

A Review of the ELEFAN System for Analysis of Length-Frequency Data in Fish and Aquatic Invertebrates*

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Abstract

Some aspects of the history and present role of length-based methods for the study of the growth, mortality and recruitment of fish and invertebrate stocks are reviewed. The recently-developed ELEFAN (Electronic Length Frequency Analysis) system of BASIC microcomputer programs is presented and some of its key features are discussed in detail.

Examples of the use of the ELEFAN system are provided; these examples are used to illustrate the need for further research on such length-based systems and to emphasize the need for adequate sampling.

Introduction

Fisheries research emerged at the turn of the century, mainly in countries bordering the North Atlantic (predominantly the North Sea area). This had the effect, among other things, that research on cod, herring and similar long-lived fish became paradigmatic for the field as a whole (Cushing 1983; Gulland 1983).

When fisheries research expanded after World War II to the developing countries of the Third World, many of the basic methods of "temperate" fisheries biology were not applicable or did not seem to be applicable to tropical fish (Menon 1953; Qasim 1973).

This is especially true of methods for aging individual fish, which, being based predominantly on "annuli" on scales, otoliths and other bony structures of fish, proved difficult to apply to tropical fish in which seasonal fluctuations of their environment are usually less marked than in temperate waters.

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Fisheries biologists working on tropical fish prior to Pannella's (1971) discovery of daily rings as an ubiquitous feature of tropical fish had to rely predominantly on length-frequency analyses to draw inferences on the growth of fish. Methods using length-frequency data to infer the growth patterns of fish can be traced to the work of Petersen (1891), who developed two basic techniques.

The first of these, the "Petersen method" (*sensu stricto*), consists of the analysis of *one sample at a time*, with different (relative) ages being attributed to the fish comprising the prominent modes of a sample (Fig. 1a).

Graphical, semi-graphical (Harding 1949; Cassie 1954; Tanaka 1956; Bhattacharya 1967) and computer-based methods (Abramson 1971; Yong and Skillman 1971) for the separation of single samples into size groups have been widely used, often with mixed results (Mathews 1974). All of these methods assume the component of the distributions investigated to be normally distributed, an assumption which has been shown not to apply in a number of cases where it has been put to test (see, e.g., Morgan, Part I, this vol.). The separation of length groups (even when computer-aided) and the attribution of ages to these length groups are two distinct steps; the latter is purely arbitrary when no additional information on recruitment periodicity is available and can be very misleading when two recruitment pulses occur per year as is common in the tropics (Pauly and Navaluna 1983), while only one is assumed or *vice versa*.

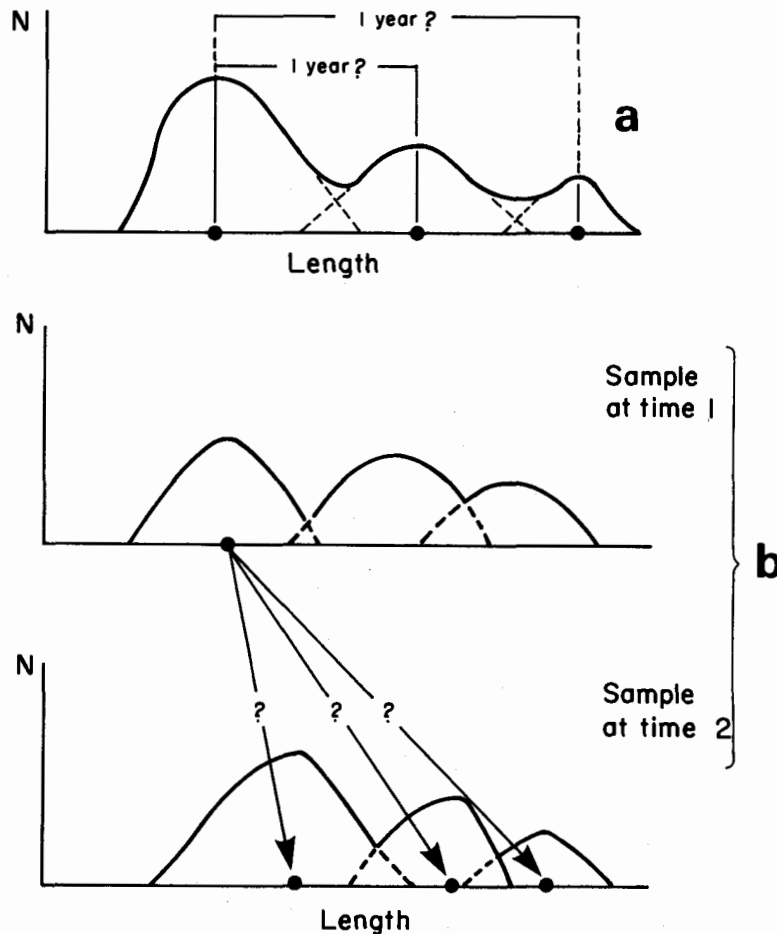


Fig. 1. Basic principles involved in traditional methods for length-frequency analysis (from Pauly et al. 1984). a) Application of the Petersen Method (*sensu stricto*) to a length-frequency sample. Note that the *time* separating peaks must be assumed, a difficult task in animals which may or may not spawn several times a year. b) Application of modal class progression analysis to a set of two samples obtained at known times. Note that the problem here is the proper identification of peaks to be interconnected, not that of time separating modes (as was the case in a).

The second of the techniques pioneered by Petersen (1891), now called “modal class progression analysis”, involves the use of several samples collected at different times, whose modes or the means of their component distributions are linked in a fashion thought to represent growth (Fig. 1b).

Various approaches exist for combining the two techniques. One, called the “integrated method” was proposed by Pauly (1978, 1980a, 1983a and see Fig. 2).

The Petersen method *sensu stricto* and the modal class progression analysis were used rather extensively in the beginning of the century in the North Atlantic area, notably by Fulton (1904) and other authors cited in Thompson (1942). Indeed, the latter was so convinced of the superiority of length-frequency analyses in growth studies that he rejected the results of Lea (e.g., Lea 1911,

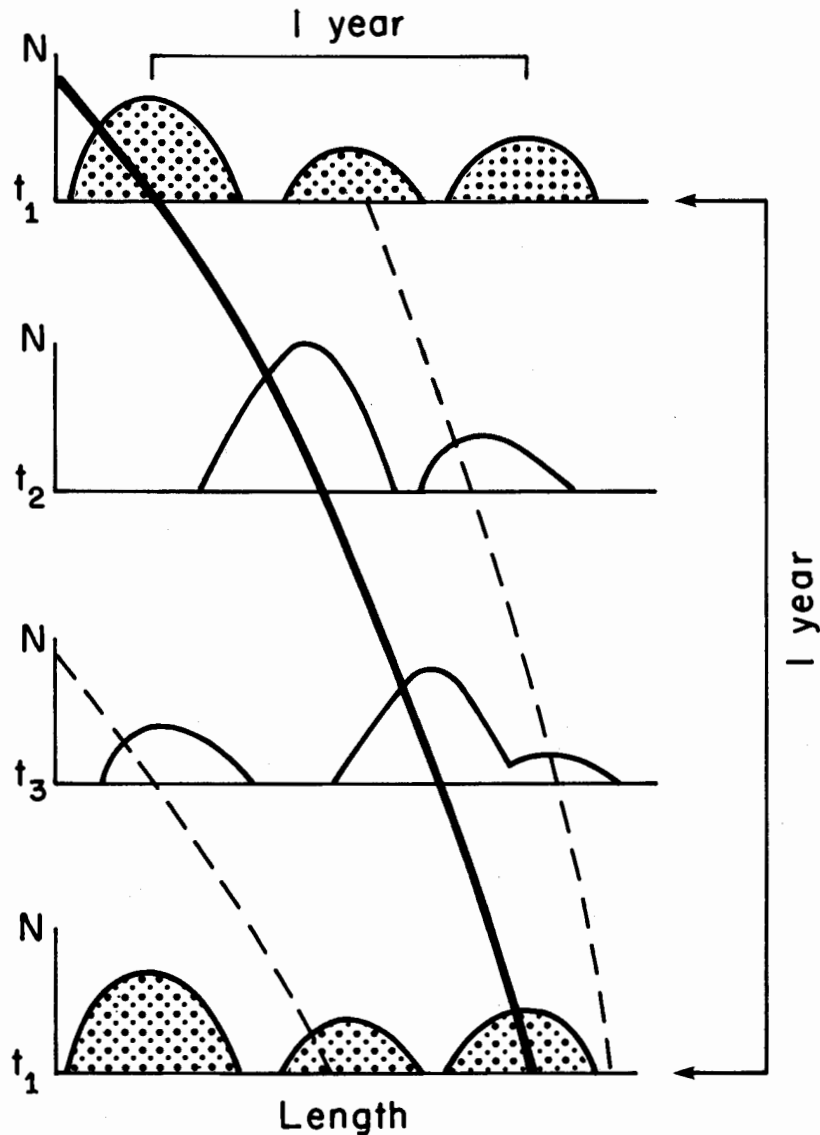


Fig. 2. An application of the ‘integrated method’ to a hypothetical set of length-frequency samples. Note that the attribution of a relative age to the third peak of sample t_1 is confirmed by the modal class progression, which suggests a growth curve passing through the major peaks of samples t_1 , t_2 , t_3 and through the third peak of sample t_1 repeated after one year (i.e., placed at the appropriate place on the time scale, after sample t_3). Thus a smooth growth curve can be traced which explains most of the peaks of a set of length-frequency samples, including those of earlier samples repeated once, twice or more along the time axis. A certain degree of reliability is achieved which could not be achieved by applying separately either of the two earlier methods (from Pauly et al. 1984).

1913) who, based on scale studies, was able to elucidate major aspects of the life history of North Sea herring. The conflict between D'Arcy Thompson (who was quite wrong) and Einer Lea delayed major advances in European fisheries research for at least a decade (Went 1972) and may be one reason why many contemporary fisheries biologists working in temperate waters are now reluctant to rely predominantly on length-frequency data when conducting growth studies.

The pendulum may have swung back too far, considering that most growth studies published in major journals now omit the *validation* of aging using independent methods or cross-validations (Beamish and McFarlane 1983).

While well-conducted growth studies based on otoliths, scales or other hard parts should generally lead to more precise inferences on growth than studies based on length frequencies only, length-based methods will remain extremely important, in the tropics at least, for the following reasons:

- (i) a number of important aquatic organisms, such as shrimp, cannot be aged individually, leaving one no choice but the use of length or of the more expensive tagging-recapture data;
- (ii) length-frequency sampling in fish markets is generally far cheaper than sampling say, for otoliths, because among other things, fish that are only measured need not be purchased; this is a factor limiting the work of fishery biologists in Southeast Asia; the phenomenon is also reported from Kuwait by Morgan (1983) and Mathews (Part I, this vol.);
- (iii) estimating growth from length-frequency data is far less work-intensive than using hard parts; when the resource under study consists of small, short-lived fish that can be aged only by counting daily rings, routine assessments based exclusively on age-structured models seem quite impractical, especially in a multispecies situation;
- (iv) large amounts of unanalyzed length-frequency data are available in most fisheries laboratories and often they are the only historical data available. Thus, for example, Ingles and Pauly (1982, 1984) were able to retrieve, from the files of various research institutions in the Philippines, length-frequency data covering more than one million measurements, from which inferences were drawn on the growth, mortality and recruitment of 56 species of Philippine fishes. Colleagues from various countries have had similar experiences and suggested that length-frequency data are probably the most underutilized type of information available on fish and other aquatic resources;
- (v) the "ages" used in many models are contrived because the process that is modelled is actually *size*-related. A number of biological and fishery-related processes involve sizes rather than ages such as predation (Ursin 1973), food conversion efficiency (Pauly 1981), gear (mesh) selection, target strength (in acoustic surveys), recruitment to fishing grounds and, quite importantly, marketability and price.

The ELEFAN System

INTRODUCTION TO THE SYSTEM

The ELEFAN system (*E*lectronic *L*ength *F*requency *A*nalysis) was developed at ICLARM in response to (1) the need for robust methods for analysis of length-frequency data; (2) the availability of cheap microcomputers. These two points provide some of the reasons why the system has found wide acceptance in developing countries, as was intended.

The system, as it now stands, consists of five programs, ELEFAN 0, I, II, III and IV.

ELEFAN 0 is used to create and modify length-frequency data files for use with the other four ELEFAN programs; the other ELEFAN programs have length-frequency data created by ELEFAN 0 as their main input (Fig. 3).

ELEFAN I is used to estimate the growth parameters of fish or invertebrates. The growth equation of which these parameters are estimated is a seasonally oscillating version of the von Bertalanffy Growth Formula (VBGF). ELEFAN I can thus be used to provide quantitative information on growth oscillations of fish and invertebrates, which can be correlated with oscillations of selected environmental parameters.

- ELEFAN II performs a variety of computations, of which the following are the main ones:
- estimation of total mortality (Z) and derived quantities from the straight, descending arm of a length-converted catch curve;
 - estimation of probabilities of capture by length and mean length at first capture (L_c) from the ascending, left arm of a length-converted catch curve;
 - expression of the seasonal changes in recruitment intensity in the form of a graphical “recruitment pattern” (which can be further subdivided into normally distributed recruitment pulses, suggestive of the number of spawning and/or recruitment seasons per year).

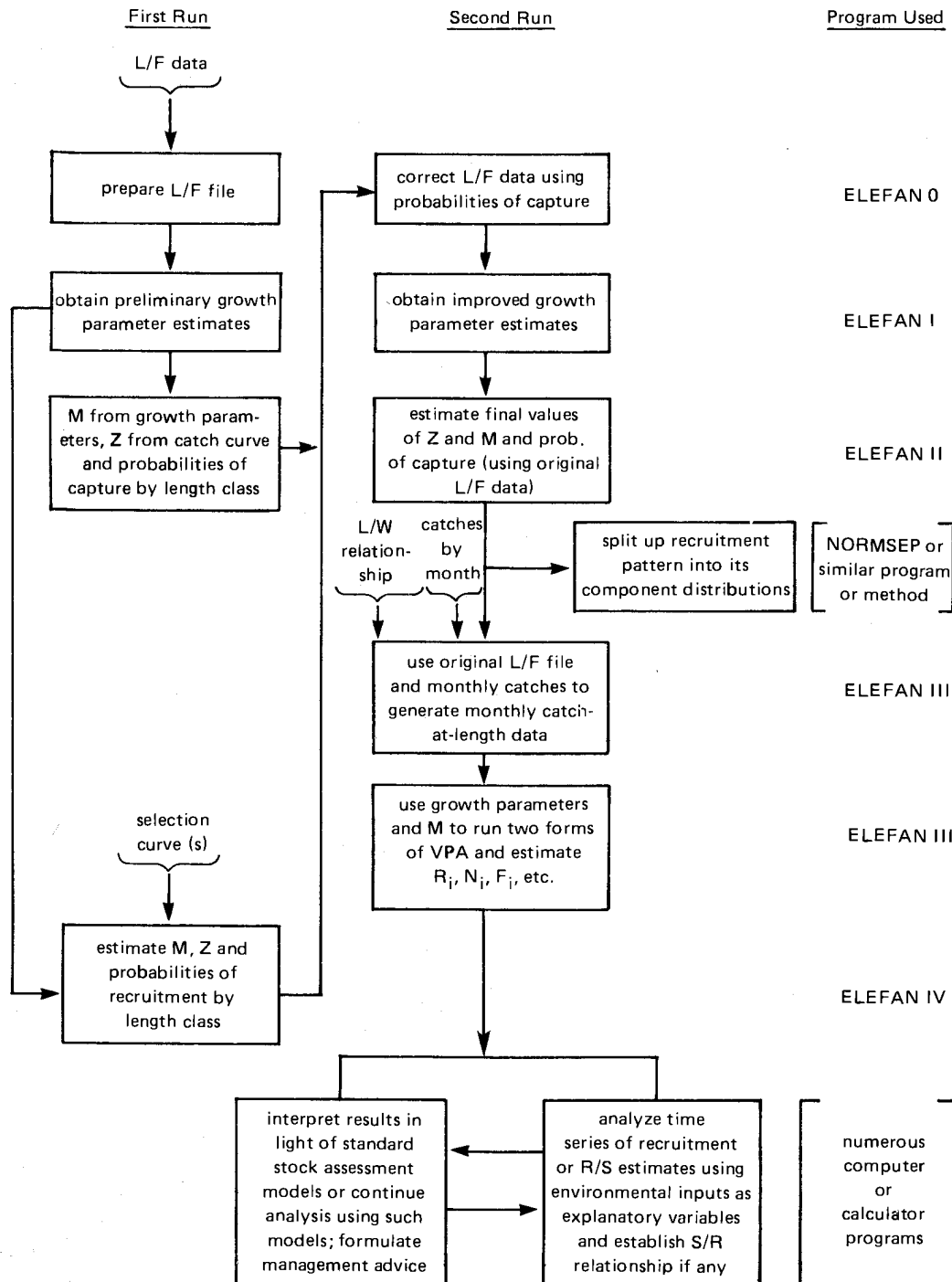


Fig. 3. Flowchart of the ELEFAN System, showing inputs, outputs and their subsequent analysis where appropriate. Definitions of parameters (Z , M , F , R , etc.) are given in the text, along with further details on system.

ELEFAN III incorporates three types of virtual population analysis (VPA), coded here VPA I, II and III.

VPA I estimates standing stock (in numbers) and fishing mortalities by time intervals (month, quarter, year, etc.). VPA II is used to estimate standing stock (in numbers) and fishing mortality by length class in a stock with stable age distribution, as can be simulated by combining data for several years. VPA III provides estimates of standing stock and fishing mortality by month and by length, which is achieved by "slicing" (pseudo-) cohorts through the catch-at-length data by means of a set of growth parameters. This approach assumes that little exchange occurs between the monthly "cohorts", which applies mainly in short-lived animals, such as anchovies or penaeid shrimps, for which the VPA III routine has been specifically designed.

ELEFAN IV is a program which, provided that gear selection is known (i.e., that probabilities of capture by length class are available), can be used to estimate M and probabilities of recruitment by length class from catch samples representative of an exploited population.

Table 1 gives a summary of the necessary inputs and of the output obtained from the ELEFAN programs. Further details are given below. As might be seen from Fig. 3, the overall system depends

Table 1. Inputs and outputs of the ELEFAN system for the analysis of length-frequency (L/F) and catch-at-length (C/L) data.

Input/output	ELEFAN program				
	0	I	II	III	IV
necessary inputs	L/F	L/F	L/F, growth parameters (excluding t_0)	L/F, monthly bulk catch, M, growth parameters (excluding t_0), length-weight relationship	L/F, selection curve, growth parameters (excluding t_0)
facultative inputs	selection curve	—	t_0 (a growth parameter)	C/L data computed externally can also be entered and used	—
output, given necessary inputs	files for use with ELEFAN I to IV	growth parameters (including seasonal growth)	Total, natural ^a and fishing mortalities, approximate selection curve, mean length at first capture, seasonal pattern of recruitment into the fishery.	Fishing mortality and population size by month and length group.	Total, natural ^a and fishing mortalities, recruitment curve.
output, given facultative inputs	L/F data corrected for selection effects (for use with ELEFAN I only)	—	seasonal pattern of recruitment with absolute time scale		

^a ELEFAN II and IV use different methods to estimate natural mortality; with ELEFAN II, M is estimated from equation (6), which is built into the program; with ELEFAN IV, M is estimated from the left, ascending side of a length-converted catch curve and the selection curve following a method devised by Munro (1984, and see text).

critically on the availability of growth parameters (mainly L_∞ and K of the VBGF) or of length-frequency data from which these parameters can be estimated. The length-frequency type of data, on the other hand, while having to be representative of the stock from which they were sampled need not have been corrected for the effects of gear selection or incomplete recruitment. This is so because it is possible to first obtain preliminary growth parameter estimates from length-frequency data not corrected for selection effects; then the available L/F data are corrected for such effects using ELEFAN 0; then growth parameters are re-estimated from the corrected L/F data (see below for an application example).

The Conceptual Basis of ELEFAN I

INTRODUCTION TO ELEFAN I

The heart of the ELEFAN system is ELEFAN I, the program for the estimation of growth parameters from length-frequency data. The first version of ELEFAN I, developed in 1978 by the author with the assistance of H. Timmermann of Kiel University, consisted of two basic steps:

- (i) separation of a number of samples into their normally distributed components using the NORMSEP program of Abramson (1971),
- (ii) identification of the growth parameters generating the growth curve which minimized the sum of the squared deviations from the means of the component distributions.

The program "worked". However, it required as input the number of broods (or age groups) in each sample, in other words, it required as *input* the very information which was wanted as an *output* (but see Sparre, Part I, this vol.; Rosenberg and Beddington, Part I, this vol.). Methods do exist to get around this problem (e.g., using the ENORMSEP program of Yong and Skillman (1971) or the method of Bhattacharya (1967) as interpreted by Pauly and Caddy (1985) to provide preliminary estimates of the number of broods in each sample). However, ELEFAN I incorporates an algorithm which bypasses this step, and which fits the growth curve to peaks defined independently of any assumed underlying distribution.

PRINCIPLES OF FITTING GROWTH CURVES

The method used in ELEFAN I to identify peaks and troughs in length-frequency histograms is a simple highpass filter, i.e., a running average which leads to definition of peaks as those parts of a length-frequency distribution that are above the corresponding running average and conversely for the troughs separating peaks (Fig. 4). The running average used in ELEFAN I is taken over five classes; analyses of the effect of the number of classes included in the running average on the results of ELEFAN I have been conducted only once, by K. Sainsbury, CSIRO (pers. comm.), who reported that the results are sensitive, but not strongly so, to changes in the number of classes included in the running average.

Fitting of the growth curves is performed by ELEFAN I through the following steps:

- calculate the maximum sum of points "available" in a (set of) length-frequency sample(s) (see Fig. 4c) ["available points" refers here to points which can possibly be "accumulated" by one single growth curve; see below]. This sum is termed "available sum of peaks" (ASP),
- "trace" through the (set of) length-frequency sample(s) sequentially arranged in time, for any arbitrary "seed" input of L_{∞} and K , a series of growth curves started from the base of each of the peaks, and projected backward and forward in time to meet all other samples of the sample set and/or the same sample repeated again and again,
- accumulate the "points" obtained by each growth curve when passing through peaks (positive points) or through the troughs separating peaks (negative points) (see Fig. 4b and 4c),
- select the curve which, by passing through most peaks and avoiding most troughs best "explains" the peaks in the (set of) sample(s) and therefore accumulates the largest number of points. This new sum is called "explained sum of peaks" (ESP).
- decrement or increment the "seeded" values of L_{∞} and K until the ratio ESP/ASP reaches a maximum, and gives the growth parameters corresponding to this optimum ratio.

THE GROWTH MODEL IN ELEFAN I

Although ELEFAN I could in principle be used to fit any type of growth curve, e.g., those proposed by Gompertz (1825) or Krüger (1964), only one type of growth curve, albeit a very versatile one, was incorporated into ELEFAN I. It is a seasonally oscillating version of the generalized von Bertalanffy Growth Function (VBGF) (*sensu* Pauly 1981) of the form

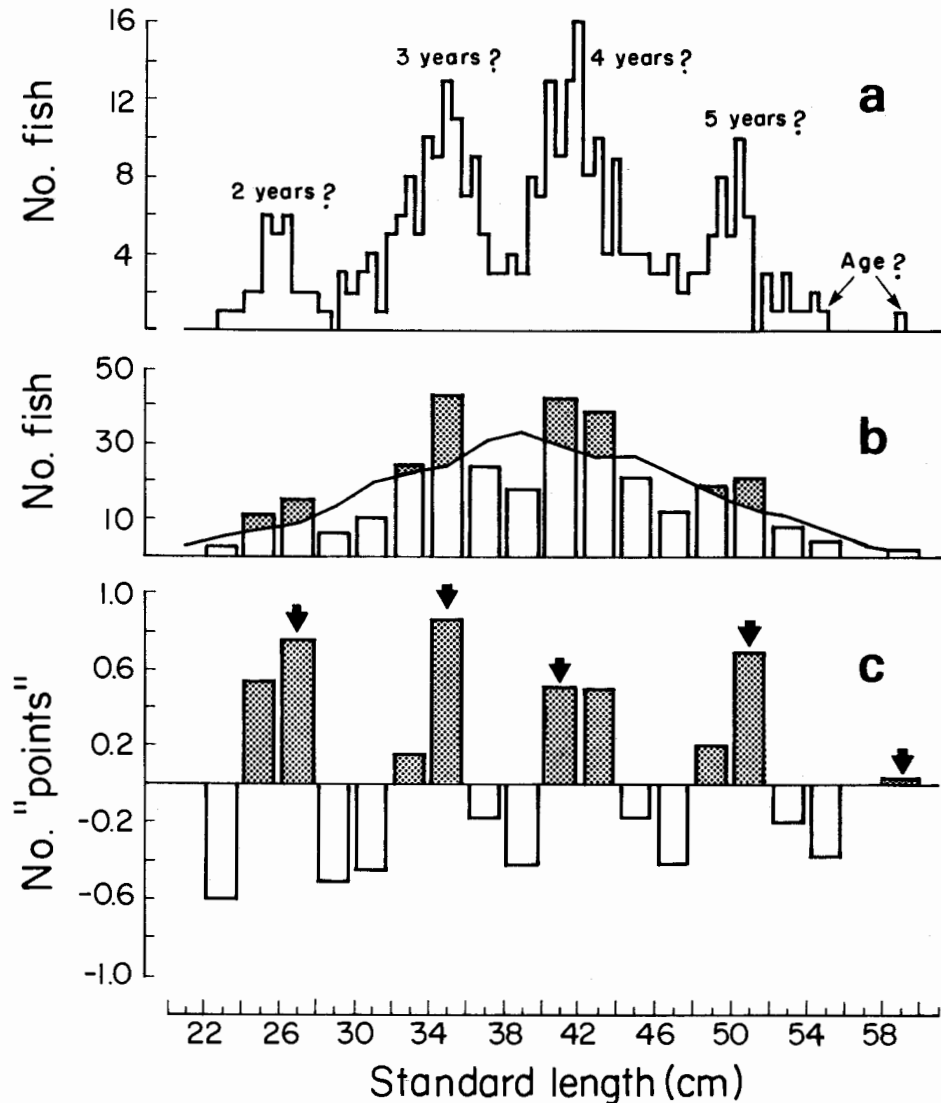


Fig. 4. Length-frequency data on coral trout (*Plectropomus leopardus*) caught near Heron Island (Great Barrier Reef, Australia) in October 1971. From Goeden (1978). a) Original data: the ages from Goeden, with question marks added; $N = 319$. Note inappropriately small class interval of 5 mm. b) Same data, replotted in 2-cm class intervals to smooth out small irregularities, showing running average frequencies (over 5 length classes) to emphasize peaks (shaded bars above running average) and intervening troughs. c) Same data as in b, after division of each frequency value by the corresponding running average frequency, subtraction of 1 from each of the resulting quotients and subsequent minor adjustments to remove potential sources of bias (see Pauly et al. 1980). Note that well-structured peaks have been allotted similar numbers of points, irrespective of the number of fish they represented. Arrows show the points used in the computation of ASP or "Available Sum of Peaks"; see also text (from Pauly and David 1981).

$$L_t = L_\infty \left(1 - e^{-KD(t-t_0)} + \frac{CKD}{2\pi} \sin 2\pi(t-t_s) \right) 1/D \quad \dots 1)$$

where L_t is the predicted length at age t

L_∞ is the asymptotic length, or the mean length the fish of a given stock would reach if they were to grow forever;

K is a growth constant ("stress factor" in Pauly 1981);

D is another growth constant ("surface factor" in Pauly 1981);

- C is a factor which expresses the amplitude of the growth oscillations (Fig. 5);
 t_o is the "age" the fish would have had at zero length if they had always grown in the manner predicted by the equation;
 t_s sets the beginning of sinusoidal growth oscillation with respect to $t = 0$ (Pauly and Gaschütz 1979).

Within ELEFAN I, equation (1) is used with two of the original parameters replaced by others; thus t_s is replaced by the Winter Point (WP), which designates the period of the year (expressed as a fraction of a year) when growth is slowest. In the northern hemisphere, WP is often found in the neighborhood of 0.2, i.e., in February, while WP often has a value of 0.7 in the southern hemisphere. The Winter Point is related to t_s through

$$t_s + 0.5 = WP \quad \dots 2)$$

The other parameter of equation (1) which requires comment is t_o . The significance of this parameter is often misunderstood. It may be described simply as a factor used to adjust a growth curve to an absolute age scale. Length-frequency data, by themselves, *never* allow the estimation of t_o and ELEFAN I is no exception. Within ELEFAN I a parameter called "T0" is used internally which fulfills the usual role of t_o (that is positioning the growth curve along the time axis). In early versions of ELEFAN I this "T0" was output, such as to enable users to draw their growth curves (e.g., White 1982). Some users have misunderstood this output for a real t_o , however, which resulted in their growth equation generating "erroneous" length-at-age data. To prevent further misunderstandings, therefore, the output of "T0" is now suppressed, and a routine has been built instead

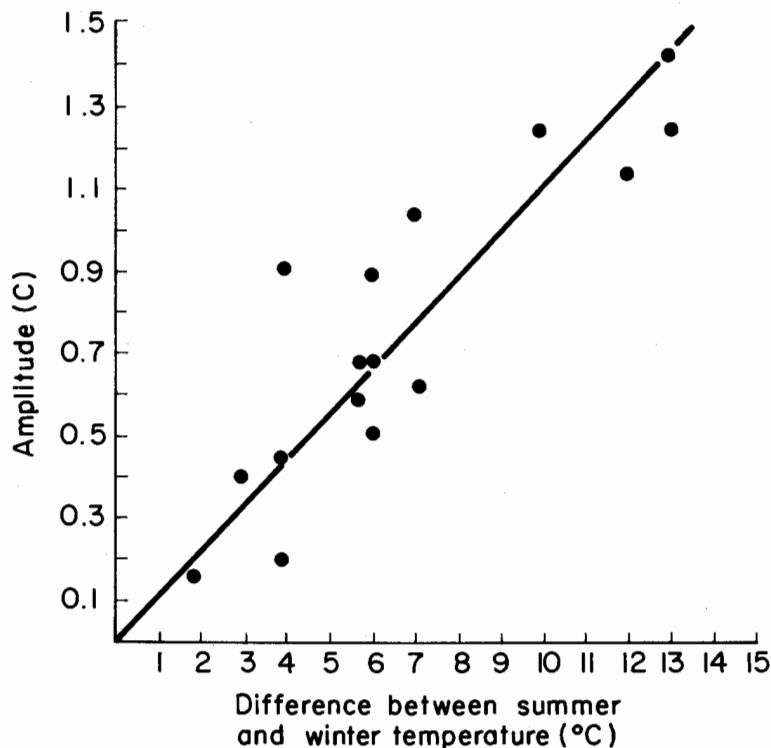


Fig. 5. Relationship between the amplitude (C) of seasonal growth oscillations in fish, penaeid shrimp and squid populations and the summer-winter temperature difference of their habitat (in $^{\circ}\text{C}$). The data points used here are documented in Pauly and Ingles (1981), Pauly (1982; 1985a), Pauly and Gaschütz (1979) and Pauly et al. (1984). Note that values of $C > 1$ do not imply that the animals in question shrink in the winter time, but rather that they undergo a period of non-growth (see Pauly and Gaschütz 1979).

into ELEFAN I which computes and outputs length in given months, and thus allows the drawing of growth curves.

The parameter C in equation (1) is dimensionless; when it has a value of zero, equation (1) becomes

$$L_t = L_\infty (1 - e^{-KD (t - t_o)})^{1/D} \quad \dots 3)$$

that is, the equation takes the form of the generalized VBGF (Pauly 1981) which has only one parameter more (D) than the original equation (von Bertalanffy 1938).

Equation (1) is defined such that growth ceases (at WP) only briefly, once a year, when $C = 1$. When $0 < C < 1$, growth oscillates seasonally, but is never completely halted. When $C > 1$, growth oscillates so strongly that the model predicts in winter a reduction of length. This latter case, it may be noted, should rarely happen in reality (as opposed to loss of weight). One paper referring to teleosts was thus found in which a significant decrease in length of 0.67 to 1.23% was reported after starvation (in captivity) for up to seven weeks (Nickelson and Larson 1974) which is unlikely to happen in nature. In most cases, therefore, values of $C > 1$ simply suggest sustained periods of nongrowth, such as may occur in cold freshwater habitats.

Extensive work with ELEFAN I and with other programs incorporating equation (1) has shown that C is generally correlated with the difference between mean monthly summer and winter water temperature, that is, with the range of temperature to which the fish of a given stock are exposed (Fig. 5). This rule may help in providing good "seed values" of C for use in ELEFAN I, although it must be restated here that C as well as WP and the parameter L_∞ and K of the VBGF are *outputs* of and not *inputs* for ELEFAN I.

The parameter D of equation (1) on the other hand probably cannot be estimated from length-frequency data and ELEFAN I alone. When $D = 1$, equation (3) becomes

$$L_t = L_\infty (1 - e^{-K (t - t_o)}) \quad \dots 4)$$

which means that it reduces to the "special" VBGF, which is the normal VBGF used in fisheries research.

When $D \neq 1$, equation (3), the generalized VBGF is actually a form of the curve proposed by Richards (1959), used to model the growth of fish and invertebrates by e.g., Mathisen and Olsen (1968) and Ebert (1980, 1981). While these authors estimated the fourth parameter (equivalent to D) of Richards' curve from size-at-age data, Pauly (1981, 1982) showed that D expresses the growth of fish gills as related to their body weight and also that D decreases with the maximum size that they can reach. Rough estimates of D can be obtained therefore, from

$$D = 3 \cdot [1 - (0.6742 + 0.03574 \cdot \log_{10} W_{\max})] \quad \dots 5)$$

where W_{\max} is the maximum weight (in grams) reached by the fish of a given stock. Equation (5) is built into ELEFAN I. However, it should be used, along with values of $D \neq 1$ only when the arguments leading to the generalized VBGF are understood and agreed with (see Pauly 1981).

The earlier version of ELEFAN I required estimated asymptotic length to be larger than the largest animal in the set of samples analyzed, or $L_\infty > L_{\max}$. This requirement has been removed from more recent versions of the program; some of the consequences are listed in Table 2.

THE PROBLEM OF MULTIPLE COHORTS

One question which seems to have caused a great deal of confusion among users of ELEFAN I, and indeed among fishery biologists generally, is the allegedly "continuous" spawning and recruitment of tropical fish and invertebrates. In fact, several colleagues suspect that it is impossible for

Table 2. Available options for definition in ELEFAN I of asymptotic length (L_{∞}) in relation to maximum length in samples (L_{\max}), with a partial list of consequences (based on pers. obs. and various contributions in this vol.).

Options	Problem(s) solved	Problem(s) created
L_{∞} must be $> L_{\max}$	“Age” and growth rate at L_{\max} are defined and hence VPA and catch curve can be used for <i>all</i> size groups; representation of growth curve still reasonable (because L_{∞} and K are inversely related)	Some available empirical equations for estimation of M (e.g., equation 6) and t_0 may produce biased estimates
$L_{\infty} \leq L_{\max}$ possible	L_{∞} and K estimates may be less biased; estimates of M and t_0 based on empirical equations (e.g., equation 6) may be improved	Another set of growth parameters must be used for length-structured VPA, and catch curve. (See also Jones, Part I, this vol., and Majkowski et al., Part II, this vol.)

any algorithm—including that built into ELEFAN I—to trace a single reliable growth curve through the jumble of modes generated by “continuous spawning”. However, consider the following:

- (i) continuous spawning in the sense of spawning with constant intensity throughout the year has never been demonstrated for any fish or aquatic invertebrate, i.e., cases of “continuous” spawning are actually cases where *some* females are reported in ripe conditions throughout the year, or *some* eggs can be sampled throughout the year. The bulk of the females, however, do spawn within identifiable seasons, even in the tropics (Qasim 1973; Weber 1976; Johannes 1978; Longhurst and Pauly 1987);
- (ii) recruitment can oscillate seasonally even if spawning is continuous. The oscillating transfer function between these two processes is also known as a “recruitment window” which opens only during certain parts of the year (Sharp 1980; Bakun et al. 1981);
- (iii) if recruitment into a population of fish or invertebrates were continuous (i.e., did not oscillate seasonally), length-frequency samples would simply not contain peaks and troughs.

For these reasons, length-frequency data obtained from fish or invertebrate stocks (unless they are collected with a highly selective gear) usually contain modes pertaining to one or two major cohorts per year, even when they are sampled from populations in which some females spawn throughout the year, such as by following a lunar/tidal periodicity (Johannes 1978).

When two cohorts occur per year, ELEFAN I will, if left to itself, fit a growth curve to the more prominent of these two cohorts. The parameters of a second growth curve can be fitted by selecting a prominent mode belonging to the second cohort, then letting ELEFAN I identify the best set of growth parameters for a curve forced through the selected mode.

DEALING WITH GEAR SELECTION

In simulation experiments constructed with perfect data, it has been observed by users at ICLARM and by others (P. Sparre, pers. comm.) that ELEFAN I recovers the growth parameters used to generate the length-frequency data (see Hampton and Majkowski, Part I, this vol.; Rosenberg and Beddington, Part I, this vol.). Real length-frequency data, however, are obtained from populations with unknown growth parameters by means of gears that often select for certain sizes, a feature which is often aggravated by the migrations and/or schooling habits of the fish themselves.

There are three approaches by which gear selection problems can be addressed in the context of the ELEFAN system, and each of them pertains to a different combination of gear type and structure of the length-frequency data as follows:

- (i) length-frequency data (a) collected with gill nets with single mesh size (or hooks of a single gap size), whose selection curve is not known and (b) consisting essentially of the same size group of fish, with few or no shifts of modes through time.
Solution: growth cannot be estimated using ELEFAN I.
- (ii) length-frequency data (a) obtained from catches of a fleet of gill nets of different mesh size or from trawl or purse seines or other similar gears whose selection curve is not known and (b) showing a wide variability in the position of modes.
Solution: preliminary estimates of growth parameters are obtained using ELEFAN I; then, using ELEFAN II, approximate probabilities of capture are computed by length for the gear(s) used in sampling the available length-frequency data. These probabilities are used with ELEFAN 0 to correct the available length-frequency data for selection effect. ELEFAN I is then reapplied to the corrected data to obtain improved estimates of the growth parameters (see Fig. 3 and third application example below).
- (iii) length-frequency data and gear as in (ii), and selection curves of gears available, as obtained from a selection experiment.
Solution: correct data for selection using appropriate routine in ELEFAN 0, then apply ELEFAN I to corrected data. Also, estimate M, Z and F and recruitment curve using ELEFAN IV.

Certain behavioral and/or life-history features of fish and invertebrates can also prevent length-frequency data sets from being truly representative of the population sampled. Such features are emigration from fishing grounds or strong growth dimorphism, the former leading to overestimation of total mortality and the latter to biased growth parameter estimates, among other things. It is necessary, when interpreting results obtained through ELEFAN I (or any other program of the ELEFAN system) to consider all known aspects of a fishery and of the resources upon which it rests, and to realize that this all-important step cannot be replaced by the user's guide, however detailed, of a computer program.

APPLICATIONS OF ELEFAN I

The ELEFAN I program has been rather widely disseminated since 1980 and a relatively large number of papers and reports have been published which relied predominantly or at least partly on this program. Table 3 gives details on some of these applications. It will be noted that they cover a wide range of animals, from cold temperate to tropical, and from invertebrates to teleost fishes. With only one exception, these applications have not involved fatal misinterpretation of the program features and output, and have helped their authors extract more out of their data than if they had used classical paper-and-pencil methods.

This is illustrated in the brief review below of typical applications of the ELEFAN I program as used by this author.

The first example presented here pertains to the shrimp *Penaeus kerathurus* and is based on length-frequency data published by Rodriguez (1977). As might be seen (Fig. 6), the seasonally oscillating growth curve fitted by ELEFAN I to the data at hand provides what appears to be a good fit. In fact, it appears necessary to reemphasize here that such a curve is derived by ELEFAN I *without* external input as to the age structure in the available length-frequency data.

The second example presented here, pertaining to the squid *Loligo pealei*, features ELEFAN I as an alternative to subjective paper-and-pencil methods, illustrated in Fig. 7a. The figure demonstrates how such methods can (and often must!) lead to erroneous interpretations:

- (i) the peaks linked by growth increments were selected in subjective fashion (also they were not linked by their bases as should be done);
- (ii) seasonal growth oscillations were not considered;
- (iii) no test was performed to determine whether the resulting growth increments identified led to an acceptable growth curve.

Table 3. Some examples of applications of ELEFAN I as of early 1985.^a

Species investigated	Area	Computer system/language	Reference
Molluscs			
<i>Asaphis deflorata</i> <i>Codakia orbicularis</i> "pearl oyster"	} Bahamas Kuwait	TRS-80 Model I/MBASIC TRS-80 Model I/MBASIC Hewlett-Packard 9845B/HPBASIC	Berg (pers. comm.), Berg and Atalo (1984) Almatar et al. (1984)
Crustaceans			
<i>Panulirus spp.</i> <i>Penaeus semisulcatus</i> <i>Metapenaeus dobsoni</i>	Galapagos Islands Kuwait off Cochin, India	n.a. Hewlett-Packard 9845B/HPBASIC n.a.	Reck (1983) Mathews et al. (Part I, this vol.) Silas et al. (1984)
Teleosteans			
<i>Gadus morhua</i> <i>Melanogrammus aeglefinus</i> <i>Merlangius merlangus</i> <i>Limanda limanda</i> <i>Clupea harengus</i>	} North Sea	PDP 10/FORTRAN V	Rohde (1982)
<i>Scomber japonicus</i> <i>Katsuwonus pelamis</i> <i>Katsuwonus pelamis</i> <i>Katsuwonus pelamis</i> <i>Thunnus albacares</i> <i>Thunnus albacares</i> <i>Pterocaeio pisang</i> <i>Stolephorus spp.</i> <i>Leiognathus spp.</i> <i>Otolithes ruber</i> <i>Hilsa kelee</i> <i>Decapterus russelli</i> <i>Epinephelus tauvina</i> <i>Pampus argenteus</i>	Peru Southern Philippines Western South Pacific Southern Philippines Western South Pacific Southern Philippines Central Philippines Papua New Guinea Manila Bay, Philippines Central Philippines } Mozambique } Kuwait	PDP10/FORTRAN V HP 85/87/HPBASIC n.a. TRS-80 Model III/MBASIC n.a. HP 85/87/HPBASIC TRS-80 Model I, III/MBASIC TRS-80 Model I, III/MBASIC TRS-80 Model I, III/MBASIC TRS-80 Model I, III/MBASIC Univac 1100/U-BASIC Hewlett-Packard 9845B/HPBASIC	Mendo (1983) White (1982) Brouard et al. (1984) Tandog (1984) Brouard et al. (1984) White (1982) Cabanban (1984a, 1984b) Dalzell (1983, 1984) Pagdilao (1982) Navaluna (1982) Gjøsaeter and Sousa (1983a, 1983b) Morgan (1983, 1985)

^aThis table does not include applications of ELEFAN I by the author (see text); "n.a." refers to "not available".

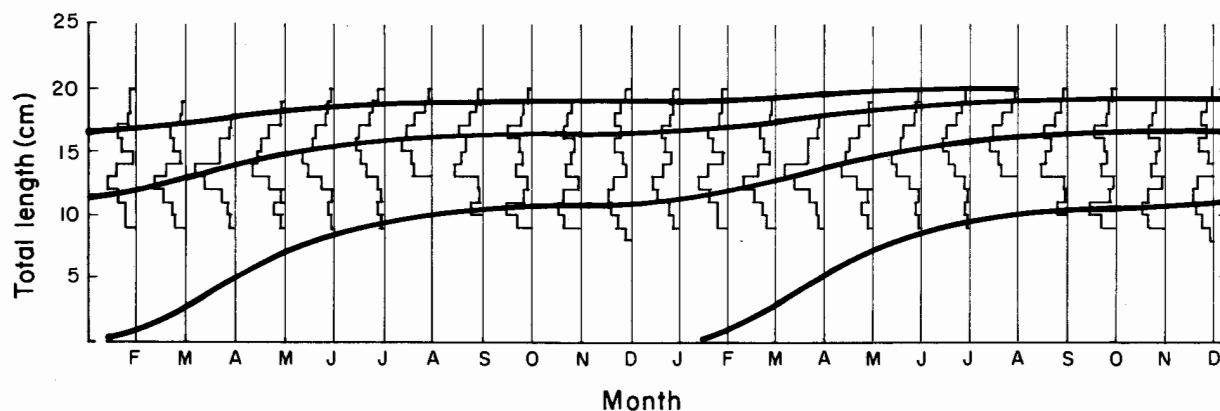


Fig. 6. Growth of females of the penaeid shrimp *Penaeus kerathurus* off Cadiz, Spain, based on length-frequency data in Rodriguez (1977) and the ELEFAN I program. The parameter estimates are: $L_{\infty} = 21.0$ (cm, total length), $K = 0.8$ (year^{-1}), $C = 0.9$. Winter Point = 0.8; the estimated ESP/ASP was 0.457. It is recalled that this growth curve was established by ELEFAN I without any external input as to the age-structure of the population or to the relative age(s) corresponding to any peak(s).

Figs. 7b and 7c show an alternative interpretation of the same data through ELEFAN I. The resulting growth curves have parameters consistent with those of other loliginid squids and the seasonal growth oscillations have an amplitude consistent with that of the oscillations of temperature in the Western Gulf of Mexico (see Pauly 1985a).

The third example pertains to the Peruvian anchoveta *Engraulis ringens* (Northern/Central stock) and demonstrates the impact of correcting length-frequency data for the effects of gear selection on growth parameter estimates, using an iterative approach first applied to *Rastrelliger brachysoma* in Burma (see Pauly and Sann Aung 1984), and illustrated in Fig. 8.

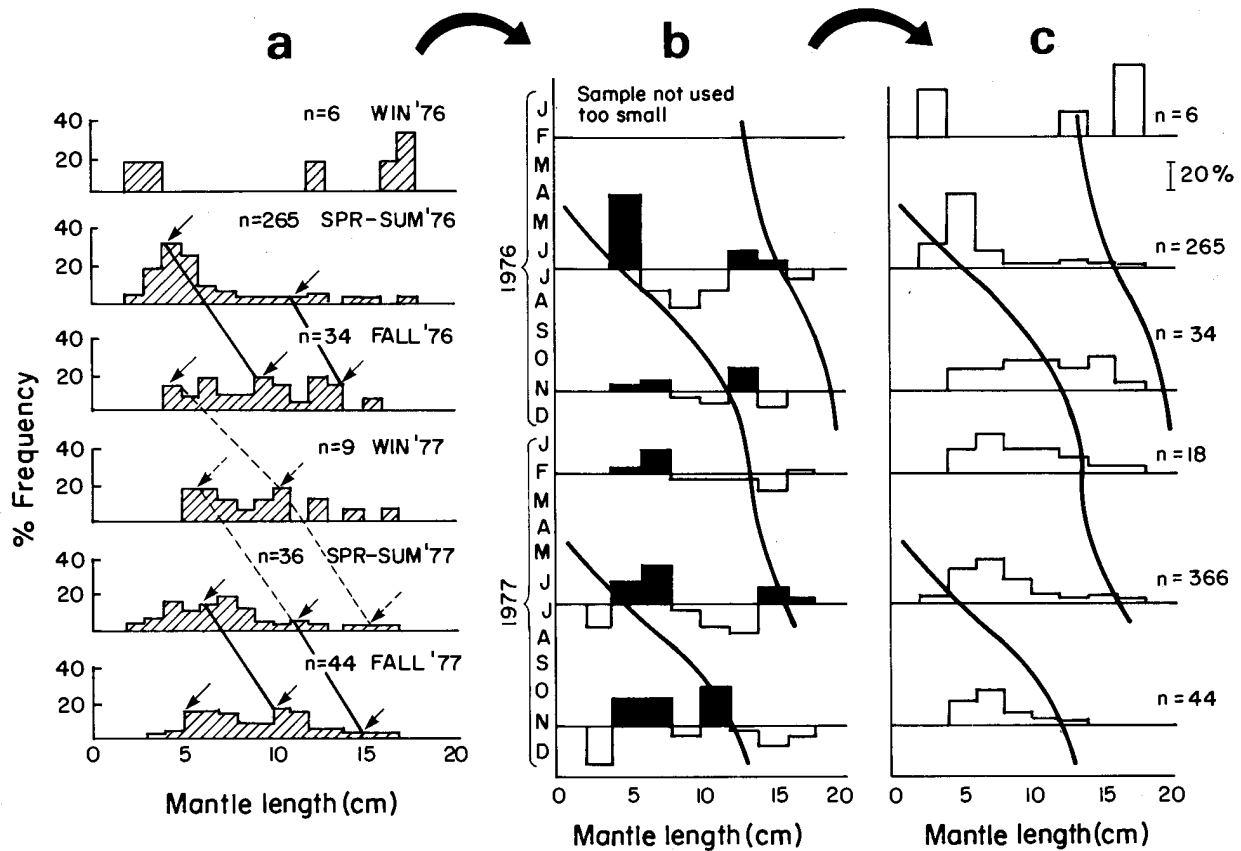


Fig. 7. Two interpretations of length-frequency data for *Loligo pealei* from the Western Gulf of Mexico (original length-frequency data from Hixon et al. 1981). a) Original interpretation (see text for comments). b) Restructured sample as created and used by ELEFAN I, with superimposed growth curves. (Note that original length-frequency data were regrouped into larger size classes for the ELEFAN I analysis). c) Length-frequency samples of Hixon et al. (1981), with superimposed growth curves as estimated using ELEFAN I (see text for comments).

In a first pass, initial estimates of L_{∞} and K obtained from the analysis of several sets of length-frequency data were averaged and used, along with length-frequency data from the two months of each year from 1953 to 1982 with the smallest fishes (i.e., the month at which recruits enter the stock) to derive a length-converted catch curve (Fig. 8b). A selection curve was then derived (Fig. 8c) which provided the probabilities of capture by means of which the original length-frequency data (here October 1963 to September 1964) were corrected. Figs. 8a and 8d show the restructured samples for the uncorrected and corrected data, respectively. As might be seen from Fig. 8d, the peaks related to the smaller fish here shifted downward, suggesting a more rapid growth (i.e., higher K) than would have been inferred from Fig. 8a.

Other applications of the ELEFAN I program to penaeid shrimps and Philippine and Indonesian teleosts are presented in Pauly et al. (1984), Ingles and Pauly (1984) and Dwiponggo et al. (1987).

One important methodological result of these various applications is the identification of a flaw in the original version of ELEFAN I, which counted peaks everytime they were "hit" by a growth curve, although each peak, representing one age group, ought to be hit only once by a well-fitting growth curve.

This flaw has now been corrected (see Pauly 1985b) and the points in a given run of positive values are counted once only when they are "hit", which completely eliminates the "drifting" of seeded K values towards unrealistically low values discussed in Pauly et al. (1980).

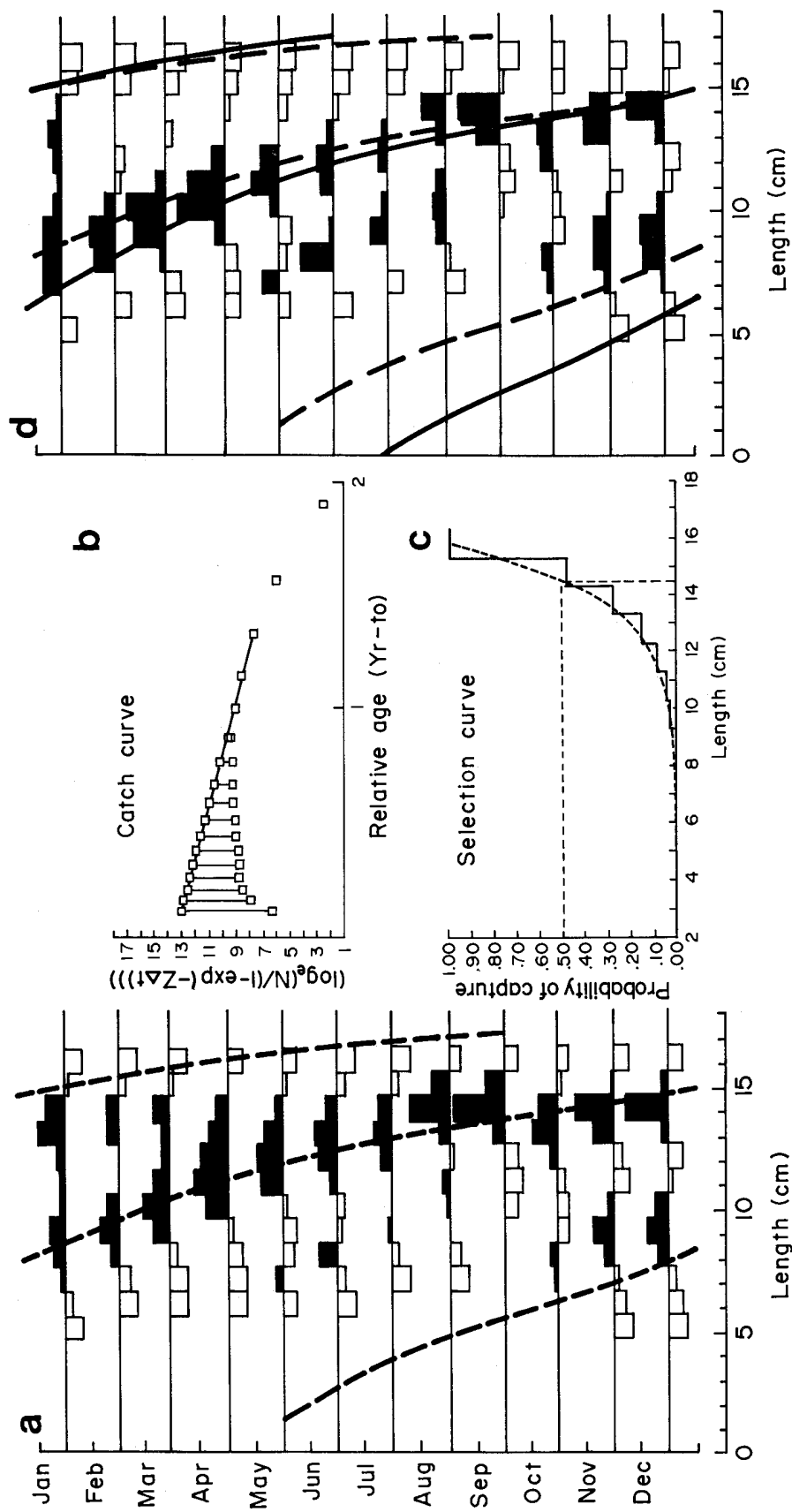


Fig. 8. Steps used to correct ELEFAN I estimates of growth parameters in Peruvian anchoveta, using the method of Pauly (1986). a) Estimation of a preliminary set of growth parameters for each cohort from 1954 to 1982 and averaging of the same. b) Derivation of a length-converted catch curve based on growth parameters estimated in (a) and an accumulated length-frequency file composed of data from the two months of each year containing the smallest fish (such as to obtain a correction for gear selection covering a size range as wide as possible; backward projection of catch curve to estimate number of fish that would have been caught, had it not been for gear selection and/or incomplete recruitment. c) Estimation of probabilities of capture from the ratio of fish caught to virtual fish, by length, and division of all original length-frequency data by the appropriate probabilities of capture, and d) Re-estimation of growth parameters. The correction leads to much improved estimates of the von Bertalanffy parameter K (Palomares et al. 1987 and see text).

ELEFAN II

INTRODUCTION TO ELEFAN II

ELEFAN II is a collection of routines which can be used, following the application of ELEFAN I to a given data set, to extract estimates of total, natural and fishing mortalities, information on the seasonality of recruitment and on probabilities of capture by length *without catch data being available or selection experiments having been conducted*. The program thus differs from ELEFAN III and IV in that it requires no inputs other than growth parameter estimates and length-frequency data.

LENGTH-CONVERTED CATCH CURVES

Total mortality in ELEFAN II is obtained via a length-converted catch curve, as described in Pauly (1980a, 1982, 1983a, 1983b, 1984a, 1984b). Important here is that, conceptually, catch curves based on length data are actually older than catch curves based on age composition data, with crude first estimates of mortality being obtained by Edser (1908), Heincke (1913) and Baranov (1918). Subsequent work has shown, however, that these early length-based catch curves were often biased and since then estimation of Z from catch curves has been based almost exclusively on age-structured catch curves (review in Ricker 1975).

Only recently have length-based catch curves been proposed which provide unbiased estimates of Z (Pauly 1980a; Gulland 1983). These "length-converted catch curves" have been shown to be far more versatile than age-structured catch curves, allowing for example, inferences to be drawn on the selection process of the gear used for sampling (Pauly 1984a, 1984b and see below) or, when used in conjunction with selection curves, the estimation of M from length samples (Munro 1984 and see below).

It is emphasized that the data used for catch curve estimates of Z must be representative of an equilibrium, or stable-age distribution. This problem, which was reviewed in great detail by Ricker (1975) in conjunction with age-structured catch curves, also occurs with length-converted catch curves, i.e., the samples used to construct the catch curve must reflect average conditions during which recruitment has varied little or randomly such that total mortality can be considered constant (see Hampton and Majkowski, Part I, this vol.).

One obvious way to simulate average conditions for construction of a length-converted catch curve is to pool length-frequency data from a longer period of time to smooth out recruitment pulses. Unfortunately, guidelines on the size of length-frequency samples suitable for the estimation of vital statistics are not presently available, although some rules of thumb have been suggested (see Munro 1982, Table 1 and Hoenig et al., Part II, this vol.). Research on this topic has been initiated by a number of authors and results should soon appear in the literature. For the time being, a routine has been incorporated into ELEFAN II which weights the samples by the square root of their size prior to combining them in a single sample for construction of the catch curve. This routine suggested by H. Lassen (pers. comm.) is based on (a) the need to use all the information incorporated in a given set of length-frequency samples (very small samples are not discarded as must be done with ELEFAN I) and (b) the fact that the standard error of means (i.e., of the mean lengths of fish in the various broods) is proportional to the square root of the number of fish used in the computation.

Obviously, schemes of sample weighting other than the dynamic range compression used here are feasible; two other approaches are incorporated in the ELEFAN system:

- (i) when catch-at-length data are available (rather than only length-frequency data), a single "sample" can be obtained by simply adding up the catches by length class. A routine provided in ELEFAN III (see below) can be used for such purpose;
- (ii) when sampling in certain periods is less intensive than in others, an adjustment can be conceived, as suggested by J.L. Munro (pers. comm.), such that those samples representing a longer period are given a larger weight than those obtained from periods represented

by many samples. Such an adjustment can be made using the appropriate routine in ELEFAN IV, where the "temporal weighting factors" are simply the distance (in time units) between a given sample and the nearest sample that precedes or succeeds it.

The ramifications of these various schemes to simulate equilibrium conditions have not been studied fully. Users of the ELEFAN system are invited to perform comparative studies of these and any other methods that might seem appropriate.

ESTIMATES OF M, F AND E

That the natural mortality (M) of fish and presumably also of invertebrates has a strong relationship with their growth parameters has been known at least since the landmark paper of Beverton and Holt (1959). Many fisheries biologists have used their empirical relationships to obtain preliminary estimates of M in cases where other approaches could not be used.

Pauly (1980b) extended the list of variables which can be used to predict M by showing that after accounting for the partial correlation between M and L_{∞} on one hand, and M and K on the other, M was strongly correlated with mean environmental temperature. These interrelationships were then expressed in the form of a multiple regression which has the form

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T \quad \dots 6)$$

and which can be used to obtain preliminary estimates of M, given L_{∞} (total length, in cm), T = mean environmental temperature (in °C) and K (expressed, as is done throughout the ELEFAN system, on an annual basis). Equation (6) is built into ELEFAN II. Readers interested in details of the derivation and of the appropriate use of this equation should consult Pauly (1980b) and Gulland (1984), respectively.

Once Z has been estimated from a catch curve and M from equation (6), preliminary estimates of F can be estimated by subtraction, i.e., $F = Z - M$, while the exploitation rate (E) is estimated from $E = F/Z$. This information is sufficient, given an estimate of mean size at first capture (L_c , see below) to perform a yield-per-recruit analysis using the method of Beverton and Holt (1966).

Alternatively, if it is accepted that the optimum value of F in a given exploited stock (F_{opt}) is about equal to M (Gulland 1971), we also have

$$E_{opt} = 0.5 = F_{opt}/(F_{opt} + M) \quad \dots 7)$$

Thus, using ELEFAN II as a follow-up to ELEFAN I, it is *in principle possible to assess whether or not a stock is overfished, based solely on length-frequency data obtained from that stock.*

It must be emphasized that this is so only *in principle*. In reality, the estimates of Z will be biased one way or the other by the sampling gear and by the behavior of the animals sampled. Also, the estimated value of M will be an overestimate or underestimate of the real rate of natural mortality prevailing in the specific stock under investigation (see Gulland 1984). Finally, equation (7) may not apply (as suggested by Francis 1974; Caddy and Csirke 1983; Beddington and Cooke 1983). Still, the principle holds, and may serve as a rationale for attempts to improve the quality of a length-based system, including data collection.

ESTIMATION OF PROBABILITIES OF CAPTURE

The estimation of probabilities of capture from the ascending, left arm of length-converted catch curves goes back to an approach developed in 1981 (see Pauly et al. 1984) and to a paper by Munro (1984) in which this approach was put on a more rigorous footing. Essentially, the method (see Fig. 9) consists of extrapolating the right, descending left side of a catch curve such that fish that "ought" to have been caught (had it not been for the effect of incomplete selection and/or recruitment) are added to the curve, with the ratio of those "expected" numbers to those that are actually caught being used to estimate probabilities of capture (Fig. 10). This approach, which is related to work done by Jensen (1982) and Hoydal et al. (1982), has been found (Anon. 1982) to

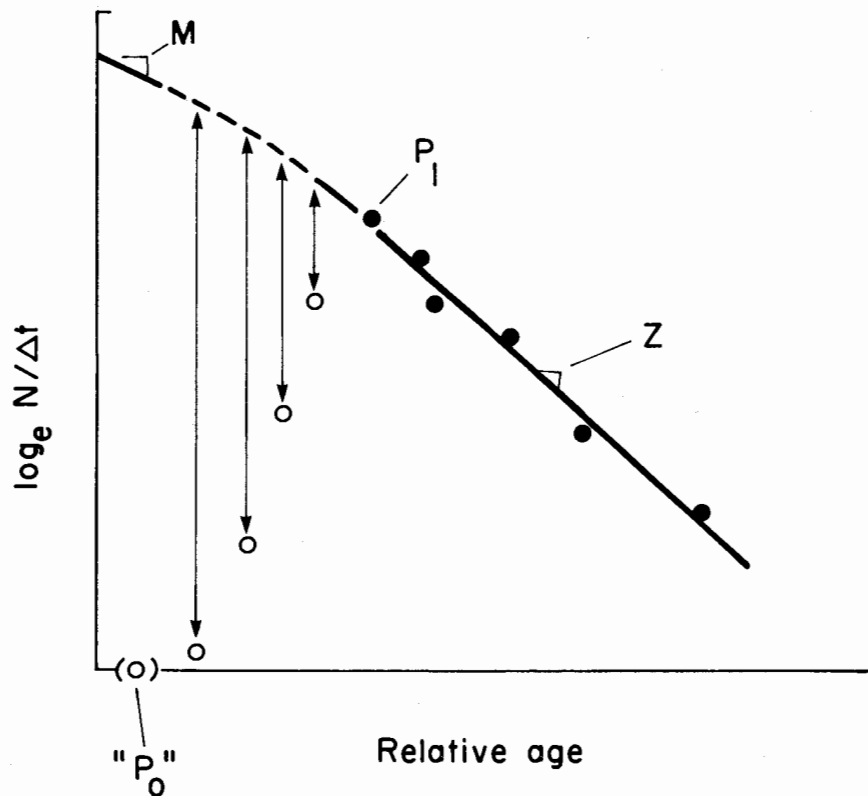


Fig. 9. Schematic representation of method to derive probabilities of capture from the left, ascending arm of a length-converted catch curve. P_1 identifies the first point from which on the probability of capture is 1, and hence the points to its right hand side which can be used for computation of Z . Point " P_0 " represents the first point (when going from right to left) where the probability of capture is 0; the mortality corresponding to this point is M , by definition. With M at P_0 , and Z at P_1 , intermediate mortalities can be interpolated, and population sizes reconstructed by backward extrapolation, starting from point P_1 . The probabilities of capture are then computed as the ratios between numbers caught and numbers expected. When $Z = M$, the method obviously requires no interpolation of mortalities and backward projection is done via the catch curve itself. The method also allows for mortality to be higher in small than in large animals; in this case, however, the value of M used is $> Z$.

provide reasonable estimates of mean size at first capture (L_c). Thus, it has the potential of making (some) mesh selection experiments superfluous, especially so when length-frequency data are available that include very small fish, i.e., covering the month(s) in which recruitment occur (M. Yahiaoui, pers. comm.).

RECRUITMENT PATTERNS

Since it is the pulsed nature of annual recruitment into a population which generates the peaks and troughs in length-frequency data, the converse also applies that, given a set of length-frequency data and growth parameters, one should be able to recover the pulsing of annual recruitment.

A routine which performs this task was incorporated into ELEFAN II; it produces what are here called "recruitment patterns", i.e., graphic descriptions of the recruitment process that generated the length-frequency data at hand.

The approach gives approximate results because recruitment patterns, while allowing statements on the number of recruitment pulses per year and on the relative importance of these pulses when compared to each other, are based on two assumptions which will hardly ever be met in reality:

- (i) all fish in a given data set grow according to the equation defined by the growth parameters used;
- (ii) one month out of twelve always has zero recruitment.

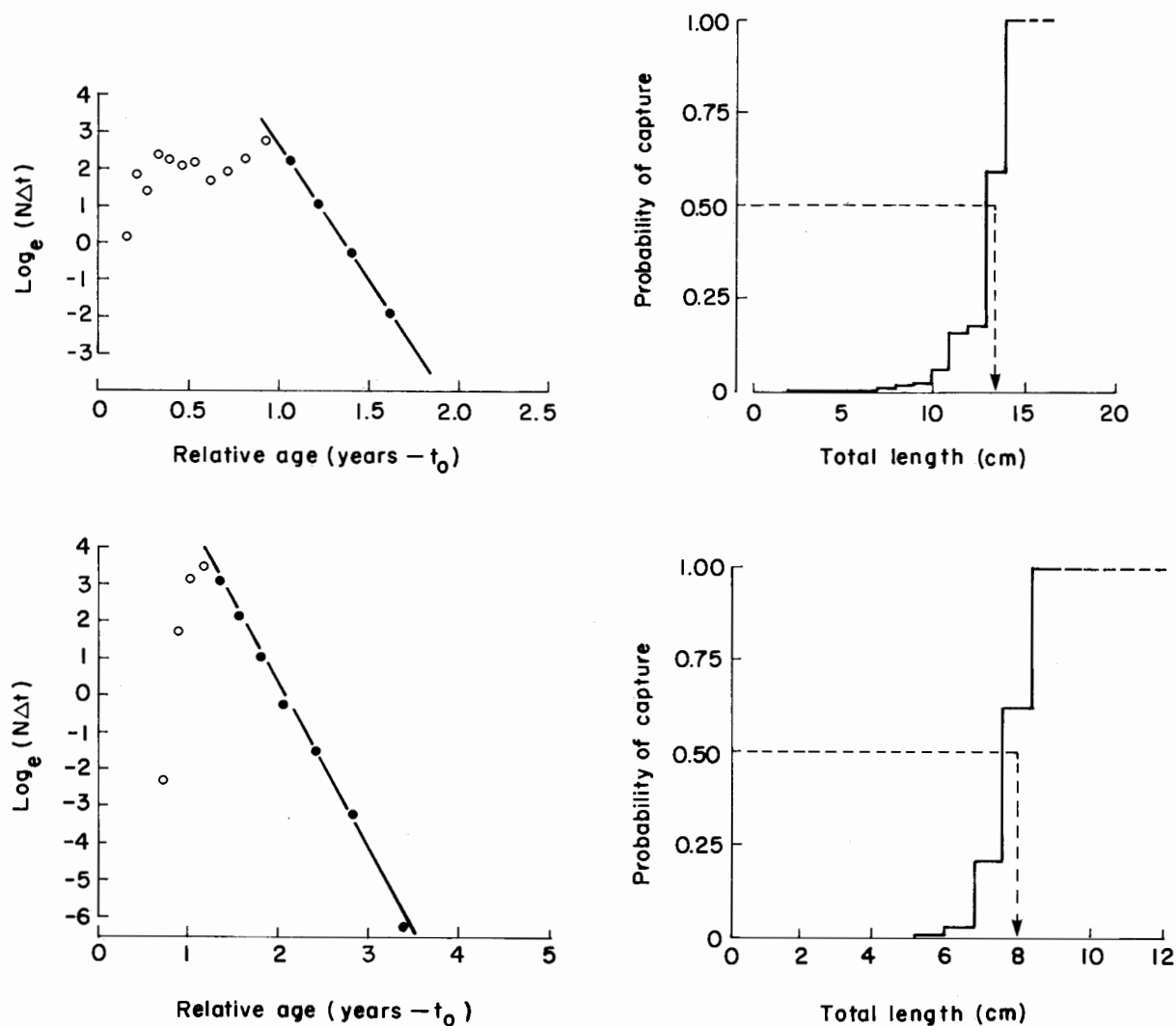


Fig. 10. Examples of length-converted catch curves and of the plots of probabilities of capture against length derived from them. Above: data on *Sardinella longiceps*, with estimated values of $Z = 5.77$ (year^{-1}) and $L_c = 13.5$ cm; below: data on *Pomadasys argyreus* with estimated values of $Z = 2.93$ (year^{-1}) and $L_c = 8.1$ cm (from Ingles and Pauly 1984).

The first of these two assumptions is common to all routines and programs in the ELEFAN system; its validity and overall impacts are discussed in Hampton and Majkowski (Part I, this vol.) and Rosenberg and Beddington (Part I, this vol.). As far as recruitment patterns are concerned, it should have relatively little impact on the result because the actual computation of these patterns assigns a very small role to older, larger fish and a larger role to smaller fish, whose deviations from the growth curve typical of the whole population are much smaller than in larger, older fish.

The second assumption will probably never be strictly met, because (a) there may be more than one month per year in which no recruits enter a stock (especially in temperate fishes and invertebrates) or because (b) some recruits may be entering a stock every month (especially in tropical fishes and invertebrates).

Fig. 11 shows the match between a recruitment pattern as obtained by means of ELEFAN II and the seasonal pattern of gonad maturity in a stock of Philippine groupers. This and a number of application examples (see Pauly and Navaluna 1983 and Fig. 12) suggest that recruitment patterns obtained by ELEFAN II do contain useful information, from which legitimate inferences on the dynamics of fish and invertebrate stocks can be drawn.

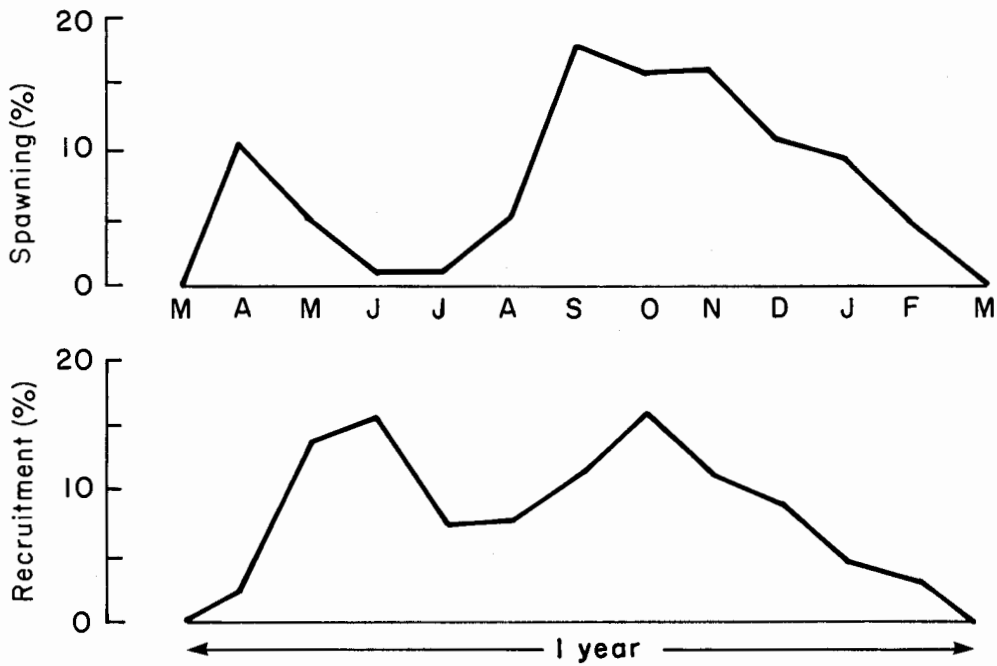


Fig. 11. Above: seasonal pattern of spawning condition in gonads for six-banded grouper (*Epinephelus sexfasciatus*) from the Visayan Sea, Philippines (data normalized by expressing as zero the month with lowest mean gonadal stage). Below: recruitment pattern in the same stock of fish. Note overall agreement of shape, suggestive of two spawning seasons and two recruitment pulses per year. Note however that absolute time scale of recruitment pattern is unknown. From Pauly and Ingles (1981).

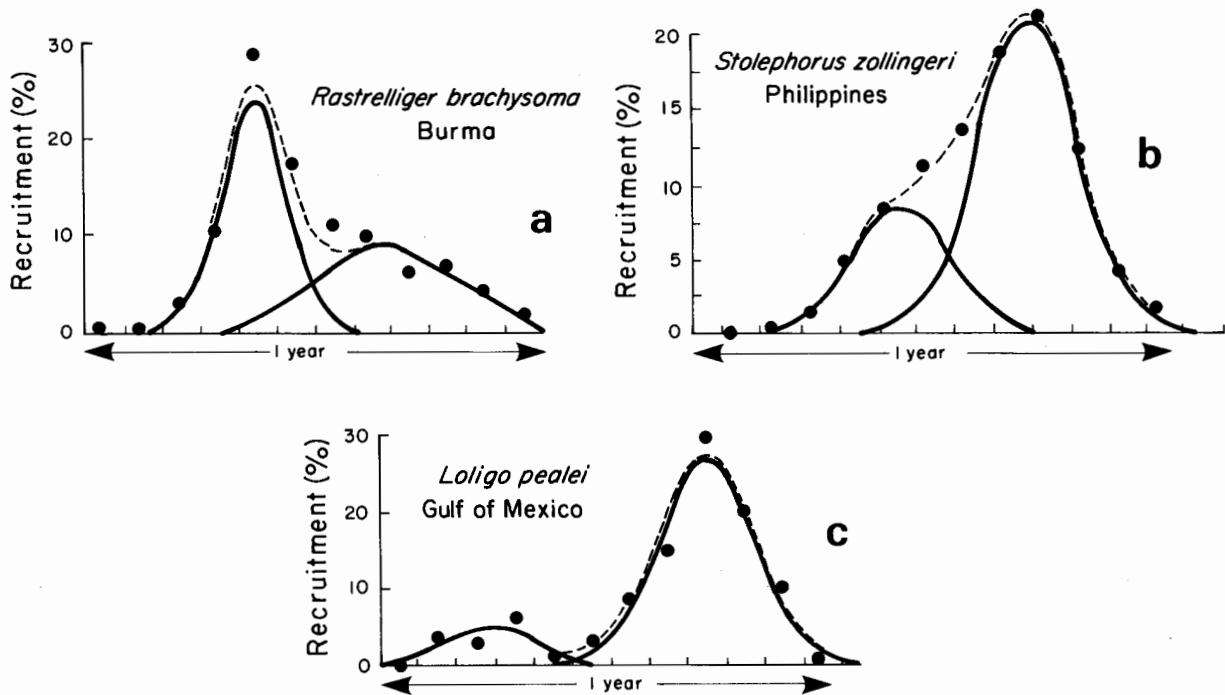


Fig. 12. Examples of recruitment patterns. a) *Rastrelliger brachysoma* (see also Fig. 9). b) *Stolephorus zollingeri* (from Pauly and Navaluna 1983). c) *Loligo pealei* (see also Fig. 8). Note in all three cases that annual recruitment consists of two pulses, one stronger than the other (see text).

ELEFAN III

INTRODUCTION TO ELEFAN III

ELEFAN III differs from ELEFAN I and II in that more data are needed to run the program than just length-frequency data. The added data which ELEFAN III requires are monthly catch data. Also, as is characteristic of most approaches based on Virtual Population Analysis (VPA), it is the *entire catch* from the whole stock which must be used, not only a part thereof.

ELEFAN III consists of four major routines:

- (i) the derivation of catch-at-length data from catch data and length-frequency samples;
- (ii) ordinary (age-structured) VPA, termed here VPA I;
- (iii) the VPA version of Jones' (1981) length cohort analysis, termed here VPA II;
- (iv) a routine to derive (pseudo-) cohorts from catch-at-length data, with subsequent application of age-structured VPA to these "cohorts"; this approach is termed VPA III.

The discussion below is limited to the principles behind these various routines and the reasons they were incorporated into ELEFAN III; further details on ELEFAN III are given in Morgan and Pauly, Part II, this vol.).

VIRTUAL POPULATION ANALYSIS (VPA I)

The principle behind VPA hinges around the concept of the "cohort", i.e., a group of fish or invertebrates born or hatched and recruited at more or less the same time and sharing throughout their lives a common pattern of exploitation by their predators and a fishery.

In most applications of VPA, the "exploitation" by predators is expressed by a single value of the rate of natural mortality M , which is assumed to apply throughout most of the life of the cohort (i.e., from the time the animals in the cohort are recruited to the time the cohort is decimated).

VPA, then, is a method to reconstruct a cohort (that is, to estimate the number of animals that were present in each age group or cohort) by using a value of M and the catch by the fishery in terms of numbers of each group in the cohort. The cohort is always reconstructed *backward* in time, starting with the last caught animals of a cohort (the "terminal catch"), which is used to obtain an approximation of the "terminal population" using a *guessed* value of the "terminal fishing mortality" exerted upon the "terminal population". Then, successive estimates of the population sizes are obtained for each age group by "adding" the catch of the fishery to a previous estimate of population size, to which the number of fish caught by predators has also been "added".

The method, which was formulated by Gulland (1965) has been reviewed by Pope (1972), Mesnil (1980) and Pauly (1984a). It is incorporated in ELEFAN III as VPA I to allow users of the ELEFAN system to acquaint themselves with VPA in its original form and to perform age-structured VPAs whenever the data for such analyses are available.

VPA II

Catch-at-length data differ from catch-at-age data (such as used in age-structured VPA or VPA I) in that they do not pertain—nor can readily be made to pertain—to a given cohort as defined above.

Still, versions of VPA can be run with catch-at-length data. Two very different versions of VPA are incorporated in ELEFAN III which use catch-at-length data. The first of these (VPA II) is conceived such that while it is not meant to help in reconstructing *any given cohort*, it can, given catch data covering the life span of several cohorts, reconstruct an *average* cohort. Thus, the results of VPA II are not structured in time; instead the population size and fishing mortalities which are typical outputs of VPAs are related to *sizes* (Table 4). These results, therefore cannot be used to manage a fishery in real time, nor to study temporal fluctuations of recruitment.

Table 4. Facsimile of printout of VPA II results obtained with the "Compleat ELEFAN" package. Data refer to West African hake *Merluccius merluccius* (see Morgan and Pauly, Part II, this vol.) for details on program used, and source of hake data.

VPA II results for MERSEN78

LENGTH CLASS (cm)	CATCHES	POPULATION	F. MORTALITY (1/year)
81.00- 87.00	46.00	92.00	0.2800
75.00- 81.00	16.00	145.79	0.1186
69.00- 75.00	96.00	304.23	0.4305
63.00- 69.00	181.00	599.59	0.4432
57.00- 63.00	228.00	1017.35	0.3364
51.00- 57.00	322.00	1626.46	0.3140
45.00- 51.00	653.00	2714.90	0.4199
39.00- 45.00	1871.00	5325.94	0.7079
33.00- 39.00	2959.00	9580.45	0.6395
27.00- 33.00	3889.00	15539.98	0.5259
21.00- 27.00	8134.00	26960.11	0.6931
15.00- 21.00	25227.00	58282.88	1.1588
9.00- 15.00	14463.00	82681.77	0.4076
3.00- 9.00	1823.00	96629.48	0.0421
Total catch :	59908	Natural mort. :	0.280 K : 0.100
Mean E :	0.620	Term. F. mort.:	0.280 Loo : 130 cm
Mean F :	0.457		

VPA III

VPA III was devised to combine the advantages of both VPA I and II, to allow catch-at-length data as input data and still to run an "age"-structured VPA, thus obtaining results that are structured both in size *and* in time (Fig. 13). This was achieved by assuming that all fish in the population under investigation have the same growth parameters, as is also assumed in the other ELEFAN programs. The effects of this assumption on the within-year estimates of recruitment variability have not been studied in detail. Exercises with the method suggest, however, that the VPA III routine of ELEFAN III generates monthly estimates of recruitment that are strongly autocorrelated (see also Mendelsohn and Mendo 1987) and which probably underestimate true within-year recruitment variability.

ELEFAN IV

THE ESTIMATION OF M

The ELEFAN IV program shares with ELEFAN III the feature of requiring more information than just length-frequency data. However, rather than requiring catch data, ELEFAN IV requires selection curves, that is, probabilities of capture by length with the gear used to obtain the available samples and of the commercial gear exploiting the stock under consideration (the two gears may be the same, in which case only one selection curve is required). Given these, and a set of length-frequency data covering a period of at least one year, ELEFAN IV can be used to estimate M and its standard error based on the method of Munro (1984) and also can be used to estimate probabilities of recruitment (by length) when recruitment overlaps with the selection range.

The basic idea behind this approach is illustrated in Fig. 14, which is based on constructed length data such as would be produced by a gill net fishery.

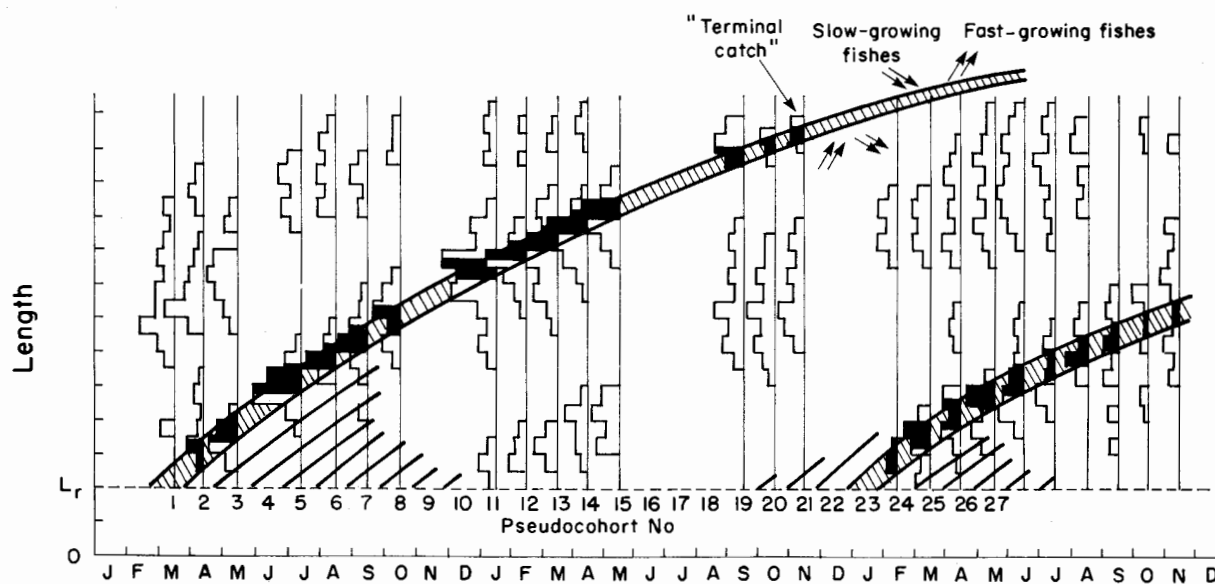


Fig. 13. Schematic representation of method to "slice" pseudo-cohorts from length-frequency data. As suggested by the arrows, the slow-growing fishes of a given pseudo-cohort will tend to be lost to preceding pseudo-cohorts and the fast-growing ones will tend to grow into the following pseudo-cohorts (from Pauly and Tsukayama 1983, redrawn).

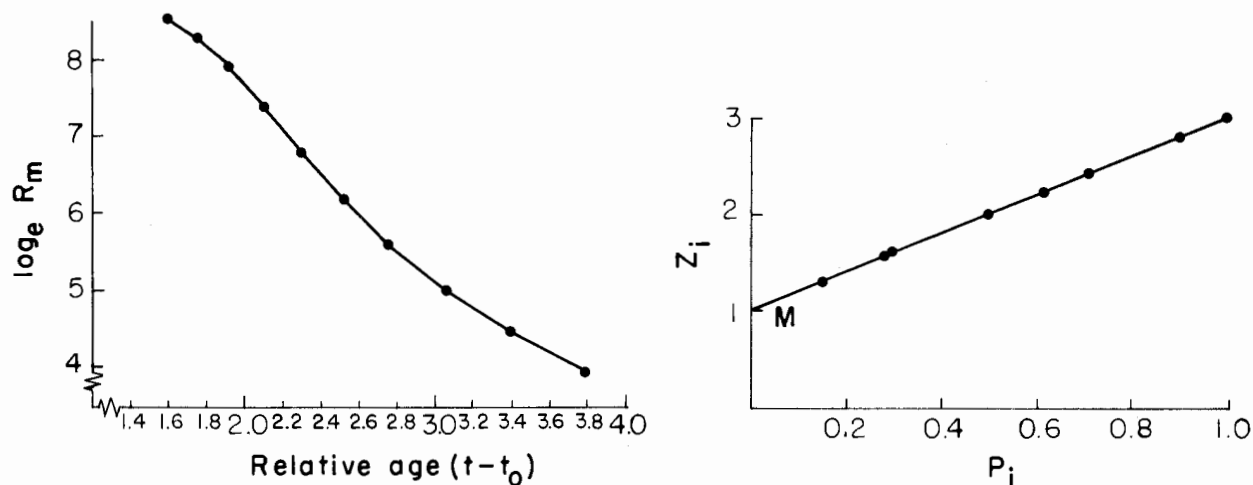


Fig. 14. Left: length-converted catch curve for fishes exploited by a single size of gill net in which the values of R_m (number caught/probability of capture) are plotted against relative age, and where the change of slope is due to mesh selectivity. Right: plot of Z_i (between successive length groups) against probability of capture P_i at the median between successive length groups. The intercept provides an estimate of M . (Both figures taken from Munro 1984).

The values of M estimated via ELEFAN IV differ from those obtained through ELEFAN II in that the former are estimated from the length-frequency data at hand, rather than from a built-in empirical equation. Therefore, it should be possible using ELEFAN IV to estimate values of M in different years, e.g., to follow the effects of predator removal on the natural mortality of a given stock of fish.

Users of ELEFAN IV will notice that this program differs also from ELEFAN II in being able to handle data that have been obtained using very selective gears, such as gill nets and hooks.

PRESENT PROBLEMS OF APPLICABILITY

Two problems must be mentioned which occur in conjunction with ELEFAN IV as it presently stands:

- (i) the method appears very sensitive to random variability in the length-frequency data used and reasonable estimates of M will generally be derived only from data that have been obtained through a rigorous, well-planned sampling design;
- (ii) because of (i) and because the idea behind ELEFAN IV has been presented only recently (in mid-1984), no data set has been found in the literature which could be used to illustrate the method, which therefore relies on a constructed example. It is therefore not certain that the approach implemented in ELEFAN IV will find wide applicability.

Discussion

The ELEFAN package of programs was developed to replace the suite of highly subjective "paper-and-pencil" methods which have been applied to length-frequency data since 1891.

Several, highly sophisticated alternatives to the ELEFAN package already exist (Sparre, Part I, this vol.; Pope and Yang, Part I, this vol.) or are presently being developed, and some may turn out to be more reliable, more robust and more rigorous than the ELEFAN programs (see Rosenberg and Beddington, Part I, this vol.).

Such programs, in order to become as useful and widespread as the ELEFAN package, will require, however, the following features:

- (i) they should run (e.g., in BASIC) on a widespread brand of microcomputer;
- (ii) their logic should be accessible to users without advanced degrees in mathematics and statistics;
- (iii) they should accommodate specific features of both temperate and tropical fishes and aquatic invertebrates, i.e.,
 - seasonally oscillating growth
 - one or two recruitment pulses per year;
- (iv) they should not require more than easy-to-obtain data such as length-frequency data with possibly some age or tagging data included (see below); particularly they should *not* require data to be weighted by C.P.U.E.;
- (v) they should accommodate data on incompletely selected and/or incompletely recruited animals.

One method which fulfills all these criteria and hence goes beyond the ELEFAN I program is that developed by Morgan (Part I, this vol.). There, the ELEFAN I approach is combined with an approach for the incorporation of age and/or tagging data such that a *single* set of growth parameters is estimated through simultaneous analysis of the combined length/age/tag returns data sets (or any paired combination thereof). It is probably approaches of this type, optimally using a variety of inputs, which will prevail in the future, since they would allow combining the wide availability of length-frequency data with the greater precision that can be obtained from age data.

Postscript: since this was written (in late 1984), numerous improvements of the ELEFAN approach—many of them based on inputs received from participants of this conference—were incorporated into ELEFAN I to IV. Only a few of these are discussed in this paper, which thus remains largely as originally presented; see Morgan and Pauly (Part II, this vol.) for a discussion of programs incorporating these changes and improvements.

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