	092 RCLD	36 14	
	093 ÷	-24	
	094 RTN	24	
	095 *LBLE	21 15	
	096 P⇄S	16-51	
	097 SPC	16-11	
	098 RCL8	36 08	
	099 RCL4	36 04	
100	100 RCL6	36 06	
	101 ×	-35	
	102 RCL9	36 09	
	103 ÷	-24	
	104 -	-45	
	105 ENT↑	-21	
	106 ENT↑	-21	
	107 RCL4	36 04	
	108 X^2	53	
	109 RCL9	36 09	
110	110 ÷	-24	
	111 RCL5	36 05	
	112 X⇄Y	-41	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used	K	used	used	Z_1	L_∞		used	used	

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
				Σx	Σx^2	Σy	Σy^2	Σxy	Σn

A	B	C	D	E	I
a	b	$\Delta L/2$	D		

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	-	-45	
114	÷	-24	
115	STOB	35 12	
116	x	-35	
117	RCL6	36 06	
118	X^2	53	
119	RCL9	36 09	
120	÷	-24	
121	CHS	-22	
122	RCL7	36 07	
123	+	-55	
124	÷	-24	
125	PRTX	-14	
126	RCL6	36 06	
127	RCL4	36 04	
128	RCLB	36 12	
129	x	-35	
130	-	-45	
131	RCL9	36 09	
132	÷	-24	
133	STOA	35 11	
134	PRTX	-14	
135	RCLB	36 12	
136	CHS	-22	
137	PRTX	-14	
138	P⇄S	16-51	
139	RTN	24	

LABELS

A $L, N \rightarrow$	B $L, N \rightarrow$	C	D	E $\rightarrow \vec{r}, a, z$
a $L_0, K, D, \Delta L \rightarrow$	b	c	d	e
0 $L \rightarrow \Delta t$	1 $L \rightarrow t'$	2 enter z & clear registers	3	4
5	6	7	8	9

FLAGS: 0, 1, 2, 3

SET STATUS

FLAGS (ON / OFF)	TRIG	DISP
0 ☐ ☐	DEG ☒	FIX ☒
1 ☐ ☐	GRAD ☐	SCI ☐
2 ☐ ☐	RAD ☐	ENG ☐
3 ☐ ☐		n = 3

Program Description

Program Title Length-converted catch curves

Name Daniel Pauly **Date** Sept. 1983

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Given inputs of L_∞, K, D and ΔL (the class interval) and length-frequency data, this program computes values of $\ln N/\Delta t$ and t' (relative age) as used for drawing length-converted catch curves of the type described by Pauly (1982a, 1983). Once the points have been graphed, the data pairs can be selected which are to be included in the estimation of Z, using linear regression (1). The points needed are then reentered and Z is estimated from

$$\ln (N/\Delta t) = a - Zt' \qquad \ldots 1)$$

The value of Z obtained from (1) can then be used as input (Z_1) in the equation of P. Sparre (pers. comm.), i.e.

$$\ln (N/1 - e^{-Z_1 \Delta t}) = a - Z_2 t' \qquad \ldots 2)$$

Where Z_2 is an improved estimate of Z. If the value of Z_1 and Z_2 differ markedly (which will rarely occur), Z_2 can be used as input for another iteration, which will then produce a value of Z improved further (Z_3), etc.

Operating Limits and Warnings Selection of points to be included in the regression must be done carefully (see text); particularly, no points belonging to the ascending part of the curve must be included, nor points estimated from lengths within 5% of L_∞.

User Instructions

Z and K FROM MEAN LENGTHS FB13

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	Estimation of Mean Size and its Standard Error				
1	Store lower class limit of lowest size considered, class interval and initialize	S'			
	($S = L$ or W)	ΔS	f	b	0.000
2	Enter frequency, starting from the lowest class (enter zero when appropriate)	N_i	A		i
3	When all frequencies have been entered, compute the mean size, the standard deviation of the size values and the standard error of the mean		B		Σn
					$\bar{S}$
					s.d.$_{(S)}$
					s.e.$_{(\bar{S})}$
	Z and K from Mean Length				
1	Initialize and enter L_r, L_1, L_2 and D	L_r	↑		
		L_1	↑		
		L_2	↑		
		D	f	a	0.000
2	Enter t_1, t_2 and $L_{(\infty)}$	t_1	↑		
		t_2	↑		
		$L_{(\infty)}$	R/S		0.000
3	Enter initial value of Z and iterate	Z	E		Z_1
					Z_2
					Z_3
					etc.
					⋮
					K
					Z

Program Description

Program Title Z and K from Mean Lengths

Name Daniel Pauly **Date** Sept., 1982

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. As demonstrated by Ebert (1973), estimates of K and Z can be obtained from 2 mean lengths, a value of $L_{(\infty)}$, a length at recruitment (L_r) and times t_1 and t_2 (corresponding to the mean lengths) by solving two equations, which become, in terms of the generalized VBGF

$$\frac{\sum_{x=0}^{N} e^{-Zx} - b\sum_{x=0}^{N} e^{-(KD(t_1+x)+Zx)}}{\sum_{x=0}^{N} e^{-Zx}} = \frac{L_1^D}{L_{(\infty)}^D} \quad \ldots 1)$$

and

$$\frac{\sum_{x=0}^{N} e^{-Zx} - b\sum_{x=0}^{N} e^{-(KD(t_2+x)+Zx)}}{\sum_{x=0}^{N} e^{-Zx}} = \frac{L_2^D}{L_{(\infty)}^D} \quad \ldots 2)$$

where $b = L_{(\infty)}^D - L_r^D / L_{(\infty)}^D$, while N is the integer portion of Y, when $Y = 1 + (-\log_e 0.0001/Z)$. As shown by Saila and Lough (1981), these equations have an explicit solution for K, i.e.

$$K = \ln \frac{L_{(\infty)}^D - L_2^D}{L_{(\infty)}^D - L_1^D} \Big/ (t_1 - t_2)\cdot D \quad \ldots 3)$$

Once K has been calculated, the value of Z is obtained using a very simplified version of the algorithm given in Ebert (1973, p. 286).

Operating Limits and Warnings Iterating time can be quite long when dealing with low values of Z; it saves time therefore, to enter initial guesses that are assumed higher than the true values (rather than the reverse).

Z is estimated with an error of less than 0.001.

User Instructions

F and M from TAGGING - RECAPTURE DATA FB14

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Initialize		f	a	0.000
2	Enter the N_r values	N_r	A		coded time
3	Calculate r^2, a and b		E		r^2
					a
					b
4	Enter N_0 and calculate F and M	N_0	f	e	F
					M

Program Listing

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	CLRG	16-53	
005	CLX	-51	
006	RTN	24	
007	*LBLA	21 11	
008	LN	32	
009	RCL0	36 00	
010	Σ+	56	
011	1	01	
012	ST+0	35-55 00	
013	RCL0	36 00	
014	1	01	
015	-	-45	
016	RTN	24	
017	*LBLE	21 15	
018	P⇄S	16-51	
019	SPC	16-11	
020	RCL8	36 08	
021	RCL4	36 04	
022	RCL6	36 06	
023	x	-35	
024	RCL9	36 09	
025	÷	-24	
026	-	-45	
027	ENT↑	-21	
028	ENT↑	-21	
029	RCL4	36 04	
030	X²	53	
031	RCL9	36 09	
032	÷	-24	
033	RCL5	36 05	
034	X⇄Y	-41	
035	-	-45	
036	÷	-24	
037	STOB	35 12	
038	x	-35	
039	RCL6	36 06	
040	X²	53	
041	RCL9	36 09	
042	÷	-24	
043	CHS	-22	
044	RCL7	36 07	
045	+	-55	
046	÷	-24	
047	PRTX	-14	
048	RCL6	36 06	
049	RCL4	36 04	
050	RCLB	36 12	
051	x	-35	
052	-	-45	
053	RCL9	36 09	
054	÷	-24	
055	STOA	35 11	
056	PRTX	-14	
057	RCLB	36 12	
058	PRTX	-14	
059	P⇄S	16-51	
060	RTN	24	
061	*LBLe	21 16 15	
062	RCLB	36 12	
063	e^x	33	
064	CHS	-22	
065	1	01	
066	+	-55	
067	x	-35	
068	RCLB	36 12	
069	CHS	-22	
070	RCLA	36 11	
071	e^x	33	
072	x	-35	
073	X⇄Y	-41	
074	÷	-24	
075	SPC	16-11	
076	PRTX	-14	
077	STO0	35 00	
078	RCLB	36 12	
079	CHS	-22	
080	RCL0	36 00	
081	-	-45	
082	PRTX	-14	
083	RTN	24	

LABELS

A N_r →	B	C	D	E → r^2, a, b
a initialize	b	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

REGISTERS

0 used	1	2	3	4	5	6	7	8	9
S0	S1	S2	S3	S4 Σx	S5 Σx^2	S6 Σy	S7 Σy^2	S8 Σxy	S9 n

A a	B b	C	D	E	I

Program Description

Program Title F and M from Tagging - Recapture Data

Name Daniel Pauly **Date** Sept. 1980

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Total mortality (Z) may be estimated from the equation

$$\ln N_r = a + br' \quad \ldots 1)$$

where N_r is the number of recoveries per time interval, where r' is the coded time interval (starting with r' = 0, then r' = 1, 2, 3 etc.), and where b, with sign changed is equal to Z.

Total mortality may then be split into F and M by means of the expression

$$F = \frac{e^a \cdot Z}{N_0 (1 - e^{-Z})} \quad \ldots 2)$$

where N_0 is the total number of fish tagged and released and a is the intercept of equation (1) (Gulland, 1969).

Operating Limits and Warnings 1) Gulland, (1969, section 6) should be consulted for details and sources of bias and errors.
2) Do not forget to put the mortality values (M, F) on an annual basis.

User Instructions

INDEPENDENT ESTIMATES OF M FB15

$L_\infty, K, T \to M$ | $W_\infty, K, T \to M$

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter L_∞, K, $\bar{T}$ and obtain M (special VBGF)	L_∞	↑		
		K	↑		
		$\bar{T}$	A		M
2	Enter W_∞, K, $\bar{T}$ and obtain M (special VBGF)	W_∞	↑		
		K	↑		
		$\bar{T}$	B		M
3	IF The estimate of M pertain to Clupeidae, or polar fishes ($\bar{T} < 3.5\,^{\circ}C$) see "operating limits and warnings."				

User Instructions

1 POPULATION SIZE (PETERSEN'S METHOD) FB16 2

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter T, n and m (fish tagged)	T	↑		
	(all captures)	n	↑		
	(recaptures of tagged fish)	m	f	a	0.
2	Estimate population size (N) and its standard error.				
	Case A		A		N
					s.e.(N)
	Case B		B		N
					s.e.(N)
	Case C		C		N
					s.e.(N)
	Case D		D		N
					s.e.(N)

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS	STEP	KEY ENTRY	KEY CODE	COMMENTS
001	001 *LBLa	21 16 11			057 RCL9	36 09	
	002 STO7	35 07			058 RCL3	36 03	
	003 R↓	-31			059 ÷	-24	
	004 STO9	35 09		060	060 ×	-35	
	005 R↓	-31			061 RCL6	36 06	
	006 STO2	35 02			062 ×	-35	
	007 2	02			063 RCL4	36 04	
	008 ÷	-24			064 x^2	53	
	009 CHS	-22			065 RCL5	36 05	
010	010 e^x	33			066 ×	-35	
	011 STO4	35 04			067 RCL7	36 07	
	012 RCL9	36 09			068 ×	-35	
	013 RCL2	36 02			069 −	-45	
	014 +	-55		070	070 STO8	35 08	
	015 STO3	35 03			071 x^2	53	
	016 RCL7	36 07			072 RCL0	36 00	
	017 ×	-35			073 X>Y?	16-34	
	018 RCL3	36 03			074 GTO1	22 01	
	019 CHS	-22			075 RCL1	36 01	
020	020 e^x	33			076 RCL5	36 05	
	021 CHS	-22			077 ×	-35	
	022 1	01			078 RCL8	36 08	
	023 +	-55			079 X⇄Y	-41	
	024 RCL9	36 09		080	080 ÷	-24	
	025 ×	-35			081 RCL9	36 09	
	026 ÷	-24			082 X⇄Y	-41	
	027 RTN	24			083 −	-45	
	028 *LBLA	21 11			084 STO9	35 09	
	029 STO7	35 07			085 GTO0	22 00	
030	030 R↓	-31			086 *LBL1	21 01	
	031 STO6	35 06			087 RCL9	36 09	
	032 RCL4	36 04			088 SPC	16-11	
	033 ×	-35			089 PRTX	-14	
	034 RCL7	36 07		090	090 RCL2	36 02	
	035 RCL2	36 02			091 +	-55	
	036 CHS	-22			092 STO3	35 03	
	037 e^x	33			093 e^x	33	
	038 ×	-35			094 RCL6	36 06	
	039 +	-55			095 ×	-35	
040	040 STO1	35 01			096 PRTX	-14	
	041 *LBL0	21 00			097 RTN	24	
	042 RCL9	36 09			098 *LBLB	21 12	
	043 CHS	-22			099 R↓	-31	
	044 e^x	33		100	100 STO6	35 06	
	045 STO5	35 05			101 R↑	16-31	
	046 RCL2	36 02			102 RCL2	36 02	
	047 RCL9	36 09			103 2	02	
	048 +	-55			104 ÷	-24	
	049 STO3	35 03			105 e^x	33	
050	050 RCL4	36 04			106 ×	-35	
	051 x^2	53			107 X⇄Y	-41	
	052 RCL5	36 05			108 RCL2	36 02	
	053 ×	-35			109 e^x	33	
	054 CHS	-22		110	110 ×	-35	
	055 1	01			111 +	-55	
	056 +	-55			112 STO5	35 05	

REGISTERS

0	1	2	3	4	5	6	7	8	9
TOL	used	M	Z	used	used	N_{i+1}	C_i	used	F
S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCL6	36 06	
114	X⇄Y	-41	
115	÷	-24	
116	LN	32	
117	CHS	-22	
118	RCL2	36 02	
119	-	-45	
120	SPC	16-11	
121	PRTX	-14	
122	RCL5	36 05	
123	PRTX	-14	
124	RTN	24	

LABELS

A → Fi , Ni	B	C	D	E
a → initialize	b	c	d	e
0 loop	1 → Fi , Ni	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☒
1	☐	☒
2	☐	☒
3	☐	☒

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 2	

Program Description

Program Title VPA and Cohort Analysis

Name J. Pope* and D. Pauly **Date** Oct. 1980
Address * MAFF Laboratory
Lowestoft, England

Program Description, Equations, Variables, etc. Program FB 18 calculates the value of F which satisfies the equation

$$\frac{N_{i+1}}{C_i} = \frac{(F_i + M)\exp\{-(F_i + M)\}}{F_i(1 - \exp\{-(F_i + M)\})} \quad \ldots 1)$$

where C_i is the catch at age i, N_i and N_{i+1} being the population sizes at the beginning and the end of the time period during which the catch C_i was taken (Gulland 1965).

The computation proceeds backward, starting from a "terminal population" (N_t) which is estimated from

$$N_t = \frac{C_t \cdot (F_t + M)}{F_t(1 - \exp\{-(F_t + M)\})} \quad \ldots 2)$$

where F_t is the (assumed) terminal fishing mortality and C_t the terminal catch.

Equation (1) is solved iteratively, using the Newton method, and Pope's equation (1972) for cohort analysis to obtain approximations of the slope of 1).

An alternative to VPA is to estimate N_i using Pope's approximation ("cohort analysis")

$$N_i \approx C_i \cdot e^{M/2} + N_{i+1} \cdot e^{M} \quad \ldots 3)$$

with F_i being estimated from N_i, N_{i+1} and M (Pope 1972).

Operating Limits and Warnings Estimation of the N_i and F_i-values must proceed backward, i.e. starting with N_t as first estimate of N_{i+1}. The values of N_i and F_i will rapidly converge toward their true values, even when F_t was a wild guess. The values of N_i and F_i immediately preceeding N_t and F_t are to be treated with suspicion, however. They may be improved by using as F_t one of the F_i-values obtained from a preliminary VPA.

When using cohort analysis, M-values should not be higher than 0.3 per time unit.

User Instructions

JONES' LENGTH COHORT ANALYSIS FB19

→ N, E　→ Z, F

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Store parameters	L_∞	STO	A	
	do either	D	↑		
		M	↑		
		K	f	a	
	or	M/KD	↑		
		D	f	b	
2	Initialize				
	a) enter upper limit of largest length class and length class interval	L_{ter}	↑		
		ΔL	f	c	
	b) enter terminal exploitation rate (a guess)* and terminal catch	E_t	↑		
		C_t	f	d	N_t
3	Run cohort analysis : enter C_{1-2} and compute N_1 and E	C_{1-2}	A		N_1
					E_{1-2}
4	To compute values of Z and F, enter M (if not done previously) and perform	M	STO	2	
		E_{1-2}	B		Z_{1-2}
					F_{1-2}
5	Repeat step(s) 3 (and 4) until smallest length is reached				

NOTE :
*A value of $E = 0.5$, corresponding to $F_t = M$ will do for most purposes.

Program Listing

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	÷	-24	
003	X⇄Y	-41	
004	STOD	35 14	
005	÷	-24	
006	STO0	35 00	
007	CLX	-51	
008	RTN	24	
009	*LBLe	21 16 15	
010	RCLA	36 11	
011	RCLD	36 14	
012	Y^x	31	
013	RCL7	36 07	
014	RCLD	36 14	
015	Y^x	31	
016	-	-45	
017	RCLA	36 11	
018	RCLD	36 14	
019	Y^x	31	
020	RCL8	36 08	
021	RCLD	36 14	
022	Y^x	31	
023	-	-45	
024	÷	-24	
025	RCL0	36 00	
026	2	02	
027	÷	-24	
028	Y^x	31	
029	STO6	35 06	
030	RTN	24	
031	*LBLA	21 11	
032	STOC	35 13	
033	GSBe	23 16 15	
034	RCL5	36 05	
035	STO9	35 09	
036	x	-35	
037	RCLC	36 13	
038	+	-55	
039	RCL6	36 06	
040	x	-35	
041	STO5	35 05	
042	RCL7	36 07	
043	STO8	35 08	
044	RCLB	36 12	
045	-	-45	
046	STO7	35 07	
047	RCL5	36 05	
048	SPC	16-11	
049	PRTX	-14	
050	RCL9	36 09	
051	-	-45	
052	RCLC	36 13	
053	X⇄Y	-41	
054	÷	-24	
055	PRTX	-14	
056	RTN	24	
057	*LBLc	21 16 13	
058	STOB	35 12	
059	X⇄Y	-41	
060	STO8	35 08	
061	X⇄Y	-41	
062	-	-45	
063	STO7	35 07	
064	CLX	-51	
065	RTN	24	
066	*LBLB	21 12	
067	CHS	-22	
068	1	01	
069	+	-55	
070	RCL2	36 02	
071	X⇄Y	-41	
072	÷	-24	
073	SPC	16-11	
074	PRTX	-14	
075	RCL2	36 02	
076	-	-45	
077	PRTX	-14	
078	RTN	24	
079	*LBLb	21 16 12	
080	STOD	35 14	
081	R↓	-31	
082	STO0	35 00	
083	CLX	-51	
084	RTN	24	
085	*LBLd	21 16 14	
086	X⇄Y	-41	
087	÷	-24	
088	STO5	35 05	
089	RTN	24	
090			

LABELS

A	B	C	D	E
→ N_1, E	Z, F			
a → M/KD	b STO M/KD	c → L_1, L_2	d → N_t	e → XL
0	1	2	3	4
5	6	7	8	9

FLAGS

Flag	
0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☒
1	☐	☒
2	☐	☒
3	☐	☒

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

REGISTERS

0	1	2	3	4	5	6	7	8	9
M/KD	K	M	Z		N_2	X_L	L_1	L_2	used
S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I
L_∞	ΔL	C_{1-2}	D		

Program Description

Program Title *Jones' Length Cohort Analysis*
Name *Daniel Pauly* **Date** *Feb., 1981*
Address *ICLARM, MCC P.O. Box 1501*
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. *Pope's (1972) cohort analysis, generalized for any time interval* Δt *is*

$$N_1 = N_1 + \Delta t \cdot e^{M\Delta t} + C_{1-2}^{M\Delta t/2} \qquad \ldots 1)$$

substituting length for age (using the generalized VBGF) and rearranging gives

$$N_1 = [(N_2 \cdot X_L) + C_{1-2}] \cdot X_L \qquad \ldots 2)$$

where

$$X_L = \left\{ \frac{L_\infty^D - L_1^D}{L_\infty^D - L_2^D} \right\}^{M/2KD} \qquad \ldots 3)$$

where N_1 *is the number of fishes at length 1, while* C_{1-2} *is the catch of fish of length* L_1 *to* L_2. *Having estimated a value of N for the largest fish, successive applications of equation (1) lead to estimates of N for the smaller fish. The rate of exploitation* ($E = F/Z$) *can be computed from*

$$E = F/Z = \text{number caught} / \text{number dying}$$

Z is then estimated from E via

$$Z = M / (1 - E) \qquad \ldots 4)$$

and F via

$$F = Z - M \qquad \ldots 5)$$

The method is based on Jones (1974, 1981).

Operating Limits and Warnings *The limitations of length cohort analysis are discussed in detail in papers by Jones (1974, 1981) and must be considered whenever this method is applied to a set of catch data. The results of length cohort analysis are sensitive to wide class intervals used for structuring the catch data; for this reason, it may be more appropriate to use length-structured VPA (program FB 20) whenever separate values of M and K are available.*

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLA	21 11	
002	STO7	35 07	
003	R↓	-31	
004	STO6	35 06	
005	RCLA	36 11	
006	RCLD	36 14	
007	Yˣ	31	
008	RCLI	36 46	
009	RCLD	36 14	
010	Yˣ	31	
011	−	-45	
012	RCLA	36 11	
013	RCLD	36 14	
014	Yˣ	31	
015	RCLI	36 46	
016	RCLE	36 15	
017	−	-45	
018	STOI	35 46	
019	RCLD	36 14	
020	Yˣ	31	
021	−	-45	
022	X⇄Y	-41	
023	÷	-24	
024	LN	32	
025	RCLC	36 13	
026	÷	-24	
027	RCLD	36 14	
028	÷	-24	
029	STOB	35 12	
030	RCL9	36 09	
031	GSBB	23 12	
032	STO9	35 09	
033	RCL2	36 02	
034	GSBB	23 12	
035	STO2	35 02	
036	2	02	
037	÷	-24	
038	CHS	-22	
039	eˣ	33	
040	STO4	35 04	
041	RCL6	36 06	
042	×	-35	
043	RCL7	36 07	
044	RCL2	36 02	
045	CHS	-22	
046	eˣ	33	
047	×	-35	
048	+	-55	
049	STO1	35 01	
050	*LBL0	21 00	
051	RCL9	36 09	
052	CHS	-22	
053	eˣ	33	
054	STO5	35 05	
055	RCL2	36 02	
056	RCL9	36 09	
057	+	-55	
058	STO3	35 03	
059	RCL4	36 04	
060	X²	53	
061	RCL5	36 05	
062	×	-35	
063	CHS	-22	
064	1	01	
065	+	-55	
066	RCL9	36 09	
067	RCL3	36 03	
068	÷	-24	
069	×	-35	
070	RCL6	36 06	
071	×	-35	
072	RCL4	36 04	
073	X²	53	
074	RCL5	36 05	
075	×	-35	
076	RCL7	36 07	
077	×	-35	
078	−	-45	
079	STO8	35 08	
080	X²	53	
081	RCL0	36 00	
082	X>Y?	16-34	
083	GTO1	22 01	
084	RCL1	36 01	
085	RCL5	36 05	
086	×	-35	
087	RCL8	36 08	
088	X⇄Y	-41	
089	÷	-24	
090	RCL9	36 09	
091	X⇄Y	-41	
092	−	-45	
093	STO9	35 09	
094	GTO0	22 00	
095	*LBL1	21 01	
096	RCL9	36 09	
097	RCLB	36 12	
098	÷	-24	
099	STO9	35 09	
100	SPC	16-11	
101	PRTX	-14	
102	RCL2	36 02	
103	RCLB	36 12	
104	÷	-24	
105	STO2	35 02	
106	+	-55	
107	GSBB	23 12	
108	eˣ	33	
109	RCL6	36 06	
110	×	-35	
111	PRTX	-14	
112	RTN	24	

REGISTERS

0	1	2	3	4	5	6	7	8	9
TOL / W_1	used / W_2	$M/Z_f \cdot \bar{w}$	Z/Z_f	used / a	used / b	$N_s/L_{min.}$	$C_f / \bar{\bar{W}}$	used	F
S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
A: L_∞	B: Δt	C: K	D: D	E: ΔL	I: L'_s				

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	*LBLB	21 12	
114	RCL8	36 12	
115	×	-35	
116	RTN	24	
117	*LBLa	21 16 11	
118	X⇄Y	-41	
119	STO9	35 09	
120	RCL2	36 02	
121	+	-55	
122	RCL9	36 09	
123	X⇄Y	-41	
124	÷	-24	
125	÷	-24	
126	RTN	24	
127	*LBLb	21 16 12	
128	CLRG	16-53	
129	STO5	35 05	
130	R↓	-31	
131	STO4	35 04	
132	CLX	-51	
133	RTN	24	
134	*LBLc	21 16 13	
135	STOE	35 15	
136	R↓	-31	
137	STO6	35 06	
138	RCL5	36 05	
139	Y^x	31	
140	RCL4	36 04	
141	×	-35	
142	STO0	35 00	
143	CLX	-51	
144	RTN	24	
145	*LBLC	21 13	
146	ST+3	35-55 03	
147	RCL6	36 06	
148	RCLE	36 15	
149	+	-55	
150	STO6	35 06	
151	RCL5	36 05	
152	Y^x	31	
153	RCL4	36 04	
154	×	-35	
155	STO1	35 01	
156	RCL0	36 00	
157	+	-55	
158	2	02	
159	÷	-24	
160	STO7	35 07	
161	×	-35	
162	ST+2	35-55 02	
163	RCL1	36 01	
164	STO0	35 00	
165	RCL7	36 07	
166	RTN	24	
167	*LBLE	21 15	
168	RCL2	36 02	
169	PRTX	-14	
170	RCL3	36 03	
171	÷	-24	
172	PRTX	-14	
173	RTN	24	

LABELS

A → $F_{1/2}$, N_t	B used	C N_i →	D	E
a → N_t	b a, b →	c L_{min}, ΔL →	d	e
0 used	1 used	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☒
1	☐	☒
2	☐	☒
3	☐	☒

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

Program Description

Program Title Length-structured VPA

Name Daniel Pauly **Date** April, 1981

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. In analogy to Jones' (1974) conversion of Pope's (1972) cohort analysis to a method suitable for the analysis of catch-at-length data, Gulland's (1965) Virtual Population Analysis (VPA) can be used to estimate fishing mortality and population sizes from catch-at-length data. Gulland's VPA has the form

$$\frac{N_{i+1}}{C_i} = \frac{(F_i + M)\exp\{-(F_i + M)\}}{F_i\{1 - \exp - (F_i + M)\}} \quad \ldots 1)$$

Generalized for any time interval Δt, this becomes

$$\frac{N_{1+\Delta t}}{C_{1-2}} = \frac{(F_{1-2} + M)\,\Delta t \cdot \exp\{-(F_{1-2} + M)\,\Delta t\}}{(F_{1-2}\cdot\Delta t)\cdot\{1 - \exp(-(F_{1-2} + M)\,\Delta t)\}} \quad \ldots 2)$$

where N_1 is the number of fish of age 1 and C_{1-2} and F_{1-2} are the catch and fishing mortality, respectively, pertaining to fishes ranging from age 1 to age 2.

Converting length to age, in terms of the generalized VBGF gives for Δt

$$\Delta t = \frac{\ln\left\{\frac{L_\infty^D - L_1^D}{L_\infty^D - L_2^D}\right\}}{KD} \quad \ldots 3)$$

where L_1 and L_2 are the lengths pertaining to ages 1 and 2, respectively.

Operating Limits and Warnings The properties of the method are essentially the same as for VPA as far as convergence towards true fishing mortality is concerned, and the same as for Jones' length cohort analysis as far as sensitivity to L_∞ and K is concerned. The method, however, is insensitive to the effects of length class intervals that are very large, something which is not the case with Jones' length cohort analysis.

User Instructions

YIELD PER RECRUIT (Special VBGF) FB21

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
	ORIGINAL VERSION (1957)				
1	Enter parameter values	W_∞	STO	B	
		K	STO	1	
		M	STO	2	
		t_{max}	STO	A	
		t_o	STO	0	
		t_c	STO	D	
		t_r	STO	I	
2	Compute Y/R	F	A		Y/R_c
					Y/R_r
	JONES' VERSION (1957)				
3	Enter parameter values as above, omitting t_{max}				
4	Compute Y/R	F	B		Y/R_c
					Y/R_r
	SIMPLIFIED VERSION (1966)				
5	Enter parameter values	M/K	STO	8	
	$(L_c/L_\infty =)$	c	STO	C	
6	Calculate relative Y'/R	E	C		Y'/R

Y/R_c = yield per recruit of age t_c

Y/R_r = yield per recruit of age t_r
when t_r is not available, set $t_r = t_o$

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	RCL2	36 02	
003	+	-55	
004	STO3	35 03	
005	RCLD	36 14	
006	RCL0	36 00	
007	-	-45	
008	STO5	35 05	
009	RCLA	36 11	
010	RCLD	36 14	
011	-	-45	
012	STO6	35 06	
013	RTN	24	
014	*LBLB	21 12	
015	STO4	35 04	
016	GSBa	23 16 11	
017	RCL3	36 03	
018	1/X	52	
019	RCL5	36 05	
020	RCL1	36 01	
021	x	-35	
022	CHS	-22	
023	e^x	33	
024	3	03	
025	x	-35	
026	RCL1	36 01	
027	RCL3	36 03	
028	+	-55	
029	÷	-24	
030	-	-45	
031	RCL5	36 05	
032	RCL1	36 01	
033	x	-35	
034	2	02	
035	x	-35	
036	CHS	-22	
037	e^x	33	
038	3	03	
039	x	-35	
040	RCL1	36 01	
041	2	02	
042	x	-35	
043	RCL3	36 03	
044	+	-55	
045	÷	-24	
046	+	-55	
047	RCL5	36 05	
048	RCL1	36 01	
049	x	-35	
050	3	03	
051	x	-35	
052	CHS	-22	
053	e^x	33	
054	RCL1	36 01	
055	3	03	
056	x	-35	
057	RCL3	36 03	
058	+	-55	
059	÷	-24	
060	-	-45	
061	RCLB	36 12	
062	x	-35	
063	RCL4	36 04	
064	x	-35	
065	*LBLb	21 16 12	
066	SPC	16-11	
067	PRTX	-14	
068	RCLD	36 14	
069	RCLI	36 46	
070	-	-45	
071	RCL2	36 02	
072	x	-35	
073	CHS	-22	
074	e^x	33	
075	x	-35	
076	PRTX	-14	
077	RTN	24	
078	*LBLA	21 11	
079	STO4	35 04	
080	GSBa	23 16 11	
081	RCL6	36 06	
082	RCL3	36 03	
083	x	-35	
084	CHS	-22	
085	e^x	33	
086	CHS	-22	
087	1	01	
088	+	-55	
089	RCL3	36 03	
090	÷	-24	
091	RCL1	36 01	
092	RCL3	36 03	
093	+	-55	
094	STO7	35 07	
095	RCL6	36 06	
096	x	-35	
097	CHS	-22	
098	e^x	33	
099	CHS	-22	
100	1	01	
101	+	-55	
102	RCL5	36 05	
103	RCL1	36 01	
104	x	-35	
105	CHS	-22	
106	e^x	33	
107	3	03	
108	x	-35	
109	x	-35	
110	RCL7	36 07	
111	÷	-24	
112	-	-45	

REGISTERS

0	1	2	3	4	5	6	7	8	9
t_0	K	M	Z	F	$t_c - t_o$	$t_{max} - t_c$	used	M/K	1 - C
S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I
t_{max}	W_∞	c	t_c	E	t_r

Program Listing (113 to end)

STEP		KEY ENTRY	KEY CODE	COMMENTS
	113	STO8	35 08	
	114	RCL1	36 01	
	115	2	02	
	116	x	-35	
	117	RCL3	36 03	
	118	+	-55	
	119	STO7	35 07	
120	120	RCL6	36 06	
	121	x	-35	
	122	CHS	-22	
	123	e^x	33	
	124	CHS	-22	
	125	1	01	
	126	+	-55	
	127	RCL5	36 05	
	128	RCL1	36 01	
	129	x	-35	
130	130	2	02	
	131	x	-35	
	132	CHS	-22	
	133	e^x	33	
	134	3	03	
	135	x	-35	
	136	RCL7	36 07	
	137	÷	-24	
	138	ST+8	35-55 08	
	139	RCL1	36 01	
140	140	3	03	
	141	x	-35	
	142	RCL3	36 03	
	143	+	-55	
	144	STO7	35 07	
	145	RCL6	36 06	
	146	x	-35	
	147	CHS	-22	
	148	e^x	33	
	149	CHS	-22	
150	150	1	01	
	151	+	-55	
	152	RCL5	36 05	
	153	RCL1	36 01	
	154	x	-35	
	155	3	03	
	156	x	-35	
	157	CHS	-22	
	158	e^x	33	
	159	x	-35	
160	160	RCL7	36 07	
	161	÷	-24	
	162	RCL8	36 08	
	163	X⇄Y	-41	
	164	-	-45	
	165	RCL8	36 12	
	166	x	-35	
	167	RCL4	36 04	
	168	x	-35	

STEP		KEY ENTRY	KEY CODE	COMMENTS
	169	GTOb	22 16 12	
170	170	*LBLC	21 13	
	171	STOE	35 15	
	172	RCLC	36 13	
	173	CHS	-22	
	174	1	01	
	175	+	-55	
	176	STO9	35 09	
	177	3	03	
	178	x	-35	
	179	RCL8	36 08	
180	180	1/X	52	
	181	RCLE	36 15	
	182	CHS	-22	
	183	1	01	
	184	+	-55	
	185	x	-35	
	186	STO7	35 07	
	187	1	01	
	188	+	-55	
	189	÷	-24	
190	190	CHS	-22	
	191	1	01	
	192	+	-55	
	193	RCL9	36 09	
	194	X^2	53	
	195	3	03	
	196	x	-35	
	197	RCL7	36 07	
	198	2	02	
	199	x	-35	
200	200	1	01	
	201	+	-55	
	202	÷	-24	
	203	+	-55	
	204	RCL9	36 09	
	205	3	03	
	206	Y^x	31	
	207	RCL7	36 07	
	208	3	03	
	209	x	-35	
210	210	1	01	
	211	+	-55	
	212	÷	-24	
	213	-	-45	
	214	RCL9	36 09	
	215	RCL8	36 08	
	216	Y^x	31	
	217	x	-35	
	218	RCLE	36 15	
	219	x	-35	
220	220	RTN	24	

LABELS

A B&H '57	B Jones '57	C B&H '66	D	E
a used	b used	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Description

Program Title Yield per Recruit

Name Daniel Pauly **Date** March, 1981

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Program FB20 estimates the yield per recruit, given growth and related parameters from any of the three equations

$$Y/R_r = F \cdot e^{-Mr_2} \cdot W_\infty \left\{ \frac{1-e^{-Zr_3}}{Z} - \frac{3e^{-Kr_1}(1-e^{-(Z+K)r_3})}{Z+K} + \frac{3e^{-2Kr_1}(1-e^{-(Z+2K)r_3})}{Z+2K} - \frac{e^{-3Kr_1}(1-e^{-(Z+3K)r_3})}{Z+3K} \right\} \quad \ldots 1)$$

or

$$Y/R_r = F \cdot e^{-Mr_2} \cdot W_\infty \left\{ \frac{1}{Z} - \frac{3e^{-Kr_1}}{Z+K} + \frac{3e^{-2Kr_1}}{Z+2K} - \frac{e^{-3Kr_1}}{Z+3K} \right\} \quad \ldots 2)$$

where $Z = F + M$, $r_1 = t_c - t_0$, $r_2 = t_c - t_r$ and $r_3 = t_{max} - t_c$

or

$$Y'/R_r = E(1-C)^{M/K} \cdot \left\{ 1 - \frac{3(1-C)}{1+\frac{K(1-E)}{M}} + \frac{3(1-C)^2}{1+\frac{2K(1-E)}{M}} - \frac{(1-C)^3}{1+\frac{3K(1-E)}{M}} \right\} \quad \ldots 3)$$

proposed by Beverton and Holt (1957), Jones (1957), Beverton and Holt (1964).

Operating Limits and Warnings These equations must be used only in conjunction with the special VBGF (when D = 1) and when weight growth is isometric.

User Instructions

FB22

YIELD PER RECRUIT VIA INCOMPLETE β-FUNCTION

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter parameters	W_∞	STO	B	
		K	STO	A	
		D	STO	D	
		b	STO	E	
		M	STO	0	
		t_0	↑		
		t_r	f	a	
		t_c	f	c	
	SPECIAL VBGF ($D = 1$):				
2	Calculate yield per recruit	F	A		β
					Y/R_c
					Y/R_r
	GENERALIZED VBGF ($D \neq 1$):				
3	Calculate yield per recruit	F	B		β
					Y/R_c
					Y/R_r

NOTES:
Y/R_c = yield per recruit of age t_c
Y/R_r = yield per recruit of age t_r
When t_r is not available, set $t_r = t_0$

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS	STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLA	21 11		057	RCL5	36 05	
002	STOI	35 46		058	×	-35	
003	P⇄S	16-51		059	RCL4	36 04	
004	RCL1	36 01		060	+	-55	
005	RCL0	36 00		061	STO5	35 05	
006	-	-45		062	CLX	-51	
007	P⇄S	16-51		063	RCL7	36 07	
008	RCLA	36 11		064	×	-35	
009	×	-35		065	RCL6	36 06	
010	CHS	-22		066	+	-55	
011	e^x	33		067	STO7	35 07	
012	STO3	35 03		068	RCL8	36 08	
013	RCLE	36 15		069	1	01	
014	RCLD	36 14		070	+	-55	
015	÷	-24		071	STO8	35 08	
016	1	01		072	RCL2	36 02	
017	+	-55		073	RCL8	36 08	
018	STO2	35 02		074	-	-45	
019	RCLI	36 46		075	×	-35	
020	RCL0	36 00		076	RCL1	36 01	
021	+	-55		077	RCL8	36 08	
022	RCLA	36 11		078	+	-55	
023	÷	-24		079	RCL8	36 08	
024	STO1	35 01		080	+	-55	
025	1	01		081	÷	-24	
026	STO7	35 07		082	LSTX	16-63	
027	STO6	35 06		083	1	01	
028	STO4	35 04		084	-	-45	
029	0	00		085	÷	-24	
030	STO8	35 08		086	RCL3	36 03	
031	STO5	35 05		087	×	-35	
032	*LBL0	21 00		088	ENT↑	-21	
033	STO9	35 09		089	ENT↑	-21	
034	RCL1	36 01		090	RCL4	36 04	
035	RCL8	36 08		091	×	-35	
036	+	-55		092	RCL5	36 05	
037	ENT↑	-21		093	•	-55	
038	ENT↑	-21		094	STO4	35 04	
039	RCL2	36 02		095	X⇄Y	-41	
040	+	-55		096	RCL6	36 06	
041	×	-35		097	×	-35	
042	RCL1	36 01		098	RCL7	36 07	
043	RCL8	36 08		099	+	-55	
044	+	-55		100	STO6	35 06	
045	RCL8	36 08		101	X≠0?	16-42	
046	+	-55		102	÷	-24	
047	÷	-24		103	RCL9	36 09	
048	LSTX	16-63		104	X⇄Y	-41	
049	1	01		105	X≠Y?	16-32	
050	+	-55		106	GTO0	22 00	
051	÷	-24		107	RCL3	36 03	
052	RCL3	36 03		108	RCL1	36 01	
053	×	-35		109	Y^x	31	
054	CHS	-22		110	×	-35	
055	ENT↑	-21		111	1	01	
056	ENT↑	-21		112	RCL3	36 03	

REGISTERS

0	1	2	3	4	5	6	7	8	9
M	P	Q	X	used	used	used	used	used	used

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
t_o	t_c	t_r							

A	B	C	D	E	I
K	W_∞		D	b	F

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	-	-45	
114	RCL2	36 02	
115	y^x	31	
116	×	-35	
117	RCL1	36 01	
118	÷	-24	
119	SPC	16-11	
120	PRTX	-14	
121	RCLB	36 12	
122	×	-35	
123	RCLI	36 46	
124	×	-35	
125	RCLA	36 11	
126	÷	-24	
127	P⇄S	16-51	
128	RCL1	36 01	
129	RCL0	36 00	
130	-	-45	
131	P⇄S	16-51	
132	RCLI	36 46	
133	RCL0	36 00	
134	+	-55	
135	×	-35	
136	e^x	33	
137	×	-35	
138	PRTX	-14	
139	P⇄S	16-51	
140	RCL1	36 01	
141	RCL2	36 02	
142	-	-45	
143	P⇄S	16-51	
144	RCL0	36 00	
145	×	-35	
146	CHS	-22	
147	e^x	33	
148	×	-35	
149	PRTX	-14	
150	RTN	24	
151	*LBLB	21 12	
152	STOI	35 46	
153	RCLA	36 11	
154	P⇄S	16-51	
155	STO5	35 05	
156	P⇄S	16-51	
157	RCLD	36 14	
158	×	-35	
159	3	03	
160	×	-35	
161	RCLE	36 15	
162	÷	-24	
163	STOA	35 11	
164	RCLI	36 46	
165	GSBA	23 11	
166	P⇄S	16-51	
167	RCL5	36 05	
168	P⇄S	16-51	
169	STOA	35 11	
170	CLX	-51	
171	RTN	24	
172	*LBLa	21 16 11	
173	P⇄S	16-51	
174	STO2	35 02	
175	R↓	-31	
176	STO0	35 00	
177	P⇄S	16-51	
178	CLX	-51	
179	RTN	24	
180	*LBLc	21 16 13	
181	P⇄S	16-51	
182	STO1	35 01	
183	P⇄S	16-51	
184	CLX	-51	
185	RTN	24	

LABELS

A $Y/R, D=1$	B $Y/R, D\neq 1$	C	D	E
a t_o, t_r →	b	c t_c →	d	e
0 Loop for β	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☒
1	☐	☒
2	☐	☒
3	☐	☒

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

Program Description

Program Title *Yield per Recruit via Incomplete B-Function*

Name *Daniel Pauly* **Date** *March 1981*

Address *ICLARM, MCC P.O. Box 1501*
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Yield per recruit, as shown by Jones (1957) can be computed, when growth conforms to the special VBGF, by using

$$Y/R_r = F/K \cdot e^{-Zr_1} \cdot e^{-Mr_2} \cdot W_\infty \{B(X, P, Q)\} \qquad \ldots 1)$$

where $X = e^{-Kr_1}$, $P = Z/K$, $Q = b+1$ (b being the exponent of the length-weight relationship) and B being the symbol of the incomplete beta function, and where $r_1 = t_c - t_0$ and $r_2 = t_c - t_r$. Note here that b may be $\neq 3$ (Jones (1957), Wilimovsky and Wicklund (1963), Ricker (1975)).

When the generalized VBGF is used to describe growth, yield per recruit can be computed from

$$Y/R_r = \frac{F \cdot b}{3KD} \cdot e^{Zr_1} \cdot e^{-Mr_2} W_\infty \{B(X, P, Q)\} \qquad \ldots 2)$$

where $X = e^{-3KDr_1/b}$, $P = Zb/3KD$, $Q = (b/D) + 1$ and r_1 and r_2 are defined as above.

The routine which estimates the values of the incomplete beta function is taken from Program 00425D, submitted by R.H. Shudde to the U.S. User's Library.

Operating Limits and Warnings Execution time is about 40 seconds.

User Instructions

CONVERSION FACTOR "k" FB23

1 F→k 2

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter parameters needed	K	STO	1	
		M*	STO	2	
		t_o	STO	0	
		t_c	STO	C	
		tk	STO	A	
2	Calculate value of factor "k"	F*	A		"k"

NOTES :

* If no separate estimates of M and F are available, enter Z instead of M, and compute k for F = 0.

Program Listing

STEP		KEY ENTRY	KEY CODE
001	001	*LBLA	21 11
	002	RCL2	36 02
	003	+	-55
	004	ST03	35 03
	005	1/X	52
	006	ST09	35 09
	007	ST05	35 05
	008	RCLC	36 13
	009	RCL0	36 00
010	010	-	-45
	011	ST07	35 07
	012	RCL1	36 01
	013	x	-35
	014	CHS	-22
	015	e^x	33
	016	3	03
	017	x	-35
	018	RCL3	36 03
	019	RCL1	36 01
020	020	+	-55
	021	÷	-24
	022	ST-9	35-45 09
	023	RCL7	36 07
	024	RCL1	36 01
	025	x	-35
	026	2	02
	027	x	-35
	028	CHS	-22
	029	e^x	33
030	030	3	03
	031	x	-35
	032	RCL1	36 01
	033	2	02
	034	x	-35
	035	RCL3	36 03
	036	+	-55
	037	÷	-24
	038	ST+9	35-55 09
	039	RCL7	36 07
040	040	RCL1	36 01
	041	x	-35
	042	3	03
	043	x	-35
	044	CHS	-22
	045	e^x	33
	046	RCL1	36 01
	047	3	03
	048	x	-35
	049	RCL3	36 03
050	050	+	-55
	051	÷	-24
	052	ST-9	35-45 09
	053	RCL5	36 05
	054	ST04	35 04
	055	RCLA	36 11
	056	RCL0	36 00
	057	-	-45
	058	ST08	35 08
	059	RCL1	36 01
060	060	x	-35
	061	CHS	-22
	062	e^x	33
	063	3	03
	064	x	-35
	065	RCL1	36 01
	066	RCL3	36 03
	067	+	-55
	068	÷	-24
	069	ST-4	35-45 04
070	070	RCL8	36 08
	071	RCL1	36 01
	072	x	-35
	073	2	02
	074	x	-35
	075	CHS	-22
	076	e^x	33
	077	3	03
	078	x	-35
	079	RCL1	36 01
080	080	2	02
	081	x	-35
	082	RCL3	36 03
	083	+	-55
	084	÷	-24
	085	ST+4	35-55 04
	086	RCL8	36 08
	087	RCL1	36 01
	088	x	-35
	089	3	03
090	090	x	-35
	091	CHS	-22
	092	e^x	33
	093	RCL1	36 01
	094	3	03
	095	x	-35
	096	RCL3	36 03
	097	+	-55
	098	÷	-24
	099	ST-4	35-45 04
100	100	RCL4	36 04
	101	RCLA	36 11
	102	RCLC	36 13
	103	-	-45
	104	RCL3	36 03
	105	x	-35
	106	CHS	-22
	107	e^x	33
	108	x	-35
	109	RCL9	36 09
110	110	÷	-24
	111	RTN	24

LABELS					FLAGS
A →K	B	C	D	E	0
a	b	c	d	e	1
0	1	2	3	4	2
5	6	7	8	9	3

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

REGISTERS

0	1	2	3	4	5	6	7	8	9
t_o	K	M	Z	used	1/Z		r_1	r_2	used
S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I
k		t_c			

Program Description

Program Title Conversion Factor "k"

Name Daniel Pauly **Date** March 1981

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Under equilibrium conditions, the proportion in the total stock (i.e. of the fish of age t_c and above) of the fish of age t_k and above is given by

$$k = \frac{\exp(-Zr_3)\cdot\left\{\frac{1}{Z} - \frac{3\exp(-Kr_2)}{Z+K} + \frac{3\exp(-2Kr_2)}{Z+2K} - \frac{\exp(-3Kr_2)}{Z+3K}\right.}{\frac{1}{Z} - \frac{3\exp(-Kr_1)}{Z+K} + \frac{3\exp(-2Kr_1)}{Z+2K} - \frac{\exp(-3Kr_1)}{Z+3K}} \quad \ldots 1)$$

where $r_1 = t_c - t_o$

$r_2 = t_k - t_o$

and $r_3 = t_k - t_c$

with the parameters K and t_o pertaining to the special VBGF (Hempel and Sarhage (1959), Pauly (1980d)).

Operating Limits and Warnings Use only in conjunction with the special VBGF (i.e. with $D = 1$).

User Instructions

FB 24

1 STOCK - RECRUITMENT CURVE of BEVERTON & HOLT 2

→initialize P↑R	P↑R (-)	P→C	→P	→r^2, α, β

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Initialize		f	a	0.000
2	Enter P and R values	P	↑		
		R	A		i
3	Remove erroneous data pair	P	↑		
		R	B		i - 1
4	Calculate r^2, α', β'		E		r^2
					α'
					β'
5	Enter P-values*	P	D		i
6	Estimate R (HM & AM) for a given P-value	P	C		$\hat{R}$ (HM)
					$\hat{R}$ (AM)
7	If P and R are expressed in the same units,				
	calculate parameters of and form of curve		f	e	A
					P_r (HM)

NOTES:
* If an erroneous value of P is entered, perform: 0 STO 1, 0 STO 3, and start entering the P-values all over again.

Program Listing

STEP	KEY ENTRY	KEY CODE
001	*LBLa	21 16 11
002	CLRG	16-53
003	P⇄S	16-51
004	CLRG	16-53
005	CLX	-51
006	RTN	24
007	*LBLA	21 11
008	ST+1	35-55 01
009	R↓	-31
010	STO0	35 00
011	R↑	16-31
012	÷	-24
013	RCL0	36 00
014	F2?	16 23 02
015	GTO0	22 00
016	Σ+	56
017	RTN	24
018	*LBL0	21 00
019	Σ-	16 56
020	RTN	24
021	*LBLB	21 12
022	SF2	16 21 02
023	GTOA	22 11
024	*LBLE	21 15
025	P⇄S	16-51
026	SPC	16-11
027	RCL8	36 08
028	RCL4	36 04
029	RCL6	36 06
030	x	-35
031	RCL9	36 09
032	÷	-24
033	-	-45
034	ENT↑	-21
035	ENT↑	-21
036	RCL4	36 04
037	X^2	53
038	RCL9	36 09
039	÷	-24
040	RCL5	36 05
041	X⇄Y	-41
042	-	-45
043	÷	-24
044	STOB	35 12
045	x	-35
046	RCL6	36 06
047	X^2	53
048	RCL9	36 09
049	÷	-24
050	CHS	-22
051	RCL7	36 07
052	+	-55
053	÷	-24
054	PRTX	-14
055	RCL6	36 06
056	RCL4	36 04
057	RCLB	36 12
058	x	-35
059	-	-45
060	RCL9	36 09
061	÷	-24
062	STOA	35 11
063	RCLB	36 12
064	PRTX	-14
065	X⇄Y	-41
066	PRTX	-14
067	P⇄S	16-51
068	RTN	24
069	*LBLD	21 14
070	RCLA	36 11
071	X⇄Y	-41
072	÷	-24
073	RCLB	36 12
074	+	-55
075	1/X	52
076	ST+2	35-55 02
077	1	01
078	ST+3	35-55 03
079	RCL3	36 03
080	RTN	24
081	*LBLC	21 13
082	SPC	16-11
083	RCLA	36 11
084	X⇄Y	-41
085	÷	-24
086	RCLB	36 12
087	+	-55
088	1/X	52
089	PRTX	-14
090	RCL1	36 01
091	RCL2	36 02
092	÷	-24
093	x	-35
094	PRTX	-14
095	RTN	24
096	*LBLe	21 16 15
097	RCLA	36 11
098	CHS	-22
099	1	01
100	+	-55
101	PRTX	-14
102	RCLB	36 12
103	X⇄Y	-41
104	÷	-24
105	1/X	52
106	PRTX	-14
107	RTN	24

LABELS

A	B	C	D	E
data input	correction	est. R	add Rest.	→ r^2, α, β
a initialize	b	c	d	e A, B
0	1	2	3	4
5	6	7	8	9

FLAGS

Flag	
0	
1	
2	correction
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☐
1	☐	☐
2	☒	☒
3	☐	☐

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used	ΣR	ΣR est.							

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
				Σx	Σx^2	Σy	Σy^2	Σxy	i

A	B	C	D	E	I
β'	α'				

Program Description

Program Title Stock-recruitment curve of Beverton & Holt

Name Daniel Pauly

Date March 1979

Address Institut für Meereskunde
Kiel, FRG

Program Description, Equations, Variables, etc. The stock-recruitment relationship proposed by Beverton and Holt (1957) has the form

$R = \frac{1}{\alpha' + \beta'/P}$, where P is the size of the parental stock and R is the number of recruits. When P and R are expressed in the same units, the formula can be rewritten as

$R = \frac{1}{1 - A(1 - P/P_r)}$, where $A = 1 - \beta'$ and $\alpha' = A/P_r$, P_r being the replacement abundance. The curve is fitted by means of:

$\frac{P}{R} = \beta' + \alpha' P$, that is by regressing P/R on P. The R-line, obtained by inverting the values of R represents the harmonic means (HM) of the expected recruitment for the various P-values. The conversion of HM-values to the corresponding arithmetic mean values (AM) follows the procedure outlined by Ricker (1975).

Operating Limits and Warnings The AM-values obtained through conversion from the HM-values are approximative (see Ricker 1975, p. 292).
When a negative value of β' is obtained, delete the values of R and P associated with the highest P/R ratio and recalculate α' and β'.

User Instructions

1	RICKER'S STOCK-RECRUITMENT CURVES FB 252				2
		→$R_{(AM)}/R_{(GM)}$	→P_r/R_r	→2nd form	
	P↑R (2)	→R GM & AM	→$R_{(GM)}$	P↑R (10)	→1st form

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS	OUTPUT DATA/UNITS
1	Initialize		f a	0.000
	1st FORM (R and P in different units)			
2	Enter P and R values	P	↑	
		R	A	i
3	Remove erroneous data pair	P	↑	
		R	f b	$i-1$
4	Calculate parameters of stock-recruitment curve		E	r^2
				α
				β
				P_m
				R_m
5	Estimate $R_{(GM)}$ for a given P-value	P	C	$\hat{R}_{(GM)}$
6	If an estimate of P_r is available, do:	P_r	f d	P_r/R_r
	2nd FORM (R and P in the Same Units)			
7-8	As 2 and 3 in 1st form			
9	Calculate parameters of stock-recruitment curve		f e	r^2
				$a (= P_r/P_m)$
				P_r
10	Reenter P and R values*	P	↑	
		R	D	i
	When all values have been entered, do:		f c	$R_{(AM)}/R_{(GM)}$
11	Estimate $R_{(GM)}$ & $R_{(AM)}$ from a given P-value	P	B	$R_{(GM)}$
				$R_{(AM)}$
	*If an erroneous value of P and/or R was entered, perform: 0 STO 6 & 0 STO 7 and start entering P & R values all over again.			

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	CLRG	16-53	
005	CLX	-51	
006	RTN	24	
007	*LBLA	21 11	
008	LN	32	
009	X⇄Y	-41	
010	STO0	35 00	
011	LN	32	
012	-	-45	
013	RCL0	36 00	
014	F2?	16 23 02	
015	GTO0	22 00	
016	Σ+	56	
017	RTN	24	
018	*LBL0	21 00	
019	Σ-	16 56	
020	RTN	24	
021	*LBLb	21 16 12	
022	SF2	16 21 02	
023	GTOA	22 11	
024	*LBLE	21 15	
025	P⇄S	16-51	
026	SPC	16-11	
027	RCL8	36 08	
028	RCL4	36 04	
029	RCL6	36 06	
030	x	-35	
031	RCL9	36 09	
032	÷	-24	
033	-	-45	
034	ENT↑	-21	
035	ENT↑	-21	
036	RCL4	36 04	
037	X^2	53	
038	RCL9	36 09	
039	÷	-24	
040	RCL5	36 05	
041	X⇄Y	-41	
042	-	-45	
043	÷	-24	
044	STOB	35 12	
045	x	-35	
046	RCL6	36 06	
047	X^2	53	
048	RCL9	36 09	
049	÷	-24	
050	CHS	-22	
051	RCL7	36 07	
052	+	-55	
053	÷	-24	
054	PRTX	-14	
055	RCL6	36 06	
056	RCL4	36 04	
057	RCLB	36 12	
058	x	-35	
059	-	-45	
060	RCL9	36 09	
061	P⇄S	16-51	
062	÷	-24	
063	e^x	33	
064	STOA	35 11	
065	F2?	16 23 02	
066	RTN	24	
067	PRTX	-14	
068	RCLB	36 12	
069	CHS	-22	
070	STOB	35 12	
071	PRTX	-14	
072	1/X	52	
073	PRTX	-14	
074	RCLA	36 11	
075	RCLB	36 12	
076	÷	-24	
077	1	01	
078	e^x	33	
079	÷	-24	
080	PRTX	-14	
081	RTN	24	
082	*LBLC	21 13	
083	STO0	35 00	
084	RCLB	36 12	
085	CHS	-22	
086	x	-35	
087	e^x	33	
088	RCL0	36 00	
089	x	-35	
090	RCLA	36 11	
091	x	-35	
092	RTN	24	
093	*LBLd	21 16 14	
094	GSBC	23 13	
095	RCL0	36 00	
096	÷	-24	
097	RTN	24	
098	*LBLe	21 16 15	
099	SF2	16 21 02	
100	GSBE	23 15	
101	LN	32	
102	PRTX	-14	
103	STO3	35 03	
104	RCLB	36 12	
105	÷	-24	
106	CHS	-22	
107	STO4	35 04	
108	PRTX	-14	
109	RTN	24	
110	*LBLD	21 14	
111	STO5	35 05	
112	R↓	-31	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used			a	R	R'	used	i		

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
				Σx	Σx^2	Σy	Σy^2	Σxy	i

A	B	C	D	E	I
a, α	b				

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	STO0	35 00	
114	RCL4	36 04	
115	÷	-24	
116	CHS	-22	
117	1	01	
118	+	-55	
119	RCL3	36 03	
120	x	-35	
121	e^x	33	
122	RCL0	36 00	
123	x	-35	
124	LOG	16 32	
125	RCL5	36 05	
126	LOG	16 32	
127	-	-45	
128	x^2	53	
129	ST+6	35-55 06	
130	1	01	
131	ST+7	35-55 07	
132	RCL7	36 07	
133	RTN	24	
134	*LBLc	21 16 13	
135	RCL6	36 06	
136	RCL7	36 07	
137	1	01	
138	-	-45	
139	STO0	35 00	
140	÷	-24	
141	RCL0	36 00	
142	x	-35	
143	RCL7	36 07	
144	÷	-24	
145	1	01	
146	.	-62	
147	1	01	
148	5	05	
149	1	01	
150	8	08	
151	x	-35	
152	10^x	16 33	
153	STO8	35 08	
154	RTN	24	
155	*LBLB	21 12	
156	STO0	35 00	
157	RCL4	36 04	
158	÷	-24	
159	CHS	-22	
160	1	01	
161	+	-55	
162	RCL3	36 03	
163	x	-35	
164	e^x	33	
165	RCL0	36 00	
166	x	-35	
167	PRTX	-14	
168	RCL8	36 08	
169	x	-35	
170	PRTX	-14	
171	RTN	24	

LABELS

A	B	C	D	E
$P, R \rightarrow$	est. $R_{(GM \& AM)}$	est. $R_{(GM)}$	reenter $P \& R$	$\rightarrow$ 1st form
a	**b**	**c**	**d**	**e**
initialize	correct.	$\rightarrow R_{(AM)}/R_{(GM)}$	$\rightarrow P_r/R_r$	$\rightarrow$ 2nd form
0	**1**	**2**	**3**	**4**
5	**6**	**7**	**8**	**9**

FLAGS

Flag	
0	
1	
2	used
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☐
1	☐	☐
2	☒	☒
3	☐	☐

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

Program Description

Program Title Ricker's Stock Recruitment Curves

Name Daniel Pauly

Date March 1981

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. The first of the stock-recruitment curves discussed in Ricker (1975) has the form

$$R = \alpha P e^{-\beta P} \quad \ldots 1)$$

where P is the parental stock size, R the corresponding number of recruits, α is an index of density-independent mortality and β an index of density dependent mortality.

The second form of the curve is

$$R = Pe^{a(1-P/P_r)} \quad \ldots 2)$$

where P_r is the replacement abundance (i.e. the point at which the replacement line cuts the stock-recruitment curve) and $a = P_r/P_m$, P_m being the parent stock size at maximum recruitment.

The fitting of the curves and the estimation of the ratio $R_{(AM)}/R_{(GM)}$ follows the method outlined in Ricker (1975, p. 282-289) which should be consulted for details and further considerations.

Operating Limits and Warnings The geometric mean values ($R_{(GM)}$) are the most probable R for the observed P-values, not the long-term (arithmetic mean) average R obtained at a given P.

User Instructions

SCHAEFER AND FOX'S MODELS FB 26

	Fox curve	Fox: f opt, MSY	Fox c/f line
Catch, Effort	correct.	Schaefer curve	Sch: f opt, MSY	Sch. c/f line

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Initialize		f	a	0.000
2	Enter catch-and-effort data	catch	↑		
		effort	A		i
3	Remove erroneous data pair	catch	↑		
		effort	B		i - 1
	SCHAEFER MODEL				
4	Plot of c/f on f		E		r^2
					a
					b
5	f opt and MSY		D		f opt
					MSY
6	Calculate catch for any level of effort	effort	C		catch
	FOX MODEL				
7	Plot of ln c/f on f		f	e	r^2
					a
					b
8	f opt and MSY		f	d	f opt
					MSY
9	Calculate catch for any level of effort	effort	f	c	catch

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	P⇄S	16-51	
004	CLRG	16-53	
005	CLX	-51	
006	RTN	24	
007	*LBLA	21 11	
008	STO0	35 00	
009	÷	-24	
010	STO1	35 01	
011	LN	32	
012	STO2	35 02	
013	RCL0	36 00	
014	ST+4	35-55 04	
015	X²	53	
016	ST+5	35-55 05	
017	RCL2	36 02	
018	ST+6	35-55 06	
019	X²	53	
020	ST+7	35-55 07	
021	RCL2	36 02	
022	RCL0	36 00	
023	x	-35	
024	ST+8	35-55 08	
025	1	01	
026	ST+9	35-55 09	
027	RCL1	36 01	
028	RCL0	36 00	
029	Σ+	56	
030	RTN	24	
031	*LBLB	21 12	
032	STO0	35 00	
033	÷	-24	
034	STO1	35 01	
035	LN	32	
036	STO2	35 02	
037	RCL0	36 00	
038	ST-4	35-45 04	
039	X²	53	
040	ST-5	35-45 05	
041	RCL2	36 02	
042	ST-6	35-45 06	
043	X²	53	
044	ST-7	35-45 07	
045	RCL2	36 02	
046	RCL0	36 00	
047	x	-35	
048	ST-8	35-45 08	
049	1	01	
050	ST-9	35-45 09	
051	RCL0	36 00	
052	RCL1	36 01	
053	Σ-	16 56	
054	RTN	24	
055	*LBLE	21 15	
056	P⇄S	16-51	
057	SPC	16-11	
058	RCL8	36 08	
059	RCL4	36 04	
060	RCL6	36 06	
061	x	-35	
062	RCL9	36 09	
063	÷	-24	
064	-	-45	
065	ENT↑	-21	
066	ENT↑	-21	
067	RCL4	36 04	
068	X²	53	
069	RCL9	36 09	
070	÷	-24	
071	RCL5	36 05	
072	X⇄Y	-41	
073	-	-45	
074	÷	-24	
075	STOB	35 12	
076	x	-35	
077	RCL6	36 06	
078	X²	53	
079	RCL9	36 09	
080	÷	-24	
081	CHS	-22	
082	RCL7	36 07	
083	+	-55	
084	÷	-24	
085	PRTX	-14	
086	√X	54	delete to obtain AM regression
087	RCLB	36 12	
088	X⇄Y	-41	
089	÷	-24	
090	STOB	35 12	
091	RCL6	36 06	
092	RCL4	36 04	
093	RCLB	36 12	
094	x	-35	
095	-	-45	
096	RCL9	36 09	
097	÷	-24	
098	STOA	35 11	
099	PRTX	-14	
100	RCLB	36 12	
101	PRTX	-14	
102	P⇄S	16-51	
103	RTN	24	
104	*LBLe	21 16 15	
105	SPC	16-11	
106	RCL8	36 08	
107	RCL4	36 04	
108	RCL6	36 06	
109	x	-35	
110	RCL9	36 09	
111	÷	-24	
112	-	-45	

REGISTERS

0	1	2	3	4	5	6	7	8	9
used	used	used	FOX →	Σx	Σx^2	Σy	Σy^2	Σxy	n

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
			SCHAEFER →	Σx	Σx^2	Σy	Σy^2	Σxy	n

A	B	C	D	E	I
intercept (a)	slope (b)				

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
	113 ENT↑	-21	
	114 ENT↑	-21	
	115 RCL4	36 04	
	116 X²	53	
	117 RCL9	36 09	
	118 ÷	-24	
	119 RCL5	36 05	
120	120 X⇄Y	-41	
	121 -	-45	
	122 ÷	-24	
	123 STOB	35 12	
	124 ×	-35	
	125 RCL6	36 06	
	126 X²	53	
	127 RCL9	36 09	
	128 ÷	-24	
	129 CHS	-22	
130	130 RCL7	36 07	
	131 +	-55	
	132 ÷	-24	
	133 PRTX	-14	
	134 √X	54	delete to obtain AM regression
	135 RCLB	36 12	
	136 X⇄Y	-41	
	137 ÷	-24	
	138 STOB	35 12	
	139 RCL6	36 06	
140	140 RCL4	36 04	
	141 RCLB	36 12	
	142 ×	-35	
	143 -	-45	
	144 RCL9	36 09	
	145 ÷	-24	
	146 STOA	35 11	
	147 PRTX	-14	
	148 RCLB	36 12	
	149 PRTX	-14	
150	150 RTN	24	
	151 *LBLC	21 13	
	152 STO0	35 00	
	153 RCLB	36 12	
	154 ×	-35	
	155 RCLA	36 11	
	156 +	-55	
	157 RCL0	36 00	
	158 ×	-35	
	159 RTN	24	
160	160 *LBLc	21 16 13	
	161 STO0	35 00	
	162 RCLB	36 12	
	163 ×	-35	
	164 RCLA	36 11	
	165 +	-55	
	166 eˣ	33	
	167 RCL0	36 00	
	168 ×	-35	
	169 RTN	24	
170	170 *LBLD	21 14	
	171 SPC	16-11	
	172 RCLA	36 11	
	173 RCLB	36 12	
	174 CHS	-22	
	175 2	02	
	176 ×	-35	
	177 ÷	-24	
	178 PRTX	-14	
	179 RCLA	36 11	
180	180 X²	53	
	181 RCLB	36 12	
	182 4	04	
	183 ×	-35	
	184 CHS	-22	
	185 ÷	-24	
	186 PRTX	-14	
	187 RTN	24	
	188 *LBLd	21 16 14	
	189 RCLB	36 12	
190	190 1/X	52	
	191 CHS	-22	
	192 SPC	16-11	
	193 PRTX	-14	
	194 RCLA	36 11	
	195 1	01	
	196 -	-45	
	197 eˣ	33	
	198 RCLB	36 12	
	199 ÷	-24	
200	200 CHS	-22	
	201 PRTX	-14	
	202 RTN	24	
210			
220			

LABELS

A	B	C	D	E
enter data	correction	catch	MSY, f opt	Schaefer Plot
a initialize	b	c catch	d MSY, f opt	e Fox Plot
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 2	

Program Description

Program Title Schaefer and Fox's Models

Name Daniel Pauly Date Sept., 1980
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Program Description, Equations, Variables, etc. When a fishery is in equilibrium, surplus yield can be described by a parabolic function of effort, i.e.

$$Y = af - bf^2 \qquad \ldots 1)$$

where a and b are constants and f is fishing effort; Maximum Sustainable Yield (MSY) and optimum effort (f opt.) can be estimated from the relationships

$$MSY = a^2/4b \qquad \ldots 2)$$

and

$$f\,opt. = a/2b \qquad \ldots 3)$$

The values of the constants a & b are generally obtained by plotting c/f on effort, a & b being the intercept and the slope, respectively of the resulting linear regression (the model used here is a GM regression; see Ricker 1975).

When ln c/f is plotted on f, a yield curve is obtained which has the form

$$Y = fe^{a} \cdot e^{-bf} \qquad \ldots 4)$$

with $MSY = e^{a-1}/b$ and $f\,opt = 1/b$ ... 5), 6)

and where a and b are the intercept and slope, respectively of a GM regression of ln c/f on f (Schaefer 1967, Fox 1970, Ricker 1975).

Operating Limits and Warnings The models are based on the assumptions that equilibrium effort and yield figures are used. When this is not the case, a bias will occur, whose magnitude is a function of both the life-span of the fish in question, and of the extent of the changes in effort (see Gulland (1969), for a method to simulate equilibrium conditions).
The results obtained here will differ slightly from those obtained using the more common AM regression.

User Instructions

SCHNUTE'S YIELD MODEL FB27

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter first pair of catch-and-effort data				
	and initialize	C	↑		
		f	f	b	0.000
2	Enter second and following data pairs	C	↑		
		f	A		i
3	Calculate R^2 and coefficients of				
	regression		E		R^2
					a
					b_1
					b_2
4	Estimate model parameters		f	e	r_m
					q
					B_∞
					$f_{opt.}$
					MSY
5	Estimate catch for any level of effort	f	C		catch

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	001 *LBLa	21 16 11	
	002 CLRG	16-53	
	003 STOA	35 11	
	004 R↓	-31	
	005 STOC	35 13	
	006 RCLA	36 11	
	007 ÷	-24	
	008 STOB	35 12	
	009 CLX	-51	
010	010 RTN	24	
	011 *LBLA	21 11	
	012 STOE	35 15	
	013 R↓	-31	
	014 STOD	35 14	
	015 RCLE	36 15	
	016 ÷	-24	
	017 STOI	35 46	
	018 RCLB	36 12	
	019 +	-55	
020	020 2	02	
	021 ÷	-24	
	022 P⇄S	16-51	
	023 STO0	35 00	
	024 RCLE	36 15	
	025 RCLA	36 11	
	026 +	-55	
	027 2	02	
	028 ÷	-24	
	029 STO1	35 01	
030	030 RCLI	36 46	
	031 RCLB	36 12	
	032 ÷	-24	
	033 LN	32	
	034 STO2	35 02	
	035 RCLE	36 15	
	036 STOA	35 11	
	037 RCLD	36 14	
	038 STOC	35 13	
	039 RCLI	36 46	
040	040 STOB	35 12	
	041 RCL2	36 02	
	042 STOI	35 46	
	043 RCL1	36 01	
	044 STOD	35 14	
	045 RCL0	36 00	
	046 STOE	35 15	
	047 P⇄S	16-51	
	048 ST+8	35-55 08	
	049 X²	53	
050	050 ST+5	35-55 05	
	051 RCLD	36 14	
	052 ST+7	35-55 07	
	053 X²	53	
	054 ST+4	35-55 04	
	055 RCLI	36 46	
	056 ST+9	35-55 09	

STEP	KEY ENTRY	KEY CODE	COMMENTS
	057 X²	53	
	058 ST+6	35-55 06	
	059 RCLE	36 15	
060	060 RCLD	36 14	
	061 ×	-35	
	062 ST+1	35-55 01	
	063 RCLD	36 14	
	064 RCLI	36 46	
	065 ×	-35	
	066 ST+2	35-55 02	
	067 RCLE	36 15	
	068 RCLI	36 46	
	069 ×	-35	
070	070 ST+3	35-55 03	
	071 1	01	
	072 ST+0	35-55 00	
	073 RCL0	36 00	
	074 RTN	24	
	075 *LBLE	21 15	
	076 SPC	16-11	
	077 RCL0	36 00	
	078 RCL4	36 04	
	079 ×	-35	
080	080 RCL7	36 07	
	081 X²	53	
	082 -	-45	
	083 STOD	35 14	
	084 RCL0	36 00	
	085 RCL3	36 03	
	086 ×	-35	
	087 RCL8	36 08	
	088 RCL9	36 09	
	089 ×	-35	
090	090 -	-45	
	091 ×	-35	
	092 STOC	35 13	
	093 RCL0	36 00	
	094 RCL1	36 01	
	095 ×	-35	
	096 RCL7	36 07	
	097 RCL8	36 08	
	098 ×	-35	
	099 -	-45	
100	100 STOA	35 11	
	101 RCL0	36 00	
	102 RCL2	36 02	
	103 ×	-35	
	104 RCL7	36 07	
	105 RCL9	36 09	
	106 ×	-35	
	107 -	-45	
	108 STOB	35 12	
	109 ×	-35	
110	110 RCLC	36 13	
	111 X⇄Y	-41	
	112 -	-45	

REGISTERS

0	1	2	3	4	5	6	7	8	9
n	Σxy	Σxz	Σyz	Σx^2	Σy^2	Σz^2	Σx	Σy	Σz

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
used	used	used							

A	B	C	D	E	I
a	b_1	b_2	used	used	used

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCLD	36 14	
114	RCL0	36 00	
115	RCL5	36 05	
116	×	-35	
117	RCL8	36 08	
118	X^2	53	
119	-	-45	
120	×	-35	
121	RCLA	36 11	
122	X^2	53	
123	-	-45	
124	÷	-24	
125	STOC	35 13	
126	RCLB	36 12	
127	RCLA	36 11	
128	RCLC	36 13	
129	×	-35	
130	-	-45	
131	RCLD	36 14	
132	÷	-24	
133	STOB	35 12	
134	RCL9	36 09	
135	RCLC	36 13	
136	RCL8	36 08	
137	×	-35	
138	-	-45	
139	RCLB	36 12	
140	RCL7	36 07	
141	×	-35	
142	-	-45	
143	RCL0	36 00	
144	÷	-24	
145	STOA	35 11	
146	RCL9	36 09	
147	×	-35	
148	RCLB	36 12	
149	RCL2	36 02	
150	×	-35	
151	+	-55	
152	RCLC	36 13	
153	RCL3	36 03	
154	×	-35	
155	+	-55	
156	RCL9	36 09	
157	X^2	53	
158	RCL0	36 00	
159	÷	-24	
160	-	-45	
161	RCL6	36 06	
162	RCL9	36 09	
163	X^2	53	
164	RCL0	36 00	
165	÷	-24	
166	-	-45	
167	÷	-24	
168	PRTX	-14	
169	RCLA	36 11	
170	PRTX	-14	
171	RCLB	36 12	
172	PRTX	-14	
173	RCLC	36 13	
174	PRTX	-14	
175	RTN	24	
176	*LBLe	21 16 15	
177	SPC	16-11	
178	RCLA	36 11	
179	PRTX	-14	
180	RCLB	36 12	
181	CHS	-22	
182	PRTX	-14	
183	RCLC	36 13	
184	RCLB	36 12	
185	×	-35	
186	RCLA	36 11	
187	÷	-24	
188	1/X	52	
189	PRTX	-14	
190	STOD	35 14	
191	RCLA	36 11	
192	RCLB	36 12	
193	CHS	-22	
194	÷	-24	
195	2	02	
196	÷	-24	
197	PRTX	-14	
198	GSBC	23 13	
199	PRTX	-14	
200	RTN	24	
201	*LBLC	21 13	
202	STOI	35 46	
203	RCLB	36 12	
204	×	-35	
205	RCLA	36 11	
206	÷	-24	
207	1	01	
208	+	-55	
209	RCLD	36 14	
210	×	-35	
211	RCLB	36 12	
212	×	-35	
213	CHS	-22	
214	RCLI	36 46	
215	×	-35	
216	RTN	24	

LABELS

A data entry	B	C f → catch	D	E → R^2, a, b_1, b_2
a initialize	b	c	d	e r_m, q, etc.
0	1	2	3	4
5	6	7	8	9

FLAGS: 0, 1, 2, 3

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☒	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☐	ENG	☐
3	☐	☒			n = 3	

Program Listing (001 to 112)

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
002	CLRG	16-53	
003	CLX	-51	
004	RTN	24	
005	*LBLA	21 11	
006	ENT↑	-21	
007	X^2	53	
008	X⇄Y	-41	
009	R↑	16-31	
010	R↑	16-31	
011	STOC	35 13	
012	R↑	16-31	
013	STOB	35 12	
014	R↑	16-31	
015	STOA	35 11	
016	7	07	
017	STOI	35 46	
018	R↓	-31	
019	GSB1	23 01	
020	8	08	
021	STOI	35 46	
022	RCLB	36 12	
023	GSB1	23 01	
024	9	09	
025	STOI	35 46	
026	RCLC	36 13	
027	GSB1	23 01	
028	RCLA	36 11	
029	RCLB	36 12	
030	x	-35	
031	ST+1	35-55 01	
032	RCLA	36 11	
033	RCLC	36 13	
034	x	-35	
035	ST+2	35-55 02	
036	RCLB	36 12	
037	RCLC	36 13	
038	x	-35	
039	ST+3	35-55 03	
040	1	01	
041	ST+0	35-55 00	
042	RCL0	36 00	
043	RTN	24	
044	*LBL1	21 01	
045	ST+i	35-55 45	
046	RCLI	36 46	
047	3	03	
048	-	-45	
049	STOI	35 46	
050	R↓	-31	
051	X^2	53	
052	ST+i	35-55 45	
053	RTN	24	
054	*LBLE	21 15	
055	RCL0	36 00	
056	RCL4	36 04	
057	x	-35	
058	RCL7	36 07	
059	X^2	53	
060	-	-45	
061	STOD	35 14	
062	RCL0	36 00	
063	RCL3	36 03	
064	x	-35	
065	RCL8	36 08	
066	RCL9	36 09	
067	x	-35	
068	-	-45	
069	x	-35	
070	STOC	35 13	
071	RCL0	36 00	
072	RCL1	36 01	
073	x	-35	
074	RCL7	36 07	
075	RCL8	36 08	
076	x	-35	
077	-	-45	
078	STOA	35 11	
079	RCL0	36 00	
080	RCL2	36 02	
081	x	-35	
082	RCL7	36 07	
083	RCL9	36 09	
084	x	-35	
085	-	-45	
086	STOB	35 12	
087	x	-35	
088	RCLC	36 13	
089	X⇄Y	-41	
090	-	-45	
091	RCLD	36 14	
092	RCL0	36 00	
093	RCL5	36 05	
094	x	-35	
095	RCL8	36 08	
096	X^2	53	
097	-	-45	
098	x	-35	
099	RCLA	36 11	
100	X^2	53	
101	-	-45	
102	÷	-24	
103	STOC	35 13	
104	RCLB	36 12	
105	RCLA	36 11	
106	RCLC	36 13	
107	x	-35	
108	-	-45	
109	RCLD	36 14	
110	÷	-24	
111	STOB	35 12	
112	RCL9	36 09	

REGISTERS

0	1	2	3	4	5	6	7	8	9
n	Σxy	Σxz	Σyz	Σx^2	Σy^2	Σz^2	Σx	Σy	Σz

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9

A	B	C	D	E	I
a	b_1	b_2	used	used	

Program Listing (113 to end)

STEP	KEY ENTRY	KEY CODE	COMMENTS
113	RCLC	36 13	
114	RCL8	36 08	
115	x	-35	
116	-	-45	
117	RCLB	36 12	
118	RCL7	36 07	
119	x	-35	
120	-	-45	
121	RCL0	36 00	
122	÷	-24	
123	STOA	35 11	
124	RCL9	36 09	
125	x	-35	
126	RCLB	36 12	
127	RCL2	36 02	
128	x	-35	
129	+	-55	
130	RCLC	36 13	
131	RCL3	36 03	
132	x	-35	
133	+	-55	
134	RCL9	36 09	
135	X²	53	
136	RCL0	36 00	
137	÷	-24	
138	-	-45	
139	RCL6	36 06	
140	RCL9	36 09	
141	X²	53	
142	RCL0	36 00	
143	÷	-24	
144	-	-45	
145	÷	-24	
146	PRTX	-14	
147	RCLA	36 11	
148	PRTX	-14	
149	RCLB	36 12	
150	PRTX	-14	
151	RCLC	36 13	
152	PRTX	-14	
153	RTN	24	
154	*LBLe	21 16 15	
155	RCLB	36 12	
156	X²	53	
157	RCLA	36 11	
158	RCLC	36 13	
159	x	-35	
160	4	04	
161	x	-35	
162	-	-45	
163	√X	54	
164	RCLB	36 12	
165	CHS	-22	
166	+	-55	
167	RCLC	36 13	
168	2	02	
169	x	-35	
170	÷	-24	
171	PRTX	-14	
172	RCLB	36 12	
173	CHS	-22	
174	RCLC	36 13	
175	2	02	
176	x	-35	
177	÷	-24	
178	PRTX	-14	
179	X⇄Y	-41	
180	-	-45	
181	PRTX	-14	
182	2	02	
183	x	-35	
184	PRTX	-14	
185	RCLB	36 12	
186	X²	53	
187	RCLC	36 13	
188	4	04	
189	x	-35	
190	÷	-24	
191	CHS	-22	
192	RCLA	36 11	
193	+	-55	
194	PRTX	-14	
195	4	04	
196	x	-35	
197	X⇄Y	-41	
198	÷	-24	
199	PRTX	-14	
200	RTN	24	
201	*LBLB	21 12	
202	ENT↑	-21	
203	X²	53	
204	RCLC	36 13	
205	x	-35	
206	X⇄Y	-41	
207	RCLB	36 12	
208	x	-35	
209	+	-55	
210	RCLA	36 11	
211	+	-55	
212	RTN	24	

LABELS

A c, Z →	B Z → c	C	D	E $(a, b_1, b_2), R^2$
a initialize	b	c	d	e → M, Z_{opt}, etc.
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☒
1	☐	☒
2	☐	☒
3	☐	☒

TRIG	
DEG	☒
GRAD	☐
RAD	☐

DISP	
FIX	☒
SCI	☐
ENG	☐
n = 3	

User Instructions

1 YIELDS FROM TWO INTERACTING SPECIES FB30 2

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Enter constants	a	STO	A	
		b	STO	B	
		d	STO	D	
		e	STO	E	
		C_1	STO	2	
		C_2	STO	3	
		F_Q	STO	0	
2	Calculate field from two interacting species	F_Q	STO	0	
		F_P	A		Y_P
					Y_Q
					Y_T
3	Calculate F_P (opt), and F_Q (opt) and MSY:				
	Enter starting value of F_P	F_P'	STO	1	
	Enter starting value of F_Q	F_Q'	STO	0	
	Enter ΔF and TOL *	ΔF	f		
		TOL	f	0	F_Q (opt)
					F_P (opt)
					MSY

NOTE :
* ΔF = initial step size
TOL = tolerated error of estimates
(e.g. 0.01)

Program Listing (001 to 112)

STEP	KEY ENTRY		KEY CODE	COMMENTS
001	001	*LBLa	21 16 11	
	002	ST09	35 09	
	003	R↓	-31	
	004	ST07	35 07	
	005	*LBLc	21 16 13	
	006	0	00	
	007	STOI	35 46	
	008	RCL7	36 07	
	009	2	02	
010	010	÷	-24	
	011	ST07	35 07	
	012	ABS	16 31	
	013	RCL9	36 09	
	014	X>Y?	16-34	
	015	GTOb	22 16 12	
	016	*LBLD	21 14	
	017	0	00	
	018	ST05	35 05	
	019	*LBLC	21 13	
020	020	1	01	
	021	RCL5	36 05	
	022	+	-55	
	023	ST05	35 05	
	024	GSBE	23 15	
	025	RCL6	36 06	
	026	X⇄Y	-41	
	027	ST06	35 06	
	028	X>Y?	16-34	
	029	GTO0	22 00	
030	030	RCL7	36 07	
	031	ST+i	35-55 45	
	032	GTOC	22 13	
	033	*LBL0	21 00	
	034	RCL5	36 05	
	035	3	03	
	036	X≤Y?	16-35	
	037	GTOB	22 12	
	038	RCL7	36 07	
	039	CHS	-22	
040	040	ST07	35 07	
	041	GTOD	22 14	
	042	*LBLB	21 12	
	043	ISZI	16 26 46	
	044	RCLI	36 46	
	045	2	02	
	046	X=Y?	16-33	
	047	GTOc	22 16 13	
	048	GTOD	22 14	
	049	*LBLb	21 16 12	
050	050	RCLi	36 45	
	051	PRTX	-14	
	052	ISZI	16 26 46	
	053	1	01	
	054	RCLI	36 46	
	055	X≤Y?	16-35	
	056	GTOb	22 16 12	

STEP	KEY ENTRY		KEY CODE	COMMENTS
	057	GSBE	23 15	
	058	CHS	-22	
	059	PRTX	-14	
060	060	R/S	51	
	061	*LBLE	21 15	
	062	RCLA	36 11	
	063	RCL1	36 01	
	064	×	-35	
	065	RCL1	36 01	
	066	X²	53	
	067	RCLB	36 12	
	068	×	-35	
	069	-	-45	
070	070	RCL2	36 02	
	071	RCL0	36 00	
	072	×	-35	
	073	RCL1	36 01	
	074	×	-35	
	075	STOC	35 13	
	076	+	-55	
	077	X<0?	16-45	
	078	SF2	16 21 02	
	079	ST04	35 04	
080	080	RCLD	36 14	
	081	RCL0	36 00	
	082	×	-35	
	083	RCL0	36 00	
	084	X²	53	
	085	RCLE	36 15	
	086	×	-35	
	087	-	-45	
	088	RCL3	36 03	
	089	RCL0	36 00	
090	090	×	-35	
	091	RCL1	36 01	
	092	×	-35	
	093	ST08	35 08	
	094	+	-55	
	095	X<0?	16-45	
	096	SF1	16 21 01	
	097	P⇄S	16-51	
	098	ST00	35 00	
	099	P⇄S	16-51	
100	100	F0?	16 23 00	
	101	RTN	24	
	102	RCL4	36 04	
	103	+	-55	
	104	CHS	-22	
	105	RTN	24	
	106	*LBLA	21 11	
	107	SPC	16-11	
	108	ST01	35 01	
	109	CF1	16 22 01	
110	110	SF0	16 21 00	
	111	GSBE	23 15	
	112	CF0	16 22 00	

REGISTERS

0	1	2	3	4	5	6	7	8	9
F_Q	F_P	c_1	c_2	used	used	used	used	used	TOL

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
used									

A	B	C	D	E	I
a	b	used	d	e	used

Program Listing (113 to end)

STEP	KEY ENTRY		KEY CODE	COMMENTS
	113	F2?	16 23 02	
	114	GTO1	22 01	
	115	F1?	16 23 01	
	116	GTO3	22 03	
	117	RCL4	36 04	
	118	X<0?	16-45	
	119	CLX	-51	
120	120	PRTX	-14	
	121	P⇄S	16-51	
	122	RCL0	36 00	
	123	P⇄S	16-51	
	124	X<0?	16-45	
	125	CLX	-51	
	126	PRTX	-14	
	127	+	-55	
	128	PRTX	-14	
	129	RTN	24	
130	130	*LBL3	21 03	
	131	RCL4	36 04	
	132	RCLC	36 13	
	133	-	-45	
	134	X<0?	16-45	
	135	CLX	-51	
	136	PRTX	-14	
	137	0	00	
	138	PRTX	-14	
	139	X⇄Y	-41	
140	140	PRTX	-14	
	141	RTN	24	
	142	*LBL1	21 01	
	143	F1?	16 23 01	
	144	GTO2	22 02	
	145	CLX	-51	
	146	PRTX	-14	
	147	P⇄S	16-51	
	148	RCL0	36 00	
	149	P⇄S	16-51	
150	150	RCL8	36 08	
	151	-	-45	
	152	X<0?	16-45	
	153	CLX	-51	
	154	PRTX	-14	
	155	PRTX	-14	
	156	RTN	24	
	157	*LBL2	21 02	
	158	CLX	-51	
	159	PRTX	-14	
160	160	PRTX	-14	
	161	PRTX	-14	
	162	RTN	24	

STEP	KEY ENTRY	KEY CODE	COMMENTS
170			
180			
190			
200			
210			
220			

LABELS

A → Y's	B used	C used	D used	E used
a → MSY	b used	c used	d	e
0 used	1 used	2 used	3 used	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☒	☒	DEG	☒	FIX	☒
1	☒	☒	GRAD	☐	SCI	☐
2	☒	☒	RAD	☐	ENG	☐
3	☐	☐			n = 2	

Program Description

Program Title Yields from Two Interacting Species

Name Daniel Pauly **Date** April, 1981

Address ICLARM, MCC P.O. Box 1501
Makati, Metro Manila, Philippines

Program Description, Equations, Variables, etc. Pope (1979) showed that, if single-species yield curves can be described by parabolas, the total yield (Y_T) of a system of two interacting species P and Q should, as long as the ratio $F_P : F_Q$ remains constant, also correspond to a parabola, i.e.

$$Y_T = \underbrace{aF_P - bF_P^2 + c_1 F_P F_Q}_{} + \underbrace{dF_Q - eF_Q^2 + c_2 F_P F_Q}_{} \quad \ldots 1)$$

$$Y_T = \quad Y_P \quad + \quad Y_Q \quad \ldots 2)$$

where a & b, and d & e are constants of the yield curves of the two different species (e.g. predator and prey) and where C_1 and C_2 express the intensity of the interactions occurring between these species (C_1 and C_2 have opposite signs in cases of predator-prey interactions). Pope (1979) also generalized equation (1) to an n-species system and showed that the overall yield curve of such systems are parabolic, as long as the F-ratios remain constant and no species drops out of the system.

This program estimates values of Y_P, Y_Q and Y_T for any combination of a, b, C_1, C_2, d, e, F_Q and F_P values as well as the MSY and optimal values of F_P and F_Q of the 2 species system.

The iterative subroutines included in this program are adapted from program # 02831D submitted by B.W. Clare to the HP 67/97 (U.S.) User's Library.

Operating Limits and Warnings There might be combinations of constants and of F_P' and F_Q' for which the MSY cannot be located by the algorithm provided here. Iteration time is quite long; don't be impatient.

When computing Y_P, Y_Q and Y_T, the combination of the interaction terms is omitted if one of the species drop out of the system; "dropping out" occurs when a partial yield (including the interaction term is smaller than zero).

Appendix III. Use of Calculators Other Than HP 67/97

In this Appendix, a brief discussion is presented of the suitability of the models included in Chapters 1 to 12, and of the Programs FB 1 to FB 30 for implementation with calculators other than the HP 67/97, specifically the HP 65, HP 41C and HP 41CV of the Hewlett-Packard Company, TI-58 and TI-59 of Texas Instruments, Inc. and miscellaneous other scientific calculators.

HP 65

Wholesale conversion of the programs in Appendix II for use on a HP 65 is possible only in the case of rather short programs (e.g., FB 14), using about half or less of the memory available on the HP 67/97. In some other cases, the sequential approach discussed under "miscellaneous calculators" may be applied (see below).

HP 41C AND HP 41CV

Programs FB 1 to FB 30 have been found to run on an HP 41C without modifications in most cases; all tests were performed using pre-programmed HP 67/97 program cards and an HP 82104A Card Reader. When such a card reader and/or pre-programmed cards are not available, conversion of the programs in Appendix II can be performed using the selection of translated keystrokes in Appendix Table III.1.

Experienced users of HP 41C/41CV may also wish to use the large amount of memory available in these calculators to improve on the programs presented here, some of which had to be condensed (and thus rendered less user friendly) to fit into the limited memory space of the HP 67/97.

TI-58

This model uses an "Algebraic Operating System" (AOS) as does the more advanced TI-59, which is radically different from the "Reverse Polish Notation" (RPN) implemented on HP calculators. The difference between AOS and RPN renders direct translation of HP programs into TI "language" particularly difficult. For this reason, a short program is presented in Appendix Fig. III.1, which, according to its author (Hoyer 1983) allows the running of programs written in RPN on TI-58 (and TI-59). The following paragraphs are a translation (from German) of the comments published along with this program.

"This program simulates on TI-58/59 the RPN as used on HP calculators. The necessary functions which operate the stack are defined by the keys A to E, as follows:

A = Enter
B = Clear stack
C = Roll up (↑)
D = Roll down (↓)
E = Last X

Addition, subtraction, multiplication and division are performed via SBR+, SBR−, SBRX and SBR÷, respectively. The use of the TI's T-register to simulate the HP's Y-register makes it possible to use tests such as X=Y?, X > Y?, etc. This allows for even large RPN programs to be used with TI calculators after only small modifications".

TI-59

Users of the more sophisticated TI-59 have, in addition to the possibility of using the program in Appendix Fig. III.1 the option of using a "RPN-simulator", available as a "Solid State Module" from Texas Instruments, Inc., which, when plugged in a TI-59, translates RPN programs (from HP 65 and HP 67/97) into AOS-compatible keystroke sequences. The very comprehensive manual which comes with the "RPN Simulator", gives all necessary details on the conversion. The memory avail-

cm — centimeter
c_1, c_2 — multiplyers for estimating Z and its standard error (p. 53, Table 5.2)
— interaction terms in Lotka-Volterra's equations and variants thereof (Chapter 12)
C — catch, in numbers (p. 13)
— parameter of the seasonally oscillating version of the VBGF (p. 37, Fig. 4.12)
— multiplicative factor for debiasing recruitment estimates in Beverton and Holt's S/R relationship (p. 132)
C_t — terminal catch, as used in VPA and cohort analysis (p. 100)
C^2 — parameter in Powell's equation for estimation of Z/K (p. 70)
$C(L_1, \infty)$ — catch in number, from the lower limit (L_1) of a given length class upward (equation 5.12)
C.V. — coefficient of variation, i.e., C.V. = $\overline{X}/\text{s.d.}_{(x_i)}$ (p. 33, 36)

d — power of weight to which anabolism is proportional (p. 23, 24)
d.f. — degree of freedom, i.e., "real" number of cases available for testing a statistical hypothesis (p. 3)
dl/dt — growth rate, in length, of an average fish in a stock (p. 37)
dw/dt — growth rate, in weight, of an average fish in a stock (p. 23)
dB/dt — growth rate of a fish population, in weight (p. 138)
dN/dt — growth rate of a fish population, in numbers (p. 163)
dY/df — increase of catch per unit of effort (p. 122)
D — gill "surface factor", a parameter of the generalized VBGF (p. 23, 24)
— a measure of the "sensitivity" of the output to changes in the inputs of a given model (p. 23, 24)
Δ — any difference; examples are:
ΔL — length increment, width of length class in grouped data (p. 79)
Δt — time difference, e.g., the time needed by an average fish to grow from the lower to the upper limit of a length class (p. 62)
$\Delta L/\Delta t$ — a growth rate expressed as difference equation (p. 45)
ΔT — a temperature difference, e.g., the difference between warmest (T_s) and coldest (T_w) mean monthly temperature (p. 40)
ΔS — size increment, when referring either to length or weight (p. 233)

e — base of the natural (or Naperian) logarithms; e = 2.71828 (p. 12)
E — exploitation rate; E = F/Z (p. 76)
— subscript to express equilibrium, steady state conditions, or stable age population. Used explicitly in Chapter 10 only, however, equilibrium assumption implicit in many models presented in this book (see p. 69-70)
E_{opt} — exploitation rate producing MSY (p. 76)
E_t — terminal exploitation rate, as used in Jones' length cohort analysis (Table 7.7)

f — fishing effort
f_{opt} — level of effort generating MSY (p. 140)
$f_{0.1}$ — level of effort at which dY/df is 1/10 of its value when f is close to zero (p. 172-173)
F — instantaneous rate of fishing mortality (p. 52)
— symbol of the F-distribution (p. 212)
FL — Fork length; length of a fish when measured up to the central rays of the caudal fin (p. 31)
F_{opt} — fishing mortality generating MSY (p. 76)
F_t — terminal fishing mortality, as used in VPA and cohort analysis (p. 100)
$F_{0.1}$ — level of fishing mortality at which the marginal increase in yield per recruit reaches 1/10 of the marginal increase computed at a very low value of F (p. 120, 121)

ϕ — "pseudovalue" of an statistic; used with the jackknife (p. 178)

g — gram (p. 6)
— a coefficient of population decline; the opposite of r_m (p. 163)
G* — biomass increase resulting from the growth of individual fishes; used in Russel's axiom (p. 1)
GM — geometric mean; used to characterize "type II", or "functional" regression (p. 31)

H — coefficient of anabolism, used in the derivation of the VBGF (p. 23)
HM — harmonic mean (p. 132)

i	— symbol or subscript used for counting items; used here only in a few equations (particularly in Chapter 7) where the need for unambiguous definitions made its use necessary
I	— Roman numeral, equal to 1; used to express age (year) groups (Table 4.3)
k	— coefficient of catabolism (equation 4.1)
	— proportion of fish above age t_k in a stock of fish (p. 121, 122)
kn	— knots = 1.852 km/h (p. 97)
K	— "stress factor", a parameter of the VBGF (p. 23)
ln	— $\log_e$, logarithm of base e (p. 13)
log	— $\log_{10}$, logarithm of base 10 (p. 5)
L	— "length" of a fish, shrimp, etc. (length itself is defined differently, depending on what is measured, see TL, SL, FL, etc.) (p. 5)
L′	— a length not smaller than the smallest length of fish fully represented in catch samples; used to compute $\bar{L}$ (p. 55)
$\bar{L}$	— mean length of fish, computed from L′ upward (p. 55)
	— mean of two lengths, e.g., mean of length at tagging (L_1) and at recapture (L_2) (p. 33, Table 4.6)
$\bar{\bar{L}}$	— overall mean length of fish in catch samples (equation 5.10)
L_c	— mean length of fish at first capture; equivalent to L_{50} of other authors (Fig. 3.1)
L_i	— length at the inflexion point of the generalized VBGF, when $D \neq 1$ (Table 4.8)
L_{max}	— maximum length reached by the fish of a given stock (p. 29)
$L_{max.\,ever}$	— largest size ever recorded from a given fish species (p. 29)
L_{min}	— smallest length represented in one, or several samples (p. 10)
L_n	— lower limit of highest length class considered in computing L_c from trawl selection experiment data (equation 3.1)
$\bar{L}_{opt}$	— mean length above L′ in a stock maintained at MSY (p. 146)
L_r	— mean length at first recruitment (p. 68, 114)
L_t	— mean length at age t (p. 23)
L_∞	— asymptotic length, i.e., the mean length the fish of a given stock would reach if they were to grow forever (p. 23)
$L_{(\infty)}$	— preliminary estimate of L_∞, obtained, e.g., through equation (4.16) (see p. 29)
m	— number of fish marked (or tagged) for a Petersen population estimate (p. 91)
m_1, m_2	— proportionality constants in the Lotka-Volterra equation (p. 163)
M	— instantaneous rate of natural mortality, i.e., of mortality due to all causes except fishing (p. 52)
M*	— biomass of fish dying of all causes other than fishing in Russel's axiom (p. 1)
MSY	— Maximum Sustainable Yield (p. 139)
n	— number of items in a sample, number of cases investigated, etc. (p. 6)
	— counter for items; similar in use to "i" (equation 3.1)
	— number of marked fish recovered in a Petersen population estimate (p. 91)
N	— size, in numbers, of a population (p. 91)
	— number of fish in a given size class of a catch sample (p. 60)
No	— abbreviation for number (p. 10)
N_o	— initial number of fish in a cohort (p. 52) or a population (p. 94)
	— total number of fish tagged and released in an experiment (p. 74)
N_r	— number of recoveries per time interval in a tagging experiment (p. 74)
N_T	— number of fish at the end of a generation started with an initial number N_o (p. 155)
N_∞	— environmental carrying capacity for a given stock, in numbers; corresponds to B_∞ (see under this symbol) and to the parameter "K" in the ecological literature (p. 152)
p	— multiplicative factor in equation (4.2a)
p_{ij}	— percentage in gut of species i of food item j (p. 170)
P	— constant in equations (8.10) and (8.11)
	— probability of capture (p. 12)
	— production (p. 53)
	— parents, or parental egg production in S/R relationships (p. 129)
P_m	— parental stock producing maximum recruitment in a Ricker curve (p. 133)
P_r	— replacement abundance of parental stock in a Ricker curve (p. 133)

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Author Index

Included here exclusively are the names *of persons*, i.e., of authors, or other persons mentioned in acknowledgements. The names of persons that are parts of eponyms (e.g., *Schaefer* model, *Lotka-Volterra* equations) are not included. Self-references are omitted.

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  Synthesizes publicly available research studies and secondary data; provides evidence of a trend towards overfishing of Philippine coastal waters, and of a willingness among fishermen to consider alternative activities to capture fishing; the shift in government programs from resource "development" to "management"; concludes with a discussion of the implications of these research findings to fisheries management and research.

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  Proceedings of a workshop in Sydney, January 1981; reviews current research and methodology used in tropical stock assessment; formulates an action plan to overcome present restraints to stock assessment and management of tropical fisheries; includes reviews of the Southeast Asian database on tropical multispecies stocks.

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