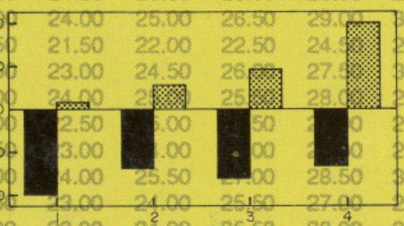
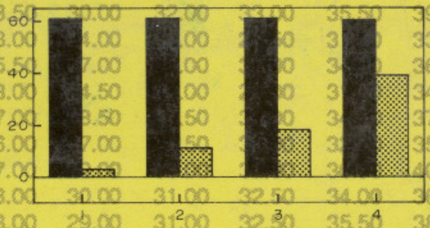
The Accuracy of Some Length-Based Methods for Fish Population Studies

Victoria J. Isaac

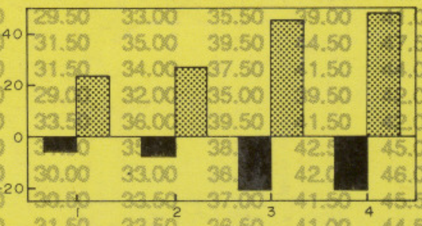
ELEFAN



P-W



SLCA



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FOREWORD

While the first methods for estimating growth from length-frequency data were proposed nearly 100 years ago, it is only in the last decades that these methods have began to be based on rigorous algorithms, rather than on subjective interpretation of hand-drawn curves. This transition was accelerated, obviously, by the wide accessibility of computers, particularly those of the personal kind.

This Technical Report presents a study of the sensitivity of three methods, developed in the 1980s for the analysis of length-frequency data, to one of their key assumptions, namely that the variability of the growth of individual fishes is negligible.

As is shown here, this assumption is not valid, for either of the three investigated methods, and indeed, all three collapse when individual growth variability becomes too high.

This problem had been previously studied - although in less detail than here - for only one of the three methods. That it is shown to also be the case for the other two methods, is a new finding, and only in part a discouraging one.

The reason for continued optimism is essentially that it is better to know one's enemies, as it allows one to take countermeasures. In this case, this possibly involves (i) estimating, from one's data set, individual variability of length about relative age, to infer the degree to which one's growth parameter estimates are affected by individual growth variability and (ii) adjusting one's estimates in the appropriate directions, by an amount determined by the results in (i).

I expect, in any case, that investigations on the reliability of length-based methods will continue, hand in hand with the development of new approaches, and that these studies will eventually lead to methods much more robust than those now in use, but still straightforward to implement. The present contribution is, I believe, a big step in the right direction.

A standard foreword would end here, perhaps after some perfunctory praise to the author. What makes this special - to me at least - is the fact that Dr. Isaac, who wrote the thesis upon which this document is based, was my first PhD student, which certainly added to her problems - not to speak of the fact that I developed, and hence became particularly attached to, one of the methods she was submitting to such cruel tests. As her text shows, she withstood all that, and is to be congratulated.

DANIEL PAULY
Manila, August 1990

ABSTRACT

Length-based methods have lately found widespread use for the estimation of growth in fish populations, especially in tropical areas, because of the various disadvantages presented by "ageing" techniques such as otolith or scale examinations or tagging experiments.

Monte-Carlo simulations of fish populations with different biological characteristics were generated to test the accuracy of some recent methods for the assessment of growth in fishes on the basis of length data. Three methods were investigated: D. Pauly and N. David's Electronic Length-Frequency Analysis (ELEFAN), J.G. Shepherd's Length Composition Analysis (SLCA) and the method derived by J.J. Wetherall from the general model of D.G. Powell referred to as the "P-W method".

The effects of different growth strategies; variability of growth between individual fishes; seasonal oscillations of growth rates; size-dependent gear selection; recruitment variability; variable width of the length classes in the data; and combination of size-at-age and length-frequency data of fish populations were analyzed.

The simulated populations were sampled at random, and the resulting length-frequency distributions were used to estimate the parameters L_∞ and K of the von Bertalanffy growth equation. To determine the magnitude of individual growth variability, the variance of the parameters L_∞ and K between fishes of *Lebistes reticulatus* and of tilapia hybrids were calculated. Additionally, length data sets for 13 species of fish of the family Sciaenidae from various parts of the world were used to test the length-based methods on field data. A sensitivity analysis of the length-converted catch curves, used for estimation of total mortality rate (Z) was performed, and the implications of the input of biased growth parameters for the derivation of mortality rates are discussed.

The principal results and conclusions of this investigation are:

- The ELEFAN and P-W methods are more adequate for fast-growing and short-lived fishes than the SLCA method, which is more suitable for slow-growing and long-lived fishes.
- In most of the experiments a general tendency to overestimate L_∞ and to underestimate K was observed.
- All methods give accurate estimates of L_∞ and K (or Z/K), if individual variability of growth parameters, recruitment variability and selection effects are small. Bias attains unacceptable levels when individual variability of growth parameters is 20% or more.
- When the individual variability of growth parameters is high, ELEFAN provides more accurate estimates of L_∞ than SLCA, which provides more accurate estimates of K. Also, in such cases, the estimates of L_∞ obtained by the P-W method are strongly biased.
- When size-dependent selection or long recruitment periods occur, the estimates of L_∞ obtained using the SLCA or P-W methods are more accurate than those obtained with ELEFAN.
- Seasonal growth oscillations, the presence of two recruitment pulses per year and the width of the length classes used to represent the samples have little effect on the bias of estimates of L_∞ and K (or Z/K).
- The three methods investigated here appear useful for the study of growth in sciaenid fishes. However, the quality of the results depends strongly on two factors: a) the representativeness of the samples and b) the growth strategy of the species in question. Slow-growing fishes were more difficult to analyze. A knowledge of the biology of the species is of considerable help in the interpretation of results.
- Length-converted catch curves underestimate Z when individual variability affects the structure of the length data, but overestimate this parameter when size-dependent selection affects the samples. However, the bias was small when both effects occur simultaneously. Length-converted catch curves tend to have a stronger bias when applied to fishes with a strategy of slow growth and low mortality rate.
- Estimates of Z obtained from length-converted catch curve have a positive correlation with the parameters L_∞ and K, but the effects of changes in K are stronger than those of changes in L_∞.

Chapter 1

INTRODUCTION

Growth studies are an essential instrument in the management of fisheries resources because these studies contribute to estimates of production, stock size, recruitment and mortality of fish populations. The estimation of growth parameters may be based on absolute or relative age of the individual fishes or derived from length-frequency data.

Ageing fishes through the identification of periodic marks on hard structures (otoliths, scales, vertebrae, etc.) and tagging experiments are expensive and time-consuming procedures. In many aquatic animals (e.g., squids, crustaceans, shrimps and various tropical fishes) age determination is very difficult or even impossible.

Moreover, random and systematic errors in age determination occur with the existing ageing techniques (Lee et al. 1983) and bias in growth rate estimates resulting from these techniques may be introduced by the particular statistical procedure used (Ricker 1969).

At the end of the 19th century the Danish biologist J. Petersen (1891) developed the first technique to assess the growth of fishes on the basis of length data. After the erroneous interpretation of the age of North Sea herring by D'Arcy Thompson at the beginning of the 20th century (Went 1972), these techniques were regarded with suspicion, and until 1970, growth studies were fundamentally based on age determinations from the analysis of otoliths, scales, vertebrae, etc. (Pauly 1987).

Since then, however, the above mentioned disadvantages of age-based methods have led to the development, in the past decades, of new methods for analysis of length data for growth and stock assessment. Length data can be collected rather cheaply, and generally do not require specialized staff. Moreover, such data are frequently available in government fishery departments or laboratories. According to Pauly (1987), length-frequency data are probably the most underutilized information on fish resources. The increasing use of microcomputers in fisheries science, even in developing countries, now permits the application of techniques involving sophisticated computing procedures.

Moreover, many biological and fishery processes, e.g. fecundity, predation, selection by gear, etc., are better correlated with size (length or weight) than with age. Many characteristics of marine ecosystems are, broadly speaking, functions of the size of the organisms (Caddy and Sharp 1986). It is therefore being recognized that there are good theoretical justifications for preferring length-based over age-based methods (Gulland 1987a; Pauly 1987).

Because most of the present-day length-based techniques are recent developments, few investigations have been done on their accuracy and sensitivity, or their limits in practice. Several scientists have cautioned against the so-called 'finger methods' (in analogy to the finger applied to the computer keyboard) (Gulland 1987b) and therefore, accuracy studies are very important to warn users of the danger associated with these methods.

This report, based on a doctoral dissertation presented to the University of Kiel (Federal Republic of Germany) analyzes the accuracy of three length-based methods: ELEFAN (Electronic Length Frequency Analysis; Pauly and David 1981), SLCA (Shepherd's Length Composition Analysis; Shepherd 1987) and the regression technique derived by Wetherall (1986) from the general model of Powell (1979) and referred to here as the P-W method.

A description of the theoretical foundations and the practical implementation of each method is presented in Chapter 2. To study the accuracy of the methods, Monte-Carlo simulations of various fish populations were produced and length samples from these simulated populations were analyzed with the three methods (Chapter 3). The bias in the estimates of the growth parameters of the different populations was related to the differences in growth strategy, individual variability, seasonal growth oscillations, recruitment variability, size-dependent selection, and width of length classes in the samples. Also, the effects of adding age information to the length data for the calculations with ELEFAN were also investigated.

To determine the magnitude of the individual variability in growth, the variance of the growth parameters L_{∞} and K was calculated based on length-at-age data obtained from tilapias and guppies kept in aquaria (Chapter 4).

The application of the three abovementioned methods on real data was undertaken in Chapter 5. Twenty-three sets of length-frequency data from various stocks of croakers (Family Sciaenidae) were analyzed. This family was selected because of its economic importance and the relatively large amount of biological information available. Moreover, length-based methods appear particularly promising for the estimation of growth patterns in this group, because it is difficult to age (Isaac 1988); the difficulty in ageing stems from the fact that the otoliths (sagitta) in this fish are usually larger and thicker than in most Perciformes (Chao 1978), and the scales of older sciaenids often present very narrow or indistinguishable rings.

Finally, some implications of the use of biased growth parameters for the estimation of total mortality (Z) using length-converted catch curves were examined (Chapter 6).

Chapter 2

LENGTH-BASED METHODS FOR GROWTH STUDIES

Introduction

Length-based methods for stock assessment may be classified into two groups: a) analytic and b) synthetic (Shepherd et al. 1987). *Analytic* methods are used to estimate vital parameters which determine the structure of a stock. *Synthetic* methods use the length data and the information obtained from analytic methods to perform assessments of a stock, e.g., yield- and biomass-per-recruit computations.

Analytic methods may be subdivided into those used to determine growth parameters, those used to estimate mortality, and those used to estimate both. Several such methods have been developed in the last decades.

However, the principle involved in methods for the estimation of growth parameters from length data is not new. Petersen (1891) developed their basic principle by attributing successive ages to the most pronounced modes of mixed distributions. This triggered the development of a variety of graphical and other methods for the separation of mixture of distribution into their components, assumed to be normal distributions (Harding 1949; Cassie 1954; Hasselblad 1966; Bhattacharya 1967; Abramson 1971; MacDonald and Pitcher 1979; Pauly and Caddy 1985).

Recently, Schnute and Fournier (1980), Fournier and Breen (1983), Sparre (1987) and Pope (1987) presented sophisticated improvements of these techniques. To follow the progression of a cohort through time, samples weighted by catch per effort are linked by a von Bertalanffy growth curve. Assumptions on mortality rate and initial cohort strength are used to calculate the location of each cohort in the next sample and how large its contribution to the mixture distribution should be. Expected frequencies and observed frequencies are then compared through a statistical criterion, such as chi-square or a maximum likelihood estimator. These methods require a large number of assumptions, and the number of parameters which must be optimized is very high, making the computation very time-consuming.

Moreover, these "mixture methods" require the lengths of the fishes of a cohort to be normally or log normally distributed, the number of cohorts in each sample to be specified, and the length frequencies to be proportional to the population.

Different approaches, perhaps not so rigorous from a statistical point of view, were presented in the form of the ELEFAN I (Electronic Length Frequency Analysis; Pauly and David 1981) and SLCA (Shepherd's Length Composition Analysis; Shepherd 1987) computer programs. The principle of these techniques is simple: given a set of growth parameters and a growth equation, an index of the coincidence between observed and expected modes of the available length-frequency data is computed and used to indicate the adequacy of the assumed growth parameters.

Finally, the P-W method constitutes a very simple and quick procedure to estimate the asymptotic length and the ratio Z/K of a population, based on the structure of a single length sample representative of the (steady-state) population.

The principal advantage of the three latter methods (ELEFAN, SLCA and P-W) is that they are relatively simple in their application and require very few assumptions to be met. This provides a strong incentive for their use. This investigation is intended to contribute to the knowledge about these techniques, the risks associated with their use and the precautions to be taken when using them.

The ELEFAN Method

The ELEFAN system was initially developed by Pauly and David (1980, 1981) and Pauly (1982) for the estimation of growth parameters and mortality in fish populations, and later improved by Brey and Pauly (1986) and Brey et al. (1988). Most of its implementations are in BASIC and are designed to be used on microcomputers. The system has recently been revised, expanded and presented as a comprehensive software package which incorporates various new routines for length-based fish stock assessment (Gayanilo et al. 1988; Gayanilo and Pauly 1989).

For the present study, a FORTRAN-77 version of ELEFAN I, which includes all routines of the original ELEFAN I and ELEFAN II programs of Brey and Pauly (1986) and Brey et al. (1988) was developed by J. Sommer (pers. comm.) for a VAX 780 computer. The listing of the program is available at the Department of Fisheries Biology of the Institute of Marine Research of the University of Kiel or from ICLARM.

Estimation of growth parameters

The first part of the program (ELEFAN I) fits a seasonally oscillating version of the von Bertalanffy growth function (VBGF),

$$L_t = L_\infty(1\text{-}\exp(-K(t\text{-}t_0)+CK/2\pi \sin 2\pi(t\text{-}t_s))) \qquad \textbf{...2.1)}^a$$

where

L_t = predicted length at age t
L_∞ = asymptotic length
K = growth constant
C = amplitude of the seasonal growth oscillations
t_0 = "age" at $L_t = 0$
t_s = age at the onset of first growth oscillation,

to one or more length-frequency distributions, estimating the parameters L_∞, K, C, and Winter Point (WP = t_s + 0.5, or the time of the year at which growth is slowest). It should be noted that when only one sample is available, the seasonally oscillating version of the VBGF cannot be applied.

Requirements of the method are:

- Samples must be representative of the structure of the population;
- Growth must follow the von Bertalanffy model modified for seasonal growth;
- Recruitment must occur in seasonal pulses.

Not required are:

- Regularly spaced samples;
- Catch and/or effort data;
- Normality of the distributions of lengths about successive ages;
- Knowledge of the number, position and standard deviation of successive mean lengths-at-age.

The identification of modes (or peaks) is obtained through a so-called "restructuring" procedure, performed for each sample via the following steps:

a. Computation of a moving average over 5 length classes;

[a]Since this was originally written, and the corresponding simulations performed, equation 2.1 has been shown to generate a bias in the estimation of t_0 (see e.g., Somers 1988 (Fishbyte)); this contribution does not deal with t_0 and hence is not affected by this bias. The most recent version of ELEFAN include a growth equation which overcomes this problem.

b. Calculation of the adjusted frequencies, by dividing the observed frequencies of each class by the corresponding moving average;
c. Computation of the relative adjusted frequencies by dividing the adjusted frequencies by the average of all adjusted frequencies within a sample, then subtracting 1;
d. A procedure to avoid the attribution of extreme values to isolated frequencies (adjacent to zero frequencies), generally at either end of the distributions;
e. A procedure to obtain equal sums of positive and negative values within a sample[b].

After restructuring a sample, either a positive value (peak), a negative value (trough) or a zero value corresponds to each length class.

Fig. 2.1 shows an example of the effect of restructuring the data in a hypothetical sample (from Pauly 1987, based on Goeden 1978). In this context, groups ("runs") of adjacent length intervals with positive values are assumed to potentially represent cohorts.

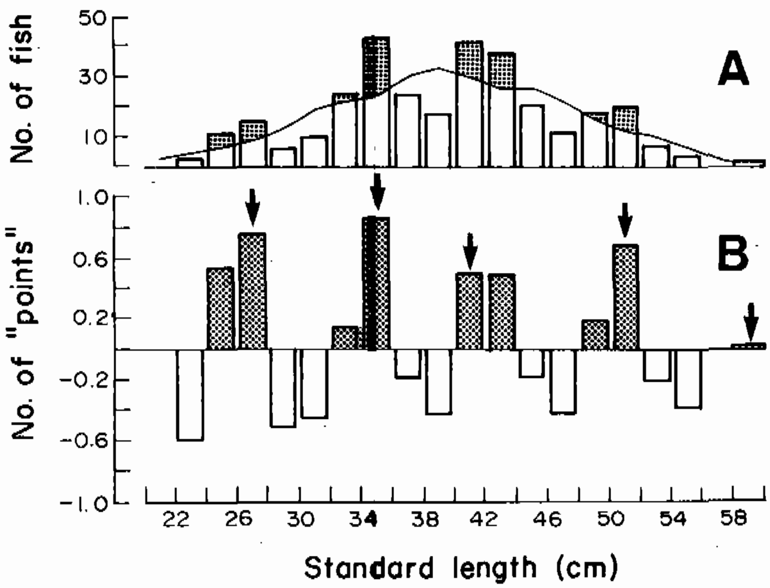

Fig. 2.1. a) Original length-frequency data and running average frequencies over 5 length classes. Peaks are represented by the shaded areas above the running average. b) Data after the restructuring process. Arrows show the points used in the computation of ASP (modified from Pauly 1987).

The Available Sum of Points (ASP) is the sum, for all samples, of the points with a maximum value in each "run" of positive values.

To fit the growth model (i.e., VBGF), ELEFAN I traces numerous growth curves through the restructured data according to a set of growth parameters chosen by the user. For a given combination of growth parameters, the Explained Sum of Points (ESP) is the sum of all points (negative and positive) over which each curve runs.

The best combination of parameters will produce a curve which hits most peaks, avoids most troughs and thus obtains the highest ESP value. The relation ESP/ASP may range from a negative value to unity (depending on the data), and higher values indicate better fit. If a curve hits a single "run" repeatedly, the recent versions of ELEFAN I, including the FORTRAN-77 version used here, add the corresponding points only once to the ESP score (Pauly 1986).

This treatment of the length-frequency data may produce undesirable effects, particularly at the end of the distribution. Table 2.1 shows the results of the restructuring process on a simulated sample with 5 cohorts. As a consequence of the algorithm, the frequency of the fourth cohort (originally 3 fishes) is converted to a negative value (-0.483), i.e., to a trough located between two "cohorts" (see arrows in Table 3). Consequently, the program will try to avoid this point.

[b]Details in Brey et al. (1988).

Table 2.1. Example of restructuring effects on a hypothetical sample with 17 classes and five cohorts. Arrows indicate the mode of the fourth cohort.

	FREQUENCY fi	Moving average MAi	fi/MAi FAi	FAi/FA-1 F'i	Adjust for 0 frequencies	All -1=0	Neutralization	Results	
	185	40.8	4.534	3.435	0.429			0.429	
	19	40.8	0.466	-0.545			-0.873	-0.873	
	0	40.8	0.000	-1.000		0.000		0	
	0	3.8	0.000	-1.000		0.000		0	
	0	0	0.000	-1.000		0.000		0	
	0	6.2	0.000	-1.000		0.000		0	
	0	10.6	0.000	-1.000		0.000		0	
	31	10.6	2.925	1.860	0.233			0.233	
	22	10.6	2.075	1.030	0.129			0.129	
	0	10.6	0.000	-1.000		0.000		0	
	0	7.4	0.000	-1.000		0.000		0	
	0	3	0.000	-1.000		0.000		0	
	15	3.6	4.167	3.075	0.384			0.384	
	0	3.6	0.000	-1.000		0.000		0	
----->	3	4.2	0.714	-0.301			-0.483	-0.483	<-----
	0	1.2	0.000	-1.000		0.000		0	
	3	1.2	2.500	1.445	0.181			0.181	

FA(mean) 1.022 SUM(+) = 1.356; SUM(-) = -0.846; RATIO = 1.603

Because the actual age of each cohort is unknown, length data alone do not permit the calculation of t_0. To fix the curve to a point of the abscissa, a "starting point" must be determined, at the base of any length class. From this point, the curve will be projected backward and forward. Thus, the Starting Point (SP) becomes the parameter of the model which replaces t_0.

Early versions of ELEFAN I were unable to estimate values of L_∞ smaller than L_{max} (i.e., the largest fish in the data), but this problem has been overcome in later versions, including the FORTRAN-77 version used in this study.

This FORTRAN-77 version of ELEFAN I allows the input of any number of samples, without a limitation as to the number of classes. The curve fitting procedure can calculate values of ESP/ASP for an unlimited number of parameter combinations, but the necessary calculations would be time-consuming. A run of the program using a file of 12 samples with 31 classes, using 10 different values each for L_∞, K, C and WP and a *fixed* Starting Point took over 12 hours CPU time on a VAX 8550 minicomputer!

For all calculations done with ELEFAN I in this study, the ESP/ASP ratio was determined for a very wide range of parameter combinations using a 'response surface' procedure. To guarantee objectivity, the combination with the highest value of goodness-of-fit (ESP/ASP) was always chosen, even when more than one maximum was found. When the same highest value of ESP/ASP corresponded to several adjacent parameter combinations, the combination closest to the simulation input parameters of the simulation was selected over the others.

Another important feature of the ELEFAN I approach is that independent information on the age of the fishes, i.e., tagging data or length-at-age data can be included and combined with the length-frequency data (Morgan 1987). Due to the mathematical problem related to the estimation of t_0 on the basis of length data (see above), a procedure to convert the length-at-age data into length increments with a structure similar to tagging/recapture data is used, thus avoiding the confusion of absolute and relative ages.

Given a set of individual ages, lengths and dates of sampling, the data are arranged in ascending order according to the age they pertain to. Combinations of lengths between adjacent ages are randomly selected to represent the size increments. With such a set of increments (L_1, t_1 ; L_2, t_2) and any combination of growth parameters, it is possible to calculate the theoretical length that an animal with length L_1 at time t_1 would have at time t_2. It is then possible to calculate the difference existing between the theoretical and the observed length increments, and the program searches for the growth parameter combination that minimizes the variance of these differences. Thus, it becomes possible to combine length-frequency data with age data. A new value of goodness-of-fit (GA = goodness-of-fit of age data; GT = goodness-of-fit of tagging-recapture data) for the length increment data procedure is calculated:

$$GA = (V_e - V_d)/V_e \qquad ...2.2)$$

where

V_e = variance of empirical length increments

V_d = variance of the difference between empirical and theoretical length increments,

and similarly for GT.

Finally, the program computes the average goodness-of-fit of both sets of data (i.e., of the length increment data and the length-frequency data).

Estimation of total mortality (Z)

The first part of the ELEFAN II program includes a routine for estimation of total mortality (Z) using a length-converted catch curve. Additionally, probabilities of capture by length and the seasonal pattern of recruitment are estimated from the left, ascending arm of the length-converted catch curve.

A set of samples representing the structure of a stable age-distributed population is required. A "pooled" sample is created with all or part of the length data, the aim here being to simulate a steady-state population. "Length-converted" catch curves are created by plotting ln $(N_i/\Delta t)$ against relative age t_i. A first estimate of Z is obtained when the following function is adjusted to the points of the right descending arm of the catch curve:

$$\ln (N_i/\Delta t) = a + b\, t_i \qquad ...2.3)$$

where

N_i = number of fish in the i-th length class

Δt = time required for the fish to grow through length class i

and

$$Z = -b \qquad ...2.4)$$

The program includes an iteration procedure (Sparre, pers. comm. to Pauly in 1984) to correct this estimate of Z for the nonlinearity of the growth model and for the mortality which occurs within each length class. However, this new estimate was not used in the present investigation, because in most of the cases it resulted in a higher bias than the linear regression estimate.

The estimation of Z requires estimates of the growth parameters and involves the following assumptions:

- Z is constant over all sizes classes included in the calculation;
- Recruitment varies little and randomly.
- The underlying selection curve is of the "trawl type" (see below).

The selection of the points to be included in the estimation of Z is probably the most sensitive part of the whole procedure. Usually the first point included is the point immediately to the right of the highest point.

Calculation of probabilities of capture

Under the assumption of a trawl-type selection, the left arm of a length-converted catch curve consists of fishes which are too small to be retained by the gear. If natural mortality (M), acting on the lowest length classes and total mortality (Z), acting on the fully recruited classes are known, the mortalities between the first and the last class of the left, ascending arm of the catch curve can be interpolated. Consequently, one can calculate the number of fishes that should have been caught in each length class if the effect of selection did not exist. The corresponding probability of capture can then be obtained from the ratio between observed and expected frequencies (Pauly 1987). Fig. 2.2 illustrates the principle of this method.

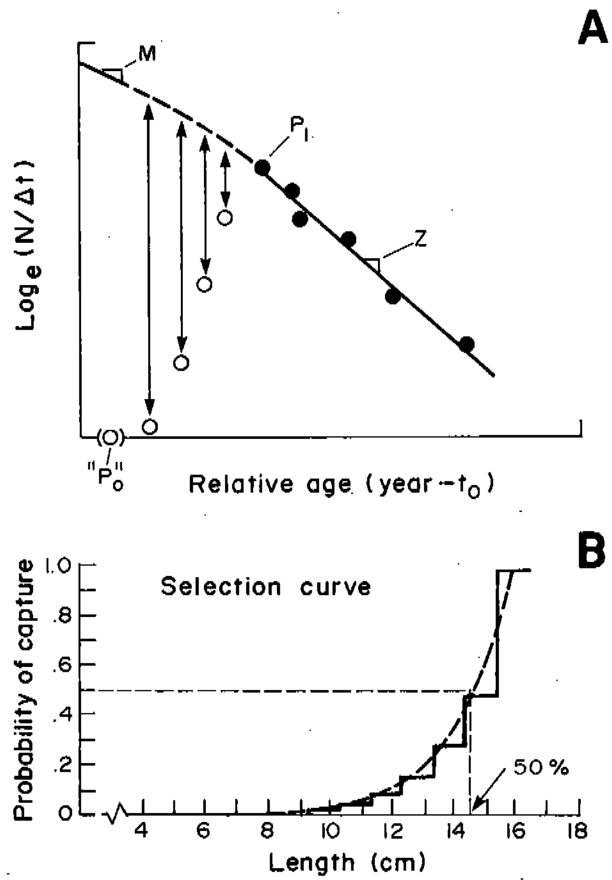

Fig. 2.2. a) Derivation of a length-converted catch curve based on growth parameters and a pooled length-frequency file; the backward projection of the catch curve is used to estimate the number of fish that would have been caught in the absence of selection. b) Estimation of the probability of capture (modified from Pauly 1987).

The method has the following assumptions:

- The gear in question is a trawl or has the selection curve of a trawl;
- The smallest fish caught are fully recruited to the fishery;
- The mortality values used for the calculation are accurate.

If the second of these assumptions is violated, the computed probabilities correspond to a resultant curve, i.e., to the product of a selection and a recruitment curve (Gulland 1983).

The probability of capture at lower sizes can be used to correct a length-frequency data set for selection effects, and the ELEFAN packages include routines which allow for easy implementation of this approach (Brey and Pauly 1986; Pauly 1987; Gayanilo et al. 1988).

Recruitment pattern calculation

The recruitment of a natural fish population does not generally represent (even in the tropics) a continuous introduction of young fishes into the exploitable stock, but rather corresponds to a seasonal pattern with one or more (usually two) pulses during an annual cycle (Longhurst and Pauly 1987). This mechanism is responsible for the existence of peaks representing cohorts in the length distributions.

Thus, if we know the cohort structure and the growth parameters of a population, it becomes possible to reconstruct the pulses of the annual recruitment. Pauly's (1982) implementation of this approach assumes the same growth parameters for all fish in samples used to derive a given recruitment pattern. This assumption is known to increase the width of apparent recruitment pulses (Pauly 1987).

The resulting recruitment pattern has the following features:

- The absolute position of the recruitment frequency on the time axis is not known, because the true value of t_0 is unknown;
- For procedural reasons, the output is standardized to give zero recruitment in one month.

Given a set of growth parameters and assuming $t_0 = 0$, the derivation of the recruitment pattern can be summarized as follows:

a. Backward projection of each length class, estimating the "month" in which length would have been zero;
b. Because the accuracy of the calculations decreases with age, the frequency of each length class is weighted by dividing it by the time (Δt) needed by the fish to grow through a length interval;
c. All values obtained for one "month" are added up;
d. The lowest monthly score is subtracted from every monthly score;
e. The relative "monthly" recruitment values are expressed as percentages of total annual recruitment.

Fig. 2.3 illustrates this procedure to estimate the recruitment pattern on the basis of length data and a set of growth parameters.

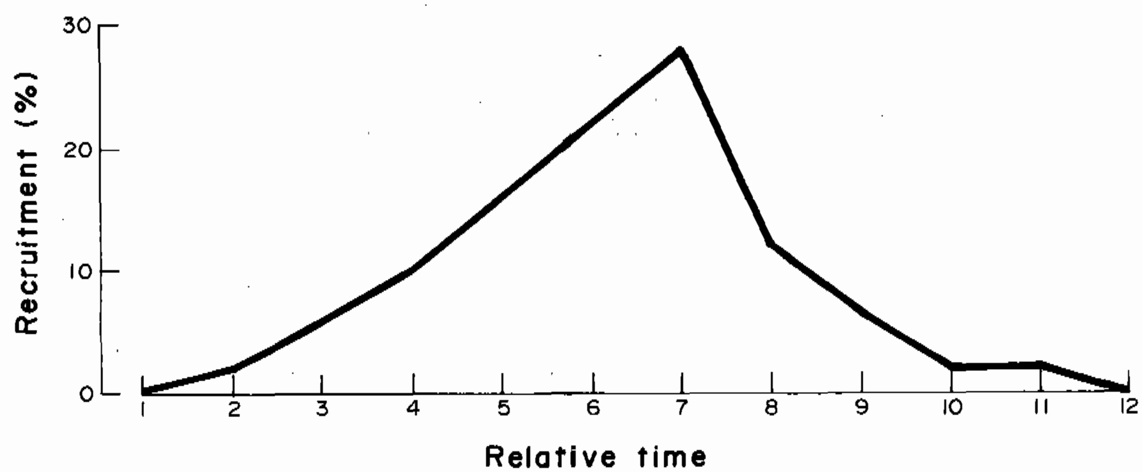

Fig. 2.3. Example of the recruitment pattern obtained with ELEFAN II. The numbers on the abscissa only correspond to successive months and not to actual months of the year.

The SLCA Method

Shepherd's Length Composition Analysis (SLCA) is conceptually similar to ELEFAN I in that it is based on the optimization of the goodness-of-fit index obtained by comparing the position of the modes of one or more length compositions with the location of expected modes (from a VBGF). SLCA has the same data requirements as ELEFAN I.

A test function is calculated for a growth curve as goodness-of-fit criterion. The algorithm is known as "complex demodulation" and is similar to that used in time series analysis. The growth parameters L_∞, K and t_0' are estimated (the latter is conceptually not the same as t_0 values that can be obtained from size-at-age data).

The original FORTRAN-77 program of Shepherd (1987) was slightly modified for the present study. Length-frequency data must be entered to the program in the same format as for the ELEFAN I program.

Score values can be obtained in a matrix of up to 100x100 combinations of L_∞ and K. The criteria used to choose the best combination of growth parameters were the same as given above for ELEFAN I.

The SLCA method uses the growth function of von Bertalanffy (VBGF) and uses as score function

$$L_t = L_\infty(1-\exp(-K(t+tsd-t_0'))) \qquad ...2.5)$$

where

L_t= predicted length at age t
L_∞= asymptotic length
K = growth constant
t_0'= "age" at L_t = 0
tsd= fraction of year until sampling date.

The published version of the method does not include a parameter for seasonal oscillations in the growth model, although it would be possible to do so.

Given values for L_∞, K and t_0, the predicted modal lengths L1, L2, L3, etc, for t = 1,2,3, etc. can be calculated using the growth function. The observed frequencies occurring at or near these predicted lengths may be interpreted as confirming the adequacy of the current parameters. On the other hand, the current parameters do not explain the observed frequencies occurring near the predicted intermodal lengths L0.5, L1.5, L2.5, etc.

The method uses a test function defined as follows:

$$T(l) = \frac{\sin c\,(t_{max} - t_{min})}{c\,(t_{max} - t_{min})} \cos 2c(t_a\text{-}tsd) \qquad ...2.6)$$

where

T(l)= test function
t_{min} = age at the lower limit of a length class
t_{max} = age at the higher limit of a length class
t_a = average of t_{max} and t_{min}

The function is positive near the predicted modal lengths and negative near the intermodal lengths.

The first term of this equation becomes small when there is more than one mode in an interval, and in this case the weight of such observations is reduced, especially for length classes near L_∞.

The sum of the values of the test function multiplied with the square root of the number of individuals observed in each class, is used as criterion of goodness-of-fit:

$$S = \sum_l \sum_i T(l,i) \sqrt{N(l,i)} \qquad ...2.7)$$

where

S = score
l = index for the length class
i = index for the sample
N = number of individuals

Since t_{min}, t_{max} and T(l) are periodic in t_0 (period=1), the procedure also allows the estimation of t_0'.

Thus, for given values for L_∞ and K,

$$t_0' = \frac{1}{2\pi} \arctan(B/A) \qquad ...2.8)$$

where

A = value of S obtained with $t_0 = 0$

B = value of S obtained with $t_0 = 0.25$

However, the relationship of the parameter t_0' to "real" t_0 values is not discussed further in this contribution.

The P-W Method

Wetherall (1986) and Wetherall et al. (1987), based on Powell (1979) developed a technique from the principle that the shape of a representative size distribution of a population is determined by the value of the asymptotic length (L_∞) and the ratio between the total mortality rate and the growth constant (i.e., by Z/K). These parameters are then estimated by means of a relatively simple regression calculation.

Requirements for the application of the method are:

- The sample is representative of a steady-state population, i.e., recruitment and mortality are constant;
- Recruitment is continuous;
- Growth follows the von Bertalanffy model (without seasonal oscillations);
- Growth is deterministic, i.e., there is no individual variability in the growth parameters.

Because a steady-state population is difficult to find in nature, the length samples available from a population with discontinuous recruitment are pooled into one sample, which will usually lead to a reasonable approximation of a steady-state distribution. Moreover, the fishes that are not fully selected are not considered.

The P-W method is based on the method of Beverton and Holt (1956) for estimating Z from mean length (L).

$$Z = K \left(\frac{L_\infty - L}{L - L'}\right) \qquad \text{...2.9)}$$

where

L_∞ = asymptotic length

K = growth constant

L = mean length of the fishes above L_c

L' = a length upward of which the fishes are fully selected.

Rearranging this equation and considering L and L' as variables,

$$L = L_\infty \left(\frac{1}{1 + Z/K}\right) + L' \left(\frac{Z/K}{1 + Z/K}\right) \qquad \text{...2.10)}$$

which implies that the mean length (L) is a linear function of the cutoff length (L').

The idea of the method is to partition the length-frequency sample using a specified sequence of L' values. Thus, for a series of arbitrary cutoff lengths (L'_i), it is possible to calculate the corresponding L_i, i.e., the mean length of all fishes longer than the actual L'. In practice, L'_i values are taken as the lowest limits of each length class (i).

A regression analysis of such a data series provides an estimate of the intercept (α) and of the slope (β) of the linear function. With

$$\alpha = \frac{L_\infty}{1 + Z/K} \qquad \text{...2.11)}$$

and

$$\beta = \frac{Z/K}{1 + Z/K} \qquad ...2.12)$$

which can be solved for the parameters L_∞ and Z/K as:

$$L_\infty = \frac{\alpha}{1 - \beta} \qquad ...2.13)$$

and

$$Z/K = \frac{\beta}{1 - \beta} \qquad ...2.14)$$

It is possible to calculate the variance of the estimates, but such calculations were not included in the program used in this study.

The method was slightly modified by Pauly (1986) and included as a subroutine in the ELEFAN package, as an option to obtain a preliminary estimate of L_∞. Thus, instead of plotting successive mean lengths (L_i) against their corresponding L'_i, the difference (L_i - L'_i) can be plotted against L'_i. Thus,

$$L_i - L'_i = \alpha + \beta L'_i \qquad ...2.15)$$

the parameters being,

$$L_\infty = \alpha/-\beta \qquad ...2.16)$$

and

$$Z/K = \frac{1 + \beta}{-\beta} \qquad ...2.17)$$

This modification permits graphic visualization of L_∞ as the point where the line intercepts the abscissa.

Because the results obtained with the P-W method depend on the length classes included in the regression, only the points belonging to the right side of the mode of the underlying distribution were used, beginning with the point corresponding to the mode itself.

Discussion

Many questions concerning the methods appropriate for stock assessment in developing countries have been raised during the last few years. Evaluations of the strengths and weaknesses of numerous recently developed techniques are of particular interest (Csirke et al. 1987), and this was one of the objectives of the present investigation.

The three methods chosen for this purpose are simple in their application and require few preliminary assumptions. All are based on the von Bertalanffy growth model and can analyze one or more irregularly-spaced length data samples.

The following advantages and disadvantages have generally been attributed to these methods:

	Advantages
ELEFAN-I	Allows the analysis of seasonal growth oscillations. Length-at-age data or tagging data can be incorporated. The program is part of a comprehensive system which also permits other analyses of the same data set.
SLCA	No preliminary treatment of the original data is needed to identify the peaks. Gives less weight to length intervals with more than one expected age mode.
P-W method	Rigorous, but simple. Allows the computation of the variance of L_∞ and Z/K.

	Disadvantages
ELEFAN-I	Pretreatment of the data may produce changes in their structure.
SLCA	Growth is calculated on the basis of the von Bertalanffy model, but does not consider seasonal growth oscillations.
P-W method	The parameter K is not estimated, i.e., only the ratio Z/K is calculated.

All three methods require representative samples of a population but catch and/or effort data are not needed.

Recently, some studies have attempted to determine possible sources of error in these and other length-based methods (Hampton and Majkowski 1987b; Damm and Herrmann 1986; Basson et al. 1988), but a comprehensive investigation has still been lacking.

Sophisticated techniques developed in industrialized nations are not immediately available in tropical countries, mainly due to lack of communication (Coates 1987; Csirke et al. 1987), even though fishery scientists in these countries have a great demand for reliable stock assessment methods which permit the management of the fish resources. Because of their simplicity, the methods analyzed here can be of considerable help in growth studies, but their limitations must also be considered.

Chapter 3

ACCURACY OF LENGTH-BASED METHODS

Introduction

Length-based methods have lately come into widespread use for determining vital parameters in exploited aquatic stocks, especially in tropical countries (Venema et al. 1988). Investigations on their accuracy, sensitivity and applicability, however, are scarce, and the theoretical and practical problems associated with these methods were the topic of an international workshop held in 1985 in Sicily, Italy (Pauly and Morgan 1987).

To determine the accuracy of vital parameter estimates obtained with a given growth assessment method, we should know the actual or theoretical value of those parameters in the population. Then we can calculate the difference between their real value and those obtained by applying the method in question.

However, when we consider a natural fish population, we never know the true values of vital parameters. Therefore, a straightforward procedure to analyze the efficiency of any method is to create (or simulate) a hypothetic "population", with known characteristics as similar as possible to those of natural populations. Then we can extract a set of data (for example length data) for the desired analysis. The difference between simulated and calculated values (in this case the growth parameter values) provides a measurement of the accuracy of the method, i.e., the bias of the method. This approach belongs to the so-called Monte-Carlo methods (Halton 1970).

An advantage of such artificial "populations" is that we can create as many sets of data as we need. A wide range of population "types" can be obtained by varying biological features of the model, i.e., the input parameters of the simulation. Today's wide accessibility of computers makes the application of Monte Carlo techniques a standard tool.

In summary, a Monte-Carlo procedure can test the ability of certain methods to describe the underlying structure of any simulated data set, and in this way, it becomes possible to indicate under which conditions a method will or will not perform acceptably in the study of natural populations.

Materials and Methods

Generation of stochastic variates

To implement the simulation of the samples, several stochastic variates must be generated to determine the structure of the simulated data. These stochastic variates may correspond to one of the following probability distributions:

a. Exponential

$$f(x) = \exp(-x) \qquad \text{...3.1)}$$

b. Normal

$$f(x) = \frac{1}{\sigma \sqrt{2\pi}} \exp\left(- \frac{(x - \mu)^2}{2\,\sigma^2} \right) \qquad \text{...3.2)}$$

c. Gamma

$$f(x) = x^{\alpha - 1}\, \beta^{\alpha} \exp(- \beta x) / \Gamma(\alpha) \qquad \text{...3.3)}$$

For the generation of *exponential* variates the method described in Ahrens and Dieter (1972) was used, based on the premise that a value x can be sampled from its probability distribution f(x) by using the inverse of the function f, i.e., f^{-1} and a random variable u [0,1], so that

$$x = f^{-1}(u) = -\ln(u) \qquad \text{...3.4)}$$

For the simulation of *normally* distributed variates, the approximation technique to obtain standardized normal variates (N[0,1]) described in Bauknecht et al. (1976) was used, in which

$$z = \left(\sum_{i=1}^{12} u_i \right) - 6 \qquad \text{...3.5)}$$

where

u_i = successive uniform-distributed random variates from interval [0,1].

A normal variate x, with mean μ and standard deviation σ is obtained as:

$$x = z\,\sigma + \mu \qquad \text{...3.6)}$$

The procedure used to generate *gamma*-distributed variates with parameters α and β implies a complex succession of procedures, which are described in Jöhnk (1964). Gamma distributions constitute a family of very flexible statistical distributions ranging from slightly skewed bell-shaped to J-shaped distributions, which include both the exponential and the chi-square distributions. Gamma-distributed variables are always positive. When the parameter α approaches ∞, the distribution approaches a normal distribution. The parameters α and β control the shape and the relative position of the curve. The mean and variance of a given variable were defined as follows (Fisz 1980):

$$\mu_1 = \alpha/\beta \qquad \text{...3.7)}$$
$$\sigma_2 = \alpha/\beta^2 \qquad \text{...3.8)}$$

Fig. 3.1 shows some gamma distributions with successively varying parameters α and β.

The quality of the random variate generators described above was tested for both normal and gamma variates. A set of 2,000 normal- and gamma-distributed variates were generated in each of 8 different experiments, with means varying from 0.01 to 1.2, and coefficients of variation varying from 10 to 40%. Averages, standard deviations and the gamma parameters α and β were then computed from each set of data. The differences between these computed values and those initially assumed in each experiment give a measure of the bias of the procedures to generate normally and gamma-distributed variates (Table 3.1).

The results show that the technique works very well for normally distributed variables; low bias occurred, even when high variabilities are simulated.

The method for the gamma variates has low bias when low variabilities are simulated. With coefficients of variation of 30 to 40% of the mean, the bias is negative and higher than 5%.

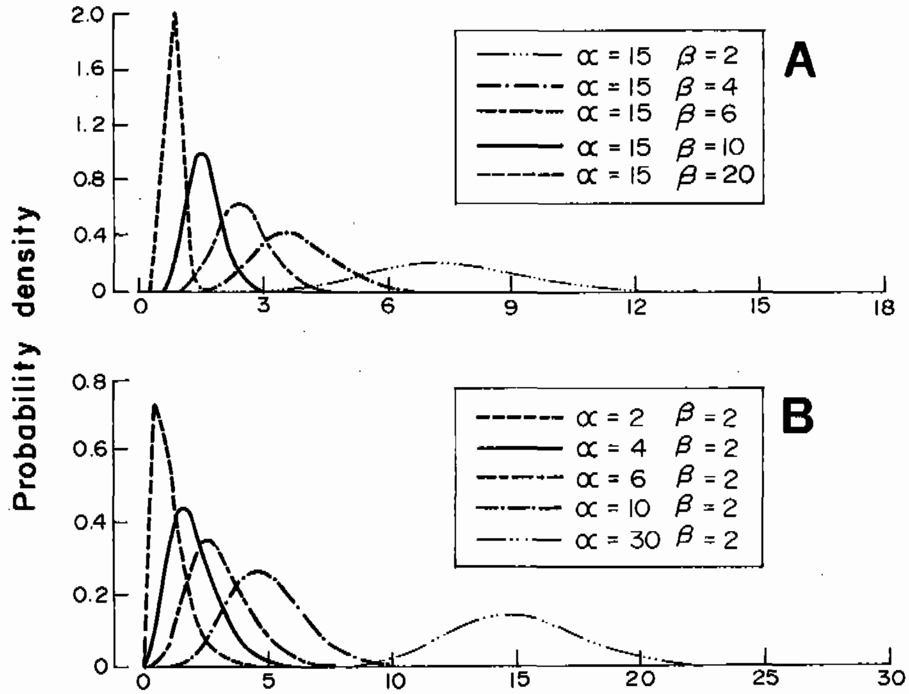

Fig. 3.1. Gamma distributions with different values for the parameters α and β.

Table 3.1. Comparison of the computed and assumed parameters in 8 experiments to generate normally and gamma-distributed variates. Bias are expressed in percentage of the assumed parameters. (N = 2,000 in all experiments).

	Parameter	1	2	3	4	5	6	7	8
	Mean	0.01	0.01	0.05	0.05	0.05	0.05	1.2	1.2
	S.D.	0.001	0.004	0.005	0.01	0.015	0.02	0.012	0.48
Simulated									
	C.V.(%)	10	40	10	20	30	40	10	40
Values	Alpha	100	6.25	100	25	11.11	6.25	100	6.25
	Beta	10,000	625	2,000	500	222.22	125	63.33	5.21
Estimated	Mean	0.0100	0.0100	0.0500	0.0499	0.0504	0.0500	1.1986	1.2066
	Bias (%)	-0.12	0.08	-0.08	0.28	-0.77	-0.06	0.11	-0.55
Values	S.D.	0.0010	0.0040	0.0050	0.0101	0.0146	0.0203	0.0117	0.4856
	Bias (%)	0.40	-0.83	0.00	-0.50	2.75	-1.45	2.13	-1.18
(Normal)	Minimum	0.0067	-0.0017	0.0320	0.0205	0.0012	-0.0121	0.8396	-0.2735
	Maximum	0.0135	0.0227	0.0650	0.0818	0.0952	0.1208	1.5576	2.6718
	Mean	0.0099	0.0107	0.0493	0.0498	0.0532	0.0534	1.1998	1.2896
	Bias (%)	1.23	-7.48	1.40	0.35	-6.30	-6.83	0.01	-7.47
Estimated	S.D.	0.0010	0.0041	0.0049	0.0100	0.0152	0.0211	0.0120	0.4952
	Bias (%)	-0.70	-3.13	1.58	-0.03	-1.38	-5.66	-0.39	-3.17
Values	Alpha	97.4300	6.7902	100.3820	24.8091	12.2161	6.3892	99.2013	6.7823
	Bias (%)	2.57	-8.64	-0.38	0.76	-9.96	-2.23	0.80	-8.52
(Gamma)	Beta	9,864.12	631.76	2,036.06	497.94	229.84	119.61	82.68	5.26
	Bias (%)	1.36	-1.08	-1.80	0.41	-3.43	4.31	0.78	-0.94
	Minimum	0.0071	0.0017	0.0340	0.0228	0.0168	0.0130	0.8376	0.2551
	Maximum	0.0135	0.0311	0.0650	0.0880	0.1145	0.1845	1.6702	3.5386

Simulation model

The size and structure of an exploited fish population is basically regulated by four processes (Russell 1931; Ricker 1975):

- *recruitment;*
- growth;
- natural mortality; and
- fishing mortality.

The simulation model used for this study, a modified version of a program developed by Hampton and Majkowski (1987a), takes these four processes into account, and implements a simulated sampling procedure to obtain length-frequency data.

The most important characteristics of the model are:

- Each cohort (i.e., all the fishes belonging to one recruitment pulse) is treated individually. The life of each recruit is traced from the time of recruitment to the time of death (due either to natural causes or to fishing);
- Yearly cohort strength (N_r) is assumed to be a random normal variate;
- Age at recruitment (t_r) is determined by generating a gamma random variate with mean α/β and variance α/β^2 (see Equations 3.3, 3.7 and 3.8);
- Recruitment can be uni- or bimodal, i.e., fishes may recruit at two different ages; in the case of bimodal recruitment, the proportion of recruits corresponding to each pulse can be determined;
- Individual growth follows a von Bertalanffy equation, modified for seasonal oscillations (Pauly and Gaschütz 1979; see Equation 2.1);
- The von Bertalanffy growth parameter L_∞ varies between individual fishes according to a normal distribution, and is always expressed in cm;
- The von Bertalanffy growth parameter K varies according to a gamma distribution, with a mean of α/β and variance of α/β^2, and is always expressed in year^{-1};
- The amplitude parameter C (Equation 2.1) and the von Bertalanffy growth parameter t_0 have the same values for all fishes; however, because $t_s = (t_r - 0.5)$ and t_r varies between individuals, t_s is variable;
- The cumulative probability distribution of time between recruitment and death due to either natural causes or encounter with the fishing gear is defined as:

$$f(t) = 1 - \exp(-(F+M)(\underline{t}-T_0)) \qquad \text{...3.9)}$$

where

$\underline{t}$ = time of natural death/encounter with the fishing gear
F = fishing mortality
M = natural mortality
T_0 = time of recruitment

The exponentially distributed variable $\underline{t}$ was generated using the inverse function method explained above (Equation 3.4). Theoretically, $\underline{t}$ can assume values ranging from T_0 to ∞, but for computational convenience the upward limit was set to T_{max} = 40 years;

- The rates of natural and fishing mortality (M and F) are assumed to be constant for all fishes;
- The probability of fish death due to natural causes is

$$P_M = M/(F+M) \qquad \text{...3.10)}$$

and the probability of death due to fishing can be estimated correspondingly.

- Size-dependent probabilities of capture were simulated. Thus, if a fish encounters a fishing gear, it must be decided whether the fish is retained by the gear, or is too small and escapes. A logistic curve (Pope et al. 1975) was used to simulate selection,

$$P_r = 1/(1 + \exp(-(a + bL_t))) \qquad \text{...3.11)}$$

where

P_r = probability of retention
L_t = length at the time of encounter
a = parameter which shifts the curve on the x (=length) axis
b = parameter indicating the steepness of the curve

- In the case of escape, the probability of future encounters is calculated;
- Each fish is followed during its entire "life", and the procedures which calculate the time of natural death/encounter with the gear are repeated until:
  a. the fish dies from natural causes;
  b. it is caught;
  c. $\underline{t}$ is greater than T_{max} (i.e., 40 years).
- After all fishes of a cohort are treated in this way, the program begins with a new cohort. A maximum of 40 cohorts are simulated. Total length and time of capture are stored in memory, and monthly length-frequency series are created for each cohort;
- Length data, which are integrated in the form of 12 monthly length-frequency samples of the entire population, are extracted and written to an ASCII file with the format required for the input data in the ELEFAN and SLCA programs;
- Four samples of length-at-age data are derived. The size and the month of capture of up to 40 fish per age group are stored in another file.

The program to implement this simulation model was written in FORTRAN-77 and runs on a VAX 8550. A seed value is required to begin the generation of pseudo-random numbers. This value was coupled to the actual time, and was therefore different for each simulation. A fixed value, however, could also have been used. A list of the input parameters required by the program is given in Appendix A.

Each run of the program produces 5 sets of 12 samples from a given population with identical input parameters. A run of the simulation program generating 5 such sets of 12 samples of a population with the following settings:

- two recruitment peaks;
- 10% individual variability in growth parameters;
- fishing without size-dependent selection;
- approximately 25 length classes

takes approximately 37 minutes CPU time on a VAX 8550.

Length-at-age data were simulated independently on the basis of the VBGF, assuming a set of growth parameters L_∞, K and t_0.

Simulated population types

The bias that occurs when using length-based methods to estimate vital parameters can be produced by two different sets of factors:

1. Bias produced by external factors during sampling or during preliminary treatment of the data, giving a false picture of the real population. In this category, we have:
   a. Gear selection acting on a part of the population;
   b. Samples which are too small or too infrequent;
   c. Systematic errors in length measurements, or nonrandom selection of the measured fishes;
   d. Errors in the method for grouping the length measurements.
2. Bias produced by intrinsic features of the population, such as:
   a. Variation in growth rates among individual fishes;
   b. Variation in time of recruitment among individual fishes;
   c. Seasonal variations of population growth rates.

Additionally, some methods may be better suited for investigation of certain population types, such as slow-growing fishes, or fast-growing fishes.

In the present study, different "populations" were created with the objective of investigating the effects of some of these factors and the magnitude of the bias that they produce when length-based methods are used to estimate growth parameters. First, a standard or *control population* was constituted, and then consecutive populations (*population types*) were created, in which only one or two input parameters or factors were varied systematically. Overall, seven series of such experiments were conducted.

For all experiments, the cohort strength (N_r) was assumed to be 10,000 fishes with a standard deviation of 1,000 fishes. The parameter t_0 of the VBGF was always assumed to be 0. Fishing mortality (F) was always assumed to be equal to natural mortality rate (M).

The growth performance index (ϕ') was calculated according to Pauly and Munro (1984) and Moreau et al. (1986) as:

$$\phi' = \log_{10} K + 2 \log_{10} L_\infty \qquad \text{...3.12)}$$

For each population type, five sets of length data were simulated, each one containing twelve samples. Growth parameters were calculated with the three methods already described, for each set of data.

In the case of ELEFAN and SLCA, the goodness-of-fit of a wide range of parameter combinations was calculated ('response surface' procedure) and the combination of parameters with the highest score was always chosen as the final result. The P-W method gives only a single solution.

Following estimation of growth parameters, a measure of the bias was obtained for each case by computing the % difference between the simulation input parameters and the results estimated with the methods. Thus,

$$\text{Bias} = \frac{(\text{Estimated parameter - Input parameter}) * 100}{\text{Input parameter}} \qquad \text{...3.13)}$$

It should be noted that the differences in the estimated parameters, as occurred frequently between the results for the five separate datasets of a given population type, are due to random effects. Although this random component increased the calculated bias, in practice it was assumed to be of minor importance and its magnitude was not computed because of the small sample size.

However, the average of the estimated parameters and of the bias was calculated for each group of five length datasets constituting a population type.

The features of each of the seven experiments are described below.

Series I. Populations with different growth strategies. The following input parameters were fixed:

Coefficient of variation of L_∞ ($C.V._{L_\infty}$)	10%
Coefficient of variation of K ($C.V._K$)	10%
Amplitude parameter (C)	0.0
Recruitment peaks (Rp)	1 $year^{-1}$
Age at recruitment (t_r)	0.0 year
Coefficient of variation of t_r	0%
Size selection (Sel)	not operating

The following input parameters of the model were varied:

Population type	L_∞ (cm)	K ($year^{-1}$)	M ($year^{-1}$)	W_{lc} (cm)
1	30	1.8	2.50	1
2	50	0.6	0.95	2
3	80	0.2	0.30	3
4	110	0.1	0.15	4

where

L_∞ = asymptotic length
K = growth constant
M = natural mortality
W_{lc}= length classes width

Series II. Effect of the variability of the parameters K and L_∞ among individual fish. Fixed input parameters:

Asymptotic length (L_∞)	50.0 cm
Growth constant (K)	0.5 $year^{-1}$
Amplitude parameter (C)	0.0
Natural mortality (M)	0.8 $year^{-1}$
Recruitment peaks (R_p)	1 $year^{-1}$
Age at recruitment (t_r)	0.0 year
Coefficient of variation of t_r	0%
Width of length classes	1.0 cm
Size selection (Sel)	not operating

The coefficient of variation of the parameters K and L_∞ was varied as follows:

Population type	C.V.$_{L\infty}$ (%)	C.V.$_K$ (%)[b]
1[a]	0	0
2	0	10
3	0	20
4	0	30
5	10	0
6	20	0
7	30	0
8	10	10
9	20	20
10	30	30

[a]control
[b]see Fig. 3.2

Series III. Influence of seasonal growth oscillations. Fixed parameters:

Asymptotic length (L_∞)	50.0 cm
Growth constant (K)	0.5 $year^{-1}$
Amplitude parameter (C)	0.65
Natural mortality (M)	0.8 $year^{-1}$
Recruitment peaks (R_p)	1 $year^{-1}$
Age at recruitment (t_r)	0.0 year
Coefficient of variation of t_r	0 %
Width of length classes	2.0 cm
Size selection (Sel)	not operating

It should be remembered that only the ELEFAN method can fit a seasonally oscillating version of the VBGF. For this reason the results obtained when C≠O were initially tested with that method, and the same method was then used assuming C=0, to permit comparison with the results obtained by SLCA and the P-W method.

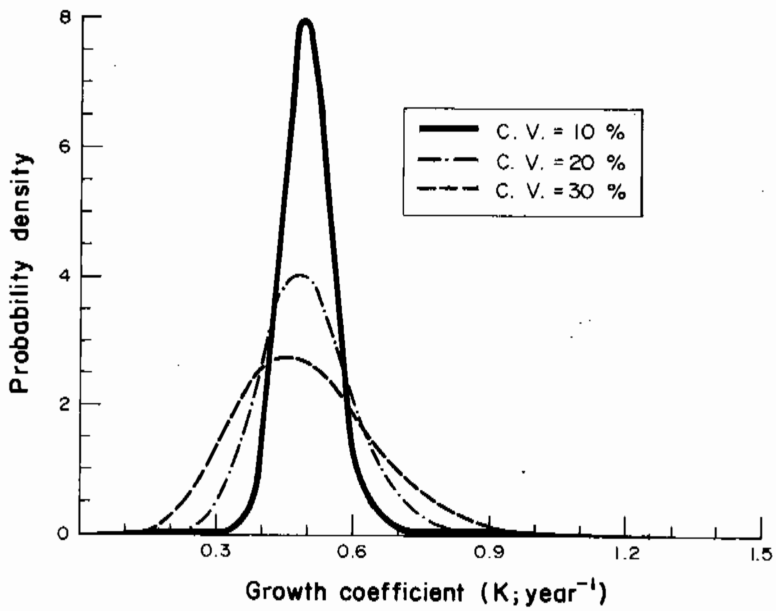

Fig. 3.2. Theoretical gamma probability density function for the parameter K when the mean is 0.5 $year^{-1}$ and the coefficients of variation (C.V.) are 10%, 20% and 30%.

In addition, the effect of variability of L_∞ and K among individuals, combined with an oscillatory pattern of the growth rate, was investigated. For that purpose, coefficients of variation of 0% and 20% were assumed, alternating for both parameters.

Series IV. Effect of size-dependent selection on the samples. Input parameters:

Asymptotic length (L_∞)	50.0 cm
Growth constant (K)	0.5 $year^{-1}$
Amplitude parameter (C)	0.0
Natural mortality rate (M)	0.8 $year^{-1}$
Recruitment peaks (R_p)	1 $year^{-1}$
Age at recruitment (t_r)	0.0 year
Coefficient of variation of t_r	0 %
Width of length classes	2.0 cm
Inflection point (b) of the selection curve	0.667

The parameter a of the selection curve (Equation 3.11) and the coefficients of variation (C.V.) of the parameters K and L_∞ were varied as follows:

Population type	Size selection	a	$C.V._{L_\infty}$ (%)	$C.V._K$ (%)
1[a]	No	-	0	0
2[a]	No	-	10	10
3	Yes	-10	0	0
4	Yes	-15	0	0
5	Yes	-20	0	0
6	Yes	-10	10	10
7	Yes	-15	10	10
8	Yes	-20	10	10

[a]controls

To evaluate whether the ELEFAN II routine is able to correct length-frequency data for selection effect, only one set of data of each population type was used. Probabilities of capture for each length class were calculated using the growth parameters previously estimated with ELEFAN I and the true value of M. The original data were corrected by dividing the frequencies of each length class by the corresponding probability of capture. New parameters were estimated once more with each method, and the results were compared with the results obtained before the correction.

Series V. Populations with different recruitment patterns. Input parameters:

Asymptotic length (L_∞)	50.0 cm
Coefficient of variation of L_∞ (C.V.$_{L\infty}$)	0 %
Growth constant (K)	0.5 year^{-1}
Coefficient of variation of K (C.V.$_K$)	0 %
Amplitude parameter (C)	0.0
Natural mortality (M)	0.8 year^{-1}
Width of length classes	2.0 cm
Size selection (Sel)	not operating

The number of recruitment peaks per year (R_p), the mean age at each recruitment peak (t_{r1}), the standard deviations of these means (s.d.$_i$) and the proportion of recruits belonging to the first recruitment peak (P) were varied as follows:

Population type	R_p	t_{r1}	s.d.$_1$	t_{r2}	s.d.$_2$	P
1	1	0.5	0	-	-	1
2	1	0.5	1 month	-	-	1
3	2	0.5	0	0.8	0	0.5
4	2	0.5	1 month	0.8	1 month	0.5

Although the two groups of fishes are simultaneously recruiting into the adult stock (but at different ages, 0.5 and 0.8 year), the resulting length distributions are comparable with those produced by a natural population with two different recruitment periods, or spawning twice a year, in which the recruits join the adult stock at equal ages, but at two different times.

Series VI. Effect produced by increasing the width of the length classes. Initially two groups of data were regrouped after sampling into length classes of 2, 3 and 4 cm, respectively. Fixed input parameters:

Using the editing facilities of the ELEFAN program, the length-frequency samples were then regrouped after sampling into length classes of 2, 3 and 4 cm, respectively. Fixed input parameters:

Asymptotic length (L_∞)	50.0 cm
Growth constant (K)	0.5 year^{-1}
Amplitude parameter (C)	0.0
Natural mortality (M)	0.8 year^{-1}
Recruitment peaks (R_p)	1 year^{-1}
Age at recruitment (t_r)	0.0 year
Coefficient of variation of t_r	0 %
Size selection (Sel)	not operating

Series VII. Effect of the addition of length-at-age data to the estimates obtained from the growth parameters with the ELEFAN method. Input parameters:

Asymptotic length (L_∞)	50.0 cm
Coefficient of variation of L_∞ ($C.V._{L_\infty}$)	10 %
Growth constant (K)	0.5 year
Coefficient of variation of K ($C.V._K$)	10 %
Amplitude parameter (C)	0.0
Natural mortality (M)	0.8 $year^{-1}$
Recruitment peaks (R_p)	1 $year^{-1}$
Age at recruitment (t_r)	0.0 year
Coefficient of variation of t_r	0 %
Width of length classes	2.0 cm
Size selection (Sel)	not operating

In addition, length-at-age data of 120 fishes were obtained through the simulation program, and three sets of hypothetical length-at-age data for 20 fishes were simulated independently, using the VBGF and the following parameters:

Population type	L_∞ (cm)	K ($year^{-1}$)	t_0
1	50	0.5	0
2	60	0.4	0
3	40	0.6	0

Results

Effects of differences in growth strategy

The average parameters obtained from five sets of simulated data for each population type in the Series I experiment, and the corresponding percentage of bias for the ELEFAN, SLCA and P-W methods are presented in Table 3.2. A complete table with all values is given in Appendix B (Table B.1). Fig. 3.3 shows the magnitude of the bias as a function of the type of population, i.e., of the growth strategies of the populations.

The ELEFAN I method proved to be more adequate for populations of small fishes with faster growth and shorter life span. However, the parameter K was always underestimated, and L_∞ was always overestimated. The bias was strongest when L_∞ was high and K was low (110 and 0.1, respectively), attaining 24% and 12%, respectively. The growth performance index (ϕ'), as a combination of L_∞ and K was less affected and only a positive bias of 4% was observed.

The SLCA method showed a relatively high variability in the estimates. As opposed to ELEFAN I, the bias was smaller for fishes with slow growth rates and greater for fishes with fast growth rates; the results are inconclusive for populations with intermediate growth strategies.

The P-W method showed a clear tendency to overestimate both L_∞ and Z/K. This is more pronounced for fishes with slow growth rate and long life span, reaching 16% and 25%, respectively (when L_∞ = 110 cm).

Table 3.2. Average parameters and percentage of bias obtained with each method in the Series I simulations. Coefficient of variation of L_∞ and K = 10%.

Method	Type	Simulated				Estimated				Bias (%)			
		L_∞ (cm)	K ($year^{-1}$)	ϕ'	Z/K	L_∞ (cm)	K ($year^{-1}$)	ϕ'	Z/K	L_∞ (cm)	K ($year^{-1}$)	ϕ'	Z/K
	1	30.00	1.80	3.210	2.778	30.57	1.654	3.187	-	1.89	-8.12	-0.69	-
ELEFAN	2	50.00	0.60	3.176	3.176	53.74	0.547	3.196	-	7.48	-8.77	0.62	-
	3	80.00	0.20	3.107	3.000	89.94	0.178	3.156	-	12.42	-11.20	1.57	-
	4	110.00	0.10	3.083	3.000	136.57	0.088	3.215	-	24.16	-12.00	4.28	-
	1	30.00	1.80	3.210	2.778	37.50	1.323	3.267	-	25.00	-26.50	1.80	-
SLCA	2	50.00	0.60	3.176	3.176	58.50	0.516	3.242	-	17.00	-13.97	2.08	-
	3	80.00	0.20	3.107	3.000	103.56	0.159	3.229	-	29.45	-20.50	3.92	-
	4	110.00	0.10	3.083	3.000	127.92	0.093	3.178	-	16.29	-7.20	3.09	-
	1	30.00	1.80	3.210	2.778	32.35	-	-	3.085	7.85	-	-	11.07
P-W	2	50.00	0.60	3.176	3.176	54.08	-	-	3.457	8.16	-	-	9.16
	3	80.00	0.20	3.107	3.000	87.01	-	-	3.446	8.77	-	-	14.87
	4	110.00	0.10	3.083	3.000	127.73	-	-	3.735	16.12	-	-	24.51

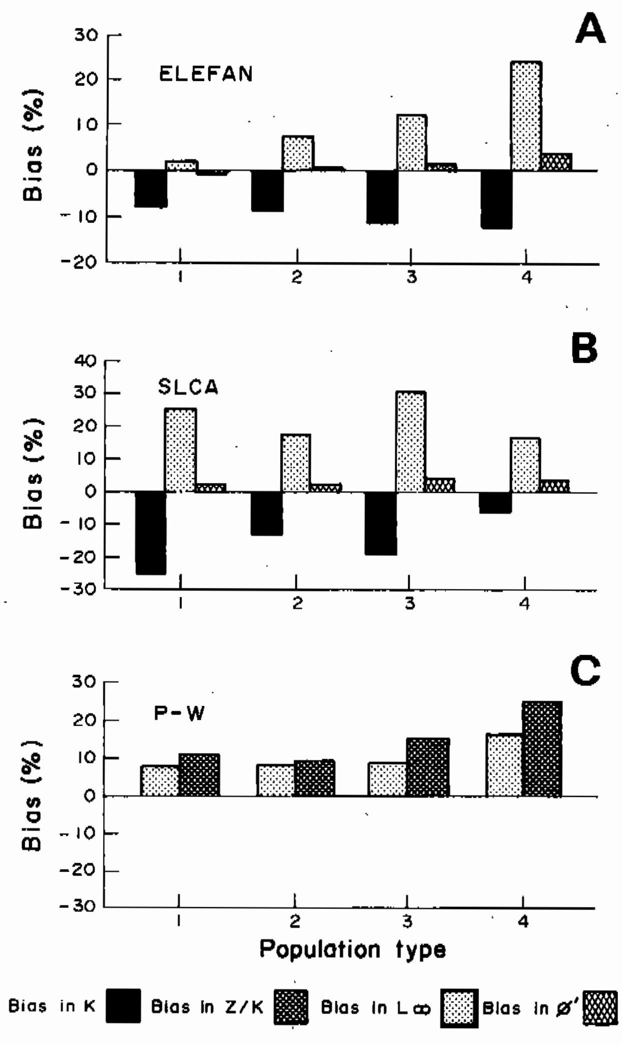

Fig. 3.3. Percentage of bias in the estimates of growth parameters with ELEFAN, SLCA and P-W methods, applied on four populations with increasing L_∞ and decreasing K.

Effects of individual variability in the parameters L_∞ and K

Table 3.3 and Fig. 3.4 (right) show the results obtained by applying ELEFAN I to populations with increasing individual variability in growth parameters. These results are the average estimates of K, L_∞ and ϕ' for five data sets and the corresponding bias. Table B.2 (in Appendix B) presents the complete results. Accurate estimations of all parameters are obtained only when the underlying length data were derived from a distribution without any individual variability in the growth parameters.

When variability was generated only for K, and L_∞ was assumed constant for all individuals, the maximum lengths (L_{max}) in the data were always smaller than the true L_∞ (see Table B.2); the values of L_∞ and ϕ' were slightly underestimated, and the underestimation of K increased with increasing variability.

Table 3.3. Average parameters and percentage of bias obtained with ELEFAN in Series II experiments, with increasing variability in L_∞ and/or K.

	Simulated		Estimated			Bias (%)		
Type	CV_{L_∞} (%)	CV_K (%)	L_∞ (cm)	K (year^{-1})	ϕ'	L_∞ (cm)	K (year^{-1})	ϕ'
1	0	0	49.88	0.502	3.097	-0.23	0.48	0.00
2	0	10	49.46	0.497	3.084	-1.09	-0.68	-0.42
3	0	20	47.93	0.489	3.050	-4.14	-2.24	-1.52
4	0	30	49.23	0.465	3.046	-1.53	-6.96	-1.65
5	10	0	48.19	0.487	3.053	-3.61	-2.52	-1.42
6	20	0	52.00	0.427	3.056	4.00	-14.60	-1.32
7	30	0	54.30	0.293	2.931	8.60	-41.40	-5.36
8	10	10	49.34	0.476	3.064	-1.31	-4.72	-1.08
9	20	20	51.57	0.303	2.898	3.15	-39.36	-6.43
10	30	30	53.28	0.277	2.875	6.56	-44.52	-7.16

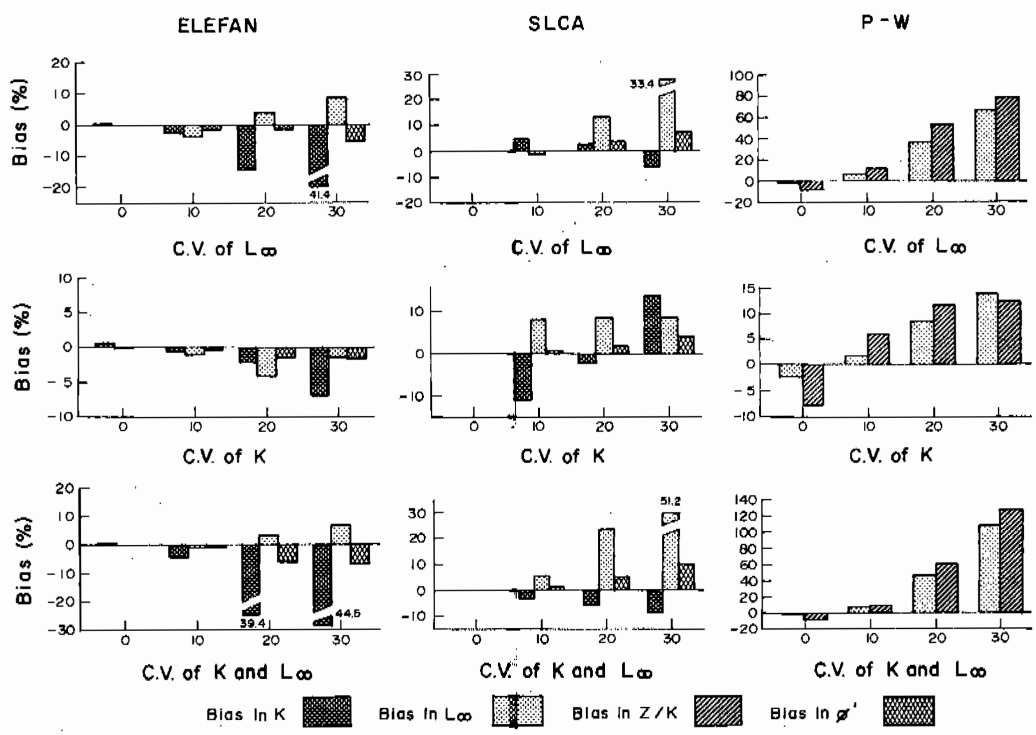

Fig. 3.4. Bias in L_∞, K, ϕ' (of Z/K where appropriate) as a function of three methods (ELEFAN, SLCA and P-W) and of coefficient of variations of L_∞ and/or K ranging from 0 to 30% (note the difference in scale).

On the other hand, when variability was generated for L_∞ only, ELEFAN I showed a tendency to overestimate this parameter, and produced a strong negative bias for the estimates of K, which reached 41% when the coefficient of variation of L_∞ was assumed to be 30%. The growth performance index ϕ' was also underestimated. Moreover, the bias of L_∞ seems to be linked to the longest length occurring in the samples (L_{max}) (see Table B.2). When the coefficient of variation of L_∞ was assumed to be 30%, the bias of this parameter varied from 0.3% to 17% for different data sets with maximum lengths of 67.5 cm and 75.5 cm, respectively. The magnitude of bias in K estimates was always quite high.

When both L_∞ and K varied among individuals, it seems that a compensatory effect occurred, the positive bias of L_∞ attaining a maximal value of 6.5%, against 8.6% obtained when only L_∞ varied. No such effect was observed for the estimates of K. This parameter was underestimated even more, the negative bias varying from 5% to 45%, according to the magnitude of the individual variability. The parameter ϕ' was also underestimated by 7%.

Multiple peaks of the ESP/ASP ratio were frequently found in the response surfaces, particularly when individual variability was high. However, the absolute maximum was always identifiable (see example in Table B.13).

The averages of the estimated parameters and the corresponding bias obtained with the SLCA method are shown in Table 3.4 and Fig. 3.4 (center). Table B.3 (Appendix B) shows all the values obtained by this method with the data of the Series II experiments.

Table 3.4. Average parameters and percentage of bias obtained with the SLCA method in Series II experiments, with increasing variability in parameters L_∞ and/or K.

	Simulated		Estimated			Bias (%)		
Type	CV_{L_∞} (%)	CV_K (%)	L_∞ (cm)	K (year^{-1})	ϕ'	L_∞ (cm)	K (year^{-1})	ϕ'
1	0	0	50.04	0.500	3.098	0.08	0.04	0.03
2	0	10	54.08	0.446	3.115	8.16	-10.76	0.59
3	0	20	54.22	0.490	3.156	8.44	-2.00	1.90
4	0	30	54.24	0.569	3.221	8.48	13.80	4.01
5	10	0	49.58	0.524	3.108	-0.84	4.76	0.36
6	20	0	56.68	0.514	3.214	13.36	2.88	3.77
7	30	0	66.72	0.469	3.313	33.44	-6.12	6.96
8	10	10	52.90	0.485	3.129	5.80	-3.00	1.04
9	20	20	61.92	0.472	3.255	23.84	-5.68	5.10
10	30	30	52.59	0.458	3.410	51.16	-8.48	10.11

As was the case with ELEFAN I, the "control population" was analyzed by SLCA with high accuracy, and L_∞ and K were reproduced without error.

When K varied among individuals, the bias in this parameter was initially negative, becoming positive with increasing coefficients of variation of K; L_∞ was always overestimated by approximately 8%.

When the variability was simulated only for L_∞, an overestimation of this parameter and of ϕ' resulted. The parameter K, initially overestimated, was underestimated when the variability in L_∞ was 30%.

When both parameters L_∞ and K varied among individuals, the bias of L_∞ was very strong, attaining more than 50% in the extreme. The parameter K was always underestimated, but by no more that 8%, and the growth performance index ϕ' was overestimated by as much as 10%.

The SLCA method showed a strong tendency to produce multiple peaks of the score function in the response surface procedures, particularly when variability was high. In several cases the parameter combinations yielding the best results were extremely different, and the choice of the best combination was difficult (Table B.13).

Individual variability of the growth parameters affected the accuracy of the results estimated with the P-W method much more than was the case with the other two methods. A complete table with all the results obtained for the series II experiments with the P-W method is given in Appendix B (Table B.4). Average parameters and the corresponding bias are shown in Table 3.5 and Fig. 3.4 (left).

Bias increased with increasing coefficients of variation of L_∞ and K, especially in the case of L_∞. Bias was under 10% only when the coefficient of variation of the growth parameters among individuals was also 10%. When both parameters varied, the bias attained very high values, more than 100% when the coefficient of variation was assumed to be 30% for both parameters.

Table 3.5. Average parameters and percentage of bias obtained with the P-W method in Series II experiments, with increasing variability in parameters L_∞ and/or K.

Type	Simulated		Estimated		Bias (%)	
	CV_{L_∞} (%)	CV_K (%)	L_∞ (cm)	Z/K	L_∞ (cm)	Z/K
1	0	0	48.86	2.954	-2.27	-7.68
2	0	10	50.88	3.393	1.76	6.02
3	0	20	54.27	3.581	8.53	11.91
4	0	30	56.98	3.601	13.96	12.52
5	10	0	53.46	3.582	6.92	11.94
6	20	0	68.19	4.903	36.39	53.21
7	30	0	83.17	5.713	66.34	78.53
8	10	10	54.01	3.511	8.03	9.71
9	20	20	73.24	5.161	46.48	61.28
10	30	30	104.09	7.309	108.18	128.41

Effects of seasonal oscillations on growth

A complete list of the results obtained in the experiments of Series III can be found in Appendix B (Table B.5). Average parameters obtained for the five data sets of each population type and the percentage of bias of the estimated parameters are presented in Table 3.6 and in Fig. 3.5. All the populations simulated for these experiments had a seasonally oscillating pattern in growth, and the magnitude of the parameter C of the VBGF was always 0.65. Estimation of C is only possible by the ELEFAN I method. The bias obtained varied from 6% to -8% (Table 3.6).

Table 3.6. Average parameters obtained for the experiments of Series III, in which growth was assumed to oscillate seasonally and the coefficient of variation of L_∞ and K was 0% and 20%.

Method	Type	Simulated		Estimated						BIAS (%)				
		CV_{L_∞} (%)	CV_K (%)	L_∞ (cm)	K ($year^{-1}$)	C	WP	φ'	Z/K	L_∞ (cm)	K ($year^{-1}$)	φ'	C	Z/K
ELEFAN (C≠0)	1	0	0	52.24	0.460	0.69	0.0	3.099	-	4.49	-7.92	0.05	6.46	-
	2	20	20	55.09	0.432	0.60	0.0	3.115	-	10.18	-13.52	0.59	-8.31	-
ELEFAN (C=0)	1	0	0	53.22	0.449	0.00	0.0	3.104	-	6.44	-10.16	0.23	-	-
	2	20	20	53.69	0.444	0.00	0.0	3.105	-	7.38	-11.16	0.27	-	-
SLCA	1	0	0	48.76	0.547	-	-	3.114	-	-2.48	9.44	0.56	-	-
	2	20	20	62.62	0.512	-	-	3.303	-	25.24	2.44	6.42	-	-
P-W	1	0	0	46.53	-	-	-	-	2.7	-6.94	-	-	-	-15.0419
	2	20	20	68.82	-	-	-	-	4.7	37.64	-	-	-	48.1140

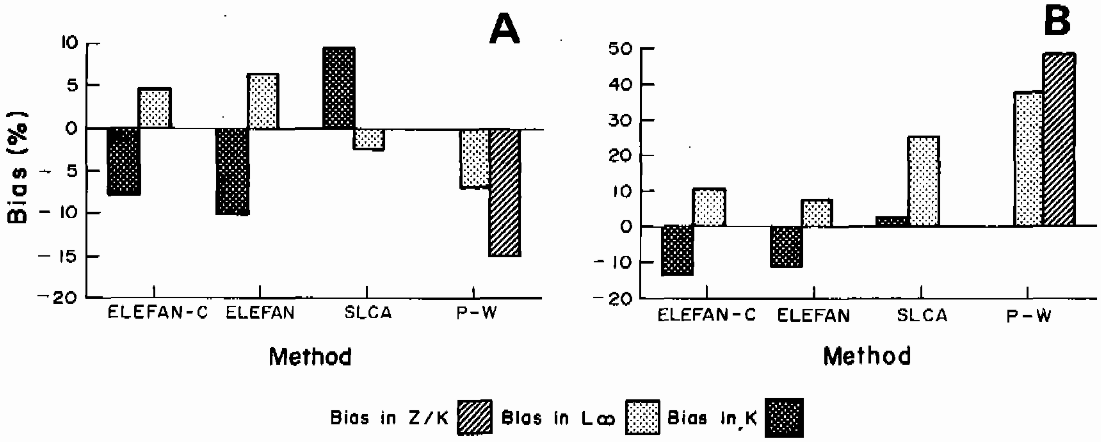

Fig. 3.5. Bias in the estimates of the parameters obtained with ELEFAN-C (i.e., C≠0), ELEFAN (C=0), SLCA and P-W methods, for populations with seasonal growth oscillations. a) without individual variability of growth parameters. b) with 20% individual variability of growth parameters L_∞ and K. (Note the differences in scale).

To appreciate the reciprocal effect of oscillation in growth and variability of the growth parameters among individuals, the results obtained in experiments II and III should be compared in those cases where both parameters, L_∞ and K, had coefficients of variation of 20% (see Tables 3.3, 3.4 and 3.5).

Among the parameter sets estimated using ELEFAN I, results were best when C was assumed variable and no individual variability was present in the samples. Second best were the estimates assuming C=0, with practically no difference in the bias between absence or presence of individual variability. Inclusion of C for the data with individual variability gave the poorest result (Table 3.6).

With the SLCA method, the existence of seasonal growth oscillations does not seem to influence the estimates of L_∞ and ϕ' very much, compared to those obtained in experiment II, producing an overestimation of K of under 10%. This overestimate is compensated by the tendency to underestimate K when variability among individuals is assumed, explaining the decrease of the positive bias to 2.4% when the coefficient of variation was 20% for the growth parameters.

The P-W method initially estimated L_∞ and Z/K with 7% and 15% negative bias, respectively, but the bias became positive when individual variability was simulated. However, the magnitude of this bias did not reach the values observed under similar circumstances in experiment II.

Effects of size-dependent selection

The use of trawl gear to sample fishes results in the escape of those individuals small enough to pass through the mesh, meaning that they will not be fully represented in the samples. The proportion of fishes of each size that escape is a function of the mesh size. In the present simulation model the effect of different mesh sizes was controlled through the parameter a in the logistic selection curve (Pope et al. 1975; see Equation 3.11), while b was left unchanged at 0.667.

Table 3.7 shows the effects of three values of a on the probability of capture of fishes with a determined total length (experiments of Series IV). When a was assumed to be -10, almost no fishes smaller than 8 cm occurred in the samples, 15 cm long fishes had a 50% probability of being captured, and almost all fishes longer than 23 cm were retained by the gear. The lower the value of a is, the less representative are the samples in relation to the population structure. When a was assumed to be -20, more than half of the length range occurring in the population failed to be correctly represented in the samples.

The combined effect of biased sampling due to size selection, and individual variability of the growth parameters was also investigated.

Table 3.8 and Fig. 3.6 show the average parameters estimated with the three methods and the corresponding percentage of bias. Complete tables with the results obtained in this experiment may be found in Appendix B (Tables B.6, B.7 and B.8).

Table 3.7. Total length (in cm) of fishes with 1%, 50% and 100% probability of being caught, when parameter a of the logistic selection curve was varied.

Probability of Capture	Value of a		
	- 10	- 15	- 20
1 %	8.0	16.0	23.0
50 %	15.0	22.5	30.0
100 %	23.0	31.0	38.0

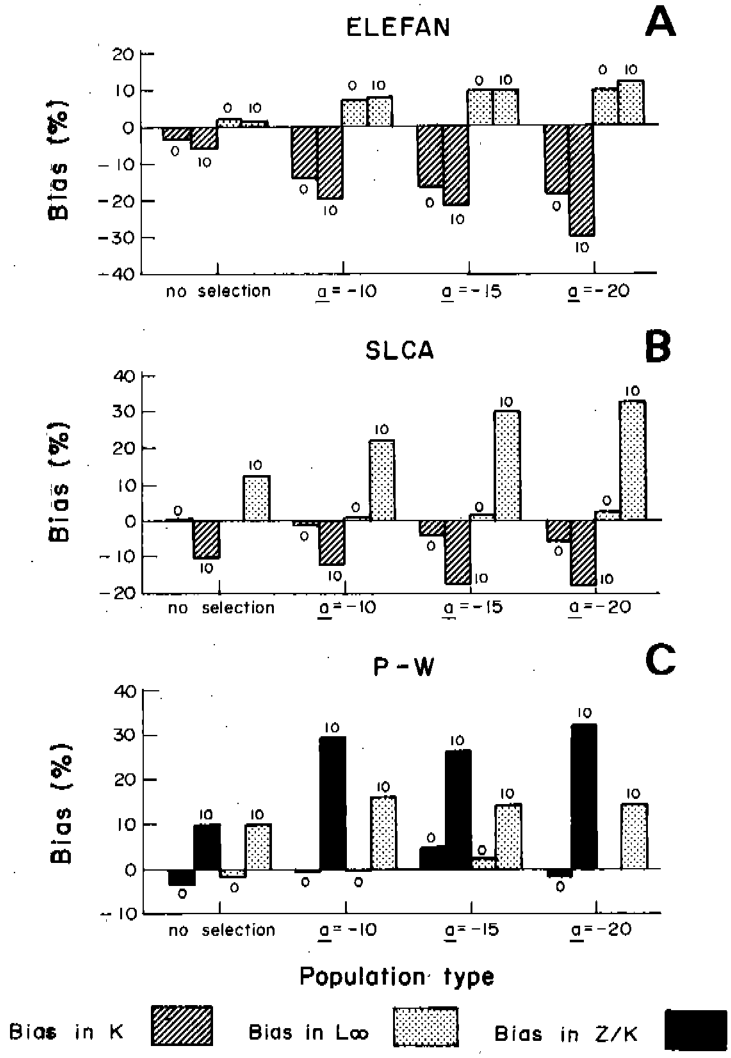

Fig. 3.6. Percentage of bias in the estimates of growth parameters obtained with ELEFAN, SLCA and P-W method applied to data with increasing size-dependent selection effects (parameter a), without and with 10% individual variability of the growth parameters. (Note the differences in scale).

For all methods, the estimates of growth parameters were again very accurate for the "control populations" without selection and variability. Bias becomes evident when selection effects were stronger and individual variability was assumed in the growth parameters.

When only selection effects were simulated, both ELEFAN I and SLCA always overestimated L_∞ and underestimated K, but the estimation by ELEFAN I were more strongly biased than those obtained with SLCA. Bias increased as the absolute value of the parameter a increased, i.e., when a higher number of length classes was not fully represented in the samples.

The additional effect of the variability of growth parameters between individuals increased the positive bias of L_∞ and the negative bias of K in all cases.

Considering the cumulative effects of selection and individual variability, L_∞ was calculated better with ELEFAN I, and SLCA estimated K more accurately.

The growth performance index ϕ' was generally estimated accurately (maximal bias was 5%) by both ELEFAN I and SLCA (Table 3.8).

The P-W method does not seem particularly sensitive to the decrease of parameter a (i.e., increase mesh size), the magnitude of the bias depending mainly on the degree of individual variation of the growth parameters. When no variability was assumed, the estimates of L_∞ and Z/K were very satisfactory.

Table 3.9. shows an evaluation of the ability to correct for selection effects in samples using the approach outlined on p. 11 and referred to as the "ELEFAN II" procedure. The corrected length frequencies were analyzed with all three methods, comparing the output with and without the correcting procedure. Results were slightly but consistently better for ELEFAN I and in most cases for SLCA, while the results obtained with the P-W method did not profit at all from the correction (Fig. 3.7).

Table 3.8. Average parameters and percentage of bias obtained with each method for samples with variable size-dependent selection effects (parameter a), without and with 10% individual variability of the growth parameters.

Method	Simulated				Estimated				Bias (%)			
	Type	CV L_∞	CV K	a	L_∞	K	ϕ'	Z/K	L_∞	K	ϕ'	Z/K
ELEFAN	1	0	0	No sel.	50.96	0.483	3.098	-	1.92	-3.36	0.05	-
	2	10	10	No sel.	50.81	0.470	3.083	-	1.62	-5.92	-0.45	-
	3	0	0	-10	53.74	0.431	3.094	-	7.47	-13.88	-0.09	-
	4	0	0	-15	54.75	0.419	3.097	-	9.49	-16.16	-0.01	-
	5	6	0	-20	54.84	0.410	3.090	-	9.68	-18.08	-0.23	-
	6	10	10	-10	53.89	0.403	3.068	-	7.78	-19.44	-0.94	-
	7	10	10	-15	54.66	0.395	3.071	-	9.32	-20.96	-0.83	-
	8	10	10	-20	55.90	0.352	3.028	-	11.79	-29.52	-2.22	-
SLCA	1	0	0	No sel.	50.10	0.502	3.100	-	0.20	0.40	0.11	-
	2	10	10	No sel.	56.20	0.449	3.150	-	12.40	-10.28	1.72	-
	3	0	0	-10	50.44	0.495	3.100	-	0.88	-1.00	0.10	-
	4	0	0	-15	51.00	0.481	3.097	-	2.00	-3.80	-0.00	-
	5	0	0	-20	51.32	0.473	3.095	-	2.84	-5.40	-0.07	-
	6	10	10	-10	61.00	0.441	3.197	-	22.00	-11.80	3.22	-
	7	10	10	-15	65.10	0.414	3.236	-	30.20	-17.28	4.48	-
	8	10	10	-20	66.54	0.413	3.250	-	33.08	-17.48	4.94	-
P-W	1	0	0	No sel.	49.15	-	-	3.088	-1.70	-	-	-3.49
	2	10	10	No sel.	54.73	-	-	3.509	9.47	-	-	9.65
	3	0	0	-10	49.85	-	-	3.182	-0.30	-	-	0.56
	4	0	0	-15	51.06	-	-	3.353	2.12	-	-	4.78
	5	0	0	-20	50.14	-	-	3.149	0.28	-	-	-1.59
	6	10	10	-10	57.87	-	-	4.133	15.73	-	-	29.15
	7	10	10	-15	57.11	-	-	4.038	14.21	-	-	26.19
	8	10	10	-20	57.29	-	-	4.228	14.59	-	-	32.12

Table 3.9. Bias of growth parameters obtained in a set of data from each population type before (b) and after (a) the correction of the frequencies for selection effects via the left ascending side of a length-converted catch curve.

Method	Simulated				Bias (%)							
		CV_{L_∞}	CV_K	Parameter	L_∞		K		ϕ'		Z/K	
	Type	(%)	(%)	a	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)
ELEFAN	3	0	0	-10	(5.05)	4.80	(-8.20)	-7.40	(0.18)	0.24	-	-
	4	0	0	-15	(2.00)	1.80	(-4.80)	-4.00	(-0.13)	-0.07	-	-
	5	0	0	-20	(9.80)	9.50	(-17.60)	-16.80	(-0.09)	-0.03	-	-
	6	10	10	-10	(10.30)	9.60	(-19.80)	-15.40	(-0.35)	0.23	-	-
	7	10	10	-15	(12.50)	11.36	(-25.20)	-23.00	(-0.77)	-0.65	-	-
	8	10	10	-20	(10.20)	10.02	(20.60)	20.20	(-0.51)	-0.49	-	-
SLCA	3	0	0	-10	(2.20)	1.00	(-4.00)	-0.60	(0.04)	0.20	-	-
	4	0	0	-15	(0.60)	0.60	(0.00)	0.00	(0.17)	0.17	-	-
	5	0	0	-20	(2.80)	2.00	(-6.00)	-2.40	(-0.09)	0.22	-	-
	6	10	10	-10	(3.80)	8.00	(6.00)	-3.00	(1.86)	1.73	-	-
	7	10	10	-15	(47.60)	23.80	(-37.00)	-16.20	(4.44)	3.51	-	-
	8	10	10	-20	(23.00)	14.00	(-2.40)	-22.60	(5.47)	0.08	-	-
P-W	3	0	0	-10	(-4.78)	-0.42	-	-	-	-	(37.00)	-0.09
	4	0	0	-15	(2.28)	8.94	-	-	-	-	(7.16)	29.72
	5	0	0	-20	(-0.34)	8.50	-	-	-	-	(-7.81)	23.41
	6	10	10	-10	(32.82)	31.08	-	-	-	-	(60.31)	87.66
	7	10	10	-15	(22.46)	27.20	-	-	-	-	(41.22)	55.13
	8	10	10	-20	(18.46)	24.10	-	-	-	-	(38.09)	63.78

Effects of variation in recruitment pattern

Young fishes are not subject to fishing until they join the exploited stock, and the effect of recruitment on length-frequency samples is somewhat comparable to the selection produced by a trawl, i.e., the smaller individuals will not be fully represented in the samples.

However, the input parameters of the Series V experiments and the gamma probability distribution assumed for the mean age-at-recruitment (t_r), led to a higher frequency of individuals in the lower length

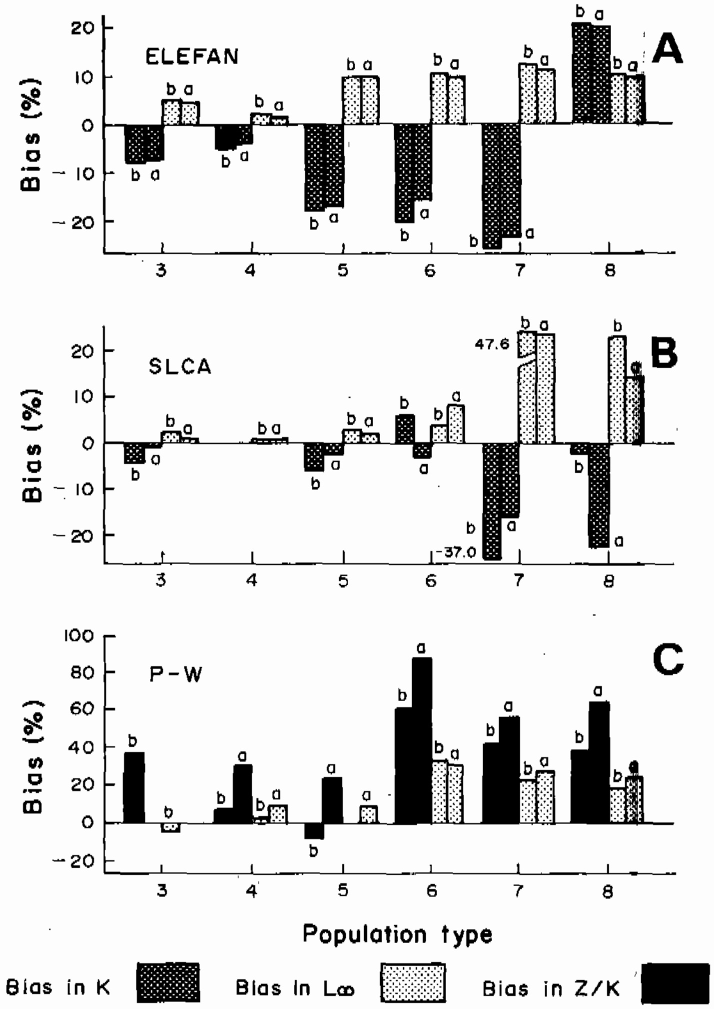

Fig. 3.7. Comparison of the bias obtained with the three methods before (b) and after (a) correction of the frequencies for selection effects by the ELEFAN II routine. The population types correspond to the different combinations of simulated parameters, as indicated in Table 3.9 (Note the differences in scale).

classes of the samples than was the case in the samples simulated in Series IV, in which the symmetrical logistic distribution was used to simulate selection. Thus, the simulated samples had a slightly better coverage over the size range. Table 3.10 shows the average parameters and the corresponding percentage of bias obtained with the three methods when t_r was varied. A complete list of the results of this experiment, including the range of lengths occurring in each set of data, can be found in Appendix B (Table B.9).

When only one recruitment peak was simulated and the age at recruitment (t_r) was assumed to be the same for all recruits (0.5 years), the samples contained fishes varying from 11 to 49 cm in length. The assumption of variability in t_r led to the occurrence of smaller fishes (down to 7 cm in length), but the maximal lengths (L_{max}) did not change, never exceeding L_∞ (50 cm).

In the second part of the experiment, two annual recruitment peaks 3 months apart were assumed. Due to the decrease in growth rate with age, the modal lengths of these two peaks can be distinguished only in the first cohort. Each mode corresponds to the 0.5 and 0.8 year old recruiting fishes, respectively. Older cohorts showed a unimodal distribution. The range of lengths occurring in the samples was similar to that described above for the first part of this experiment.

When age at recruitment was fixed and constant for all individuals, the ELEFAN method underestimated K and overestimated L_∞. However, it is to be expected that the magnitude of this bias should be correlated with the value assumed for t_r. Thus, the older the fishes are when they join the adult stock, the less representative the samples will be of the population, intensifying the tendency of the bias.

When variability in the mean age at recruitment was assumed, the ELEFAN I estimates improved, most probably because of the presence of smaller fishes in the samples.

Table 3.10. Average parameters and percentage of bias obtained with ELEFAN, SLCA and P-W method for the data created for experiment V. tr1 and tr2 are the simulated mean ages (in years) at the corresponding standard deviations. Asterisks indicate the results of the ELEFAN method using a length class belonging to the second recruitment peak as "starting point". P = proportion of recruits included in the first peak.

		Simulated					Estimated				Bias (%)			
	Type	P	tr1	SD 1	tr2	SD 2	L_∞ (cm)	K (year^{-1})	ϕ'	Z/K	L_∞ (cm)	K (year^{-1})	ϕ'	Z/K
ELEFAN	1	1	0.5	0	-	-	54.62	0.422	3.100	-	9.24	-15.60	0.10	-
	2	1	0.5	1 month	-	-	51.59	0.471	3.097	-	3.18	-5.84	0.02	-
	3	0.5	0.5	0	0.8	0	54.41	0.448	3.122	-	8.82	-10.36	0.80	-
	*						52.20	0.445	3.083	-	4.41	-10.92	-0.44	-
	4	0.5	0.5	1 month	0.8	1 month	54.21	0.461	3.131	-	8.42	-7.80	1.10	-
	*						51.56	0.447	3.074	-	3.11	-10.64	-0.74	-
SLCA	1	1	0.5	0	-	-	50.32	0.498	3.101	-	0.64	-0.36	0.13	-
	2	1	0.5	1 month	-	-	49.36	0.536	3.116	-	-1.28	7.28	0.62	-
	3	0.5	0.5	0	0.8	0	48.10	0.605	3.146	-	-3.80	20.96	1.58	-
	4	0.5	0.5	1 month	0.8	1 month	46.04	0.707	3.175	-	-7.92	41.32	2.52	-
P-W	1	1	0.5	0	-	-	50.23	-	-	3.208	0.47	-	-	0.26
	2	1	0.5	1 month	-	-	49.29	-	-	3.079	-1.42	-	-	-3.77
	3	0.5	0.5	0	0.8	0	50.94	-	-	3.369	1.87	-	-	5.29
	4	0.5	0.5	1 month	0.8	1 month	49.92	-	-	3.176	-0.16	-	-	-0.74

In populations with two annual recruitment peaks, the ELEFAN method permits adjustment of a growth curve across the length class corresponding either to the first or to the second peak. This is implemented by changing the "starting point" of the curve. Fig. 3.8 illustrates the results of this procedure on a set of 12 samples with two recruitment peaks and a standard deviation for t_r of one month.

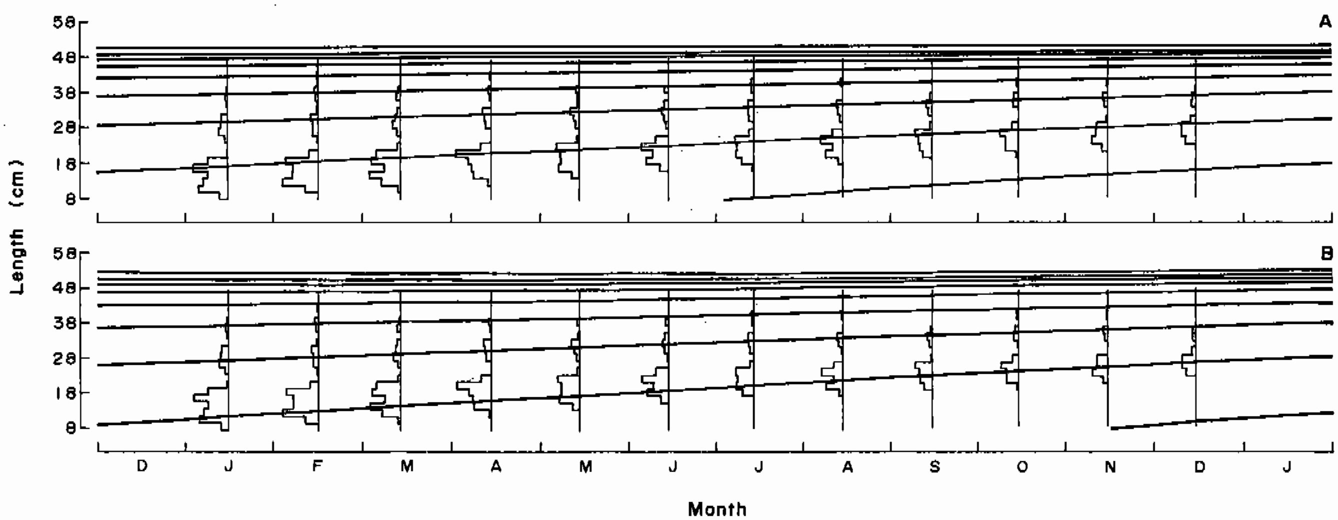

Fig. 3.8. Growth curve estimates of ELEFAN with data from a population of type 4 of the experiment of Series VI (see 3.2.3) with two annual recruitment peaks. a) "Starting point" fixed at the second recruitment peak. b) "Starting point" fixed at the first recruitment peak.

For each population type with two recruitment peaks, two possible results for the population were calculated, corresponding to the adjustment for either peak. The values for the second peak are marked with asterisks in Table 3.10; a comparison shows that the estimates of L_∞ and K were lower in the adjustment for the second recruitment peak.

The SLCA method produced rather accurate estimates of the growth parameters when t_r was assumed constant, but had an increasing tendency to underestimate L_∞ and to overestimate K in all other cases. The bias of K was relatively high (41%) when two recruitment pulses with variable t_r were assumed (Fig. 3.9).

The estimates of the growth performance index ϕ' were always very accurate with both ELEFAN I and SLCA.

As in the experiment with selection effects, the P-W method was not very sensitive to the part of the population lacking in the samples. Bias remained low and constant in all the cases.

The efficiency of ELEFAN II in determining the recruitment pattern was investigated on a set of data from each population type, using the growth parameters previously estimated with ELEFAN I. The results (Fig. 3.10) show that the procedure reproduced the peaks adequately in relation to the number of pulses and the distance between them. The temporal distribution of the calculated pulses was wider than in the original input data, as expected.

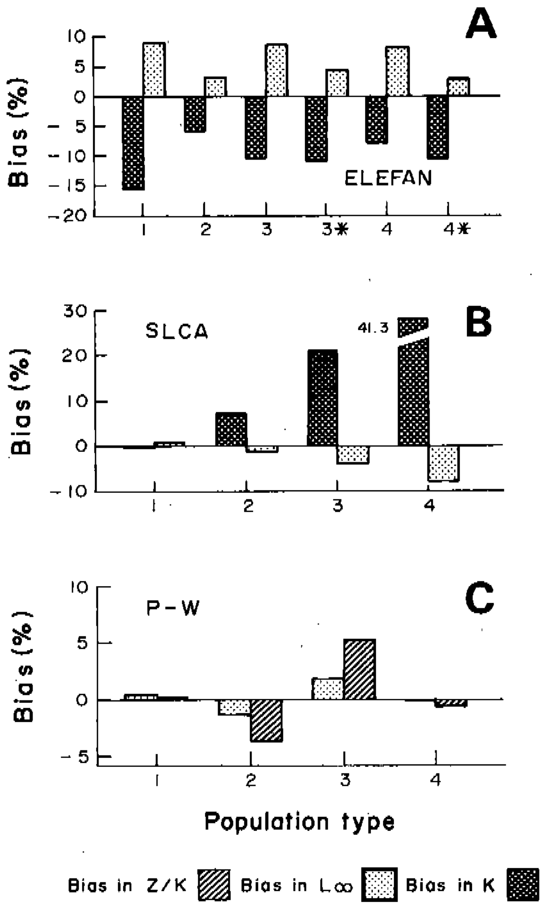

Fig. 3.9. Percentage of bias obtained with ELEFAN, SLCA and P-W method on populations with one and two annual recruitment peaks. Asterisks indicate the results of ELEFAN when using a "starting point" fixed in a length class corresponding to the second recruitment peak.

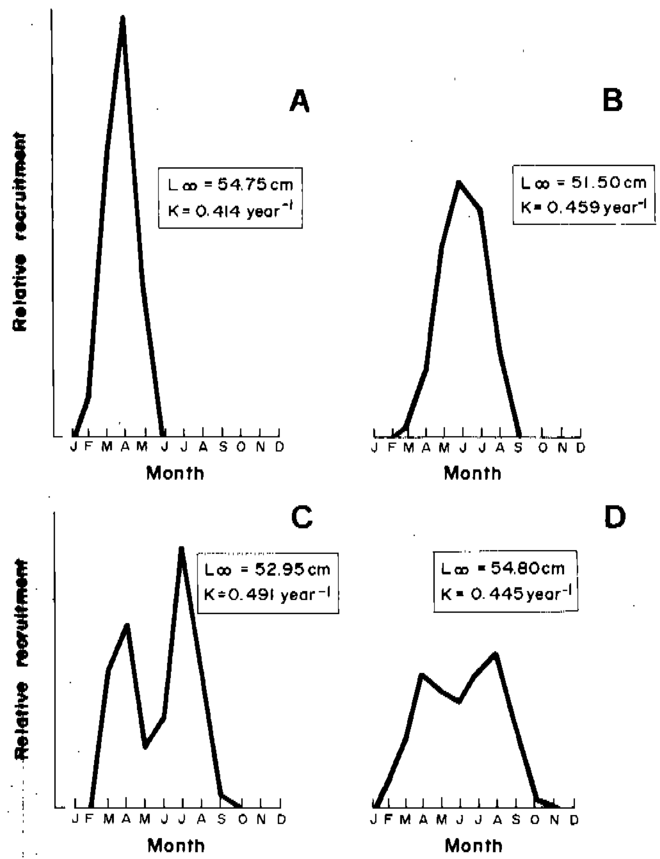

Fig. 3.10. Recruitment patterns obtained using ELEFAN II and a data set from each population type in Table 3.10 (Series V).

Effects of length class width

The objective of the experiments of Series VI was to estimate growth parameters for the same data sets, but grouping the frequencies in wider length classes. The average results and the corresponding percentage of bias for each method are given in Table 3.11 and in Fig. 3.11. A list of all estimates can be found in Appendix B (Table B.10, B.11 and B.12).

Table 3.11. Average parameters and percentage of bias obtained with each method in the Series VI experiment, with varying width of length classes.

Method	Type	Simulated CV_{L_∞} (%)	Simulated CV_K (%)	Class Interval	Estimated L_∞ (cm)	Estimated K ($year^{-1}$)	Estimated φ'	Estimated Z/K	Bias (%) L_∞ (cm)	Bias (%) K ($year^{-1}$)	Bias (%) φ'	Bias (%) Z/K
ELEFAN	1	0	0	1	49.89	0.502	3.097	-	-0.22	0.48	0.00	-
	2	0	0	2	50.59	0.489	3.097	-	1.19	-2.28	0.00	-
	3	0	0	3	56.82	0.418	3.130	-	13.64	-16.32	1.08	-
	4	0	0	4	60.06	0.404	3.163	-	20.13	-19.16	2.14	-
	5	20	20	1	51.57	0.303	2.898	-	3.15	-39.36	-6.43	-
	6	20	20	2	55.66	0.362	3.044	-	11.32	-27.60	-1.71	-
	7	20	20	3	59.15	0.339	3.070	-	18.29	-32.28	-0.87	-
	8	20	20	4	69.68	0.366	3.247	-	39.36	-26.84	4.84	-
SLCA	1	0	0	1	50.02	0.500	3.098	-	0.04	0.08	0.02	-
	2	0	0	2	50.54	0.495	3.102	-	1.08	-1.00	0.16	-
	3	0	0	3	50.56	0.498	3.105	-	1.12	-0.36	0.26	-
	4	0	0	4	51.30	0.492	3.112	-	2.60	-1.60	0.49	-
	5	20	20	1	61.92	0.472	3.255	-	23.84	-5.68	5.10	-
	6	20	20	2	63.66	0.463	3.262	-	27.32	-7.48	5.32	-
	7	20	20	3	72.96	0.400	3.322	-	45.92	-20.00	7.26	-
	8	20	20	4	74.44	0.400	3.339	-	48.88	-19.92	7.81	-
P-W	1	0	0	1	48.81	-	-	2.950	-2.38	-	-	-7.81
	2	0	0	2	49.01	-	-	2.964	-1.98	-	-	-7.39
	3	0	0	3	49.44	-	-	2.996	-1.12	-	-	-6.38
	4	0	0	4	49.97	-	-	3.027	-0.06	-	-	-5.39
	5	20	20	1	51.57	-	-	5.161	3.15	-	-	61.28
	6	20	20	2	55.66	-	-	5.165	11.32	-	-	61.41
	7	20	20	3	59.15	-	-	5.174	18.29	-	-	61.70
	8	20	20	4	69.68	-	-	5.140	39.36	-	-	60.64

Without individual variability, ELEFAN I showed an increasing tendency to overestimate L_∞ and underestimate K as the width of the length classes increased. Bias was relatively low for the data with length class intervals of 1 cm and 2 cm (48 and 24 classes, respectively), but attained 20% for the 4 cm intervals. The estimates of the parameter φ' always had a low bias.

When the effect of individual variability of the growth parameters was combined with the increase in length class width, the bias in L_∞ of ELEFAN I increased proportionally with the width of the length classes, and the bias in K was relatively high for all four cases.

When no individual variability of the growth parameters was assumed, the increase in length class width did not influence the estimates of SLCA strongly; bias was always low. However, when individual variability was assumed, the bias of SLCA for both parameters L_∞ and K increased with the length class width, L_∞ being overestimated and K underestimated.

The P-W method had a slight tendency to produce improved estimates of L_∞ and Z/K when length class width was increased, but the differences were too small to be conclusive.

When individual variability of the growth parameters was combined with the increase in length class width, the bias for L_∞ of the P-W method increased with increasing length class width. Z/K was reproduced with 60% bias independently of the length class width, this value being similar to that found in the experiments of Series II, when individual variability of the growth parameters was 20% (see Table 3.5).

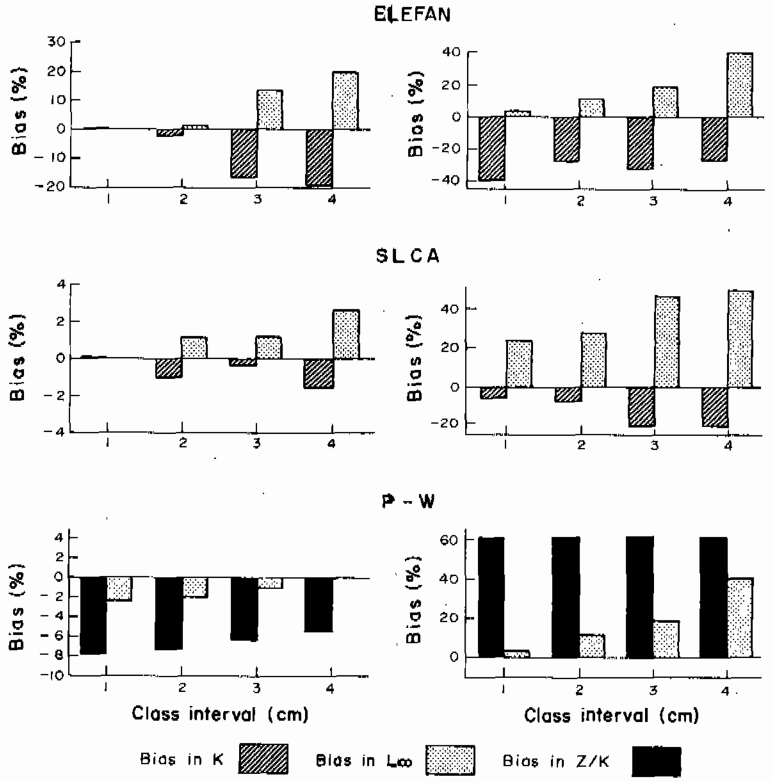

Fig. 3.11. Percentage of bias in growth parameters estimated with ELEFAN, SLCA and P-W methods in the experiments of Series VI. Left: data without individual variability. Right: data with a coefficient of variation of 20% for individual growth parameters. (Note the differences in scale).

Effects of the addition of length-at-age data

Table 3.12 shows the parameters estimated for the data in the experiment of Series VII. Probably because of its similarity to the length data, the additional length-at-age data, which had been generated together with the simulation model, did not improve the estimates of the growth parameters obtained with ELEFAN I. Bias was -7% for K and 1.4% for L_∞, which are the same as before the addition of the length-at-age data.

Table 3.12. Results obtained with a set of length data and the ELEFAN method, when including length-at-age data in the adjusting procedure. Bias is always calculated in relation to the parameters used for the simulation of the length-frequency data.

Origin of age/lt data	Simulated parameters lt/age data		Number lt/age data included	Estimated parameters		Bias (%)	
	L_∞	K		L_∞	K	L_∞	K
Simulated	50.0	0.50	0	50.72	0.465	1.44	-7.00
together with	50.0	0.50	36	50.72	0.465	1.44	-7.00
length data	50.0	0.50	120	50.72	0.465	1.44	-7.00
Simulated							
independently	50.0	0.50	5	50.71	0.468	1.42	-6.40
of length data	50.0	0.50	20	50.71	0.468	1.42	-6.40
*= only of age 0	50.0	0.50	5	50.71	0.468	1.42	-6.40
** = only of age 4	50.0	0.50	5	50.71	0.468	1.42	-6.40
Simulated	60.0	0.40	20	51.30	0.435	2.60	-9.40
independently							
of length data	40.0	0.60	20	49.35	0.514	-1.30	2.80

When length-at-age data were simulated separately, but with the same assumed growth parameters, ELEFAN I still reproduced the same estimates as before. The inclusion of data corresponding only to a particular year class, omitting the others, did not affect the estimates either.

On the other hand, when the length-at-age data originated from populations with different parameters as those of the length-frequency data, the magnitude of the bias changed, because the estimates tend to approximate the parameters assumed for the length-at-age data. The influence on K was stronger than for L_∞. While a value for L_∞ of 60.0 cm in the length-at-age data produced an estimate only 1% greater than the control, a value for K of 0.4 $year^{-1}$ reduced the estimates by 8% in relation to the control (Table 3.12).

Discussion

The von Bertalanffy equation, still the most frequently used model for describing growth in fishes, was derived by considering growth as the balance between anabolic and catabolic processes in an animal's body (von Bertalanffy 1934, 1938, 1957; Pauly 1980).

The deterministic nature of the von Bertalanffy equation is the primary problem when individual variability in growth exists, each fish in a group being considered to grow according to the model, but with its own L_∞ and K.

Individual variability is probably the most arguable point in fitting the VBGF to average values, since one should expect that individual variability of the growth parameters is a general feature of natural populations. Every individual organism is a unique result of heredity and environment, so that no two organisms in a population will grow at precisely the same rate and attain the same size at a given age (DeAngelis and Mattice 1979). The present study uses a simulation model which considers each fish individually, in contrast to most simulation experiments found in the literature, in which different overlapping cohorts are simulated (Jones 1987; Rosenberg and Beddington 1987).

Additionally, some authors have already shown that if a deterministic age-length-key is used to determine the age frequency of catches on the basis of length data, biased results are to be expected (Kimura 1977; Westrheim and Ricker 1978).

Bartoo and Parker (1983) incorporated a stochastic element in von Bertalanffy's relationship to improve this approach. Sainsbury (1980) developed a stochastic version of the VBGF for size increment data and affirmed that K will be underestimated when data obtained from populations with different individual growth parameters are analyzed with the classic deterministic equation. Schnute (1981) developed a new growth model, which includes von Bertalanffy's, Gompertz's and other models as special cases, and in which an error component for the size-at-age is incorporated.

Given that all three methods tested in the present study assume a deterministic model of growth, it is not surprising that they were highly sensitive to the individual variability of growth parameters.

The ELEFAN I program has been rather widely disseminated since 1980, and used on a relatively large number of fish and invertebrate stocks (see e.g., Table 3 of Pauly 1987 or Venema et al. 1988). SLCA and the P-W method are more recent, and therefore, only a few critical applications have been found (Damm and Herrmann 1986; Lozano 1987; Basson et al. 1988).

The ELEFAN method

In the present study, ELEFAN I always overestimated L_∞ and underestimated K when individual variability of growth parameters was assumed. Because the bias on L_∞ and K compensate each other, at least partially, the estimates of ϕ' were generally very accurate. The bias in K was only acceptable ($\leq$10%) when the coefficient of variation of the parameters L_∞ and K did not exceed 10%. Bias increased strongly when variability was high. This may be partially attributed to the procedure used for the generation of the stochastic variate for K, which had an intrinsic tendency towards negative bias. The magnitude of this bias, however (under 8%; see Table 3.1), is quite small compared to the bias resulting from variability in the growth parameters (more than 40% in some cases). Additionally, it was demonstrated that a coefficient of variation of L_∞ greater than 10% also produced an important bias in K (see Table 3.3).

The tendency of ELEFAN I to underestimate K may also be partially due to the fact that the identification of peaks (or modes) is quite difficult when the cohorts overlap, especially in older age groups. Moreover, the occurrence in the samples of fishes longer that L_∞ leads to an overestimation of L_∞ and underestimation of K, since both parameters are strongly correlated. Hampton and Majkowski (1987b) showed that the elimination of the largest length classes from the original length data slightly improves the estimates.

Additionally, as mentioned above, the deterministic nature of the VBGF is certainly the principal source of error in K, and the solution to this problem will be the implementation of a stochastic model for all the methods used in growth studies.

Factors such as seasonal changes in growth rate, variable recruitment period, size-dependent selection, or data grouped in greater length class intervals did not essentially change the tendency of the bias of L_∞ and K in ELEFAN I. Because seasonal oscillations in growth are expected to be very frequent in natural populations, the oscillating version of the VBGF can be used in conjunction with the ELEFAN I method. However, the results of this investigation are inconclusive with regard to the effects of such inclusion on the accuracy of L_∞ and K.

Variation in the growth rates due to seasonal effects, and variation in time of recruitment did not have a great influence on ELEFAN I results, and even the presence of two annual recruitment peaks produced a bias of less than 10%. The ELEFAN II procedure to determine the recruitment pattern is useful to estimate the number of peaks per year, but their temporal spread was wider than in reality, as has already been suggested by Pauly (1987).

The combination of growth variability and the effect produced by size-dependent selection reduced the accuracy of the growth parameter estimates (particularly K) obtained with ELEFAN I. The estimates of L_∞ were not strongly biased (always less than 12%) by the influence of these factors, but the bias of K was in these cases always greater than 12%.

The size range of fishes not fully sampled due to the selection of the fishing gear must not exceed 50% of the value of L_∞, if bias is to be kept near 10%. The correction of the frequencies by the ELEFAN II procedure produced a slight improvement of the estimates, but a reasonable estimate of natural mortality (M) should be used in this case.

Size-dependent selection effects and recruitment processes eliminate slow-growing fishes (i.e., the smallest ones) from the first cohort in the samples. Therefore, the difference between the modal lengths of the first and second cohorts is smaller in the samples than the true size difference in the natural population. This leads to the computation of a smaller annual growth rate and therefore an underestimation of K.

The same applies when two annual recruitment peaks occur, generating lower values of K when ELEFAN I is used for fitting the second recruitment peak. This must be taken into account when populations with two annual recruitment pulses are analyzed, in order to avoid the attribution of a slow growth pattern to the fishes corresponding to the second recruitment peak. Therefore, if two recruitment peaks are evident, a length class corresponding to the first peak should be used as starting point.

On the other hand, a bimodality in the length-frequency distribution of the first cohorts can also be caused by other ecological or biological circumstances (DeAngelis and Coutant 1982), and a good understanding of the biology of the species studied is needed in order to interpret the results obtained with length-based methods.

In simulation studies, Rosenberg and Beddington (1987) and Hampton and Majkowski (1987b) investigated the combined effect of variable recruitment time and individual variation of growth parameters, and their results had the same tendency as those of the present study.

The way in which length classes were grouped was another source of error, particularly in the ELEFAN I method. A reduction of the number of length classes resulted in "aliasing", i.e., hiding some cohorts, thus increasing the bias. In practice, 25 to 35 classes are generally adequate for all three methods.

The SLCA method

The SLCA method is also affected by variability between individuals. The bias in K increased with increasing coefficients of variation of this parameter, confirming the results of Basson et al. (1988). However, this tendency is reversed when only L_∞ or both L_∞ and K varied between individuals. In these cases (not previously tested by other authors), the tendency of the bias was similar to that of ELEFAN I, i.e., overestimation of L_∞ and underestimation of K. With SLCA, the estimates of K were relatively accurate (bias ≤ 10%), but L_∞ was more strongly overestimated than in ELEFAN. The truncation of the last length classes may improve the results (Hampton and Majkowski 1987b).

Another critical factor relevant to this method was the variability in time of recruitment. A long recruitment period produced positive bias in K, as has also been observed by Basson et al. (1988). A similar bias was also produced by seasonal growth oscillations. These factors affect cohort structure, and the modes can be obscured to such an extent that the SLCA method attempts to interpret the entire distribution as representing a single first cohort, overestimating K (Basson et al. 1988). However, it remains unclear why the tendency of this bias is reversed when variability is also assumed for L_∞ and size selection is in operation. Under these circumstances, the same explanation proposed for the ELEFAN I method may apply, i.e, the occurrence of larger fishes in the samples may force the values of L_∞ upward, provoking an underestimation of K.

When small fishes are not well represented in the samples but the individual variability is very low, the SLCA estimates of L_∞ and K are less biased than those obtained using ELEFAN I.

The SLCA method frequently showed a tendency to generate multiple maxima of the score function. This phenomenon was most pronounced in the populations which had the highest variability or the most complicated structure. In these cases the maxima were harmonically generated by extremely different combinations of L_∞ and K values, making it difficult to define the most adequate pair of growth parameters. This constitutes a significant disadvantage of the method, and although multiple maxima also occur in ELEFAN I results, it was generally easier to find the best parameter combination with the latter method.

The P-W method

According to Wetherall et al. (1987) the regression method to estimate L_∞ and Z/K should be insensitive to individual variability, since the estimates are based on the mean length (L_i). However, these authors tested the method on data without variability. The present study shows that individual variability of the growth parameters is critical for the estimates of the P-W method; the bias was the greatest of all methods, and prevailed in all experiments (in some cases reaching over 100%) (see Table 3.5).

The presence of larger fishes in the samples led to higher mean length values, especially at the end of the distribution, producing a moderate slope in the regression line and decreasing the absolute value of β. As a result, the values of L_∞ and Z/K are systematically inflated.

Wetherall et al. (1987) recognized that the length class interval, and thus the number of classes, should strongly affect the estimates of their method. In the present study, length class intervals affected the estimates of L_∞ only when variability between individuals was high. In all other cases, the way in which the data were grouped did not change the results significantly. Laurec and Mesnil (1987) tested the efficiency of the Beverton and Holt (1956) method, from which the P-W method is derived, and found that the differences in the results obtained for different length class widths are considerable only for populations with large values of Z.

The P-W method should be more efficient if the points for the regression are weighted by the covariance matrix A. However, this implies more computation time, and weighing the points by the sample size, as used in the present study, should also perform acceptably (Wetherall et al. 1987).

Seasonal oscillations in growth pattern, variable recruitment and size selection in the samples also seem to be sources of error, but the resulting bias is lower than that produced by individual variability. Damm and Herrmann (1986) showed that if the part of the size distribution unaffected by selection is one-half or less of the overall size range, the method will not produce accurate results. In addition, the correction procedure of ELEFAN II for selection effects increased the bias of the P-W method even more, and although there is no plausible explanation for this phenomenon, it is suggested that the correction procedure should not be used for this method (see Table 3.9).

Chapter 4

INDIVIDUAL VARIABILITY OF GROWTH

Introduction

Most published growth data on fishes refer to mean length-at-age values for entire populations. However, as shown above, the impact of individual growth variability on the growth parameter estimates is considerable. Therefore, data with individual observations of length and age over a considerable period of time were required, in order to calculate the growth parameters for each individual fish and the variability between fishes, i.e., the variance of L_∞ and K occurring in real fish population.

To assess the individual variability of growth parameters in a population, it is necessary to follow the growth of individual fishes during the course of their lives, and to compute the parameters for each individual from its length at various points in time. This type of data is very scarce. The present section is an attempt to estimate the magnitude of this variability with two different data sets.

Materials and Methods

The first data set was collected by Ursin (1967), who reared seven newborn females and four males of *Lebistes reticulatus* (guppy) individually for 58 weeks under experimental conditions, and periodically recorded their lengths.

In the same way, length-at-age data from Dr. R. Doyle (pers. comm.; see Doyle and Talbot 1989) were also obtained for 70 young hybrids of *Oreochromis mossambicus* and *O. hornorum* (tilapia) also reared individually for approximately 25 weeks.

In both cases, the VBGF was fitted to the data of each fish using the nonlinear method of Allen (1966). Additionally the data of tilapia were also fitted with a nonlinear method developed by Soriano et al. (1990) which allows the fitting of a two-phase growth curve. The equation used was:

$$L_t = L_\infty (1 - \exp(-KB(t-t_0))) \quad \text{...4.1)}$$

where

$$B = 1 - (h/((t-t_h)^2 + 1)) \quad \text{...4.2)}$$

and

h = measure of the strength of the deviation from the standard VBGF

t_h = age at which the deviation is strongest

The analysis of the length-at-age data of guppy and tilapia permitted the approximate estimation of the individual variability of the growth parameters within these populations. The parameters K, L_∞ and t_0 were estimated for each individual fish. Average, variance and coefficient of variation between the individual sets of growth parameters were also calculated.

Results

Theoretically, the variability of the growth pattern of a cohort can only be produced by individual variations in the growth parameters. However, the distribution pattern of the length-at-age values and their variance can be very useful to make inferences on the growth parameters variability. Fig. 4.1 shows growth curves with varying K and/or L_∞, and constant t_0. When only L_∞ varies, the variance of length-at-age increases with age and length. When only K varies, the younger and intermediate age classes represent the greater variation in length. If both parameters vary, a combination of both patterns of variation is observed.

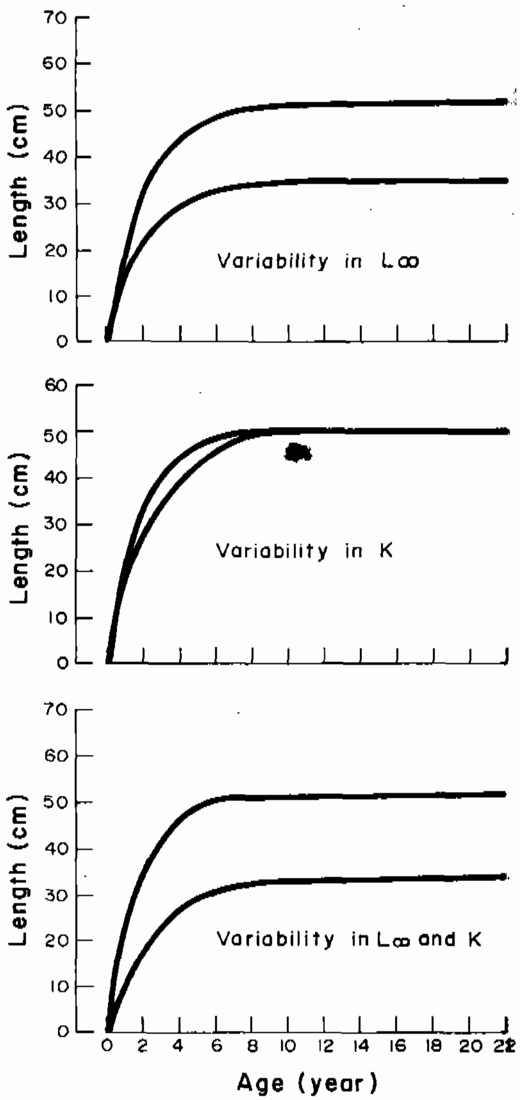

Fig. 4.1. Theoretical growth curves of the fish of a cohort with individual variability in growth parameters L_∞ and/or K.

Figs. 4.2 and 4.3 show the mean length for each age and the corresponding standard deviations for the female guppies and for the tilapias. The inflection point in the tilapia growth curve was an artefact resulting from the transfer of the fish to larger tanks in the 10th week of the laboratory experiment (R. Doyle, pers. comm.). The original length-at-age data and the values of the estimated individual growth parameters for both experimental populations are given in Appendix B (Tables B.14, B.15, B.16, and B.17).

Table 4.1 shows the results obtained with Allen (1966) method on the average values of the growth parameters and their variation. Both parameters (L_∞ and K) vary among individuals. The variation was stronger in the tilapias and in K, with a maximum of 30%.

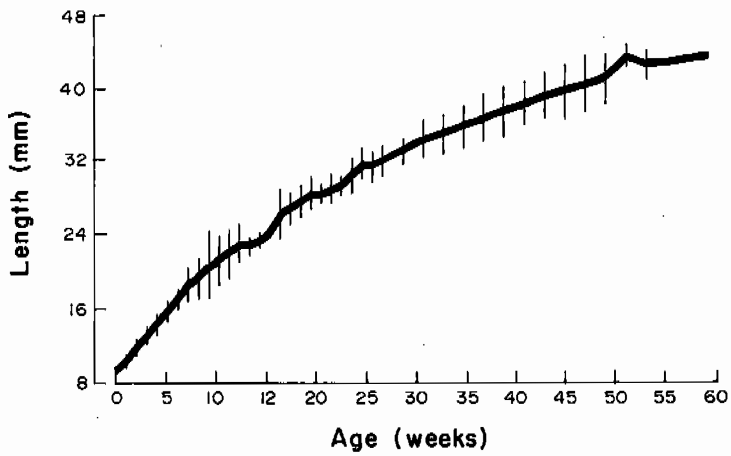

Fig. 4.2. Mean length-at-age and standard deviation of 7 young female guppies reared individually during 58 weeks under experimental conditions.

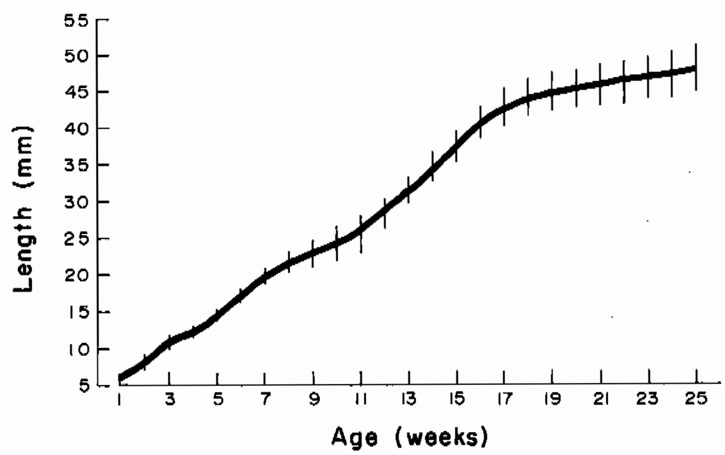

Fig. 4.3. Mean length-at-age and standard deviation of 70 young hybrids of tilapia reared individually during 58 weeks under experimental conditions.

Table 4.1. Means and coefficients of variation of the parameters L_∞ and K in experimental guppy and tilapia populations.

Species	N	L_∞ (cm)	CV_{L_∞} (%)	K ($year^{-1}$)	CV_K (%)
L. reticulatus (females)	7	4.91	12	0.035	22
L. reticulatus (males)	4	2.38	5	0.12	11
Tilapia	70	9.25	26	0.035	30

The exclusion of some outlying points for young tilapias reduced the coefficient of variation of L_∞ to 20% but did not change the corresponding value for K. When the same data were fitted for the two-phase growth, a reduction of the coefficient of variation of L_∞ to 15% was observed. However in this case, K had a coefficient of variation of 44%. The fit of a two-phase growth model seems to explain better the change in growth pattern produced by the transfer of the fishes to larger tanks (Fig. 4.4).

Table 4.2 summarizes the coefficients of variation of L_∞ and K obtained with the different fitting methods applied to the tilapia length-at-age data. These coefficients of variation ranged from 15% to 44%, but independently of the method used, the individual variability of K was always stronger than that of L_∞.

Discussion

The questions underlying this chapter were: how and how much do L_∞ and K vary in natural populations?

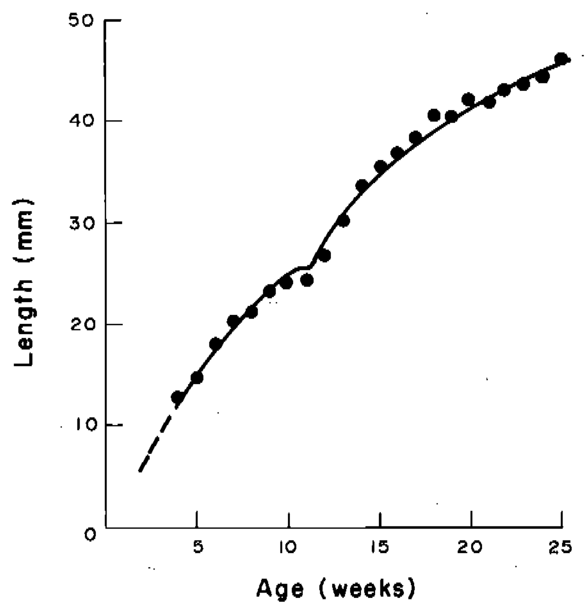

Fig. 4.4. Two-phase growth curve fitted for the length-at-age data of an individual tilapia and estimated parameters.

Table 4.2. Coefficients of variation of L_∞ and K.

Method	CV of L_∞ (%)	CV of K (%)	Notes
Allen (1966)	25.6	30.0	all points included
Allen (1966)	20.0	30.1	outlying points not included
Soriano et al. (1990)	15.5	44.4	outlying points not included

The results presented above demonstrate that individual variability in fishes can be quite large. Indeed, the coefficients of variation of K were as high as 40%, always higher than those of L_∞. Different methods indicate differences in the variability of growth parameters. However, the coefficients of variation of L_∞ and K seem to be inversely correlated, i.e. when L_∞ varied more, K varied less and vice versa.

The results on the individual variability of growth parameters are only an approximation, because they were gained under experimental conditions. Interferences during the experiments due to population density, size of the tanks (Yoshihara 1952), type of food, temperature, etc., probably affected individual growth rates. However, considering the results obtained with these experimental populations suggests that the coefficients of variation of 10%, 20% and 30% assumed in the simulation model of Chapter 3 were probably realistic and should probably include the true values for natural populations.

Rosenberg and Beddington (1987) presented a compilation of several values for the coefficient of variation of L_∞ between years or between populations for a number of species. The differences are smaller for the data between years, never exceeding 10%, but the estimates were made by taking the average of the mean size at age in the oldest age group, or by averaging several estimates of L_∞, and could therefore be biased.

Differences in growth pattern, caused by intrinsic or extrinsic factors, between different populations or for different time periods, are amply documented (e.g., Bannister 1978; Craig 1978; Anthony and Waring 1980; Mollow 1984). These differences reflect, in average, modifications in the budget of catabolism and anabolism, and are expressed by the parameters L_∞ (or W_∞) and K (Beverton and Holt 1957). According to these authors, changes in the rate of food consumption probably directly affect the rate of anabolism, whereas catabolism should be affected to a greater extent by the amount of body material available to be broken down, i.e., the weight of the organism and the general metabolic activity.

The parameter L_∞ of the VBGF is proportional to the ratio of anabolism and catabolism (H/k), and the parameter K is proportional to the coefficient of catabolism (k). Thus, factors which affect the food consumption rate should produce changes in the coefficient of anabolism and therefore in L_∞. Other differences in general metabolic activity should affect more the rate of catabolism and therefore the parameter K (Beverton and Holt 1957).

It is reasonable to suppose that the differences between the individuals of a population, which live under similar external conditions, should mostly be caused by genetic factors and affect the general metabolic activity of the organism, and probably indirectly both parameters L_∞ and K. The proportion of the variability of each parameter probably differs according to the species in question, but this preliminary investigation suggested that K varied more strongly than L_∞.

In many fishes the variance of length-at-age increases with increasing age (see e.g. Steinmetz 1974; Westrheim and Ricker 1978). This has led some authors to suppose that L_∞ constitutes the major source of variation between individuals (Jones 1987; Rosenberg and Beddington 1987). However, in other fishes (mostly pelagic and fast-growing species) and in many molluscs, variance in length-at-age first increases and then decreases (Wolf and Daugherty 1961; Feare 1970; Poore 1972; Bartoo and Parker 1983), suggesting that it is the variance of K which is high. Moreover, it could also be argued that bias in the determination of age or sampling errors are the cause of such patterns in the data. Natural variability and sampling bias are probably combined in real data, and therefore, further investigation is needed to clarify these questions.

The pattern of variation of length-at-age (see Fig. 4.1) may be used to gain an idea of the variation of the growth parameters between individuals of a species (Sainsbury 1980) until better methods are developed for the purpose, unveiling the underlying ecological and physiological relationships. Experimental research must nevertheless be intensified in the future, if we are to learn more about individual variations of growth within populations. This will be essential, in order to permit at least a partial correction of the bias resulting from high variability.

Chapter 5

LENGTH-BASED METHODS APPLIED TO SCIAENID FISHES

Introduction

The sciaenids, commonly known as croakers or drums are a large family of mainly coastal demersal marine fishes inhabiting all tropical and most temperate oceans, comprising approximately 200 species (Wheeler 1979). Many are found in brackish waters, at least seasonally, and some are endemic to fresh waters. Many species use estuarine environments as nursery grounds during their juvenile phase and as feeding grounds during the adult phases. Others are estuarine inhabitants throughout their lives (Fischer 1978).

For this part of the present study, biological information was compiled on several species of Sciaenidae from different regions of the world. Most of the sciaenids have large and thick otoliths (which are difficult to read), and therefore I was interested to investigate the application of length-based methods on these fishes.

The objective of the present study was to apply the length-based methods tested in Chapter 3 to natural populations, in order to examine their usefulness in practice and to compare simulated and real data.

Materials and Methods

For the present study, length data for the following sciaenid species were analyzed:

Species	Area
• *Umbrina canosai* • *Micropogonias furnieri* • *Cynoscion striatus* • *Cynoscion jamaicensis* • *Macrodon ancylodon*	Southwest and West-Central Atlantic
• *Cynoscion regalis* • *Leiostomus xanthurus* • *Cynoscion nobilis*	Northwest Atlantic and Northeast Pacific
• *Johnieops vogleri* • *Protonibea diacanthus* • *Pseudosciaena coibor*	Northern Indian Ocean
• *Pseudotolithus senegalensis* • *Umbrina canariensis*	East-Central Atlantic

The length data used in the present investigation and general information on the samples are summarized in Table 5.1.

Table 5.1. Sources of length-frequency data used in the present study. Names without year denote personal communications by the researcher/institution indicated. C = commercial catch. S = research survey.

	Code name	Species	Source	Sampling period	Sampling area	Sampling method	L_{min} (cm)	L_{max} (cm)	Class interval	Number classes	Number samples	Observations
1	CAS1	*Umbrina canosai*	M. Haimovici/FURG-Brazil	1976-1979	Brazil/S	C/trawl	15.0	40.0	1.0	26	4	pooled
2	CAS2	*Umbrina canosai*	J. Kotas/CEPSUL-Brazil	1986	Brazil/S	C/trawl	16.5	41.5	1.0	26	4	
3	CJAMA	*Cynoscion jamaicensis*	H. Valentini/IP-Brazil	1982	Brazil/SE	C/trawl	14.0	33.0	0.5	39	12	pooled
4	CJAM1	*C. jamaicensis* (males)	Santos, 1968	1959-1962	Brazil/SE	C/trawl	16.3	30.3	1.0	15	4	pooled
5	CJAM2	*C. jamaicensis* (females)	Santos, 1968	1959-1962	Brazil/SE	C/trawl	16.3	30.3	1.0	15	4	pooled
6	CJAM3	*Cynoscion jamaicensis*	Vazzoler & Braga, 1983	1975	Brazil/SE-S	S/trawl	5.5	26.5	1.0	23	4	
7	CSTRI	*Cynoscion striatus*	Haimovici & Maceira, 1981	1978-1980	Brazil/S	S/trawl	4.0	52.0	2.0	25	4	
8	CSTRI1	*Cynoscion striatus*	J. Kotas/CEPSUL-Brazil	1986	Brazil/S	C/trawl	13.5	53.5	1.0	41	4	
9	CORV	*Micropogonias furnieri*	M. Rey/INAPE-Uruguay	1980	Uruguay	C/trawl	21.5	61.5	1.0	41	8	pooled
10	MIFUR	*Micropogonias furnieri*	Vazzoler et al., 1973	1972	Brazil/S	S/trawl	20.0	62.0	2.0	22	4	
11	MIFUR1	*Micropogonias furnieri*	J. Kotas/CEPSUL-Brazil	1986	Brazil/S	C/trawl	16.5	70.5	1.0	55	4	
12	MIFUR2	*Micropogonias furnieri*	J. Kotas/CEPSUL-Brazil	1986	Brazil/SE	C/trawl	19.5	64.5	1.0	46	3	
13	CORV1	*Micropogonias furnieri*	Lowe-McConnell, 1966	1958-1959	Guyana	S/trawl	22.0	45.0	1.0	24	10	
14	CREGA	*Cynoscion regalis*	Massmann, 1963	1954-1958	USA/Chesapeake B.	C/pound net	15.5	36.5	0.5	43	6	
15	CYNOB	*Cynoscion nobilis*	Thomas, 1968	1960	USA/California	C/gill net	72.5	142.5	5.0	15	1	
16	JVOG	*Johnieops vogleri*	Muthiah, 1982	1973-1975	India/Bombay	C/trawl	1.5	29.5	2.0	15	12	
17	LXANT	*Leiostomus xanthurus*	Pacheco, 1962	1956	USA/Virginia	C/pound & S/trawl	2.0	26.5	0.5	50	7	
18	PESC	*Macrodon ancylodon*	Martin Juras, 1980	1976-1977	Brazil/S	C/trawl	13.5	40.5	1.0	28	12	
19	PESC1	*Macrodon ancylodon*	J. Kotas/CEPSUL-Brazil	1986	Brazil/S	C/trawl	9.5	44.5	1.0	36	4	
20	PCOIB	*Pseudosciaena caibor*	Rajan, 1967	1960	India/Chilka lake	C/several nets	6.3	81.3	2.5	31	12	
21	PDIAC	*Protonibea diacanthus*	Rao, 1966	1958-1961	India/Bombay	C/trawl	22.5	107.5	5.0	18	12	
22	PSENE	*Pseudotolithus senegalensis*	Poinsard & Troadec, 1966	1963-1964	Congo	S/trawl	9.5	55.5	1.0	47	12	pooled
23	UCANA	*Umbrina canariensis*	Dardignac, 1961	1960	Morrocco	C/trawl	6.0	39.0	1.0	34	5	

Table 5.2. Growth parameters estimated for 23 sets of length data on *Sciaenidae* with ELEFAN, ELEFAN-C, SLCA and P-W methods.

	Code		ELEFAN						ELEFAN-C							SLCA					P-W			
	name	Species	L_∞	K	C	Sta. Point	ESP/ASP	ϕ'	L_∞	K	C	WP	Sta.Point	ESP/ASP	ϕ'	L_∞	K	t_0	Score	ϕ'	Cl.	L_∞	Z/K	r^2
1	CAS1	*Umbrina canosai*	52.53	0.355	0	3 /24.00	0.373	2.991	49.60	0.624	1.00	0.80	1 /19.00	0.465	3.186	43.30	0.320	0.5	61.30	2.778	13	37.50	2.337	0.954
2	CAS2	*Umbrina canosai*	47.90	0.302	0	1 /26.50	0.443	2.841	43.45	0.630	0.75	0.30	3 /37.50	0.511	3.075	39.30	0.470	0.8	63.80	2.861	10	38.51	2.028	0.984
3	CJAMA	*Cynoscion jamaicensis*	33.56	0.315	0	4 /19.00	0.261	2.550	35.00	0.250	0.50	0.86	5 /28.00	0.323	2.486	31.00	0.435	0.9	24.60	2.621	19	35.32	5.722	0.899
4	CJAM1	*C. jamaicensis* (males)	40.12	0.361	0	1 /25.25	0.527	2.764	40.34	0.222	1.00	0.00	2 /20.25	0.581	2.558	33.50	0.552	0.6	33.90	2.792	7	31.88	3.867	0.985
5	CJAM2	*C. jamaicensis* (females)	32.60	0.380	0	2 /25.25	0.571	2.606	32.80	0.376	0.38	0.00	2 /25.25	0.581	2.607	29.90	0.400	0.9	10.20	2.553	7	34.03	4.526	0.959
6	CJAM3	*Cynoscion jamaicensis*	35.70	0.262	0	2 / 7.50	0.528	2.524	28.78	0.371	0.86	0.00	3 /20.50	0.564	2.487	44.50	0.355	0.8	61.70	2.847	15	31.44	4.706	0.921
7	CSTRI	*Cynoscion striatus*	62.75	0.525	0	4 / 6.00	0.499	3.315	58.06	0.580	0.37	0.70	2 /10.00	0.547	3.291	53.80	0.460	0.9	68.90	3.124	19	53.32	2.731	0.978
8	CSTRI1	*Cynoscion striatus*	60.62	0.495	0	1 /37.50	0.275	3.260	64.06	0.318	0.89	0.22	2 /27.50	0.369	3.116	56.30	0.490	0.7	73.50	3.191	28	51.50	1.550	0.995
9	CORV	*Micropogonias furnieri*	68.39	0.150	0	1 /49.50	0.429	2.846	63.72	0.232	1.00	0.00	7 /24.50	0.498	2.974	56.00	0.510	0.8	162.50	3.204	17	66.09	3.750	0.932
10	MIFUR	*Micropogonias furnieri*	71.90	0.160	0	4 /36.00	0.399	2.918	62.43	0.322	0.98	0.50	1 /32.00	0.608	3.099	62.75	0.235	0.1	35.75	2.966	12	68.33	4.795	0.913
11	MIFUR1	*Micropogonias furnieri*	77.11	0.177	0	2 /31.50	0.407	3.022	74.80	0.232	1.00	0.62	1 /47.50	0.542	3.113	78.80	0.370	0.7	203.40	3.361	19	67.90	1.960	0.920
12	MIFUR2	*Micropogonias furnieri*	70.57	0.153	0	1 /32.50	0.481	2.882	72.80	0.177	0.91	0.43	1 /37.50	0.606	2.972	71.90	0.260	0.2	46.60	3.128	19	67.53	2.954	0.992
13	CORV1	*Micropogonias furnieri*	51.80	0.220	0	4 /39.50	0.402	2.771	48.13	0.435	0.48	0.60	1 /33.50	0.467	3.003	39.50	0.510	0.9	28.80	2.901	11	47.72	4.854	0.789
14	CREGA	*Cynoscion regalis*	43.10	0.241	0	3 /25.50	0.307	2.651	39.75	0.204	1.00	0.00	5 /30.00	0.372	2.508	39.10	0.140	0.9	22.70	2.330	18	39.84	4.568	0.987
15	CYNOB	*Cynoscion nobilis*	181.15	0.308	0	1 /77.50	1.000	4.005	-	-	-	-	- -	-	-	144.8	0.520	0.2	11.00	4.038	8	154.24	2.908	0.951
16	JVOG	*Johnieops vogleri*	34.40	0.590	0	1 /11.10	0.714	2.844	34.88	0.570	0.10	0.50	3 /13.50	0.722	2.841	42.50	0.440	0.5	144.90	2.900	3	29.65	0.658	0.989
17	LXANT	*Leiostomus xanthurus*	28.23	0.202	0	4 / 7.00	0.436	2.207	27.98	0.284	0.80	0.00	6 /11.50	0.427	2.347	28.40	0.160	0.9	60.80	2.111	34	26.45	2.451	0.995
18	PESC	*Macrodon ancylodon*	45.90	0.240	0	9 /29.50	0.463	2.704	45.80	0.244	0.30	0.80	6 /23.50	0.474	2.709	34.70	0.700	0.4	413.10	2.926	18	43.53	2.269	0.951
19	PESC1	*Macrodon ancylodon*	49.68	0.388	0	3 /26.50	0.290	2.981	48.70	0.253	0.40	0.74	1 /28.50	0.340	2.778	42.50	0.210	0.2	25.00	2.579	15	43.16	5.159	0.932
20	PCOIB	*Pseudosciaena caibor*	89.00	0.250	0	9 /78.80	0.387	3.297	89.14	0.255	0.44	0.17	6 /38.80	0.430	3.307	87.30	0.400	0.6	250.50	3.484	25	91.16	4.379	0.860
21	PDIAC	*Protonibea diacanthus*	135.79	0.228	0	8 /92.50	0.437	3.624	125.62	0.279	0.65	0.70	1 /97.50	0.518	3.644	108.30	0.400	0.4	82.80	3.671	15	111.37	3.241	0.882
22	PSENE	*Pseudotolithus senegalensis*	57.32	0.361	0	1 /14.10	0.276	3.074	57.52	0.354	0.10	0.80	1 /14.00	0.318	3.069	59.60	0.380	0.3	223.80	3.130	20	57.21	3.476	0.994
23	UCANA	*Umbrina canariensis*	43.20	0.238	0	5 /14.00	0.619	2.648	43.28	0.242	0.85	0.00	2 /21.00	0.661	2.656	38.40	0.120	0.4	32.90	2.248	13	40.13	1.422	0.934

The data were taken from tables when available, but in some cases they had to be read off from graphs. Some original length frequencies were pooled by month or year, when more than one sample per month or year was available from the same source. These cases are indicated in Table 5.1.

ELEFAN I, SLCA and the P-W methods were applied to the length data in the same way as done previously for the simulated data (see Chapter 3.4).

I selected the results of the calculations exclusively according to the best goodness-of-fit, regardless of whether they agreed with my personal knowledge on the biology or growth of the species in question. In the case of ELEFAN I, when the maximum value of ESP/ASP could be attributed to several adjacent values of K and L_∞ ('response surface procedure'; see Chapter 2), the combination with the lowest L_∞ and the highest K was preferred, because of the demonstrated bias in ELEFAN (see Chapter 3).

Although seasonal oscillation of growth rates is to be expected in natural populations, the parameters corresponding to a non-oscillatory ("ELEFAN") and to an oscillatory ("ELEFAN-C") curve of VBGF were calculated for each set of data, to observe the differences between the estimates and to compare the results with the other methods which do not consider seasonal oscillation in the growth equation.

The correction of the length frequencies for size-selection with the ELEFAN-II procedure was not applied to the Sciaenidae data.

Results

Table 5.2 displays the growth parameters obtained with ELEFAN, ELEFAN-C (i.e., when the parameter $C \neq 0$), SLCA and the P-W methods. Length distributions of the species with slow growth rates were more difficult to analyze due to the occurrence of multiple maxima of the score functions of ELEFAN I and SLCA.

A statistical examination of the growth parameters estimated for all the length data sets (except *C. nobilis*) is summarized in Table 5.3.

ELEFAN generally computed the highest values for central tendency and measures of deviation of estimates of L_∞, and the lowest values for central tendency of K, followed by ELEFAN-C, SLCA and the P-W method. SLCA and the P-W method led to very similar values. The measures of deviation of K were lowest in ELEFAN. The central tendency of ϕ' shows that errors in L_∞ and K compensate each other at least in part. Measures of deviation of ϕ' were highest in SLCA.

Fig. 5.1 shows a box-and-whisker plot of the results. The central box covers the central 50% of the values, between the lower and upper quartiles. The vertical lines ('whiskers') extend out to the minimum and maximum values and the central line represents the median. The points represent outliers (more than 1.5 times the interquartile range).

The range of variation (interquartile range) shows a wide overlapping region of the estimates of the growth parameters, and a slight tendency of decreasing L_∞ and increasing K from left to right (Fig. 5.1).

Table 5.3. Mean, median, mode, standard deviation, coefficient of variation, minimum and maximum of the estimates of L_∞, K and ϕ' obtained with ELEFAN, ELEFAN-C, SLCA and P-W method on 22 length data sets of sciaenid fishes.

Parameter	Method	Mean	Median	Mode	SD	CV (%)	min	max
L_∞	ELEFAN	56.01	50.74	47.90	24.01	42.87	28.23	135.79
	ELEFAN-C	53.94	48.42	45.80	22.57	41.84	27.98	125.62
	SLCA	50.97	42.90	42.50	20.50	40.22	28.40	108.30
	P-W	50.62	43.35	40.13	21.20	41.88	26.45	111.37
K	ELEFAN	0.300	0.256	0.361	0.122	40.67	0.150	0.590
	ELEFAN-C	0.339	0.282	0.232	0.141	41.59	0.177	0.630
	SLCA	0.378	0.400	0.400	0.145	38.36	0.120	0.700
ϕ'	ELEFAN	2.878	2.845	2.841	0.314	10.91	2.207	3.624
	ELEFAN-C	2.901	2.973	2.841	0.330	11.38	2.347	3.644
	SLCA	2.896	2.901	2.861	0.390	13.47	2.111	3.671

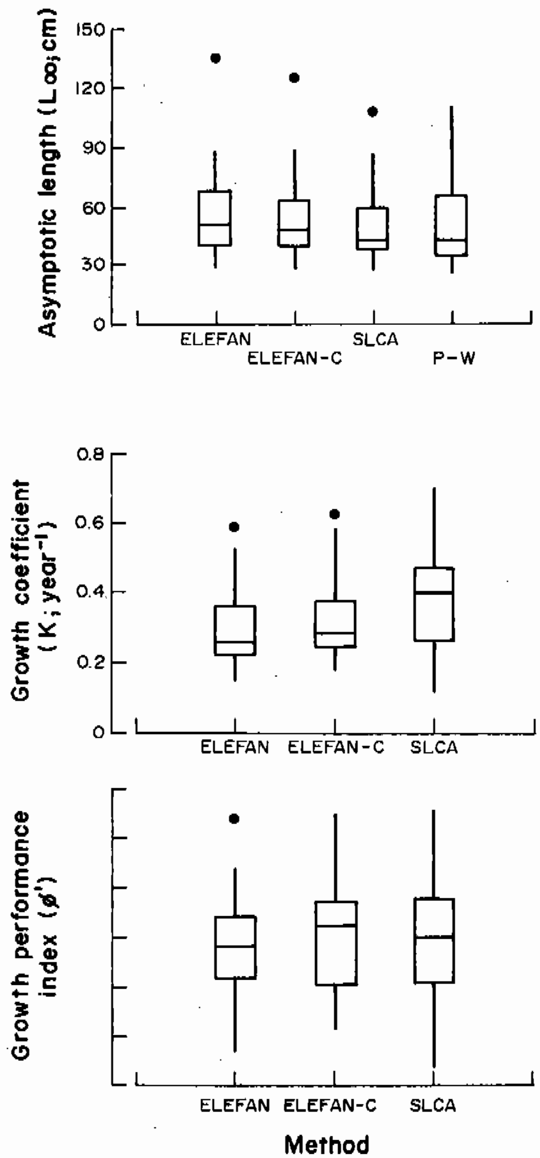

Fig. 5.1. Box-and-whisker plot for L_∞, K and ϕ' estimated with ELEFAN, ELEFAN-C, SLCA and P-W method on 22 length data sets of sciaenid fishes (see explanation in text).

However, no systematic differences between the methods could be shown for the estimates of K and ϕ' by means of a Friedman rank test (Table 5.4). There were, however, significant differences (5% level) between methods in the estimates of L_∞. The highest values were produced by ELEFAN, followed by ELEFAN-C, SLCA and the P-W method (Table 5.5, top). A test for multiple comparison (Conover 1980) demonstrated that the estimates of the two ELEFAN methods on one hand, and those of SLCA and the P-W method on the other are significantly different at the 5% level (Table 5.5, top).

Discussion

The results of the present section demonstrated that ELEFAN tends to overestimate L_∞ more than the SLCA or P-W methods. In the test on the samples simulated in Chapter 3, ELEFAN estimates of L_∞ were more positively biased than those of SLCA and P-W only when the populations had no individual variability in growth parameters, and size-dependent selection or when variable recruitment were assumed (see Tables 3.9 and 3.11). Assuming that a comparison between simulated and real data is valid, it follows that, at least for the sciaenid data analyzed here, selection effects and recruitment variability influenced the samples more than the individual variability of growth parameters.

Table 5.4. Friedman test (by ranks) to compare the growth parameters.

		Parameter K			Table of ranks		
File	Code	ELEFAN	ELEFAN-C	SLCA	ELEFAN	ELEFAN-C	SLCA
1	CAS1	0.355	0.624	0.320	2	3	1
2	CAS2	0.302	0.630	0.470	1	3	2
3	CJAMA	0.315	0.250	0.435	2	1	3
4	CJAM1	0.361	0.222	0.552	2	1	3
5	CJAM2	0.380	0.376	0.400	2	1	3
6	CJAM3	0.262	0.371	0.355	1	3	2
7	CSTRI	0.525	0.580	0.460	2	3	1
8	CSTRI1	0.495	0.318	0.490	3	1	2
9	CORV	0.150	0.232	0.510	1	2	3
10	MIFUR	0.160	0.322	0.235	1	3	2
11	MIFUR1	0.177	0.232	0.370	1	2	3
12	MIFUR2	0.153	0.177	0.260	1	2	3
13	CORV1	0.220	0.435	0.510	1	2	3
14	CREGA	0.241	0.204	0.140	1	2	3
16	JVOG	0.590	0.570	0.440	3	2	1
17	LXANT	0.202	0.284	0.160	2	3	1
18	PESC	0.240	0.244	0.700	1	2	3
19	PESC1	0.388	0.253	0.210	3	2	1
20	PCOIB	0.250	0.255	0.400	1	2	3
21	PDIAC	0.228	0.279	0.400	1	2	3
22	PSENE	0.361	0.354	0.380	2	1	3
23	UCANA	0.238	0.242	0.120	2	3	1
				SUM =	36	46	50

Calculated statistic = 2.528

F = 3.22; 0.05; 2; 42 ===> No significant differences

		Parameter φ'			Table of ranks		
File	Code	ELEFAN	ELEFAN-C	SLCA	ELEFAN	ELEFAN-C	SLCA
1	CAS1	2.991	3.186	2.778	2	3	1
2	CAS2	2.841	3.075	2.861	1	3	2
3	CJAMA	2.550	2.486	2.621	2	1	3
4	CJAM1	2.764	2.558	2.792	2	1	3
5	CJAM2	2.606	2.607	2.553	2	3	1
6	CJAM3	2.524	2.487	2.847	2	1	3
7	CSTRI	3.315	3.291	3.124	3	2	1
8	CSTRI1	3.260	3.116	3.191	3	1	2
9	CORV	2.846	2.974	3.204	1	2	3
10	MIFUR	2.918	3.099	2.966	1	3	2
11	MIFUR1	3.022	3.113	3.361	1	2	3
12	MIFUR2	2.882	2.972	3.128	1	2	3
13	CORV1	2.771	3.003	2.901	1	3	2
14	CREGA	2.651	2.508	2.330	3	2	1
16	JVOG	2.844	2.841	2.900	2	1	3
17	LXANT	2.207	2.347	2.111	2	3	1
18	PESC	2.704	2.709	2.926	1	2	3
19	PESC1	2.981	2.778	2.579	3	2	1
20	PCOIB	3.297	3.307	3.484	1	2	3
21	PDIAC	3.624	3.644	3.671	1	2	3
22	PSENE	3.074	3.069	3.130	2	1	3
23	UCANA	2.648	2.656	2.248	2	3	1
				SUM =	39	45	48

Calculated statistic = 0.952

F = 3.22; 0.05; 2; 42 ===> No significant differences

Table 5.5. Friedman rank test comparing the estimates of L_∞ (top) between methods and results of the test for multiple comparison (Conover 1980).

	Code	Asymptotic Length (L_∞)				Table of Ranks			
		ELEFAN	ELEFAN-C	SLCA	P-W	ELEFAN	ELEFAN-C	SLCA	P-W
1	CAS1	52.53	49.60	43.30	37.50	4	3	2	1
2	CAS2	47.90	43.45	39.30	38.51	4	3	2	1
3	CJAMA	33.56	35.00	31.00	35.32	2	3	1	4
4	CJAM1	40.12	40.34	33.50	31.88	3	4	2	1
5	CJAM2	32.60	32.80	29.90	34.03	2	3	1	4
6	CJAM3	35.70	28.78	44.50	31.44	3	1	4	2
7	CSTRI	62.75	58.06	53.80	53.32	4	3	2	1
8	CSTRI1	60.62	64.06	56.30	51.50	3	4	2	1
9	CORV	68.39	63.72	56.00	66.09	4	2	1	3
10	MIFUR	71.90	62.43	62.75	68.33	4	1	2	3
11	MIFUR1	77.11	74.80	78.80	67.90	3	2	4	1
12	MIFUR2	70.57	72.80	71.90	67.53	2	4	3	1
13	CORV1	51.80	48.13	39.50	47.72	4	3	1	2
14	CREGA	43.10	39.75	39.10	39.84	4	2	1	3
15	JVOG	34.40	34.88	42.50	29.65	2	3	4	1
16	LXANT	28.23	27.98	28.40	26.45	3	2	4	1
17	PESC	45.90	45.80	34.70	43.53	4	3	1	2
18	PESC1	49.68	48.70	42.50	43.16	4	3	1	2
19	PCOIB	89.00	89.14	87.30	91.16	2	3	1	4
20	PDIAC	135.79	125.62	108.30	111.37	4	3	1	2
21	PSENE	57.32	57.52	59.60	57.21	2	3	4	1
22	UCANA	43.20	43.28	38.40	40.13	3	4	1	2
					SUM =	70	62	45	43

Calculated statistic = 5.719

F = 2.76; 0.05; 3; 60 ===> Significant differences

Multiple comparison ===> Calculated statistic = 15.533

Methods	Rank difference	Significant
ELEFAN - ELEFAN-C	8	no
ELEFAN - SLCA	25	yes
ELEFAN - P-W	27	yes
ELEFAN-C - SLCA	17	yes
ELEFAN-C - P-W	19	yes
SLCA - P-W	2	no

The number of small Sciaenidae discarded by the commercial trawlers may reach more than 60% of the catch in some areas, such as in the USA and southern Brazil (Chittenden and McEachran 1976; Haimovici and Maceira 1981). The data sets with the higher estimates of L_∞ in ELEFAN or ELEFAN-C (rank=4 in Table 5.4, e.g., CORV1, CAS1, CAS2, PESC) are those with strong selection effects, generally obtained from a commercial trawl fishery. On the other hand, data sets such as LXANT, JVOG or CJAM3, in which small fishes are well represented, have higher estimates of L_∞ in SLCA than in ELEFAN. This indicates that the effect of selection is more important for the ELEFAN method than has been assumed, and strongly suggests that the ELEFAN II procedure should be used to correct this bias (at least partially) whenever "real" length-frequency data are analyzed.

In summary, the estimates of L_∞ obtained with ELEFAN or ELEFAN-C will be more biased than those obtained with SLCA and the P-W method when selection effects are important and cannot be corrected. When selection is negligible, only the individual variability in growth parameters should affect the estimates, and the estimates of L_∞ will be least biased with ELEFAN. The estimates of ϕ', being a combination of both L_∞ and K, will compensate the opposing tendencies of bias, and therefore, this index can indeed be considered a useful indicator of growth performance.

Chapter 6

ACCURACY OF TOTAL MORTALITY ESTIMATES

Introduction

Several of the commonly-used methods for estimation of mortality rates, cohort strength and fishery yields require previous estimates of the von Bertalanffy growth parameters. Therefore, the accuracy of the estimates of mortality are related to the magnitude of the bias in growth parameters.

In this section, the bias of the estimates of Z obtained from a length-converted catch curve is investigated. Additionally, a sensitivity analysis of the procedure in relation to uncertainties in L_∞ and K is performed.[a]

Materials and Methods

Some simulated length-frequency data of Series I, II and IV (see Chapter 3) were selected to investigate the sources of bias in the length-converted catch curves. Such curves can be created by the ELEFAN II program from a pooled data set of length-frequencies and values for L_∞ and K. Total mortality is calculated from a regression between $\ln(N_i/\Delta t)$ and relative age t_i. (For more details on the procedure, see Chapter 2.)

The following effects were investigated:

- selection of the points included in the regression;
- different growth strategies;
- individual variability of the growth parameters; and
- size-dependent selection.

The effects of the exclusion of some points of the catch curve on the estimates of Z were analyzed on a control population with the following parameters:

Asymptotic length (L_∞)	50.0 cm
Coefficient of variation of L_∞	0
Growth constant (K)	0.5 year^{-1}
Coefficient of variation of K	0
Natural mortality rate (M)	0.8 year^{-1}
Total mortality rate (Z)	1.6 year^{-1}
Age at recruitment (t_r)	0.0
Width of length classes	2.0 cm
Size selection	not operating
Number total of points in the catch curve	24

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[a]Note added in proof:

The December 1990 issue of Fishbyte (ICLARM, Manila) presents papers by P. Sparre and D. Pauly which discuss the biasing effect of seasonal growth on catch curve estimates of Z, and a simple modification of the standard length converted catch curve which eliminates this bias, respectively.

For the analysis of the effects of different growth strategies, 4 sets of 12 length data samples were analyzed, corresponding to fish populations with the following parameters:

Population type	L_∞ (cm)	K ($year^{-1}$)	Z ($year^{-1}$)	W_{lc} (cm)
1	30	1.8	5.00	1
2	50	0.6	1.90	2
3	80	0.2	0.60	3
4	110	0.1	0.30	4

where

L_∞ = asymptotic length (cm)
K = growth constant ($year^{-1}$)
Z = total mortality rate ($year^{-1}$)
W_{lc} = width of the length classes (cm)

The following input parameters were fixed:

Coefficient of variation of K ($C.V._K$)	10 %
Coefficient of variation of L_∞ ($C.V.L_\infty$)	10 %
Age at recruitment (t_r)	0.0
Size selection (Sel)	not operating
Natural mortality rate (M)	Z/2

For the analysis of the effects of individual growth variability, one set of 12 samples of each of following population types was used:

C.V. of L_∞	C.V. of K
0[a]	0[a]
0	10
0	20
10	0
20	0
10	10
20	20

[a]control

Fixed input parameters:

Asymptotic length (L_∞)	50.0 cm
Growth constant (K)	0.5 $year^{-1}$
Natural mortality rate (M)	0.8 $year^{-1}$
Total mortality rate (Z)	0.8 $year^{-1}$
Age at recruitment (t_r)	0.0 year
Width of length classes	1.0 cm
Size selection (Sel)	not operating

In all the experiments described above, the fishes were not selected by the gear, thus being available to the fishery from the moment of hatching. In the last experiment, two sets of 12 samples of length data with size-dependent selection were used for the calculations of Z. One set had no individual variability in growth parameters, and the other had a coefficient of variation of 10% for both L_∞ and K. In both cases, the parameter a of the logistic curve (see Equation 3.11) was assumed to be -10.

In all cases, catch curves were computed using two different sets of growth parameters: a) the true values of L_∞ and K from the original data simulation; b) the values of L_∞ and K estimated by ELEFAN I.

For the selection of the points of the catch curve to be included in the regression calculations in the last three experiments, the following criteria were used:

1. When size-dependent selection was not operating:
   a. All points were included.
   b. Some of the outlying last points were excluded.
2. When size-dependent selection affected the samples:
   a. The highest point of the curve was the first point included.
   b. The point immediately to the right of the highest point of the curve was the first point included.
   c. The point immediately to the right of the point described in b) was the first point included.

Each of these three options was combined with the following two:

a. The last point included is the last point of the curve.
b. Some of the outlying last points were excluded.

For the sensitivity analysis, Z was calculated from a set of length data sampled from a simulated population with the following parameters:

Asymptotic length (L_∞)	50.0 cm
Coefficient of variation of L_∞	0
Growth constant (K)	0.5 $year^{-1}$
Coefficient of variation of K	0
Natural mortality rate (M)	0.8 $year^{-1}$
Total mortality rate (Z)	1.6 year
Width of length classes	1.0 cm
Size selection	not operating
Number of classes of the catch curve	47

Results

Effects of the number of points included in the calculation

The catch curve for the control population is shown in Fig. 6.1. Because size-dependent selection was lacking, the distribution of the 24 points follow a continuously decreasing decay pattern. Table 6.1 shows the effects of the exclusion of different groups of points in the catch curve on the estimates of Z.

When only the points corresponding to the smaller (younger) fishes are included, a slight negative bias in the estimates of Z is observed. On the other hand, the points of the greater and older fishes produce an overestimation of Z of up to 13%. The inclusion of all the points produces a slight overestimation.

The effects of the exclusion of the last points of the catch curve on the estimates of Z is described further below.

Effects of differences in growth strategy

As expected, estimates of Z were always less biased when the true growth parameters were used to compute the catch curve. The exclusion of the last point of the catch curve in the calculation always produced more accurate estimates of Z (Table 6.2).

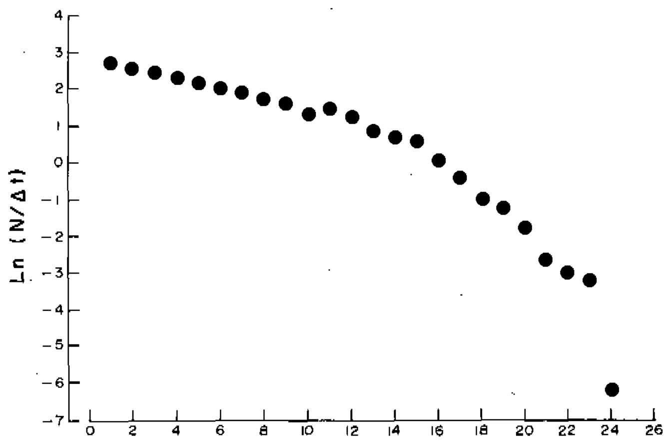

Fig. 6.1. Catch curve obtained with ELEFAN II using length data sampled from a control population with the true growth parameters: L_∞=50 and K=0.5.

Table 6.1. Estimates of Z obtained with different combinations of points of the catch curve. Parameters: L_∞ = 50, K = 0.5, Z = 1.6. Number of classes: 24

Points included	Z	Bias (%)
1 - 24	1.660	3.75
1 - 10	1.576	-1.50
1 - 20	1.590	-0.63
10 - 20	1.758	9.87
20 - 24	1.813	13.31

Table 6.2. Estimates of Z obtained from catch curves of populations with different growth strategies, calculated with the original growth parameters and with the growth parameters estimated by ELEFAN I.

Parameters									
True			Estimated		Parameters	No. of	Last class		Bias
L_∞	K	Z	L_∞	K	used	classes	included	Z	(%)
30	1.8	5.0	30.46	1.449	true	30	30	5.376	7.52
					estimated	30	30	4.197	-16.06
					estimated	30	29	4.471	-10.58
50	0.6	1.9	55.40	0.489	true	26	26	1.872	-1.47
					estimated	26	26	1.957	3.00
					estimated	26	25	1.965	3.42
50	0.2	0.6	91.90	0.179	true	30	30	0.598	-0.33
					estimated	30	30	0.643	7.17
					estimated	30	29	0.672	12.00
110	0.1	0.3	139.80	0.088	true	31	31	0.291	-3.00
					estimated	31	31	0.408	36.00
					estimated	31	30	0.416	38.67

Samples of the population with low asymptotic length (L_∞=30) and high value of K (=1.8) generated negative bias in Z. The estimates obtained with all other population types showed a tendency to produce positive bias in Z. This bias is higher with increasing L_∞ and decreasing K (Table 6.2). The bias was not excessive for the intermediate populations, but exceeded 35% for fishes with a high asymptotic length (L=110 cm) and low value of K (=0.1 $year^{-1}$) (Table 6.2).

Effects of individual variability in growth

As before, the estimates in this experiment were always more accurate when the catch curves were calculated from the true growth parameters and when some of the last points were excluded from the regression. This last procedure was relatively efficient when only the parameter L_∞ varied between individuals, producing an important improvement in the estimates of Z (Table 6.3).

In the control population without variability, a slight tendency to underestimate Z was observed. However, this bias oscillates between ± 3%, depending on the number of classes in the length-frequency data (see the first lines of Tables 6.1 and 6.3).

The individual variability of the growth parameters L_∞ and K appears to produce an underestimation of Z, which increases with increasing coefficients of variation. Variability in both parameters produces strong negative bias in estimates of Z, which attained 40% when the coefficients of variation of L_∞ and K were 20% (Table 6.3).

Effects of size-dependent selection

The effects of size-dependent selection on the catch curve are shown in Fig. 6.2. The left arm of the curve consists of fishes which are too small to be caught by the gear. Their frequency in the samples increases with length.

When the small fishes were not well represented in the samples, the catch curve method had a tendency to overestimate Z (Table 6.4). Although the estimates were more accurate when the true growth parameters were used to create the catch curves, a positive bias in the Z estimates occurred, exceeding 10% in all these cases. The biases were lower when the first point included in the calculation was the highest point of the curve and when two of the last points were excluded from the regression.

Table 6.3. Estimation of Z based on samples from populations with increasing coefficients of variation of parameters L_∞, K and both together.

CV (%) L_∞	CV (%) K	Parameters used	L_∞	K	No. of classes	Last class included	Z	Bias (%)
0	0	true	50.00	0.500	47	47	1.545	-3.44
		estimated	50.01	0.500	47	47	1.545	-3.44
		estimated	50.01	0.500	47	42	1.610	0.63
0	10	true	50.00	0.500	46	46	1.691	5.69
		estimated	49.74	0.504	46	46	1.686	5.37
		estimated	49.74	0.504	46	42	1.649	3.06
0	20	true	50.00	0.500	48	48	1.536	-4.00
		estimated	45.97	0.601	45	45	1.300	-18.75
		estimated	45.97	0.601	45	42	1.372	-14.25
10	0	true	50.00	0.500	49	49	1.530	-4.38
		estimated	51.53	0.483	51	51	1.472	-8.00
		estimated	51.53	0.483	51	49	1.613	0.81
20	0	true	50.00	0.500	49	49	1.377	-13.94
		estimated	49.98	0.471	49	49	1.296	-19.00
		estimated	49.98	0.471	49	44	1.510	-5.63
10	10	true	50.00	0.500	49	49	1.478	-7.63
		estimated	49.37	0.431	49	49	1.225	-23.44
		estimated	49.37	0.431	49	47	1.296	-19.00
20	20	true	50.00	0.500	49	49	1.308	-18.25
		estimated	55.85	0.286	52	52	0.930	-41.88
		estimated	55.85	0.286	52	51	0.979	-38.81

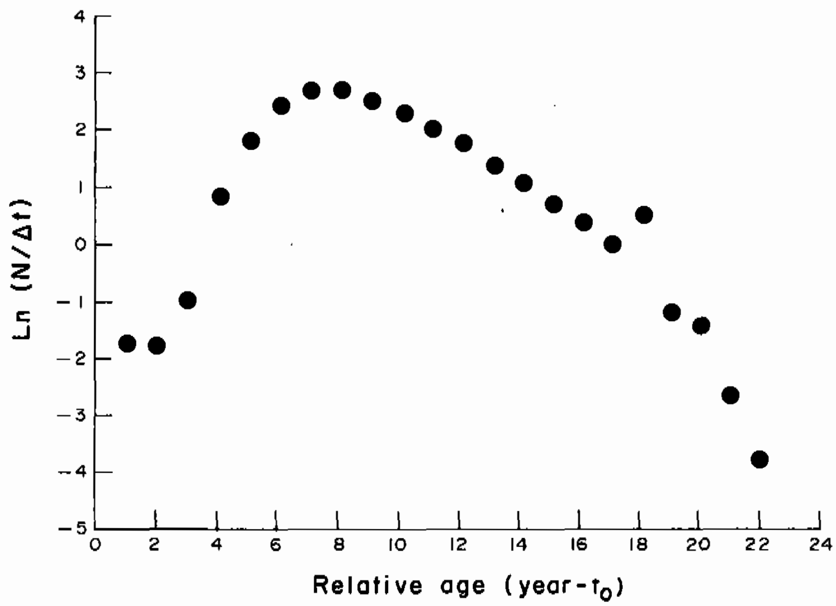

Fig. 6.2. Catch curve obtained from populations with size-dependent effects and individual growth variability.

Table 6.4. Estimates of Z obtained from samples with size-dependent selection effects, without and with 10% individual variability of the growth parameters.

CV (%)		Parameters used		No. of classes	Classes used	Z	Bias (%)
L_∞	K	L_∞	K				
0	0	50	0.5	21	6-21	1.801	12.56
					7-21	1.822	13.88
					8-21	1.842	15.13
					6-19	1.785	11.56
					7-19	1.821	13.81
					8-19	1.858	16.13
0	0	52.53	0.459	21	6-21	1.876	17.25
					7-21	1.908	19.25
					8-21	1.938	21.12
					6-19	1.804	12.75
					7-19	1.848	15.50
					8-19	1.893	18.31
10	10	50	0.5	22	7-22	1.552	-3.00
					8-22	1.559	-2.56
					9-22	1.552	-3.00
					7-20	1.552	-3.00
					8-20	1.579	-1.31
					9-20	1.568	-2.00
10	10	55.15	0.401	25	7-25	1.428	-10.75
					8-25	1.431	-10.56
					9-25	1.425	-10.94
					7-23	1.546	-3.38
					8-23	1.560	-2.50
					9-23	1.561	-2.44

When individual growth variability was simulated in the samples, the effect of the underestimation of Z already described in last section predominated. However, the positive bias produced by size-dependent selection partially compensated for this effect, and the underestimates of Z were only between 1 and 11% (Table 6.4).

Sensitivity analysis of the length-converted catch curve method for estimation of Z

The bias in estimates of Z resulting from a wide range of input values for L_∞ and K is shown in Fig. 6.3. The samples are from a control population without individual variability or size-dependent selection effects. The lines represent points with the same Z values, expressed as percentage of the true value.

The estimates of Z are positively correlated with both L_∞ and K. Thus, overestimations of L_∞ will produce an overestimation of Z and underestimations of K will produce an underestimation of Z. Since L_∞ and K are inversely correlated, the bias tend to compensate Z, but the effects of changes in K are stronger than those of changes in L_∞ (Fig. 6.3).

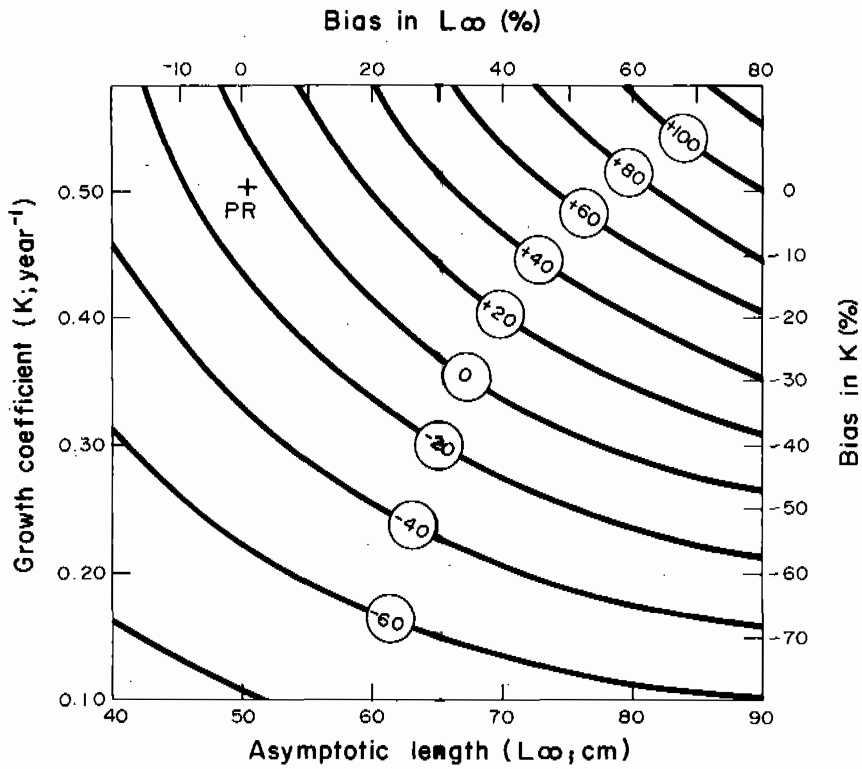

Fig. 6.3. Isolines of estimates of Z obtained with ELEFAN-II and varying input values of the growth parameters L_∞ and K for samples from a control population. Estimates of Z are expressed as percentage of the true value. PR = point of reference, calculated with the true growth parameters, L_∞ = 50 and K = 0.5.

Discussion

Length-converted catch curves are obtained from the length frequencies and from growth parameters. Changes in the structure of the samples or in the input growth parameters will alter the shape of the curve and thus the estimates of Z, which are derived from the slope of the curve.

When size-dependent selection is not operating and no individual variability affects the growth parameters, the population is adequately represented in the samples and the points do not deviate significantly from the calculated regression line. Thus, very accurate estimates of Z are obtained.

Variability in growth produces outlying points in catch curves. That is particularly critical in the case of the older fishes, when individuals are scarce and need a long time to grow through the length classes. The inclusion of all the points of the catch curve generally produces a decrease in the slope of the regression and therefore an underestimation of Z. The estimates can be improved by eliminating some of the points corresponding to the oldest (largest) fishes.

The effects of variability in growth parameters has already been investigated by Laurec and Mesnil (1987) for the estimates of Z obtained with the method of Beverton and Holt (1956) (see Equation 2.9). They reported a moderate bias of 1.5% in Z estimates when the C.V. of K was 20%. These authors also recommended the use for cohort analyses of a value of L_∞ not higher than 70% of the estimated value, in order to improve the estimates of fishing mortality. This procedure would probably be useful for the calculation of the length-converted catch curve as well, although the bias of Z resulting from growth parameter variability is greater for length-converted catch curves than the results obtained by Laurec and Mesnil (1987).

The results of this investigation suggest that a compensation of the bias in Z will occur if both size-dependent selection and individual variability affect the samples. In these cases (see Table 6.4, last two boxes) negative bias was moderate (only 3%) when the last points were not included in the calculation.

Similarly, such a compensation should be expected if the parameter L_∞ is overestimated and K underestimated, which is the general pattern for ELEFAN I. However, that compensation is only partial, because the method is more sensitive to changes in K than in L_∞. Moreover, according to this investigation, bias in K is stronger that in L_∞, increasing the tendency to underestimate Z. This combination of effects must be taken into account when evaluating the accuracy of Z estimates. As an example, let us consider the average bias produced by ELEFAN I in Table 3.3, obtained from the analysis of populations with 20% individual variability in both growth parameters; the average bias of L_∞ estimates was 6.5%, whereas the average bias of K was -40%, and according to Fig. 6.3, the input of those parameters will produce a negative bias of Z of 50%. In the same experiment SLCA produced an average bias of +33% and -6% for L_∞ and K, respectively (Table 3.4). This combination of biased input growth parameters will produce an overestimation of Z of approximately 20%.

Although the present sensitivity analysis of Z is based on a single simulated control population, its results can serve to evaluate the magnitude of possible bias in the estimates of Z obtained with length-converted catch curves.

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Appendix A

Appendix Table A.1. Input parameters used in the simulation.

am1	mean age at recruitment for major peak.
asd1	standard deviation of am1.
am2	mean age at recruitment for minor peak.
asd2	standard deviation of am2.
p	proportion of the recruitment in the major peak.
rm	mean cohort strength (= 10,000 fish).
rsd	standard deviation of rm.
lmax	mean asymptotic length (cm) (VBGF).
lmaxsd	standard deviation of lmax.
km	mean K ($year^{-1}$) (VBGF).
ksd	standard deviation of km.
t0	age at L_t=0 (=0 year) (VBGF).
c	oscillation amplitude parameter (VBGF).
iselect	if =0, no operating size-depending selection function.
a	parameter of selection logistic curve
b	inflection point of selection logistic curve (0<b>1).
m	rate of natural mortality ($year^{-1}$).
f	rate of fishing mortality($year^{-1}$).
range	amplitude of a length class (cm).
mmax	number of samples to be extracted for length analysis.

Appendix B

Supplementary tables

Appendix Table B.1. Simulated and estimated parameters, and percentage of bias obtained with ELEFAN, SLCA and P-W method on the length-frequency data created for the Series I experiments.

B.1. Simulated and estimated parameters, and percentage of bias obtained with ELEFAN, SLCA and P-W method on the length-frequency data created for the Series I experiments.

ELEFAN

Simulated					Estimated					Bias (%)		
L_∞	K	ϕ'	M	L_{max}	L_∞	K	St.Point	ESP/ASP	ϕ'	L_∞	K	ϕ'
30.0	1.80	3.210	2.50	32.5	30.460	1.449	1/ 3.01	0.521	3.129	1.53	-19.50	-2.52
30.0	1.80	3.210	2.50	31.5	29.050	1.692	2/ 5.80	0.515	3.155	-3.17	-6.00	-1.71
30.0	1.80	3.210	2.50	34.5	32.230	1.788	2/ 5.40	0.428	3.269	7.43	-0.67	1.85
30.0	1.80	3.210	2.50	30.5	30.740	1.626	3/ 8.80	0.488	3.187	2.47	-9.67	-0.72
30.0	1.80	3.210	2.50	32.5	30.360	1.714	2/ 5.01	0.488	3.199	1.20	-4.78	-0.34
50.0	0.60	3.176	0.95	51.0	55.400	0.498	2/ 2.80	0.700	3.164	10.80	-17.00	0.26
50.0	0.60	3.176	0.95	51.0	59.200	0.497	5/41.00	0.648	3.241	18.40	-17.17	2.04
50.0	0.60	3.176	0.95	57.0	50.850	0.589	2/ 3.80	0.566	3.183	1.70	-1.83	0.21
50.0	0.60	3.176	0.95	51.0	53.250	0.553	1/ 0.20	0.720	3.195	6.50	-7.83	0.61
50.0	0.60	3.176	0.95	53.0	50.000	0.600	1/ 1.20	0.768	3.176	0.00	0.00	0.00
80.0	0.20	3.107	0.30	88.5	91.900	0.179	6/ 6.90	0.577	3.179	14.88	-10.50	2.33
80.0	0.20	3.107	0.30	82.5	86.785	0.181	1/ 0.60	0.661	3.135	8.48	-9.50	0.88
80.0	0.20	3.107	0.30	76.5	92.000	0.184	6/ 6.30	0.672	3.192	15.00	-8.00	2.74
80.0	0.20	3.107	0.30	91.5	88.100	0.190	6/ 6.90	0.592	3.169	10.12	-5.00	1.98
80.0	0.20	3.107	0.30	82.5	90.900	0.154	7/ 8.10	0.639	3.105	13.63	-23.00	-0.08
110.0	0.10	3.083	0.15	122.0	139.800	0.088	8/54.00	0.461	3.235	27.09	-12.00	4.95
110.0	0.10	3.083	0.15	110.0	140.750	0.086	7/ 6.00	0.485	3.231	27.95	-14.00	4.82
110.0	0.10	3.083	0.15	118.0	133.725	0.087	3/ 2.00	0.341	3.192	21.57	-13.00	3.54
110.0	0.10	3.083	0.15	122.0	130.775	0.093	1/ 0.80	0.359	3.202	18.89	-7.00	3.85
110.0	0.10	3.083	0.15	122.0	137.820	0.086	1/ 1.20	0.436	3.213	25.29	-14.00	4.23

SLCA

Simulated					Estimated					Bias (%)		
L_∞	K	ϕ'	M	L_{max}	L_∞	K	t_0	Score	ϕ'	L_∞	K	ϕ'
30.0	1.80	3.210	2.50	32.5	38.600	1.277	0.0	481.8	3.279	28.67	-29.06	2.18
30.0	1.80	3.210	2.50	31.5	36.700	1.358	0.0	443.9	3.262	22.33	-24.56	1.64
30.0	1.80	3.210	2.50	34.5	36.200	1.384	0.0	467.6	3.259	20.67	-23.11	1.53
30.0	1.80	3.210	2.50	30.5	40.500	1.141	1.0	460.6	3.272	35.00	-36.61	1.95
30.0	1.80	3.210	2.50	32.5	35.500	1.455	0.0	475.7	3.263	18.33	-19.17	1.68
50.0	0.60	3.176	0.95	51.0	64.200	0.445	0.0	361.6	3.263	28.40	-25.83	2.75
50.0	0.60	3.176	0.95	51.0	60.500	0.482	0.0	357.7	3.247	21.00	-19.67	2.22
50.0	0.60	3.176	0.95	57.0	80.500	0.501	0.0	329.1	3.263	21.00	-16.50	2.75
50.0	0.60	3.176	0.95	51.0	51.800	0.600	0.0	364.9	3.207	3.60	0.00	0.97
50.0	0.60	3.176	0.95	53.0	55.500	0.553	0.0	352.4	3.231	11.00	-7.83	1.74
80.0	0.20	3.107	0.30	88.5	95.900	0.172	0.1	191.2	3.199	19.88	-14.00	2.96
80.0	0.20	3.107	0.30	82.5	110.500	0.150	0.1	213.7	3.263	38.13	-25.00	5.01
80.0	0.20	3.107	0.30	76.5	96.900	0.171	0.1	211.2	3.206	21.13	-14.50	3.17
80.0	0.20	3.107	0.30	91.5	103.800	0.160	0.1	197	3.237	29.75	-20.00	4.16
80.0	0.20	3.107	0.30	82.5	110.700	0.142	0.0	216.5	3.241	38.38	-29.00	4.29
110.0	0.10	3.083	0.15	122.0	125.000	0.091	0.0	89.5	3.153	13.64	-9.00	2.27
110.0	0.10	3.083	0.15	110.0	133.300	0.091	0.1	89.3	3.209	21.18	-9.00	4.08
110.0	0.10	3.083	0.15	118.0	137.500	0.091	0.1	99.3	3.236	25.00	-9.00	4.96
110.0	0.10	3.083	0.15	122.0	109.200	0.101	0.0	91.4	3.081	-0.73	1.00	-0.07
110.0	0.10	3.083	0.15	122.0	134.600	0.090	0.1	96.4	3.212	22.36	-10.00	4.20

P-W Method

Simulated					Estimated				Bias (%)	
L_∞	K	ϕ'	M	Z/K	L_{max}	Z/K	L_∞	r^2	Z/K (%)	L_∞ (%)
30.0	1.80	3.210	2.50	2.778	32.5	2.916	31.298	0.997	4.98	4.33
30.0	1.80	3.210	2.50	2.778	31.5	2.939	31.258	0.997	5.80	4.19
30.0	1.80	3.210	2.50	2.778	34.5	3.208	33.671	0.997	15.49	12.24
30.0	1.80	3.210	2.50	2.778	30.5	2.976	31.450	0.999	7.14	4.83
30.0	1.80	3.210	2.50	2.778	32.5	3.388	34.093	0.999	21.97	13.64
50.0	0.60	3.176	0.95	3.167	51.0	3.880	56.906	0.996	22.53	13.81
50.0	0.60	3.176	0.95	3.167	51.0	3.148	52.631	0.994	-0.59	5.26
50.0	0.60	3.176	0.95	3.167	57.0	3.503	54.878	0.996	10.62	9.76
50.0	0.60	3.176	0.95	3.167	51.0	3.561	54.067	0.998	12.45	8.13
50.0	0.60	3.176	0.95	3.167	53.0	3.192	51.927	0.992	0.80	3.85
80.0	0.20	3.107	0.30	3.000	88.5	3.145	84.351	0.990	4.83	5.44
80.0	0.20	3.107	0.30	3.000	82.5	3.303	82.570	0.989	10.10	3.21
80.0	0.20	3.107	0.30	3.000	76.5	3.577	88.683	0.991	19.23	10.85
80.0	0.20	3.107	0.30	3.000	91.5	3.156	83.082	0.989	5.20	3.85
80.0	0.20	3.107	0.30	3.000	82.5	4.049	96.376	0.990	34.97	20.47
110.0	0.10	3.083	0.15	3.000	122.0	3.380	120.673	0.995	12.67	9.70
110.0	0.10	3.083	0.15	3.000	110.0	3.553	122.902	0.997	18.43	11.73
110.0	0.10	3.083	0.15	3.000	118.0	4.332	139.427	0.972	44.40	26.75
110.0	0.10	3.083	0.15	3.000	122.0	3.695	128.779	0.995	23.17	17.07
110.0	0.10	3.083	0.15	3.000	122.0	3.716	126.880	0.993	23.87	15.33

Appendix Table B.2. Simulated and estimated parameters, and percentage of bias obtained with ELEFAN on the length-frequency data created for the Series II experiments. CV = coefficient of individual variation.

ELEFAN

Simulated			Estimated					Bias (%)		
CV_{L_∞} (%)	CV_K (%)	L_{max}	L_∞	K	St. Point	ESP/ASP	ϕ'	L_∞	K	ϕ'
0	0	48.5	50.01	0.500	1/ 0.999	0.977	3.097	0.02	0.00	0.01
		45.5	49.93	0.499	1/ 1.00	0.997	3.095	-0.15	-0.20	-0.07
		45.5	49.63	0.509	2/21.60	0.985	3.098	-0.74	1.80	0.04
		47.5	49.85	0.504	1/20.3	1.000	3.098	-0.29	0.80	0.03
		48.5	50.00	0.500	1/ 0.999	0.996	3.097	0.00	0.00	0.00
0	10	45.5	49.74	0.504	2/21.5	0.587	3.096	-0.51	0.80	-0.03
		46.5	49.10	0.509	3/ 4.50	0.591	3.089	-1.80	1.80	-0.26
		47.5	49.23	0.504	4/ 6.50	0.528	3.087	-1.55	0.80	-0.33
		48.5	50.94	0.461	4/ 6.50	0.540	3.078	1.88	-7.80	-0.62
		44.5	48.28	0.505	5/ 8.50	0.594	3.071	-3.45	1.00	-0.85
0	20	47.5	45.97	0.501	12/35.5	0.331	3.025	-8.06	0.20	-2.33
		49.5	47.80	0.490	5/ 7.50	0.347	3.049	-4.40	-2.00	-1.55
		48.5	48.75	0.500	3/ 4.50	0.315	3.075	-2.50	0.00	-0.71
		48.5	48.62	0.500	7/11.5	0.305	3.073	-2.76	0.00	-0.78
		48.5	48.50	0.453	4/21.5	0.325	3.028	-3.00	-9.40	-2.24
0	30	49.5	48.30	0.498	1/ 0.50	0.299	3.065	-3.40	-0.40	-1.03
		48.5	50.28	0.322	2/ 2.80	0.230	2.911	0.56	-35.60	-6.01
		49.5	49.65	0.486	9/ 4.50	0.227	3.078	-0.70	-2.80	-0.60
		48.5	48.49	0.506	2/ 2.60	0.248	3.075	-3.02	1.20	-0.69
		48.5	49.45	0.514	7/14.5	0.238	3.099	-1.10	2.80	0.08
10	0	51.5	51.53	0.483	3/ 4.80	0.443	3.108	3.06	-3.40	0.36
		53.5	45.86	0.493	5/ 8.50	0.455	3.016	-8.28	-1.40	-2.62
		49.5	48.70	0.498	1/ 0.90	0.407	3.072	-2.60	-0.40	-0.80
		48.5	48.84	0.474	11/36.5	0.433	3.053	-2.33	-5.20	-1.41
		55.5	46.05	0.489	4/ 7.00	0.408	3.016	-7.91	-2.20	-2.62
20	0	60.5	49.98	0.471	2/ 3.30	0.269	3.071	-0.04	-5.80	-0.85
		57.5	56.80	0.315	1/16.50	0.262	3.007	13.60	-37.00	-2.90
		59.5	51.85	0.492	2/ 2.30	0.255	3.121	3.70	-1.60	0.79
		58.5	48.58	0.419	4/20.40	0.259	2.995	-2.85	-16.20	-3.29
		56.5	52.80	0.438	3/ 4.50	0.248	3.087	5.60	-12.40	-0.33
30	0	67.5	50.18	0.255	3/ 4.50	0.302	2.808	0.35	-49.00	-9.34
		70.5	55.79	0.293	6/ 9.50	0.235	2.960	11.58	-41.40	-4.42
		75.5	58.50	0.281	2/ 2.50	0.233	2.983	16.99	-43.80	-3.68
		65.5	51.53	0.375	2/40.5	0.234	2.998	3.05	-25.00	-3.19
		69.5	55.52	0.261	2/ 2.00	0.281	2.906	11.04	-47.80	-6.18
10	10	53.5	50.13	0.517	5/ 5.80	0.364	3.114	0.26	3.40	0.54
		51.5	49.37	0.431	3/ 4.20	0.413	3.021	-1.26	-13.80	-2.44
		51.5	49.56	0.486	3/ 4.50	0.376	3.077	-0.88	-2.80	-0.65
		52.5	49.56	0.470	3/ 4.70	0.373	3.062	-0.88	-6.00	-1.12
		54.5	48.10	0.478	3/ 4.80	0.357	3.044	-3.80	-4.40	-1.72
20	20	55.5	55.85	0.286	2/25.5	0.242	2.950	11.70	-42.80	-4.73
		63.5	48.74	0.380	2/ 2.40	0.292	2.956	-2.52	-24.00	-4.56
		61.5	49.00	0.352	2/ 2.50	0.292	2.927	-2.00	-29.60	-5.49
		62.5	53.63	0.222	2/ 2.80	0.288	2.805	7.25	-55.60	-9.42
		57.5	50.66	0.276	3/25.2	0.268	2.850	1.32	-44.80	-7.97
30	30	66.5	55.56	0.230	4/30.0	0.295	2.851	11.12	-54.00	-7.93
		76.5	48.00	0.458	4/ 5.50	0.242	3.023	-4.00	-8.40	-2.38
		76.5	51.50	0.249	2/ 2.50	0.267	2.820	3.00	-50.20	-8.95
		77.5	55.57	0.200	3/32.0	0.242	2.791	11.14	-60.00	-9.89
		71.5	55.76	0.250	2/ 2.50	0.227	2.891	11.52	-50.00	-6.66

Appendix Table B.3. Simulated and estimated parameters and percentage of bias obtained with SLCA on the length-frequency data created for the Series II experiments. CV = coefficient of individual variation.

SLCA

Simulated			Estimated					Bias (%)		
CV_{L_∞} (%)	CV_K (%)	L_{max}	L_∞	K	t_0	Score	ϕ'	L_∞	K	ϕ'
0	0	48.5	50.10	0.499	1.0	482.1	3.098	0.20	-0.20	0.03
		45.5	50.00	0.501	1.0	509.9	3.098	0.00	0.20	0.03
		45.5	50.10	0.500	1.0	490.5	3.099	0.20	0.00	0.06
		47.5	50.10	0.500	1.0	515.9	3.099	0.20	0.00	0.06
		48.5	49.90	0.501	1.0	490.9	3.096	-0.20	0.20	-0.03
0	10	45.5	53.50	0.453	0.0	594.6	3.113	7.00	-9.40	0.51
		46.5	52.30	0.469	0.0	579.2	3.108	4.60	-6.20	0.36
		47.5	54.60	0.440	1.0	593.1	3.118	9.20	-12.00	0.68
		48.5	56.00	0.422	1.0	587.2	3.122	12.00	-15.60	0.80
		44.5	54.00	0.447	0.0	568.5	3.115	8.00	-10.60	0.59
0	20	47.5	49.30	0.553	0.0	460.0	3.128	-1.40	10.60	1.02
		49.5	53.70	0.495	0.0	475.3	3.155	7.40	-1.00	1.86
		48.5	55.00	0.480	0.0	451.5	3.162	10.00	-4.00	2.10
		48.5	54.10	0.485	0.0	437.9	3.152	8.20	-3.00	1.78
		48.5	59.00	0.437	0.0	506.1	3.182	18.00	-12.60	2.75
0	30	49.5	51.70	0.619	0.1	344.6	3.219	3.40	23.80	3.93
		48.5	59.50	0.510	0.1	386.9	3.257	19.00	2.00	5.16
		49.5	53.90	0.560	0.1	364.7	3.211	7.80	12.00	3.70
		48.5	50.00	0.612	0.1	385.2	3.185	0.00	22.40	2.83
		48.5	56.10	0.544	0.1	389.0	3.234	12.20	8.80	4.41
10	0	51.5	51.00	0.505	0.0	518.5	3.118	2.00	1.00	0.69
		53.5	52.40	0.480	0.0	485.5	3.120	4.80	-4.00	0.74
		49.5	47.00	0.560	0.0	502.1	3.092	-6.00	12.00	-0.15
		48.5	50.50	0.510	0.0	505.1	3.114	1.00	2.00	0.56
		55.5	47.00	0.564	0.0	498.0	3.095	-6.00	12.80	-0.05
20	0	60.5	60.10	0.480	0.1	414.0	3.239	20.20	-4.00	4.59
		57.5	54.40	0.548	0.1	405.9	3.210	8.80	9.60	3.65
		59.5	48.90	0.578	0.1	382.5	3.141	-2.20	15.60	1.41
		58.5	61.90	0.470	0.1	407.4	3.255	23.80	-6.00	5.12
		56.5	58.10	0.496	0.1	412.2	3.224	16.20	-0.80	4.10
30	0	67.5	65.60	0.440	0.1	302.7	3.277	31.20	-12.00	5.82
		70.5	54.30	0.556	0.1	329.6	3.215	8.60	11.20	3.80
		75.5	70.40	0.457	0.1	342.5	3.355	40.80	-8.60	8.34
		65.5	66.30	0.465	0.1	301.6	3.310	32.60	-7.00	6.90
		69.5	77.00	0.429	0.1	340.4	3.405	54.00	-14.20	9.96
10	10	53.5	53.80	0.474	0.0	462.3	3.137	7.60	-5.20	1.31
		51.5	55.90	0.459	0.0	502.8	3.157	11.80	-8.20	1.93
		51.5	54.80	0.461	0.0	474.8	3.141	9.60	-7.80	1.43
		52.5	54.00	0.460	0.0	468.6	3.128	8.00	-8.00	0.99
		54.5	46.00	0.571	0.0	470.2	3.082	-8.00	14.20	-0.48
20	20	55.5	59.10	0.486	0.1	342.2	3.230	18.20	-2.80	4.29
		63.5	60.10	0.469	0.1	366.9	3.229	20.20	-6.20	4.26
		61.5	68.20	0.405	0.1	368.5	3.275	36.40	-19.00	5.75
		62.5	60.60	0.502	0.1	345.4	3.266	21.20	0.40	5.45
		57.5	61.60	0.496	0.1	349.4	3.275	23.20	-0.80	5.74
30	30	66.5	75.00	0.450	0.1	276.0	3.403	50.00	-10.00	9.89
		76.5	66.00	0.522	0.1	276.5	3.357	32.00	4.40	8.39
		76.5	66.90	0.476	0.1	305.3	3.328	33.80	-4.80	7.48
		77.5	82.00	0.390	0.1	293.9	3.419	64.00	-22.00	10.39
		71.5	88.00	0.450	0.1	279.4	3.542	76.00	-10.00	14.38

Appendix Table B.4. Simulated and estimated parameters and percentage of bias obtained with the P-W method on the length-frequency data created for the Series II experiments. CV = coefficient of individual variation.

P-W Method

Simulated			Estimated			Bias (%)	
$CV_{L\infty}$ (%)	CV_K (%)	L_{max}	Z/K	L_∞	r^2	Z/K	L_∞
0	0	48.5	2.593	46.43	0.994	-18.97	-7.14
		45.5	2.840	46.49	0.996	-11.25	-7.02
		45.5	2.822	49.26	0.993	-11.81	-1.48
		47.5	3.570	52.69	0.999	11.56	5.38
		48.5	2.946	49.45	0.999	-7.94	-1.10
0	10	45.5	3.226	49.86	0.999	0.81	-0.28
		46.5	3.267	49.63	0.999	2.09	-0.74
		47.5	3.559	53.13	0.998	11.22	6.26
		48.5	4.060	55.89	0.994	26.87	11.78
		44.5	2.852	45.88	0.997	-10.88	-8.24
0	20	47.5	3.481	53.43	0.997	8.78	6.86
		49.5	3.800	55.08	0.998	18.75	10.16
		48.5	3.975	58.30	0.997	24.22	16.60
		48.5	2.865	49.84	0.994	-10.47	-0.32
		48.5	3.785	54.68	0.998	18.28	9.36
0	30	49.5	3.855	58.80	0.995	20.47	17.60
		48.5	3.272	54.03	0.995	2.25	8.06
		49.5	3.647	57.49	0.995	13.97	14.98
		48.5	3.871	59.63	0.997	20.97	19.26
		48.5	3.358	54.95	0.998	4.94	9.90
10	0	51.5	4.214	57.73	0.974	31.69	15.46
		53.5	3.457	53.58	0.996	8.03	7.16
		49.5	3.196	49.43	0.997	-0.13	-1.14
		48.5	3.502	52.70	0.999	9.44	5.40
		55.5	3.541	53.87	0.997	10.66	7.74
20	0	60.5	4.909	68.85	0.994	53.41	37.70
		57.5	5.343	71.54	0.990	66.97	43.08
		59.5	3.931	59.87	0.982	22.84	19.74
		58.5	6.175	77.88	0.956	92.97	55.76
		56.5	4.155	62.83	0.991	29.84	25.66
30	0	67.5	4.947	76.45	0.978	54.59	52.90
		70.5	6.339	89.90	0.990	98.09	79.80
		75.5	6.206	86.31	0.990	93.94	72.62
		65.5	4.988	77.52	0.980	55.88	55.04
		69.5	6.085	85.66	0.992	90.16	71.32
10	10	53.5	3.212	52.36	0.995	0.38	4.72
		51.5	3.728	56.02	0.999	16.50	12.04
		51.5	3.493	53.18	0.995	9.16	6.36
		52.5	3.636	55.47	0.995	13.63	10.94
		54.5	3.485	53.04	0.997	8.91	6.08
20	20	55.5	5.759	78.49	0.985	79.97	56.98
		63.5	5.972	78.60	0.995	86.63	57.20
		61.5	4.760	69.92	0.992	48.75	39.84
		62.5	4.452	67.08	0.989	39.12	34.16
		57.5	4.861	72.11	0.997	51.91	44.22
30	30	66.5	7.688	109.22	0.958	140.25	118.44
		76.5	7.174	102.12	0.991	124.19	104.24
		76.5	7.371	101.33	0.983	130.34	102.66
		77.5	7.533	108.79	0.981	135.41	117.58
		71.5	6.779	98.99	0.991	111.84	97.98

Appendix Table B.5. Simulated and estimated parameters and percentage of bias obtained with ELEFAN (C=0), ELEFAN (C≠0), SLCA and P-W methods on the length-frequency data created for the Series III experiments. CV = coefficient of individual variation.

B.5. Simulated and estimated parameters, and percentage of bias obtained with ELEFAN (C=0), ELEFAN (C≠0), SLCA and P-W methods on the length-frequency data created for the Series III experiments. CV = coefficient of individual variation.

ELEFAN (C = 0)

Simulated			Estimated							Bias (%)		
$CV_{L\infty}$ (%)	CV_K (%)	L_{max}	L_∞	K	C	WP	St. Point	ESP/ASP	φ'	L_∞	K	φ'
0	0	47.0	52.70	0.460	0.0	0.0	1/0.001	0.717	-8.00	5.41	3.108	0.30
0	0	47.0	53.04	0.441	0.0	0.0	1/0.001	0.672	-11.80	6.08	3.094	-0.11
0	0	45.0	51.25	0.479	0.0	0.0	1/0.001	0.621	-4.20	2.50	3.100	0.09
0	0	49.0	54.38	0.441	0.0	0.0	1/0.200	0.879	-11.80	8.75	3.115	0.59
0	0	47.0	54.74	0.425	0.0	0.0	1/0.001	0.674	-15.00	9.48	3.105	0.26
20	20	55.0	56.80	0.405	0.0	0.0	3/3.60	0.414	-19.00	13.60	3.116	0.62
20	20	55.0	51.90	0.481	0.0	0.0	3/3.60	0.410	-3.80	3.80	3.112	0.50
20	20	53.0	52.90	0.486	0.0	0.0	4/5.80	0.438	-2.80	5.80	3.134	1.18
20	20	51.0	51.57	0.440	0.0	0.0	3/3.00	0.516	-12.00	3.14	3.068	-0.93
20	20	53.0	55.28	0.409	0.0	0.0	4/5.20	0.491	-18.20	10.56	3.097	0.00

ELEFAN (C ≠ 0)

Simulated			Estimated							Bias (%)			
$CV_{L\infty}$ (%)	CV_K (%)	L_{max}	L_∞	K	C	WP	St. Point	ESP/ASP	φ'	L_∞	K	φ'	C
0	0	47.0	52.46	0.456	0.65	0.0	1/0.80	0.959	3.099	4.92	-8.80	0.05	0.00
0	0	47.0	50.00	0.495	0.85	0.0	1/0.60	0.998	3.093	0.00	-1.00	-0.14	0.00
0	0	45.0	52.80	0.455	0.80	0.0	1/1.00	0.929	3.103	5.60	-9.00	0.20	23.08
0	0	49.0	53.50	0.440	0.71	0.0	1/1.00	0.975	3.100	7.00	-12.00	0.10	9.23
0	0	47.0	52.46	0.456	0.65	0.0	1/0.80	0.961	3.099	4.91	-8.80	0.05	0.00
20	20	55.0	58.00	0.400	0.52	0.0	3/2.60	0.481	3.129	16.00	-20.00	1.03	-20.00
20	20	55.0	55.74	0.477	0.85	0.0	3/2.40	0.448	3.171	11.48	-4.80	2.38	0.00
20	20	53.0	52.70	0.495	0.65	0.0	4/4.60	0.415	3.138	5.40	-1.00	1.33	0.00
20	20	51.0	53.91	0.388	0.50	0.0	4/4.60	0.557	3.052	7.82	-22.40	-1.45	-23.08
20	20	53.0	55.10	0.402	0.66	0.0	4/4.80	0.530	3.087	10.20	-19.60	-0.34	1.54

SLCA

Simulated			Estimated					Bias (%)		
$CV_{L\infty}$ (%)	CV_K (%)	L_{max}	L_∞	K	t_0	Score	φ'	L_∞	K	φ'
0	0	47.0	48.80	0.548	0.10	360.3	3.116	-2.40	9.60	0.60
0	0	47.0	48.40	0.554	0.10	372.5	3.113	-3.20	10.80	0.52
0	0	45.0	48.30	0.557	0.10	376.8	3.114	-3.40	11.40	0.54
0	0	49.0	49.10	0.538	0.10	357.3	3.113	-1.80	7.60	0.51
0	0	47.0	49.20	0.539	0.10	370.6	3.116	-1.60	7.80	0.60
20	20	55.0	63.30	0.505	0.10	251.1	3.306	26.60	1.00	6.75
20	20	55.0	52.60	0.595	0.10	231.8	3.216	5.20	19.00	3.86
20	20	53.0	59.80	0.540	0.10	264.9	3.286	19.60	8.00	6.10
20	20	51.0	72.30	0.436	0.10	258.4	3.358	44.60	-12.80	8.42
20	20	53.0	65.10	0.485	0.10	261.2	3.313	30.20	-3.00	6.97

P-W Method

Simulated			Estimated			Bias (%)	
$CV_{L\infty}$ (%)	CV_K (%)	L_{max}	Z/K	L_∞	r^2	Z/K	L_∞
0	0	47.0	2.699	46.17	0.860	-15.66	-7.66
0	0	47.0	2.846	47.00	0.834	-11.06	-6.00
0	0	45.0	2.657	45.53	0.860	-16.97	-8.94
0	0	49.0	2.867	49.07	0.846	-10.41	-1.86
0	0	47.0	2.524	44.87	0.853	-21.13	-10.26
20	20	55.0	4.346	65.41	0.826	35.81	30.82
20	20	55.0	4.180	64.39	0.833	30.62	28.78
20	20	53.0	5.894	78.70	0.742	84.19	57.41
20	20	51.0	4.246	64.23	0.838	32.69	28.46
20	20	53.0	5.032	71.36	0.833	57.25	42.72

Appendix Table B.6. Simulated and estimated parameters and percentage of bias obtained with ELEFAN on the length-frequency data created for the Series IV experiments. A = Parameter of the selection curve, whose absolute value is correlated to the mesh size. CV = coefficient of individual variation.

ELEFAN

Simulated				Estimated					Bias (%)		
CV_{L_∞} (%)	CV_K (%)	A	Length range	L_∞	K	St.Point	ESP/ASP	φ'	K	L_∞	φ'
0	0	No sel.	1-45	51.10	0.478	1/ 1.40	0.944	3.096	2.20	-4.40	-0.02
0	0	No sel.	1-45	49.90	0.499	1/ 1.20	0.890	3.094	-0.20	-0.20	-0.08
0	Q	No sel.	1-47	51.20	0.473	1/ 1.20	0.922	3.093	2.40	-5.40	-0.11
0	0	No sel.	1-47	51.40	0.481	8/13.20	0.913	3.104	2.80	-3.80	0.23
0	0	No sel.	1-47	51.20	0.485	4/ 6.80	0.943	3.104	2.40	-3.00	0.24
10	10	No sel.	1-51	48.00	0.497	1/ 1.80	0.667	3.059	-4.00	-0.60	-1.23
10	10	No sel.	1-61	53.80	0.430	4/ 7.00	0.690	3.095	7.60	-14.00	-0.06
10	10	No sel.	1-57	52.85	0.452	1/ 1.20	0.704	3.101	5.70	-9.60	0.14
10	10	No sel.	1-55	49.00	0.482	2/ 3.60	0.696	3.063	-2.00	-3.60	-1.08
10	10	No sel.	1-57	50.40	0.491	1/ 1.20	0.646	3.096	0.80	-1.80	-0.03
0	0	-10	7-47	52.53	0.459	9/28.60	0.908	3.103	5.05	-8.20	0.18
0	0	-10	3-49	54.35	0.423	1/ 2.00	0.901	3.097	8.70	-15.40	-0.01
0	0	-10	7-47	53.30	0.434	8/13.80	0.915	3.091	6.60	-13.20	-0.19
0	0	-10	3-47	53.90	0.421	8/13.80	0.906	3.087	7.80	-15.80	-0.31
0	0	-10	5-45	54.60	0.416	8/13.60	0.928	3.093	9.20	-16.80	-0.11
0	0	-15	11-47	51.00	0.476	8/36.40	0.913	3.093	2.00	-4.80	-0.13
0	0	-15	9-47	57.83	0.360	1/45.00	0.881	3.081	15.66	-28.00	-0.53
0	0	-15	13-49	55.10	0.416	8/37.00	0.816	3.101	10.20	-16.80	0.14
0	0	-15	13-49	54.80	0.424	8/37.00	0.788	3.105	9.60	-15.20	0.26
0	0	-15	11-49	55.00	0.420	8/37.00	0.805	3.104	10.00	-16.00	0.23
0	0	-20	21-47	54.90	0.412	4/41.00	0.828	3.094	9.80	-17.60	-0.09
0	0	-20	19-49	53.05	0.442	1/39.40	0.767	3.095	6.10	-11.60	-0.07
0	0	-20	19-47	55.80	0.382	5/24.80	0.798	3.075	11.60	-23.60	-0.70
0	0	-20	19-47	54.50	0.423	1/39.60	0.905	3.099	9.00	-15.40	0.07
0	0	-20	21-49	55.95	0.389	1/39.80	0.843	3.086	11.90	-22.20	-0.37
10	10	-10	5-59	55.15	0.401	6/11.40	0.603	3.086	10.30	-19.80	-0.34
10	10	-10	5-51	52.60	0.417	6/11.60	0.711	3.062	5.20	-16.60	-1.12
10	10	-10	3-57	53.90	0.415	7/13.00	0.660	3.081	7.80	-17.00	-0.51
10	10	-10	5-57	53.60	0.385	6/11.00	0.582	3.044	7.20	-23.00	-1.72
10	10	-10	9-51	54.20	0.396	8/14.20	0.624	3.066	8.40	-20.80	-1.01
10	10	-15	13-59	56.30	0.374	3/23.20	0.623	3.074	12.60	-25.20	-0.74
10	10	-15	15-53	52.50	0.407	12/31.60	0.490	3.050	5.00	-18.60	-1.52
10	10	-15	11-59	54.10	0.365	10/19.00	0.524	3.029	8.20	-27.00	-2.20
10	10	-15	13-51	54.70	0.414	11/20.00	0.478	3.093	9.40	-17.20	-0.13
10	10	-15	7-51	55.70	0.416	1/21.60	0.462	3.111	11.40	-16.80	0.45
10	10	-20	19-53	55.10	0.397	1/32.60	0.358	3.081	10.20	-20.60	-0.51
10	10	-20	21-51	55.30	0.366	5/49.00	0.370	3.049	10.60	-26.80	-1.55
10	10	-20	19-53	59.50	0.205	2/41.00	0.349	2.861	19.00	-59.00	-7.62
10	10	-20	19-51	57.28	0.375	8/51.00	0.485	3.090	14.56	-25.00	-0.22
10	10	-20	21-51	52.30	0.419	5/37.20	0.519	3.059	4.60	-16.20	-1.22

Appendix Table B.7. Simulated and estimated parameters and percentage of bias obtained with SLCA on the length-frequency data created for the Series IV experiments. A = Parameter of the selection curve, whose absolute value is correlated to the mesh size. CV = coefficient of individual variation.

SLCA

Simulated				Estimated					Bias (%)		
$CV_{L\infty}$ (%)	CV_K (%)	A	Length range	L_∞	K	t_0	Score	ϕ'	L_∞	K	ϕ'
0	0	No sel.	1-45	50.00	0.505	0.0	382.7	3.101	0.00	1.00	0.14
0	0	No sel.	1-45	50.00	0.505	1.0	397.3	3.101	0.00	1.00	0.14
0	0	No sel.	1-47	49.90	0.505	0.0	405.6	3.099	-0.20	1.00	0.08
0	0	No sel.	1-47	50.50	0.495	0.0	372.4	3.101	1.00	-1.00	0.14
0	0	No sel.	1-47	50.10	0.500	1.0	422.6	3.099	0.20	0.00	0.06
10	10	No sel.	1-51	58.10	0.425	0.0	318.4	3.157	16.20	-15.00	1.93
10	10	No sel.	1-61	56.70	0.435	0.0	337.7	3.146	13.40	-13.00	1.57
10	10	No sel.	1-57	52.60	0.495	0.0	349.0	3.137	5.20	-1.00	1.28
10	10	No sel.	1-55	58.30	0.435	0.0	349.6	3.170	16.60	-13.00	2.35
10	10	No sel.	1-57	55.30	0.453	0.0	301.8	3.142	10.60	-9.40	1.44
0	0	-10	7-47	51.10	0.480	1.0	290.8	3.098	2.20	-4.00	0.04
0	0	-10	3-49	50.10	0.505	0.0	294.2	3.103	0.20	1.00	0.20
0	0	-10	7-47	50.20	0.500	0.0	290.2	3.100	0.40	0.00	0.11
0	0	-10	3-47	50.40	0.495	1.0	288.7	3.099	0.80	-1.00	0.08
0	0	-10	5-45	50.40	0.495	1.0	289.3	3.099	0.80	-1.00	0.08
0	0	-15	11-47	50.30	0.500	0.0	230.6	3.102	0.60	0.00	0.17
0	0	-15	9-47	51.00	0.480	1.0	217.5	3.096	2.00	-4.00	-0.02
0	0	-15	13-49	51.00	0.480	1.0	222.6	3.096	2.00	-4.00	-0.02
0	0	-15	13-49	52.40	0.445	0.9	230.4	3.087	4.80	-11.00	-0.32
0	0	-15	11-49	50.30	0.500	0.0	218.4	3.102	0.60	0.00	0.17
0	0	-20	21-47	51.40	0.470	1.0	142.1	3.094	2.80	-6.00	-0.09
0	0	-20	19-49	50.20	0.510	0.1	153.4	3.109	0.40	2.00	0.39
0	0	-20	19-47	51.30	0.475	1.0	144.5	3.097	2.60	-5.00	0.00
0	0	-20	19-47	51.40	0.470	1.0	150.8	3.094	2.80	-6.00	-0.09
0	0	-20	21-49	52.30	0.440	0.9	142.6	3.080	4.60	-12.00	-0.53
10	10	-10	5-59	51.90	0.530	0.1	166.1	3.155	3.80	6.00	1.86
10	10	-10	5-51	57.60	0.460	0.1	158.8	3.184	15.20	-8.00	2.80
10	10	-10	3-57	54.90	0.500	0.1	162.9	3.178	9.80	0.00	2.62
10	10	-10	5-57	78.30	0.290	0.0	169.3	3.250	56.60	-42.00	4.94
10	10	-10	9-51	62.30	0.425	0.1	146.2	3.217	24.60	-15.00	3.89
10	10	-15	13-59	73.80	0.315	0.1	68.6	3.234	47.60	-37.00	4.44
10	10	-15	15-53	57.40	0.493	0.2	72.7	3.211	14.80	-1.40	3.67
10	10	-15	11-59	62.30	0.433	0.2	73.0	3.225	24.60	-13.40	4.15
10	10	-15	13-51	65.00	0.452	0.3	71.7	3.281	30.00	-9.60	5.94
10	10	-15	7-51	67.00	0.375	0.1	75.4	3.226	34.00	-25.00	4.17
10	10	-20	19-53	61.50	0.488	0.3	13.3	3.266	23.00	-2.40	5.47
10	10	-20	21-51	66.40	0.285	0.6	21.6	3.099	32.80	-43.00	0.07
10	10	-20	19-53	76.90	0.360	0.3	24.6	3.328	53.80	-28.00	7.47
10	10	-20	19-51	65.50	0.430	0.3	21.2	3.266	31.00	-14.00	5.46
10	10	-20	21-51	62.40	0.500	0.4	25.0	3.289	24.80	0.00	6.21

Appendix Table B.8. Simulated and estimated parameters and percentage of bias obtained with the P-W method on the length-frequency data created for the Series IV experiments. A = Parameter of the selection curve, whose absolute value is correlated to the mesh size. CV = coefficient of individual variations.

P-W Method

Simulated				Estimated			Bias (%)	
CV_{L_∞} (%)	CV_K (%)	A	Length range	L_∞	Z/K	r^2	L_∞	Z/K
0	0	No sel.	1-45	50.01	3.255	0.998	0.02	1.72
0	0	No sel.	1-45	49.79	3.228	0.998	-0.42	0.88
0	0	No sel.	1-47	51.71	3.202	0.996	3.42	0.06
0	0	No sel.	1-47	48.55	2.892	0.996	-2.90	-9.63
0	0	No sel.	1-47	45.68	2.865	0.998	-8.64	-10.47
10	10	No sel.	1-51	52.75	3.179	0.998	5.50	-0.66
10	10	No sel.	1-61	52.91	3.272	0.990	5.82	2.25
10	10	No sel.	1-57	57.93	4.017	0.997	15.86	25.53
10	10	No sel.	1-55	55.72	3.806	0.997	11.44	18.94
10	10	No sel.	1-57	54.36	3.270	0.997	8.72	2.19
0	0	-10	7-47	47.61	2.816	0.991	-4.78	-12.00
0	0	-10	3-49	47.64	2.770	0.984	-4.72	-13.44
0	0	-10	7-47	52.52	3.545	0.993	5.04	10.78
0	0	-10	3-47	52.73	3.875	0.997	5.46	21.09
0	0	-10	5-45	48.76	2.904	0.994	-2.48	-9.25
0	0	-15	11-47	51.14	3.429	0.984	2.28	7.16
0	0	-15	9-47	54.07	3.866	0.965	8.14	20.81
0	0	-15	13-49	47.57	2.758	0.991	-4.86	-13.81
0	0	-15	13-49	52.23	3.534	0.990	4.46	10.44
0	0	-15	11-49	50.29	3.178	0.996	0.58	-0.69
0	0	-20	21-47	49.83	2.950	0.996	-0.34	-7.81
0	0	-20	19-49	48.45	2.792	0.980	-3.10	-12.75
0	0	-20	19-47	51.90	3.527	0.980	3.80	10.22
0	0	-20	19-47	50.27	3.186	0.986	0.54	-0.44
0	0	-20	21-49	50.24	3.291	0.933	0.48	2.84
10	10	-10	5-59	66.41	5.130	0.982	32.82	60.31
10	10	-10	5-51	57.83	4.156	0.984	15.66	29.87
10	10	-10	3-57	55.82	4.103	0.967	11.64	28.22
10	10	-10	5-57	56.64	3.786	0.992	13.28	18.31
10	10	-10	9-51	52.63	3.489	0.993	5.26	9.03
10	10	-15	13-59	61.23	4.519	0.968	22.46	41.22
10	10	-15	15-53	53.11	3.490	0.958	6.22	9.06
10	10	-15	11-59	58.51	4.340	0.923	17.02	35.62
10	10	-15	13-51	57.43	4.095	0.960	14.86	27.97
10	10	-15	7-51	55.25	3.746	0.993	10.50	17.06
10	10	-20	19-53	59.23	4.419	0.944	18.46	38.09
10	10	-20	21-51	54.01	3.325	0.996	8.02	3.91
10	10	-20	19-53	55.90	4.221	0.949	11.80	31.91
10	10	-20	19-51	57.60	4.170	0.963	15.20	30.31
10	10	-20	21-51	59.73	5.004	0.974	19.46	56.37

Appendix Table B.9. Simulated and estimated parameters and percentage of bias obtained with ELEFAN, SLCA and the P-W method on the length-frequency data created for the Series V experiments. P = proportion of recruits in the first peak. tr1 = mean age (year) at peak i of recruitment. SD1 = standard deviation of the mean age at recruitment i.

ELEFAN

Simulated						Estimated					Bias (%)		
P	tr1	SD 1	tr2	SD 2	Range	L_∞	K	St.Point	ESP/ASP	ϕ'	L_∞	K	ϕ'
1	0.5	0	-	-	11-47	54.75	0.414	2/13.60	0.863	3.094	9.50	-17.20	-0.10
1	0.5	0	-	-	11-47	53.90	0.426	2/13.60	0.929	3.093	7.80	-14.80	-0.14
1	0.5	0	-	-	11-49	55.10	0.417	1/12.00	0.770	3.102	10.20	-16.60	0.18
1	0.5	0	-	-	11-49	55.10	0.416	1/12.00	0.891	3.101	10.20	-16.80	0.14
1	0.5	0	-	-	11-47	54.26	0.437	1/11.80	0.786	3.109	8.52	-12.60	0.40
1	0.5	1 month	-	-	9-49	51.50	0.459	3/15.20	0.910	3.085	3.00	-8.20	-0.37
1	0.5	1 month	-	-	7-47	51.60	0.476	3/14.60	0.945	3.103	3.20	-4.80	0.19
1	0.5	1 month	-	-	7-47	53.10	0.440	5/17.60	0.962	3.094	6.20	-12.00	-0.11
1	0.5	1 month	-	-	7-47	50.85	0.487	1/11.80	0.964	3.097	1.30	-2.60	-0.01
1	0.5	1 month	-	-	7-45	51.10	0.492	6/18.80	0.997	3.109	2.20	-1.60	0.38
0.5	0.5	0	0.8	0	11-49	52.95	0.491	1/10.60	0.530	3.139	5.90	-1.80	1.35
*						50.80	0.476	4/21.00	0.595	3.086	1.20	-4.80	-0.36
0.5	0.5	0	0.8	0	11-47	56.70	0.410	2/13.40	0.577	3.120	13.40	-18.00	0.74
*						51.98	0.451	2/18.80	0.692	3.086	3.96	-9.80	-0.36
0.5	0.5	0	0.8	0	11-47	53.55	0.456	2/13.20	0.567	3.116	7.10	-8.80	0.63
*						52.22	0.443	2/19.00	0.687	3.082	4.44	-11.40	-0.48
0.5	0.5	0	0.8	0	11-47	53.64	0.455	2/13.20	0.597	3.117	7.28	-9.00	0.65
*						51.82	0.453	2/18.80	0.641	3.085	3.64	-9.40	-0.38
0.5	0.5	0	0.8	0	11-47	55.20	0.429	2/13.40	0.580	3.116	10.40	-14.20	0.63
*						54.40	0.404	4/21.00	0.682	3.078	8.80	-19.20	-0.62
0.5	0.5	1 month	0.8	1 month	7-47	54.80	0.445	2/13.20	0.663	3.126	9.60	-11.00	0.94
*						52.85	0.432	2/30.60	0.753	3.081	5.69	-13.80	-0.50
0.5	0.5	1 month	0.8	1 month	9-47	52.67	0.500	2/13.20	0.616	3.142	5.34	0.00	1.46
*						50.85	0.465	4/21.00	0.759	3.080	1.70	-7.00	-0.54
0.5	0.5	1 month	0.8	1 month	7-47	53.30	0.485	1/11.80	0.586	3.139	6.60	-3.00	1.37
*						50.40	0.475	4/21.00	0.737	3.082	0.80	-5.00	-0.50
0.5	0.5	1 month	0.8	1 month	7-47	55.23	0.434	1/11.80	0.654	3.122	10.45	-13.20	0.80
*						51.90	0.430	2/19.00	0.737	3.064	3.80	-14.00	-1.07
0.5	0.5	1 month	0.8	1 month	7-47	55.05	0.441	3/14.20	0.616	3.126	10.10	-11.80	0.94
*						51.78	0.432	7/24.40	0.750	3.064	3.56	-13.60	-1.07

SLCA

Simulated						Estimated					Bias (%)		
P	tr1	SD 1	tr2	SD 2	Range	L_∞	K	t_0	Score	ϕ'	L_∞	K	ϕ'
1	0.5	0	-	-	11-47	50.30	0.499	0.5	356.4	3.101	0.60	-0.20	0.14
1	0.5	0	-	-	11-47	50.60	0.493	0.5	366.4	3.101	1.20	-1.40	0.14
1	0.5	0	-	-	11-49	50.10	0.503	0.5	357.7	3.101	0.20	0.60	0.14
1	0.5	0	-	-	11-49	50.20	0.500	0.5	391.2	3.100	0.40	0.00	0.11
1	0.5	0	-	-	11-47	50.40	0.496	0.5	335.5	3.100	0.80	-0.80	0.11
1	0.5	1 month	-	-	9-49	49.40	0.532	0.6	388.0	3.113	-1.20	6.40	0.53
1	0.5	1 month	-	-	7-47	49.70	0.525	0.5	432.2	3.113	-0.60	5.00	0.52
1	0.5	1 month	-	-	7-47	48.50	0.559	0.6	405.0	3.119	-3.00	11.80	0.71
1	0.5	1 month	-	-	7-47	50.00	0.520	0.5	422.6	3.114	0.00	4.00	0.55
1	0.5	1 month	-	-	7-45	49.20	0.546	0.6	406.2	3.121	-1.60	9.20	0.78
0.5	0.5	0	0.8	0	11-49	47.20	0.631	0.5	310.1	3.148	-5.60	26.20	1.65
0.5	0.5	0	0.8	0	11-47	48.60	0.586	0.5	307.5	3.141	-2.80	17.20	1.43
0.5	0.5	0	0.8	0	11-47	48.80	0.599	0.5	312.8	3.154	-2.40	19.80	1.85
0.5	0.5	0	0.8	0	11-47	47.90	0.606	0.5	307.6	3.143	-4.20	21.20	1.49
0.5	0.5	0	0.8	0	11-47	48.00	0.602	0.5	294.8	3.142	-4.00	20.40	1.46
0.5	0.5	1 month	0.8	1 month	7-47	47.10	0.670	0.6	320.5	3.172	-5.80	34.00	2.43
0.5	0.5	1 month	0.8	1 month	9-47	45.40	0.737	0.6	302.2	3.182	-9.20	47.40	2.73
0.5	0.5	1 month	0.8	1 month	7-47	46.80	0.672	0.6	310.8	3.168	-6.40	34.40	2.29
0.5	0.5	1 month	0.8	1 month	7-47	45.50	0.721	0.6	313.1	3.174	-9.00	44.20	2.49
0.5	0.5	1 month	0.8	1 month	7-47	45.40	0.733	0.6	288.3	3.179	-9.20	46.60	2.66

P-W Method

Simulated						Estimated			Bias (%)	
P	tr1	SD 1	tr2	SD 2	Range	L_∞	Z/K	r^2	L_∞	Z/K
1	0.5	0	-	-	11-47	50.27	3.224	0.999	0.54	0.75
1	0.5	0	-	-	11-47	48.21	2.838	0.998	-3.58	-11.31
1	0.5	0	-	-	11-49	54.00	3.800	0.997	8.00	18.75
1	0.5	0	-	-	11-49	50.83	3.409	0.998	1.66	6.53
1	0.5	0	-	-	11-47	47.86	2.770	0.999	-4.28	-13.44
1	0.5	1 month	-	-	9-49	47.27	2.555	0.998	-5.46	-20.16
1	0.5	1 month	-	-	7-47	52.06	3.641	0.996	4.12	13.78
1	0.5	1 month	-	-	7-47	48.83	3.322	0.995	-0.34	3.81
1	0.5	1 month	-	-	7-47	50.06	3.240	0.997	0.12	1.25
1	0.5	1 month	-	-	7-45	47.22	2.639	0.995	-5.56	-17.53
0.5	0.5	0	0.8	0	11-49	51.65	3.607	0.998	3.30	12.72
0.5	0.5	0	0.8	0	11-47	49.73	3.227	0.997	-0.54	0.84
0.5	0.5	0	0.8	0	11-47	53.15	3.644	0.993	6.30	13.88
0.5	0.5	0	0.8	0	11-47	49.76	3.335	0.994	-0.48	4.22
0.5	0.5	0	0.8	0	11-47	50.39	3.034	0.999	0.78	-5.19
0.5	0.5	1 month	0.8	1 month	7-47	50.51	3.399	0.995	1.02	6.22
0.5	0.5	1 month	0.8	1 month	9-47	52.82	3.731	0.993	5.64	16.59
0.5	0.5	1 month	0.8	1 month	7-47	50.32	3.161	0.999	0.64	-1.22
0.5	0.5	1 month	0.8	1 month	7-47	47.49	2.801	0.998	-5.02	-12.47
0.5	0.5	1 month	0.8	1 month	7-47	48.46	2.790	0.996	-3.08	-12.81

Appendix Table B.10. Simulated and estimated parameters and percentage of bias obtained with ELEFAN on the length-frequency data created for the Series VI experiments. CV = coefficient of individual variation.

ELEFAN

Simulated					Estimated					Bias (%)		
CV_{L_∞} (%)	CV_K (%)	Class interval	L_{max}	Number classes	L_∞	K	St.Point	ESP/ASP	φ'	L_∞	K	φ'
0	0	1	46.5	47	50.03	0.500	1/ 0.999	0.978	3.097	0.06	0.00	0.02
			45.5	46	49.93	0.499	1/ 1.00	0.977	3.095	-0.15	-0.20	-0.07
			45.5	46	49.63	0.509	2/21.60	0.985	3.098	-0.74	1.80	0.04
			47.5	48	49.85	0.504	1/20.30	1.000	3.098	-0.29	0.80	0.03
			45.5	46	50.00	0.500	1/ 0.999	0.996	3.097	0.00	0.00	0.00
0	0	2	47.0	24	50.54	0.491	1/ 0.999	0.926	3.098	1.08	-1.80	0.05
			45.0	23	51.07	0.476	1/ 1.20	0.952	3.094	2.14	-4.80	-0.10
			45.0	23	51.36	0.480	1/ 1.20	0.948	3.102	2.72	-4.00	0.18
			47.0	24	50.00	0.500	1/ 1.00	0.897	3.097	0.00	0.00	0.00
			45.0	23	50.00	0.496	1/ 1.00	0.851	3.093	0.00	-0.80	-0.11
0	0	3	46.5	16	56.00	0.434	3/ 4.20	0.846	3.134	12.00	-13.20	1.19
			46.5	16	57.35	0.415	3/ 4.50	0.824	3.135	14.70	-17.00	1.23
			46.5	16	56.75	0.422	3/ 4.50	0.830	3.133	13.50	-15.60	1.17
			46.5	16	56.65	0.406	1/ 1.50	0.846	3.115	13.30	-18.80	0.58
			46.5	16	57.35	0.415	3/ 4.50	0.862	3.135	14.70	-17.00	1.23
0	0	4	46.0	12	61.65	0.391	6/10.00	0.810	3.172	23.30	-21.80	2.43
			46.0	12	57.50	0.429	1/ 1.20	0.810	3.152	15.00	-14.20	1.77
			46.0	12	60.07	0.415	1/ 0.40	0.732	3.175	20.14	-17.00	2.53
			46.0	12	61.60	0.380	6/10.00	0.740	3.159	23.20	-24.00	2.00
			46.0	12	59.50	0.406	1/ 1.60	0.753	3.158	19.00	-18.80	1.96
20	20	1	55.5	56	55.85	0.286	8/29.50	0.296	2.950	11.70	-42.80	-4.73
			63.5	64	48.74	0.380	2/ 2.40	0.292	2.956	-2.52	-24.00	-4.56
			61.5	62	49.00	0.352	2/ 2.50	0.292	2.927	-2.00	-29.60	-5.49
			62.5	63	53.63	0.222	2/ 2.80	0.306	2.805	7.25	-55.60	-9.42
			57.5	58	50.66	0.276	3/25.20	0.277	2.850	1.32	-44.80	-7.97
20	20	2	55.0	28	52.50	0.459	1/ 1.25	0.551	3.102	5.00	-8.20	0.17
			63.0	32	54.80	0.304	12/33.0	0.515	2.960	9.60	-39.20	-4.41
			61.0	31	56.40	0.387	1/ 1.00	0.420	3.090	12.80	-22.60	-0.21
			63.0	32	58.77	0.307	2/ 3.00	0.466	3.025	17.54	-38.60	-2.31
			57.0	29	55.82	0.353	1/ 2.00	0.411	3.041	11.64	-29.40	-1.79
20	20	3	55.5	19	56.90	0.416	1/ 1.20	0.617	3.129	13.80	-16.80	1.05
			61.5	21	57.75	0.297	12/52.5	0.603	2.996	15.49	-40.60	-3.27
			61.5	21	61.40	0.301	3/ 5.40	0.620	3.055	22.80	-39.80	-1.36
			61.5	21	60.75	0.345	4/ 6.90	0.582	3.105	21.50	-31.00	0.26
			55.5	19	58.94	0.334	5/49.50	0.577	3.065	17.88	-33.20	-1.04
20	20	4	54.0	14	62.70	0.397	1/ 1.20	0.732	3.193	25.40	-20.60	3.11
			62.0	16	69.14	0.323	1/ 1.60	0.693	3.189	38.28	-35.40	2.96
			58.0	15	72.67	0.340	1/ 0.40	0.711	3.254	45.34	-32.00	5.08
			62.0	16	71.35	0.395	1/ 0.40	0.711	3.303	42.70	-21.00	6.67
			58.0	15	72.55	0.374	6/10.4	0.697	3.294	45.10	-25.20	6.37

Appendix Table B.11. Simulated and estimated parameters and percentage of bias obtained with SLCA on the length-frequency data created for the Series VI experiments. CV = coefficient of individual variation.

SLCA

Simulated					Estimated					Bias (%)		
CV_{L_∞} (%)	CV_K (%)	Class interval	L_{max}	Number classes	L_∞	K	t_0	Score	ϕ'	L_∞	K	ϕ'
0	0	1	46.5	47	50.00	0.500	1.0	482.0	3.097	0.00	0.00	0.00
			45.5	46	50.00	0.501	1.0	509.9	3.098	0.00	0.20	0.03
			45.5	46	50.10	0.500	1.0	490.5	3.099	0.20	0.00	0.06
			47.5	48	50.10	0.500	1.0	515.9	3.099	0.20	0.00	0.06
			45.5	46	49.90	0.501	1.0	490.7	3.096	-0.20	0.20	-0.03
0	0	2	47.0	24	50.10	0.500	0.0	370.2	3.099	0.20	0.00	0.06
			45.0	23	50.30	0.499	0.0	394.5	3.101	0.60	-0.20	0.14
			45.0	23	51.50	0.484	1.0	378.6	3.108	3.00	-3.20	0.37
			47.0	24	50.50	0.494	1.0	398.6	3.100	1.00	-1.20	0.11
			45.0	23	50.30	0.498	0.0	375.9	3.100	0.60	-0.40	0.11
0	0	3	46.5	16	50.60	0.498	0.0	322.1	3.106	1.20	-0.40	0.28
			46.5	16	50.40	0.500	0.0	340.9	3.104	0.80	0.00	0.22
			46.5	16	50.90	0.493	0.0	326.0	3.106	1.80	-1.40	0.30
			46.5	16	50.40	0.500	0.0	345.5	3.104	0.80	0.00	0.22
			46.5	16	50.50	0.500	0.0	327.3	3.106	1.00	0.00	0.28
0	0	4	46.0	12	50.80	0.500	0.0	269.2	3.111	1.60	0.00	0.45
			46.0	12	51.90	0.483	0.0	287.8	3.114	3.80	-3.40	0.56
			46.0	12	51.40	0.491	0.0	272.6	3.113	2.80	-1.80	0.52
			46.0	12	51.30	0.490	0.0	291.7	3.110	2.60	-2.00	0.44
			46.0	12	51.10	0.496	0.0	274.0	3.112	2.20	-0.80	0.50
20	20	1	55.5	56	59.10	0.486	0.1	342.2	3.230	18.20	-2.80	4.29
			63.5	64	60.10	0.469	0.1	366.9	3.229	20.20	-6.20	4.26
			61.5	62	68.20	0.405	0.1	368.5	3.275	36.40	-19.00	5.75
			62.5	63	60.60	0.502	0.1	345.4	3.266	21.20	0.40	5.45
			57.5	58	61.60	0.496	0.1	349.4	3.275	23.20	-0.80	5.74
20	20	2	55.0	28	58.90	0.500	0.1	239.9	3.239	17.80	0.00	4.59
			63.0	32	56.50	0.520	0.1	257.7	3.220	13.00	4.00	3.98
			61.0	31	67.70	0.403	0.1	256.5	3.266	35.40	-19.40	5.48
			63.0	32	77.30	0.360	0.1	249.6	3.333	54.60	-28.00	7.61
			57.0	29	57.90	0.530	0.1	245.9	3.250	15.80	6.00	4.93
20	20	3	55.5	19	70.10	0.410	0.1	195.3	3.304	40.20	-18.00	6.69
			61.5	21	86.60	0.337	0.1	214.3	3.403	73.20	-32.60	9.87
			61.5	21	69.00	0.400	0.1	206.7	3.280	38.00	-20.00	5.90
			61.5	21	74.40	0.391	0.1	200.1	3.335	48.80	-21.80	7.70
			55.5	19	64.70	0.462	0.1	198.6	3.286	29.40	-7.60	6.12
20	20	4	54.0	14	65.30	0.470	0.1	164.1	3.302	30.60	-6.00	6.62
			62.0	16	85.40	0.355	0.1	183.0	3.413	70.80	-29.00	10.21
			58.0	15	66.40	0.424	0.1	175.4	3.272	32.80	-15.20	5.64
			62.0	16	73.70	0.394	0.1	169.9	3.330	47.40	-21.20	7.54
			58.0	15	81.40	0.359	0.1	166.8	3.376	62.80	-28.20	9.02

Appendix Table B.12. Simulated and estimated parameters and percentage of bias obtained with the P-W method on the length-frequency data created for the Series VI experiments. CV = coefficient of individual variation.

P-W Method

Simulated					Estimated			Bias (%)	
CV_{L_∞} (%)	CV_K (%)	Class interval	L_{max}	Number classes	Z/K	L_∞	r^2	Z/K	L_∞
0	0	1	46.5	47	2.593	46.43	0.994	-18.97	-7.14
			45.5	46	2.840	46.49	0.996	-11.25	-7.02
			45.5	46	2.822	49.26	0.993	-11.81	-1.48
			47.5	48	3.570	52.69	0.999	11.56	5.38
			45.5	46	2.925	49.17	0.999	-8.59	-1.66
0	0	2	47.0	24	2.603	46.57	0.994	-18.66	-6.86
			45.0	23	2.838	46.60	0.997	-11.31	-6.81
			45.0	23	2.858	49.67	0.993	-10.69	-0.66
			47.0	24	3.576	52.83	0.998	11.75	5.65
			45.0	23	2.943	49.40	0.999	-8.03	-1.21
0	0	3	46.5	16	2.659	47.19	0.994	-16.91	-5.62
			46.5	16	2.875	47.02	0.996	-10.16	-5.97
			46.5	16	2.904	50.19	0.993	-9.25	0.39
			46.5	16	3.586	53.06	0.999	12.06	6.12
			46.5	16	2.955	49.74	0.999	-7.66	-0.52
0	0	4	46.0	12	2.655	47.42	0.993	-17.03	-5.16
			46.0	12	2.875	47.27	0.996	-10.16	-5.46
			46.0	12	2.942	50.77	0.991	-8.06	1.54
			46.0	12	3.667	54.07	0.999	14.59	8.14
			46.0	12	2.998	50.32	0.999	-6.31	0.64
20	20	1	55.5	56	5.759	55.85	0.985	79.97	11.70
			63.5	64	5.972	48.74	0.995	86.63	-2.52
			61.5	62	4.760	49.00	0.992	48.75	-2.00
			62.5	63	4.452	53.63	0.982	39.12	7.25
			57.5	58	4.861	50.66	0.997	51.91	1.32
20	20	2	55.0	28	5.762	52.50	0.985	80.06	5.00
			63.0	32	5.982	54.80	0.995	86.94	9.60
			61.0	31	4.760	56.40	0.992	48.75	12.80
			63.0	32	4.461	58.77	0.989	39.41	17.54
			57.0	29	4.860	55.82	0.998	51.88	11.64
20	20	3	55.5	19	5.837	56.90	0.986	82.41	13.80
			61.5	21	5.922	57.75	0.995	85.06	15.49
			61.5	21	4.813	61.40	0.994	50.41	22.80
			61.5	21	4.419	60.75	0.991	38.09	21.50
			55.5	19	4.881	58.94	0.998	52.53	17.88
20	20	4	54.0	14	5.708	62.70	0.985	78.38	25.40
			62.0	16	5.986	69.14	0.998	87.06	38.28
			58.0	15	4.650	72.67	0.995	45.31	45.34
			62.0	16	4.470	71.35	0.990	39.69	42.70
			58.0	15	4.888	72.55	0.998	52.75	45.10

Appendix Table B.13. Response surfaces of the goodness-of-fit criterion calculated with ELEFAN (top) and SLCA (bottom) for a set of simulated length data with individual variability in growth parameters; peaks are remarked.

	Value of K															
L_∞	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40
54.0	174	112	216	222	273	387	400	488	452	466	341	288	390	429	379	415
55.0	137	236	197	288	354	442	447	381	343	285	368	414	379	432	543	560
56.0	174	226	358	425	470	478	342	296	335	385	426	459	556	539	512	430
57.0	280	377	438	450	367	294	308	374	449	453	542	**603**	516	508	394	396
58.0	350	447	423	327	263	308	386	495	510	538	570	508	502	393	357	395
59.0	396	410	322	249	359	395	498	574	**614**	536	520	410	405	411	398	413
60.0	351	257	266	366	454	497	564	602	551	517	430	352	371	413	358	333
61.0	250	269	371	442	497	529	559	543	502	419	357	355	365	341	317	236
62.0	255	391	442	547	540	586	566	504	356	424	355	364	343	329	190	166
63.0	403	416	499	540	575	580	493	359	382	335	360	317	324	234	208	212
64.0	415	509	533	**612**	570	466	374	370	311	334	314	311	213	232	272	260
65.0	461	527	605	555	516	362	376	316	334	338	316	203	232	271	280	227
66.0	563	609	535	516	435	387	316	336	301	330	214	297	271	314	227	183
67.0	546	537	510	431	356	306	321	316	330	282	297	257	283	212	193	150

	Value of K										
L_∞	0.33	0.35	0.37	0.39	0.41	0.43	0.45	0.47	0.49	0.51	0.53
51.0	243.2	284.2	324.6	360.8	386.2	405.1	423.2	437.5	446.7	451.7	452.6
52.0	258.9	305.0	344.0	372.3	396.7	418.3	433.5	444.2	452.4	456.6	454.6
53.0	281.0	322.7	356.7	386.5	409.0	426.3	442.0	454.8	460.8	457.4	446.1
54.0	297.7	338.2	372.4	396.4	417.2	439.4	456.7	**462.2**	456.7	445.6	433.1
55.0	315.3	354.7	380.2	406.3	435.5	454.7	459.9	456.1	448.4	439.4	428.1
56.0	332.9	361.1	392.7	427.2	448.9	456.4	456.4	453.3	446.5	434.2	416.7
57.0	339.2	374.5	414.3	439.8	451.3	457.4	458.4	452.1	438.9	421.0	400.9
58.0	351.7	396.2	426.6	445.2	456.7	460.9	457.0	444.9	426.5	405.5	385.5
59.0	372.3	410.0	435.4	452.3	461.9	461.8	450.7	431.9	411.0	392.3	376.4
60.0	388.5	420.7	444.0	460.7	465.2	455.9	437.9	418.2	400.4	384.9	370.1
61.0	400.5	430.7	455.4	**466.2**	460.5	444.6	426.3	409.2	393.4	377.9	362.1
62.0	411.4	444.5	463.8	463.9	451.4	434.7	418.2	402.1	386.1	369.7	353.2
63.0	426.5	456.4	465.0	457.4	443.1	427.2	411.2	394.7	378.0	361.1	344.4
64.0	441.8	461.9	461.6	450.7	436.2	420.4	403.9	387.0	369.9	352.7	335.6

Appendix Table B.14. Individual length-at-age data, mean and variation coefficients (in %) of 7 females (f) and 4 males (m) of *Lebistes reticulatus* reared for 58 weeks in experimental tanks.

Age (weeks)	1 f	2 f	3 f	4 f	5 f	6 f	7 f	Mean	Variance	CV (%)	1 m	2 m	3 m	4 m	Mean	Variance	CV (%)
0	46	47	43	44	43	43	43	44.14	2.81	3.80	45	46	46	40	44.25	8.25	6.49
1	53	55	50	53	51	48	50	51.43	5.62	4.61	51	53	49	49	50.50	3.67	3.79
2	60	66	58	59		56	58	59.50	11.90	5.80	59	60	58	54	57.75	6.92	4.56
3	64	73	63	66	62	66	69	66.14	14.48	5.75	65	64	65	61	63.75	3.58	2.97
4	72	81	66	71	67	70	74	71.57	24.95	6.98	71	71	73	67	70.50	6.33	3.57
5	79	87		78	76	74	79	78.83	19.77	5.64	78	79	83	71	77.75	24.92	6.42
6	85	94		83	84	81	83	85.00	21.20	5.42	83	84	89	73	82.25	44.92	8.15
7	91	106		87	89			93.25	74.92	9.28	92	90	101		94.33	34.33	6.21
8	101	110	81	92	95			95.80	115.70	11.23	96	93	105		98.00	39.00	6.37
9	107	120	84					103.67	332.30	17.58	99	97			98.00	2.00	1.44
10	113	124	90			103	97	105.40	179.30	12.70	101	100		84	95.00	91.00	10.04
11	116	128	96			107	99	109.20	170.70	11.96	105	103		89	99.00	76.00	8.81
12	121	133		108	112	112	106	115.33	101.47	8.73	104	104	111	93	103.00	55.33	7.22
13				108	116	117	110	112.75	19.58	3.92			113	95	104.00	162.00	12.24
14			112	116	120	118		116.50	11.67	2.93			115	97	106.00	162.00	12.01
15			118	120	123	121	119	120.20	3.70	1.60			117	99	108.00	162.00	11.79
16	132	150	121				123	131.50	175.00	10.06	108	108			108.00	0.00	0.00
17	134	151	126	128	135	130	133	133.86	67.81	6.15	108	107	120	101	109.00	63.33	7.30
18	137	152	128		143	132	136	138.00	72.40	6.17	109	107		104	106.67	2.00	1.33
19	139	158		139	146	133	140	142.50	74.70	6.07	109	108	118	101	109.00	48.67	6.40
20				141	149	138	140	142.00	23.33	3.40			118	102	110.00	128.00	10.29
21	142	161	137	143	149	139	144	145.00	64.33	5.53	112	109	118	108	111.75	20.25	4.03
22			141	148	150			146.33	22.33	3.23			119		119.00		0.00
23	151	170	143	149		148	151	152.00	86.40	6.12	111	113	118	106	112.00	24.67	4.43
24	155	171				152	157	158.75	70.92	5.30	110	116		105	110.33	30.33	4.99
25	159	173	151	156	154	148	157	156.86	64.48	5.12	109	112	121	106	112.00	42.00	5.79
26	162	175		157	157	151	159	160.17	65.77	5.06	111	112	121	107	112.75	34.92	5.24
27																	
28	167	176		160	164	158	165	165.00	40.00	3.83	111	111	121	106	112.25	39.58	5.60
29																	
30	176	192	163	174	171	161	169	172.29	105.24	5.95	112	112	121	106	112.75	38.25	5.49

a) f=females; m = males

Continued

Appendix Table B.14. Continued

Age (weeks)	1 f	2 f	3 f	4 f	5 f	6 f	7 f	Mean	Variance	CV (%)	1 m	2 m	3 m	4 m	Mean	Variance	CV (%)
31																	
32	179	197	168	171	170	167	171	174.71	111.57	6.05	115	112	121	106	113.50	39.00	5.50
33																	
34	181	204	176	172	177	173	174	179.57	124.95	6.22	116	114	123	109	115.50	33.67	5.02
35																	
36	192	209	187	176	179	174	174	184.43	164.29	6.95	117	114	128	110	117.25	59.58	6.58
37																	
38	192	216	188	178	181	180	176	187.29	192.24	7.40	118	114	128	113	118.25	46.92	5.79
39																	
40	192	216	191	183	186	197	181	192.29	139.90	6.15	117	115	126	113	117.75	32.92	4.87
41																	
42	198	218	196	192	199	196	177	196.57	145.29	6.13	122	116	131	110	119.75	80.25	7.48
43																	
44	203	223		188	201	198	179	198.67	223.47	7.52	120	116	131	113	120.00	62.00	6.56
45																	
46	212	227		193	206	201	181	203.33	250.67	7.79	126	123	136	116	125.25	68.92	6.63
47																	
48	213	221		189	201			206.00	196.00	6.80	121	118	135		124.67	82.33	7.28
49																	
50	215	223						219.00	32.00	2.58	123	118			120.50	12.50	2.93
51																	
52	216	221				205		214.00	67.00	3.82	124	123		117	121.33	14.33	3.12
53																	
54					215			215.00					134		134.00		0.00
55																	
56																	
57																	
58	218							218.00			124	121			122.50	4.50	1.73

Appendix Table B.15. Individual growth parameters (L_∞, K and t_0) of 7 females and 4 males of *Lebistes reticulatus* calculated from Ursin's (1967) data with Allen's (1966) method. The variances and variation of coefficients in the lines below the parameter values represent the variation within each individual. The values of the last column correspond to the averages, variances and variation coefficients between individuals. N = number of data available for each individual.

FEMALES								
Parameters	F1	F2	F3	F4	F5	F6	F7	Average (F)
L_∞	5.058	5.026	6.056	4.450	4.732	4.937	4.112	4.910
Var (L_∞)	0.014	0.012	0.105	0.007	0.014	0.026	0.009	0.372
CV (%)	2.354	2.143	5.343	1.904	2.477	3.248	2.292	12.415
K	0.0320	0.0408	0.0212	0.0380	0.0361	0.0305	0.0456	0.0349
Var (K)	3.70E-06	6.54E-06	4.03E-06	3.65E-06	5.45E-06	5.13E-06	8.99E-06	6.29E-05
CV (%)	6.015	6.269	9.488	5.025	6.478	7.428	6.572	22.747
t_0	-6.802	-5.576	-7.489	-6.025	-5.780	-6.812	-5.173	-6.237
Var (t_0)	0.239	0.236	0.255	0.133	0.251	0.297	0.216	0.673
CV (%)	7.184	8.712	6.736	6.064	8.665	8.004	8.977	0.132
Res. var.	15.060	22.949	7.185	7.925	16.076	14.850	15.910	-
r^2	0.995	0.993	0.997	0.997	0.994	0.994	0.992	-
N	36	34	25	32	32	33	32	-

MALES					
Parameters	M1	M2	M3	M4	Average (M)
L_∞	2.372	2.331	2.555	2.257	2.379
Var (L_∞)	4.17E-04	2.32E-04	6.85E-04	2.60E-04	1.60E-02
CV (%)	0.861	0.653	1.024	0.714	5.326
K	0.1274	0.1321	0.1295	0.1018	0.1227
Var (K)	7.90E-05	5.24E-05	1.03E-04	2.29E-05	1.97E-04
CV (%)	6.976	5.481	7.842	4.697	11.448
t_0	-3.596	-3.601	-3.047	-4.500	-3.686
Var (t_0)	0.201	0.122	0.196	0.110	0.362
CV (%)	12.479	9.691	14.529	7.371	16.329
Res. var.	14.053	8.127	19.764	4.625	-
r^2	0.971	0.982	0.971	0.990	-
N	36	36	33	33	-

Appendix Table B.16. Individual length-at-age data, averages, standard deviations and coefficients of variation (in %) for 70 *Oreochromis ossambicus hornorum* reared for 25 weeks in experimental tanks (calculated after original data from Doyle, pers. comm.).

B.16. Individual length-at-age data, averages, standard deviations and coefficients of variation (in %) for 70 *Oreochromis mossambicus hornorum* reared for 25 weeks in experimental tanks (calculated after original data from Doyle, pers. comm.).

TIME (in weeks)

Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	N
1	6.08	7.68	10.48	11.52	13.68	17.60	21.12	23.00	23.50	24.00	24.50	29.00	33.00	36.50	39.00	40.00	42.00	42.50	44.00	44.50	44.50	45.50	45.5	46.00	45.50	25
2	6.08	7.92	11.84	12.96	15.52	18.24	21.12	22.50	23.50	25.00	26.50	30.00	35.00	38.50	42.50	42.50	43.00	45.00	46.00	48.00	49.50	49.50	50.0	52.00	51.00	25
3	5.92	7.44	11.12	12.40	14.32	17.60	19.84	21.00	23.00	23.50	24.00	26.50	30.00	33.00	35.00	36.50	38.00	40.00	40.00	41.50	41.50	42.50	43.0	44.00	45.50	25
4	5.52	7.36	11.12	12.32	14.24	16.64	19.20	22.00	22.50	23.50	24.00	26.50	31.50	35.00	37.50	38.00	39.00	41.00	42.00	43.00	42.50	42.50	-	-	-	22
5	5.76	7.76	10.64	12.32	14.48	17.04	19.44	20.00	21.00	22.00	24.00	27.50	32.50	36.50	38.50	39.00	40.00	41.00	41.00	41.50	42.00	42.00	43.0	43.00	44.00	25
6	5.84	7.92	11.20	12.16	13.68	16.00	18.16	19.00	19.50	21.00	22.00	25.50	31.00	35.00	37.50	38.50	39.50	40.50	41.50	43.00	43.00	44.50	44.5	45.50	46.00	25
7	6.16	7.84	11.76	13.12	14.32	17.04	20.00	22.00	23.00	24.50	26.50	29.50	34.50	37.50	40.50	41.50	43.00	45.00	47.00	46.50	47.00	49.50	50.0	52.50	52.50	25
8	5.36	7.20	10.40	11.60	13.76	17.60	19.52	21.00	21.00	21.50	22.50	26.00	31.00	36.00	39.00	42.50	43.50	44.00	44.00	45.50	45.00	45.00	45.5	46.00	45.50	25
9	6.08	7.76	11.20	12.40	14.24	16.96	20.00	22.00	22.50	24.50	25.50	28.00	31.50	35.50	38.50	41.00	43.00	45.00	46.00	47.00	46.00	46.00	46.5	46.50	46.50	25
10	5.52	7.92	11.04	12.08	13.84	16.40	19.04	20.50	22.00	22.00	23.00	28.50	33.50	39.00	42.00	43.00	45.00	46.50	46.50	47.00	46.00	49.00	50.0	51.50	53.00	25
11	5.76	7.60	11.04	12.56	14.16	16.56	19.52	21.50	22.50	23.50	25.00	29.50	34.00	37.50	39.00	40.00	41.00	44.50	45.00	44.50	46.00	46.00	47.0	47.50	49.00	25
12	6.08	8.32	11.52	12.48	14.96	17.28	20.32	22.50	23.50	24.00	25.50	30.00	33.50	36.50	38.50	41.00	42.50	43.00	43.50	45.00	46.00	46.00	48.0	47.50	-	24
13	5.28	8.40	11.84	13.12	15.28	17.04	20.80	22.50	23.00	23.50	24.00	28.00	32.00	34.50	38.00	40.50	42.50	45.00	46.00	47.00	48.00	49.00	48.5	48.00	49.00	25
14	6.40	8.08	11.52	12.64	14.88	17.20	20.00	22.00	22.00	23.00	24.00	28.50	33.50	37.50	40.00	42.50	43.50	44.50	45.00	46.00	46.00	46.50	47.0	-	-	23
15	5.92	6.16	11.44	12.72	14.64	17.36	19.52	21.50	22.50	22.50	23.50	27.00	31.50	34.00	37.50	40.00	41.50	42.50	44.00	43.50	44.50	44.00	44.5	44.00	-	24
16	5.68	7.92	11.28	12.32	14.80	17.04	19.20	20.50	21.50	22.00	22.50	26.50	30.50	33.00	34.50	36.00	37.50	38.50	41.00	41.00	41.50	42.50	43.5	44.00	44.50	25
17	6.08	7.12	9.44	10.72	13.68	15.84	18.24	20.00	20.00	21.00	21.00	26.50	32.00	36.00	38.00	40.00	40.50	42.00	42.00	42.50	43.00	43.00	-	-	-	22
18	5.44	8.32	11.52	12.64	15.04	18.00	20.40	22.00	23.00	24.50	24.50	29.00	33.00	36.50	40.50	42.00	43.50	45.50	46.00	46.50	46.00	47.50	48.5	48.50	49.00	25
19	6.08	8.00	11.52	12.32	14.72	16.40	18.56	20.50	21.00	21.50	22.00	25.50	30.50	34.50	36.00	37.00	38.00	40.50	42.00	43.00	43.00	44.00	44.5	46.50	47.00	25
20	6.24	8.24	11.36	12.88	15.44	18.08	20.80	22.00	23.00	23.50	24.50	28.50	34.00	38.00	39.50	41.00	42.50	44.50	45.00	45.50	45.50	46.00	47.0	47.50	48.00	25
21	5.76	7.68	11.84	12.32	14.32	15.60	17.60	19.00	18.50	18.50	19.00	24.00	30.00	33.50	36.00	37.50	38.50	39.00	40.00	39.50	40.00	40.00	41.0	40.50	41.50	25
22	5.60	6.24	9.12	11.12	13.92	16.64	19.52	21.50	22.50	24.00	26.00	31.00	35.50	39.50	40.50	42.00	43.00	44.50	46.00	46.50	46.50	46.50	46.5	48.00	49.00	25
23	6.32	7.52	11.20	12.64	15.04	17.76	19.68	21.00	22.00	22.00	23.00	27.00	32.00	34.00	35.50	38.50	40.50	43.00	43.00	44.50	44.00	44.00	43.5	-	-	23
24	6.32	8.40	11.92	13.04	14.88	17.36	20.32	21.50	21.50	22.00	22.50	27.00	32.00	34.00	37.00	39.00	40.50	42.00	43.00	43.50	43.50	45.00	45.5	46.00	46.50	25
25	6.24	8.00	11.20	12.56	14.56	16.56	19.12	20.50	21.50	21.50	23.00	26.50	32.00	36.50	39.50	42.00	42.50	44.00	45.00	44.50	45.00	45.00	46.0	46.50	47.00	25
26	6.00	7.52	10.00	12.40	14.64	17.28	19.36	21.00	21.50	22.50	23.50	25.50	30.50	34.00	35.00	37.50	39.50	40.50	40.50	41.50	42.00	43.50	43.0	44.50	44.00	25
27	6.24	8.80	11.36	12.48	14.72	17.12	19.60	21.00	22.00	22.50	23.50	27.50	33.50	38.00	39.50	42.50	45.00	46.50	46.50	47.00	47.00	48.50	46.5	48.00	49.00	25
28	6.08	8.16	11.20	12.16	15.04	16.72	19.04	20.50	20.50	21.50	22.50	27.00	33.00	36.50	40.00	41.50	42.50	43.50	44.50	45.50	46.50	47.00	49.0	49.50	50.00	25
29	6.08	7.92	10.40	11.76	13.84	15.84	17.20	18.00	19.00	20.00	22.00	25.50	30.00	34.00	36.00	37.00	37.50	39.00	40.00	41.00	41.00	43.00	43.5	45.00	44.50	25
30	5.44	8.32	10.88	12.00	14.16	16.72	19.36	21.00	21.50	22.00	24.00	27.50	32.00	36.00	39.00	41.00	42.00	43.50	44.50	45.00	45.50	45.50	46.0	49.00	49.50	25
31	5.44	7.52	10.56	11.60	13.84	15.92	19.04	20.00	19.50	20.00	21.00	25.50	30.50	32.50	33.50	35.50	37.50	38.50	39.50	40.00	40.50	42.00	42.0	43.50	44.00	25
32	6.08	7.76	10.88	11.92	13.84	15.76	17.92	18.50	19.50	20.00	21.50	25.00	31.00	34.00	36.00	40.00	40.00	40.50	41.00	41.00	41.00	41.00	-	-	-	22
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
34	5.76	6.32	11.68	12.32	14.80	18.40	20.96	22.00	24.00	25.00	26.50	28.50	30.00	34.00	37.50	41.50	45.00	45.00	45.50	46.00	47.50	48.00	49.0	49.50	51.00	25
35	6.40	8.16	11.20	12.32	14.48	17.60	20.32	22.50	24.00	25.00	26.00	28.00	29.00	33.00	36.00	41.50	45.00	46.00	47.00	47.50	48.00	49.00	49.5	49.50	50.00	25
36	5.84	8.24	11.84	13.20	15.76	18.56	20.80	23.00	24.00	25.00	26.50	29.00	30.00	32.50	35.00	40.00	43.50	45.50	47.00	47.00	48.00	49.50	50.0	50.00	50.50	25
37	6.64	7.92	11.04	12.08	14.24	17.44	19.68	20.50	21.50	22.00	22.50	24.50	27.00	31.00	34.50	39.00	43.50	45.00	45.50	47.00	47.00	48.00	48.0	47.00	48.00	25
38	6.08	8.16	11.36	12.48	14.64	17.28	19.12	21.50	23.00	24.50	26.00	27.50	30.00	33.50	35.00	39.50	42.00	43.00	43.50	43.00	43.00	44.00	43.5	-	-	23
39	6.24	7.92	10.96	12.32	14.72	16.96	19.68	22.00	24.00	25.00	25.50	28.00	29.00	32.50	36.00	41.00	43.50	43.50	44.50	44.50	44.50	45.00	45.0	44.50	-	24
40	5.92	7.68	11.20	12.32	14.72	17.60	20.16	22.00	22.50	25.00	26.50	29.00	29.00	32.50	36.00	41.50	46.00	47.00	49.00	48.50	50.00	51.50	52.5	52.00	52.00	25
41	6.08	7.76	11.04	12.16	14.88	18.24	21.12	22.50	23.00	24.00	25.00	28.00	29.50	34.50	36.50	41.00	43.00	44.00	45.50	48.00	46.00	48.00	45.5	45.00	45.00	25
42	6.32	8.16	11.52	12.40	14.72	17.28	20.32	23.00	24.00	25.50	27.00	28.50	30.00	33.00	36.00	41.00	44.50	46.00	48.50	48.00	47.50	49.00	48.5	48.00	49.50	25
43	5.76	7.92	11.36	12.48	14.88	17.60	20.00	21.50	23.00	24.00	25.50	27.00	28.50	30.50	33.50	37.50	40.50	42.00	42.50	41.50	41.50	42.50	42.5	42.00	-	24
44	6.00	8.00	11.36	12.40	14.40	16.80	19.52	21.00	23.00	24.00	25.50	28.00	30.50	33.50	37.50	41.00	44.00	45.50	46.00	45.50	46.00	46.50	46.5	46.00	46.50	25
45	5.28	7.44	10.72	11.92	14.24	17.68	20.80	24.00	26.50	28.50	30.00	32.00	33.00	35.50	39.00	43.00	46.00	46.50	46.50	47.00	47.50	48.00	47.0	47.00	47.00	25
46	6.24	7.84	10.88	12.00	14.08	16.72	18.64	21.00	22.00	23.00	24.00	26.00	27.50	31.00	33.50	38.50	41.00	42.00	43.50	44.00	44.00	43.50	44.5	44.00	-	24
47	5.84	7.84	11.20	12.48	14.32	17.28	20.16	22.00	23.50	25.50	27.00	29.00	30.00	34.00	36.00	39.50	41.00	42.50	42.00	43.00	43.00	43.50	43.0	43.00	-	24
48	5.92	8.00	10.80	11.68	14.00	16.32	18.88	20.50	22.00	23.00	24.50	26.00	28.00	31.00	34.00	38.50	42.00	42.50	43.00	43.50	44.00	44.00	44.5	44.00	45.00	25
49	6.08	8.00	11.12	11.92	14.08	17.20	20.00	23.00	25.00	27.00	28.50	30.50	32.00	34.00	37.00	42.50	44.50	45.00	45.50	45.50	46.00	46.00	46.0	46.50	-	24
50	5.68	7.20	10.40	11.76	13.76	16.72	20.00	23.00	24.00	26.00	27.00	29.50	30.00	32.50	35.50	38.50	41.50	42.00	43.50	45.00	45.50	45.50	46.5	45.50	45.00	25
51	5.76	8.00	11.88	12.08	14.48	18.32	21.04	23.00	24.50	27.00	29.00	31.00	32.00	36.00	40.50	44.00	47.00	48.50	49.50	50.50	52.00	52.00	52.5	54.00	55.00	25
52	6.16	8.24	11.04	12.16	14.40	18.16	20.80	23.00	25.50	28.00	30.00	31.00	32.50	34.00	36.50	41.50	44.00	45.50	47.00	47.00	48.50	49.00	50.5	51.00	51.00	25
53	5.92	8.32	11.36	12.32	14.72	18.00	20.72	23.00	25.50	28.00	29.00	31.00	32.50	35.50	38.50	43.00	45.50	46.50	48.00	48.50	48.50	48.00	48.0	-	-	23
54	5.92	8.16	11.12	12.24	13.92	16.64	19.52	20.50	22.00	24.00	25.00	28.00	29.50	33.00	35.50	39.00	41.00	41.00	41.00	41.00	41.50	41.00	41.0	41.00	-	24
55	6.08	8.00	11.04	11.92	14.40	18.00	21.12	23.50	24.00	26.00	27.50	30.00	31.50	35.00	39.50	44.50	47.50	48.50	49.50	49.00	50.50	51.50	52.5	53.50	54.00	25
56	5.68	7.76	11.28	12.08	14.32	16.56	19.20	21.50	23.00	25.00	27.00	29.00	31.50	34.00	37.50	41.50	44.00	44.50	45.00	45.00	46.00	45.50	46.0	46.00	46.50	25
57	5.12	8.00	10.88	12.00	13.92	16.00	18.88	19.50	21.00	22.50	24.50	27.00	29.00	32.00	35.00	39.50	42.00	43.50	44.00	43.50	44.50	45.00	45.5	46.00	46.50	25
58	6.40	8.24	11.20	12.24	15.52	19.52	22.00	23.50	25.00	26.50	28.00	30.00	33.50	36.00	39.50	41.50	42.00	42.00	41.50	42.00	42.00	-	-	-	-	22
59	6.08	8.08	11.20	12.40	15.04	18.00	20.64	23.50	24.50	27.00	28.00	29.50	31.00	35.00	38.50	42.50	45.00	45.00	46.00	46.00	46.50	46.00	46.0	-	-	23
60	6.08	8.00	11.36	12.40	14.80	17.92	20.24	22.00	23.00	25.00	26.50	28.50	30.00	33.00	36.00	42.00	46.00	47.00	47.50	48.00	49.50	50.00	50.5	51.50	52.00	25
61	5.76	7.68	10.96	11.84	14.08	17.20	20.16	22.50	23.50	26.00	27.00	29.00	30.50	33.50	37.00	41.50	45.50	46.58	47.00	48.00	48.00	49.00	50.0	50.50	49.50	25
62	6.40	8.00	11.04	12.40	14.48	17.60	20.64	23.00	25.50	27.50	28.50	30.00	31.50	33.50	36.50	41.00	44.50	45.00	48.00	46.00	46.00	46.50	46.5	46.50	46.50	25
63	6.08	8.32	11.36	12.72	14.80	17.44	20.56	22.50	25.00	27.50	28.50	30.50	32.50	35.50	39.00	44.50	48.00	47.50	48.50	49.00	49.00	51.00	50.5	49.50	50.50	25
64	6.08	8.16	10.96	11.84	14.40	17.92	21.20	24.00	26.50	29.00	30.00	31.50	33.00	35.50	39.00	44.00	47.00	48.00	48.00	48.00	48.00	48.00	48.0	47.50	47.00	25
65	6.16	8.16	11.68	12.48	15.04	18.40	20.72	23.00	24.50	27.00	28.50	29.00	30.50	34.00	37.50	42.00	44.00	45.50	45.50	45.00	45.00	45.00	45.0	45.00	45.50	25
66	5.80	7.68	10.24	11.76	14.08	17.60	20.96	22.50	25.00	27.00	26.50	30.00	31.00	34.00	36.00	41.00	44.00	45.50	46.50	46.50	47.50	49.00	49.0	48.50	49.00	25
67	6.32	8.08	11.20	12.00	14.00	16.80	19.52	21.50	24.00	26.00	27.50	29.00	30.50	34.00	36.50	41.00	42.50	43.00	44.00	44.00	44.50	45.00	45.5	44.50	45.00	25
68	6.08	7.92	10.96	11.84	14.00	17.28	20.40	23.00	25.00	27.50	28.50	30.50	32.50	35.50	38.50	42.00	44.00	44.00	44.50	45.00	45.50	45.50	46.5	46.00	46.50	25
69	6.24	8.16	11.12	12.08	14.00	17.04	20.00	22.00	25.00	27.00	28.50	30.50	32.00	35.50	39.00	43.50	47.00	49.00	50.00	51.00	51.50	52.00	52.5	53.00	54.00	25
70	6.08	7.76	11.04	12.00	14.24	17.68	21.28	24.00	26.00	29.00	29.50	32.00	32.50	36.00	38.50	43.50	46.50	48.00	48.00	48.00	49.00	50.00	50.0	50.00	50.00	25
Mean	5.957	7.904	11.096	12.231	14.461	17.203	19.857	21.688	22.879	24.200	25.357	28.236	31.264	34.600	37.379	40.621	42.786	43.957	44.721	45.143	45.564	46.114	46.	47.115	48.000	
SD	0.310	0.382	0.510	0.437	0.487	0.712	0.904	1.292	1.760	2.357	2.470	1.865	1.744	1.946	2.042	2.065	2.556	2.500	2.532	2.548	2.737	2.872	2.	3.083	3.010	
CV	0.052	0.048	0.046	0.036	0.034	0.041	0.046	0.060	0.077	0.097	0.097	0.066	0.056	0.056	0.055	0.051	0.060	0.057	0.057	0.056	0.060	0.062	0.	0.065	0.083	
AV -	5.646	7.522	10.586	11.794	13.974	16.492	18.953	20.394	21.119	21.843	22.887	26.371	29.520	32.654	35.337	38.556	40.230	41.457	42.190	42.595	42.827	43.242	43.	44.032	44.990	
AV +	6.267	8.286	11.606	12.668	14.948	17.915	20.761	22.977	24.638	26.557	27.827	30.100	33.008	36.546	39.421	42.686	45.342	46.458	47.253	47.691	48.301	48.986	49.	50.197	51.010	

Appendix Table B.17. Individual growth parameters (L_∞, K and t_0), variances and variation coefficients for 70 individuals of *Oreochromis mossambicus hornorum* calculated after Doyle's data (pers. comm.) with Allen's (1966) method. Overall averages, variances and variation coefficients for each parameter are in the last lines.

	L_∞ (mm)	Var_{L_∞}	CV_{L_∞}	K	Var_K	CV_K	t_0 (week)	Var_{t_0}	CV_{t_0}	N
1	68.915	62.427	11.465	0.0488	1.03E-04	20.753	-0.191	0.249	260.891	25
2	92.980	223.161	16.066	0.0341	7.20E-05	24.863	-0.507	0.253	99.317	25
3	73.532	58.886	10.436	0.0382	4.34E-05	17.234	-0.918	0.161	43.773	25
4	93.148	589.966	26.076	0.0292	1.16E-04	36.917	-0.868	0.340	67.113	22
5	64.269	69.853	13.004	0.0500	1.44E-04	23.994	-0.306	0.356	195.171	25
6	96.429	752.825	28.454	0.0271	1.22E-04	40.769	-0.820	0.540	89.652	25
7	108.653	433.077	19.153	0.0270	5.44E-05	27.289	-0.658	0.229	72.731	25
8	78.817	294.868	21.787	0.0395	1.96E-04	35.443	-0.146	0.557	511.113	25
9	78.406	164.937	16.379	0.0406	1.22E-04	27.196	-0.338	0.361	178.002	25
10	117.403	1518.072	33.187	0.0250	1.30E-04	45.680	-0.321	0.511	222.626	25
11	81.680	143.041	14.642	0.0384	8.25E-05	23.679	-0.335	0.254	150.640	25
12.	86.716	187.067	15.772	0.0348	7.21E-05	24.381	-0.679	0.234	71.244	24
13	100.976	567.117	23.584	0.0284	9.45E-05	34.285	-0.783	0.403	81.062	25
14	111.181	1689.037	36.965	0.0253	1.64E-04	50.553	-0.820	0.575	92.434	23
15	82.825	336.453	22.146	0.0348	1.42E-04	34.326	-0.776	0.477	89.036	24
16	80.437	144.205	14.929	0.0328	5.79E-05	23.186	-1.105	0.251	45.359	25
17	136.309	8378.356	67.152	0.0184	2.38E-04	83.674	-0.718	0.785	123.503	22
18	84.666	205.065	16.914	0.0373	1.02E-04	27.116	-0.428	0.332	134.562	25
19	108.540	979.212	28.830	0.0227	8.01E-05	39.436	-1.277	0.440	51.975	25
20	78.486	150.762	15.644	0.0405	1.12E-04	26.138	-0.528	0.353	112.651	25
21	73.492	415.964	27.752	0.0357	2.52E-04	44.378	-0.881	0.967	111.642	25
22	72.947	75.676	11.925	0.0490	1.07E-04	21.091	0.339	0.217	-137.496	25
23	107.206	1478.739	35.870	0.0241	1.38E-04	48.775	-1.166	0.556	63.959	23
24	89.431	395.338	22.233	0.0304	1.03E-04	33.482	-1.109	0.470	61.824	25
25	85.420	427.928	24.217	0.0347	1.71E-04	37.730	-0.512	0.597	150.980	25
26	74.147	112.559	14.309	0.0384	8.15E-05	23.508	-0.728	0.285	73.298	25
27	95.326	656.199	26.873	0.0316	1.62E-04	40.305	-0.506	0.597	152.652	25
28	119.014	1823.742	35.883	0.0227	1.21E-04	48.525	-0.781	0.574	97.005	25
29	97.826	789.441	28.722	0.0253	1.04E-04	40.352	-0.983	0.499	71.852	25
30	96.112	482.635	22.858	0.0298	1.00E-04	33.611	-0.561	0.389	111.189	25
31	84.795	322.384	21.175	0.0298	8.81E-05	31.522	-0.979	0.389	63.728	25
32	144.479	14941.590	84.605	0.0160	2.75E-04	103.369	-1.238	1.127	85.733	22
33	77.176	197.598	18.214	0.0404	1.49E-04	30.178	-0.344	0.443	193.599	25
34	103.402	476.883	21.119	0.0277	7.14E-05	30.493	-0.834	0.313	67.070	25
35	115.324	1207.446	30.131	0.0240	9.99E-05	41.566	-0.879	0.475	78.426	25
36	123.201	1225.977	28.420	0.0217	6.93E-05	38.326	-1.209	0.380	50.983	25
37	176.566	19726.293	79.545	0.0133	1.64E-04	95.932	-1.324	1.085	78.661	25
38	88.417	397.464	22.548	0.0315	1.10E-04	33.323	-0.942	0.364	64.023	23
39	82.121	284.129	20.526	0.0360	1.35E-04	32.192	-0.681	0.428	96.008	24
40	167.533	6865.210	49.457	0.0158	9.33E-05	61.252	-0.893	0.520	80.778	25
41	74.333	149.499	16.449	0.0426	1.44E-04	28.104	-0.462	0.426	141.416	25
42	98.596	490.330	22.459	0.0296	9.59E-05	33.126	-0.759	0.397	83.025	25
43	71.366	131.906	16.093	0.0404	1.17E-04	26.779	-0.895	0.369	67.893	24
44	82.177	248.666	19.189	0.0373	1.32E-04	30.780	-0.453	0.430	144.791	25
45	65.620	29.333	8.253	0.0597	9.58E-05	16.394	0.233	0.166	174.651	25
46	107.812	1435.823	35.147	0.0232	1.23E-04	47.789	-1.161	0.572	65.159	24
47	65.666	46.497	10.384	0.0496	8.71E-05	18.806	-0.431	0.201	103.981	24
48	85.936	369.085	22.356	0.0318	1.17E-04	33.929	-0.772	0.465	88.345	25
49	74.762	94.693	13.016	0.0448	9.90E-05	22.197	-0.277	0.236	175.558	24
50	71.928	53.380	10.158	0.0445	6.16E-05	17.614	-0.295	0.167	138.758	25
51	118.267	605.433	20.805	0.0261	5.81E-05	29.157	-0.450	0.233	107.288	25
52	91.472	112.205	11.580	0.0343	3.82E-05	17.992	-0.555	0.136	66.429	25
53	96.551	347.258	19.301	0.0327	8.67E-05	28.510	-0.520	0.243	94.798	23
54	63.065	69.449	13.214	0.0497	1.43E-04	24.034	-0.496	0.337	116.933	24
55	121.493	1010.740	26.168	0.0248	7.99E-05	36.099	-0.502	0.334	115.132	25
56	74.243	100.578	13.508	0.0440	1.04E-04	23.198	-0.227	0.279	233.108	25
57	94.476	507.968	23.856	0.0290	1.01E-04	34.784	-0.630	0.408	101.431	25
58	80.471	269.766	20.411	0.0356	1.23E-04	31.137	-0.982	0.333	58.725	21
59	85.365	254.422	18.685	0.0370	1.15E-04	29.011	-0.555	0.304	99.272	23
60	139.677	2698.505	37.191	0.0194	8.77E-05	48.320	-0.907	0.458	74.626	25
61	100.677	448.223	21.029	0.0298	8.44E-05	30.828	-0.450	0.316	125.009	25
62	70.541	59.715	10.955	0.0485	9.29E-05	19.876	-0.307	0.236	158.338	25
63	87.470	212.172	16.653	0.0383	1.06E-04	26.841	-0.263	0.319	214.985	25
64	68.055	50.177	10.409	0.0567	1.31E-04	20.203	0.095	0.251	529.337	25
65	65.495	51.868	10.996	0.0537	1.29E-04	21.126	-0.294	0.297	185.123	25
66	84.385	128.257	13.421	0.0381	6.75E-05	21.580	-0.271	0.205	167.002	25
67	68.578	58.057	11.111	0.0481	9.32E-05	20.087	-0.333	0.241	147.466	25
68	65.948	30.943	8.435	0.0549	7.91E-05	16.203	-0.058	0.165	705.850	25
69	121.441	902.898	24.743	0.0251	7.36E-05	34.190	-0.410	0.297	132.862	25
70	78.754	79.283	11.306	0.0452	7.84E-05	19.572	-0.084	0.196	527.123	25
AV	92.470			0.0346			-0.603			
Var	558.626			1.08E-04			0.128			
CV	25.560			30.028			59.314			

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