Application to shrimp stocks of objective methods for the estimation of growth, mortality and recruitment-related parameters from length-frequency data (ELEFAN I and II)*

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Abstract

This paper presents applications to several shrimp stocks of a new, computer-based set of methods for the detailed analysis of length-frequency data. These applications include the objective estimation of growth parameters, including seasonally oscillating growth, and of total mortality as estimated from length-converted catch curves and from mean lengths. A method for obtaining estimates of natural mortality in shrimps is discussed. Methods are also presented by which inferences can be drawn on the pattern of mesh selection prevailing in the fishery from which the length-frequency data were obtained. Finally, a method is presented which helps assessment of the seasonality of the recruitment of young shrimps into a fishery.

Introduction

Reasonably reliable estimates of the growth and mortality parameters of exploited shrimp populations are essential for their proper management. However, as opposed to the situation prevailing in fish where periodic markings can be used for precise and accurate aging (Brothers, 1980), the growth of shrimps is very difficult to estimate reliably, because no calcareous structure survives the periodic shedding of the exoskleleton.

Methods that have been used involved the establishment of calibrating growth curves from shrimp grown in captivity (Zein-Eldin and Griffith 1969, Forster 1970), the study of the growth increments of tagged and recaptured shrimps (Lindner and Anderson 1956, Berry 1967), the detailed study of the growth increments associated with moultings (Forster, 1970) as well as the study of size-frequency data (Kutkuhn 1962, Boschi 1969). Unfortunately, none of these methods approaches the degree of reliability generally obtained in fish aging by means of their otoliths, scales or other bones. This applies to techniques for the analysis of length-frequency data, which have remained essentially unmodified since they were proposed

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by Petersen (1872), as well as to the analysis of mark-recapture data, which have been the principal method for estimation of growth parameters to date. The latter method is limited by the fact that many marks interfere with successful completion of moulting. Thus growth estimates, at best, are for short period–requiring considerable extrapolation–and at worst, do not represent growth because growth of shrimps occurs only at the time of moulting. Some marks have been developed that are retained through moulting (Neal, 1969) although they probably inhibit growth to some extent. Another problem is the effect of seasonal temperature oscillations, which until recently were difficult to account for (see Pauly and Ingles, 1981, and Nichols, this volume).

The methods introduced by Petersen (1892) for the analysis of length-frequency data consists of two approaches:

– the Petersen method (*sensu stricto*), and
– the *modal* class progression analysis.

The first of these approaches involves the attribution of assumed (relative) ages to the distinct peaks of a single, multi-peaked-length-frequency sample. The problems here are of identifying the 'real' peaks, representing distinct broods, and attributing the proper relative age to the peaks representing broods (*Fig 1*).
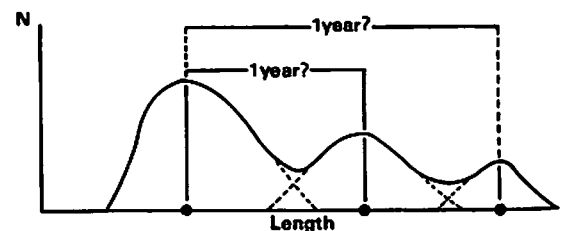

Fig 1 Application of the 'Petersen method' (*sensu stricto*) to a hypothetical length-frequency sample. Note that the *time* separating various peaks must be assumed, a difficult task in animals which may, or may not, spawn several times a year.

Much thought has been devoted to the problem of identifying 'real' peaks and splitting up single, multi-peaked samples into their constituent broods; milestones here include papers by Harding (1949), Cassie (1954), and Tanaka (1956), as well

as the computer programs NORMSEP (Tomlinson, 1971), and ENORMSEP (Young and Skillman, 1975). All of these methods assume the constituent broods of a multi-peaked sample to be normally distributed.

On the other hand, relatively little attention has generally been devoted to improving what George and Banerji (1964) called 'modal class progression analysis' in which individual peaks are followed through a time series of length-frequency samples.

The problem with this method (in addition to the separation of broods) is the identification of those peaks (=broods) that are to be connected with each other – by no means a trivial problem (see *Fig 2*). Thus, as in the case of *Fig 1*, it appears that the use of complex methods (*eg* ENORMSEP) for the separation of multipeaked samples into normally distributed subsets ('broods') and the subsequent computation of their means and standard deviations helps little in identifying the peaks that should be interconnected or, as in *Fig 1*, in defining the time separating peaks.
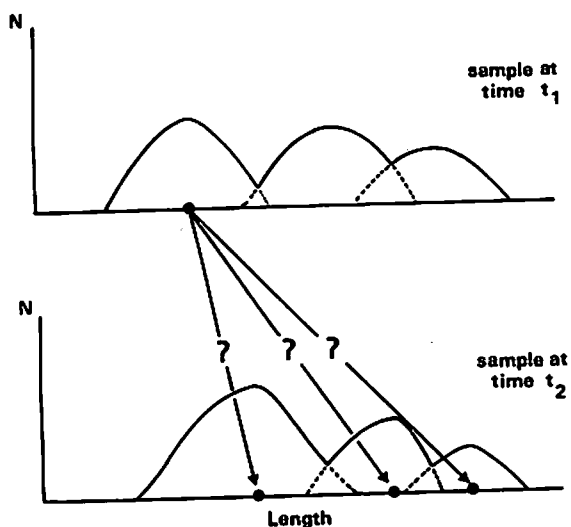
Fig 2 Application of the 'modal progression analysis' to a set of two samples obtained at known times (t_1, t_2). Note that the problem is the proper identification of peaks to be interconnected, and not the problem of time (as was the case in Fig. 1).

Pauly (1978, 1983) suggested a method involving an explicit criterion by which the 'Petersen method' and the 'modal class progression analysis' can be used to validate each other (*Fig 3*). This method, called 'integrated method', although it represents an improvement over the separate use of the two earlier approaches, is still subjective in that different workers can obtain different results from the same set of data.

In this paper, the applicability to shrimp stocks

of a set of new methods for the detailed analysis of length-frequency data is demonstrated. Also, it is shown that the new methods allow for the extraction from the length-frequency data available of a large amount of information on the biology of shrimps, information which normally is embedded in any set of length-frequency data but cannot be extracted by the methods used to date. All rates (growth, mortality) discussed in this paper are put on an annual basis, unless mentioned otherwise.
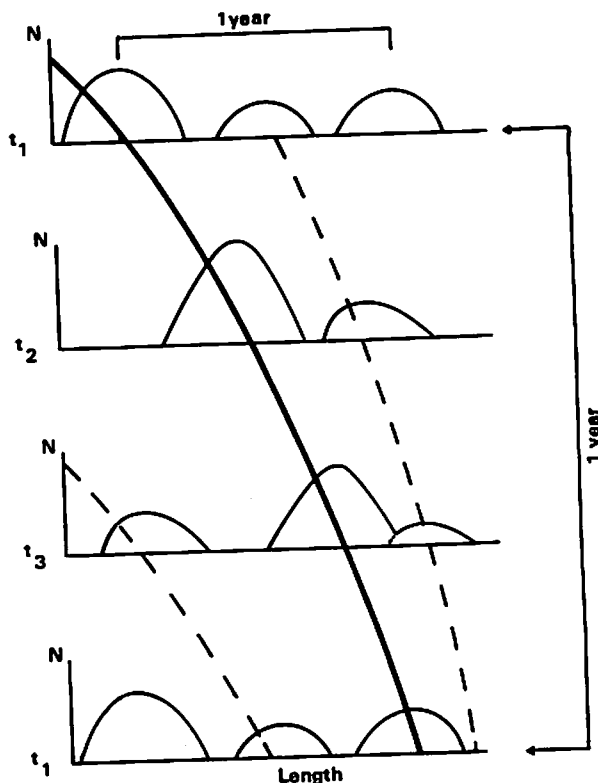
Fig 3 An application of the 'integrated method' to a hypothetical set of length-frequency samples. Note that the attribution of a relative age to the third peak of sample t_1 is confirmed by the modal class progression, which suggests a growth curve passing through the major peaks of samples t_1, t_2, t_3 and through the third peak of sample t_1 *repeated* after one year (*ie*, 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 either of the two earlier methods.

Methods

Estimation of growth parameters

The method presented here for the extraction of growth parameters from length-frequency data may be considered an extension of the integrated method, yet is wholly objective, *ie*, allows for fully

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reproducible results (Pauly and David, 1980, 1981). The method, which is called ELEFAN I (*E*lectronic *LE*ngth *F*requency *AN*alysis) involves the following steps:

- identify peaks, and the troughs separating peaks in terms of the deviation of each length class frequency from the corresponding running average frequency (peaks are positive, troughs negative deviations)–note that this definition involves no assumption of normality for the distribution of the broods in each sample,
- attribute to each positive deviation a number of positive points, proportional to its deviation from the running average and attribute, similarly, a certain number of negative points to each trough,
- identify the set of growth parameters, which, by generating a growth curve which passes through a maximum number of peaks and avoiding troughs as much as possible, accumulates the largest number of points, termed 'Explained Sum of Peaks' or ESP, and
- divide the ESP by the sum of points 'available' in a set of length-frequency samples, *ie*, by the 'Available Sum of Peaks' (ASP) to obtain an estimator of the goodness of fit, the ESP/ASP ratio, which generally ranges between 0 and 1 may be considered analogous to a coefficient of determination (r^2).

Figure 4 depicts a set of restructured length-frequency samples of penaeid shrimps, showing the peaks and troughs as defined above, together with the best growth curve estimated from the data

set. This procedure assumes that:

- the length-frequency data are representative of the population,
- the growth patterns are repeated from year to year,
- the von Bertalanffy Growth Formula (VBGF) describes the mean growth in the population, and
- all shrimps in the samples have the same growth parameters, *ie*, all differences in size reflect difference in age.

Of these four assumptions, the fourth is the least realistic, since it is known that shrimps of different lengths can have the same age. However, the error involved by making this (essential) assumption is probably small. The procedure for ELEFAN I is fully described in Pauly *et al* (1980).

An aspect of ELEFAN I which adds considerably to the versatility of the program is that the growth equation used for generating the growth curves is a seasonally oscillating version of the VBGF which has the form

$$L_t = L_\infty(1 - e^{-[K(t-t_0)+C(K/2\pi)\sin 2\pi(t-t_s)]}) \quad (1)$$

where L_t is the length at age t, L_∞ is the length the fish would reach if they were to grow indefinitely, and t_0 is the computed length at age zero while t_s and C are parameters which control seasonal growth oscillations of period one year; t_s is the start of a sinusoid growth oscillation with respect to $t = 0$ and C is a parameter exposing the intensity of the seasonal growth oscillation. C has values generally ranging from zero (when there are no oscillations) to a value of unity (in which case dL/dt has one
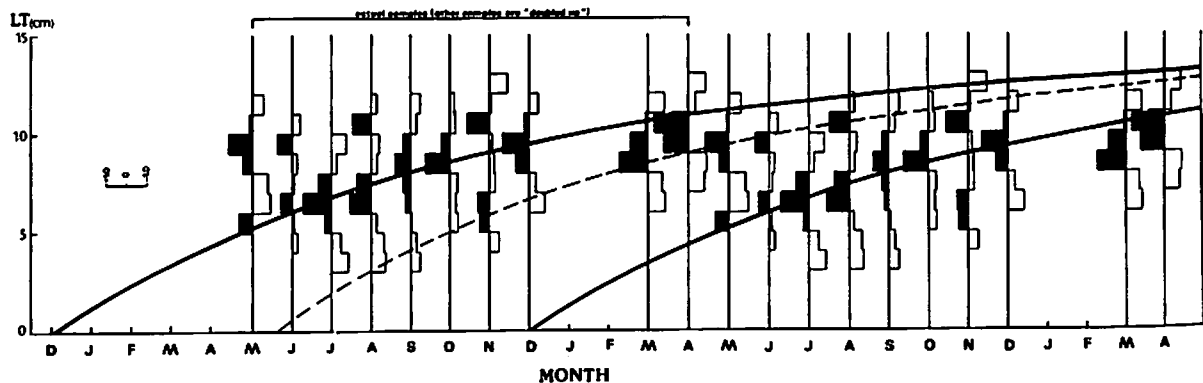

Fig 4 Growth curves estimated by ELEFAN I from a 'restructured' set of shrimp length-frequency data (stock #6, see *Table 1*). Note that 'peaks' are here expressed as positive, and troughs as negative points. The growth curve (a von Bertalanffy curve) as fitted by ELEFAN I goes through as many peaks as possible, while avoiding as many troughs as possible resulting in ESP/ASP = 0·418 for the main curve (solid line) and ESP/ASP = 0·209 for the secondary curve (dotted line), *ie* a sum of 62·7% of the available peaks are expressed by the curves. It will be noted that, as in *Fig 3*, there is a multiple use of some samples, to allow for a better visualization of the shape of the growth curves, and of the peaks they explain.

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zero value per year). Equation (1) can be reduced to the form of the VBGF commonly used in fishery biology by setting $C = 0$, ie,

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (2)$$

The seasonally oscillating growth model built into ELEFAN I is a feature which is essential to the use of this program in conjunction with sets of data pertaining to temperate or subtropical shrimp stock, as will be shown below.

Finally, a parameter, the Winter Point (WP) is defined as

$$WP = t_s + 0 \cdot 5 \qquad (3)$$

or as the time of the year (expressed as a decimal fraction) where growth is slowest ie, in 'winter' (Pauly and Gaschütz, 1979).

Estimation of total mortality from length-frequency samples

Although the estimation of total mortality based on a 'catch curve' was used by Edser (1908) in conjunction with a length-frequency sample, the catch-curve method of estimating total mortality is generally applied to animals that have been aged, using the relationship

$$\log_e N = a + bt \qquad (4)$$

where N is the number of fully recruited and vulnerable animals of a given age t, and $-b = Z$, the exponential rate of total mortality, as commonly used in fishery biology (see Robson and Chapman, 1961 or Ricker, 1975 for reviews).

When animals cannot be aged individually, as in shrimps, one could conceive of replacing N in equation (4) by the number of animals in a given length class, and replacing t by the relative age (t') of the animals at the mid-length of that class ($L_{t'}$), where t' is obtained by solving the VBGF

$$t' = \frac{\log_e \{1 - (L_{t'}/L_\infty)\}}{-K} \qquad (5)$$

This method was applied to shrimp, eg, by Berry (1970). However, the method is subject to a large bias, because larger shrimps need a longer time to grow through a length class than small shrimps, this being due to the fact that shrimp growth in length is not linear. Thus, large, old shrimps 'pile up' in the larger size groups and Z is under-estimated. A correction for this effect can be achieved by dividing each value of N by the time needed to grow through a length class (Δt) computed as

$$\Delta t = \frac{\log_e \{(L_\infty - L_1)/(L_\infty - L_2)\}}{K} \qquad (6)$$

where L_1 and L_2 are the lower and upper limits of the length class, respectively. Thus, a length-converted catch curve should (as suggested by J A Gulland, pers. comm.) have the form

$$\log_e (N/\Delta t) = a + bt' \qquad (7)$$

The differences between Z values obtained from equation (7) and those obtained when not accounting for the non-linearity of shrimp growth can be considerable (see Fig 5).
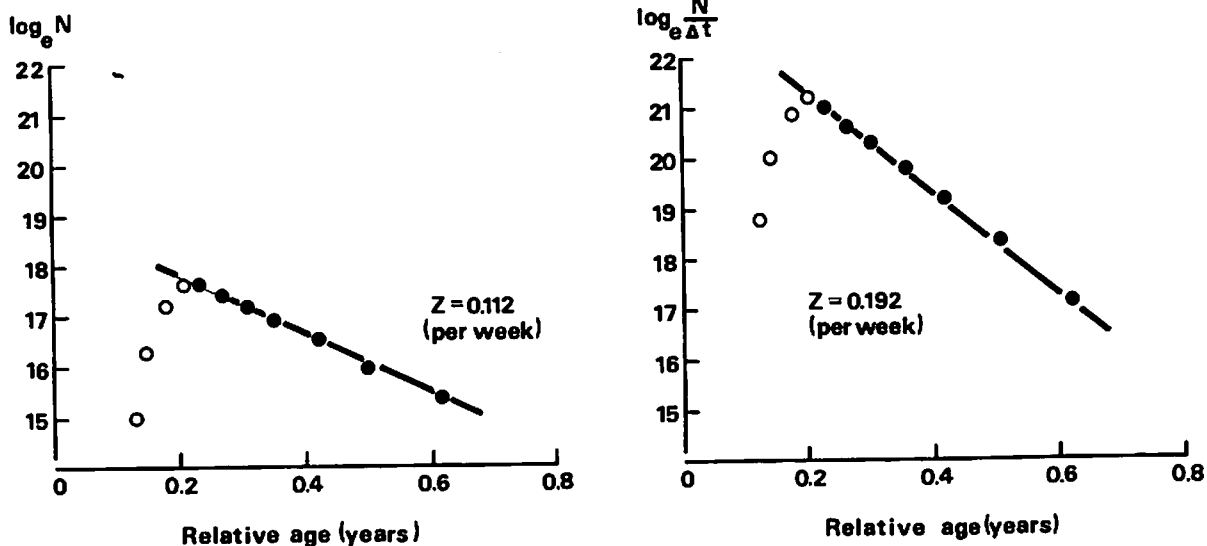

Fig 5 Two methods for the estimation of total mortality (Z) from length-converted catch curves. Left: straightforward conversion of lengths to relative ages. Right: conversion of lengths to ages with compensation for non-linearity of growth. Note large deviation (58%) between the estimates of Z. The catch data ($P.\ duorarum\ \male$) are from Berry (1970, Fig. 1) whose growth parameters ($L_\infty = 20 \cdot 5, k = 0 \cdot 08$ per week) were also used.

The computer program ELEFAN II (a sequel to ELEFAN I) can be used to estimate values of Z using the method presented here, based on any combination of length-frequency samples believed to be representative of the population, as well as any set of growth parameters (Pauly *et al*, 1981).

A feature of this program is that it allows for the selection of data points to use in the analysis. Thus, it is possible to disregard both the points pertaining to the 'ascending' part of the curve and those points (generally one only) derived from lengths so close to L_∞ that unrealistically high 'age' is generated by equation (5) (see *Figs 7–9* for examples).

Identification of selection patterns

As will be noted in the results section, the descending limb of length-converted catch curve is generally remarkably straight. This suggests that Z would also be constant for at least part of the ascending part of the curve, were it not for the effects of incomplete selection and/or recruitment. Thus, by dividing, for each length class in the ascending part of the curve, the numbers actually sampled by the expected numbers (as obtained by projecting backward the straight portion of the catch curve) as series of ratios are obtained which resemble a selection curve, but is in fact akin to a 'resultant curve' (Gulland, 1969), *ie* the result of the interactions of a recruitment with a selection curve (*Fig 6*).

The key assumption of this method, which generates what will be called "selection patterns", is that the straight portion of the catch curve could legitimately be extrapolated backward, *ie* that Z would be constant over a range of values larger than the range from which it is estimated, if it were not for the effect of mesh selection. (It will be realized that this assumption is fully met only when $Z = M$.)

Estimation of natural and fishing mortality

When the growth of animals can be described by the VBGF, and if it can be assumed that the oldest animals of a given stock reach approximately 95% of their L_∞ value, then the VBGF can be solved such that

$$t_{max} \approx 3/K \qquad (8)$$

where K is the growth coefficient of the VBGF and t_{max} the longevity. That natural mortality should be related to longevity, hence to K is thus obvious, and has been demonstrated on the basis of a vast amount of data by Beverton and Holt (1959). Similarly, animals with small L_∞ (*ie* animals that stay small) should have more predators than
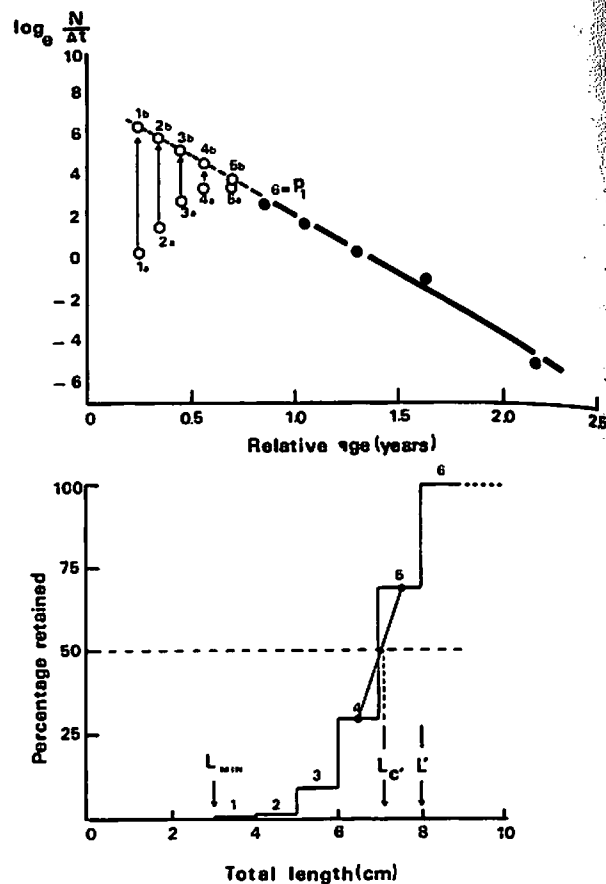

Fig 6 Construction of 'selection patterns' from catch curves. Above: backward projection of straight portion of catch curve, and computation of 'expected' numbers (1b-to 5b). Below: percentage retained, as obtained by performing 1a/1b, 2a/2b *etc*, and plotting the resulting fractions (expressed in %) against the corresponding lengths. L_{min}, L'_c and L' are defined. Catch curve and selection patterns shown here pertain to stock #8 in *Tables 1* to *4*.

animals having a large size. Hence, small animals should generally have, for constant K, a higher natural mortality than large animals. Mean environmental temperature – at least in fishes – can also be demonstrated to have a direct relationship with natural mortality (Pauly, 1980a). On the basis of 175 independent data sets, it was thus possible to establish for fishes the relationship

$$\log M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T \qquad (9)$$

where L_∞ is expressed in cm (total length), where K is put on an annual basis and T is expressed in °C. This relationship, which can be used to predict reasonable values of M in any species of fish can be expected to generate equally reasonable estimates

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of M in shrimps for the reasons that shrimps and fish generally share the same habitats, resources and predators, and that therefore, they are not likely to differ widely in their vital parameters (see Discussion).

Equation (9) thus allows a rough estimation of M in shrimp stocks where L_∞, K and T are known. Subtraction of these estimates of M from the estimates of Z (obtained by using one of the methods presented above) gives values of fishing mortality via the definition

$$Z = M + F \qquad (10)$$

Also, the exploitation rate $E = F/Z$ can be computed for a preliminary assessment of whether a stock is lightly ($E < 0.5$) or strongly exploited ($E > 0.5$), based on the assumption that a stock is optimally exploited when $F = M$ or $E = 0.5$ (Gulland, 1971).

Derivation of recruitment patterns

It has been a common practice, when using the traditional methods for the analysis of length-frequency data to make inferences, once patterns of growth have emerged, as to

- the length of the spawning season (more precisely the length of the period during which animals are recruited into the set of length-frequency samples under investigation),
- the number of times 'spawning' occurs per year (recruitment again is actually considered),
- the relative magnitude of the various 'spawning' (recruitment) events.

However, these inferences, although helpful, are as subjective as the growth estimates obtained by these methods. ELEFAN II incorporates a routine which, by projecting the length-frequency data available backward onto the time axis (by means of a set of growth parameters) generates 'recruitment patterns' which can be used to obtain objective information pertaining to the recruitment processes (Fig 7).

Material

Table 1 indicates the source of the data used here to demonstrate the applicability of ELEFAN I and II to shrimps.

Except for data collected in the Philippines (Ingles, 1980) all length-frequency data used in the present analysis stem from the literature. There are two reasons for this:

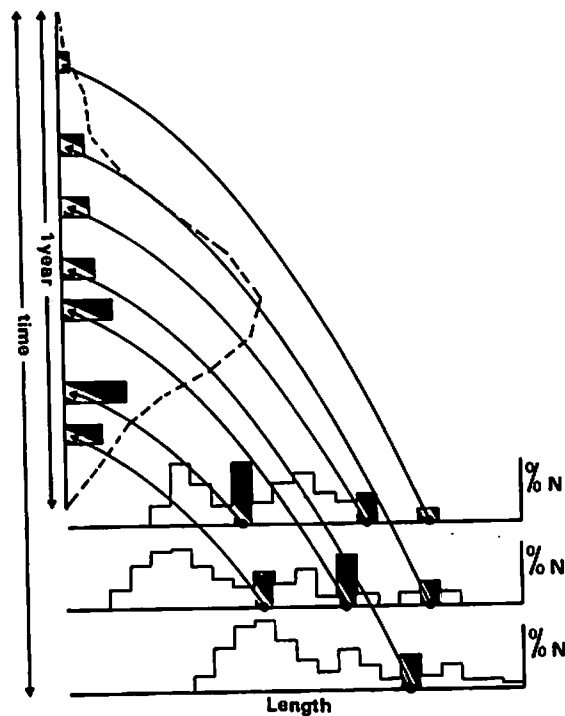- we do not have enough original data to illus-

Fig 7 Schematic representation of method for obtaining recruitment patterns. The steps involved are: (1) projection onto the time axis of the frequencies of a set of length-frequency data (this process includes a correction for non-linearity of growth, not shown here), (2) summation for each month (and irrespective of year) of the frequencies projected onto each month, (3) subtraction, from each monthly sum, of the lowest monthly sum to obtain a zero value where apparent recruitment is lowest, (4) output of monthly recruitment, in percent of annual recruitment.

Concerning points 3 and 4, it must be noted that the monthly values pertain to real times of the year only when t_0 is available. Otherwise, the times of maximum and minimum recruitment are not known—hence the use of '1 year' as a time scale in the various figures presented below.

trate sufficiently all possible applications of the ELEFAN programs, and
- one of our aims is to demonstrate that length-frequency data in the literature have generally been underutilized, ie, the data allow for a much deeper analysis.

Results

Growth parameter estimates

The growth parameters estimated by ELEFAN I from the data in Table 1 are summarized in Table 2. Some of the growth curves involved are illustrated in Figures 8 and 9.

An 'auximetric' grid (Pauly, 1970, 1980c) is presented which allows comparison of the growth patterns of the shrimp stocks investigated here (Fig. 10). It will be noted that for given K-values

the *Penaeus* spp. have higher values of W_∞ than the other Penaeidae ie, they grow faster. Pauly (1979, 1980c) notes other inferences and comparisons, eg, with fish, which can be made using an auximetric grid.

As will be noted from *Table 2*, seasonally oscillating growth curves have not been fitted to tropical stocks, but only to temperate and subtropical stocks, ie, to 7 of the 19 cases considered here (see eg, *Fig 9*). Thus, for these stocks, the value of *C* in

Table 1

SUMMARY OF DATA ON THE SHRIMP STOCKS USED FOR THE ANALYSIS

Fig. No.	Stock No.	Species, sex	Locality and date	Water temperature (monthly means)			ΔT	Source of length-frequency data
				Min	Max	Mean		
8	1	*Hymenopenaeus robustus* ♀	Northeast Florida, 100 fathoms, 1957	—	—	15[a]	—	Anderson and Lindner (1971, App. Table 6)
	2	*Metapenaeopsis durus* ♀ and ♂	Visayan Sea, Philippines, 1976/77	25·1	28·3	26·8[b]	3·2	Ingles (1980, Appendix IIIc)
9	3	*Metapenaeus brevicornis* ♀ and ♂	Off Kutch, India, 1960/61	17·7	29·3	25·0[c]	11·6	Ramamurthy (1965, Fig 6)
	4	*Metapenaeus brevicornis* ♀ and ♂	Off Kutch, India, 1961/62	16·5	29·1	24·0[c]	12·6	Ramamurthy (1965, Fig 6)
	5	*Metapenaeus affinis* ♀ and ♂	Off Versoba, India, 1958/59	24·6	28·1	26·7[c]	3·5	Mohamed (1967, Fig 3)
	6a	*Metapenaeus kutchensis* ♀ and ♂	Off Kandla, India, 1959/60	21·3	29·0	25·0[d]	7·7	Ramamurthy (1965, Fig 3)
	6b	*Metapenaeus kutchensis* ♀ and ♂	Off Kandla, India, 1959/60	21·3	29·0	25·0[d]	7·7	Ramamurthy (1965, Fig 3)
	7	*Metapenaeus kutchensis* ♀ and ♂	Off Kandla, India, 1960/61	17·7	29·3	25·0[d]	11·6	Ramamurthy (1965, Fig 3)
	8	*Metapenaeus kutchensis* ♀ and ♂	Off Kandla, India, 1961/62	16·5	29·1	24·0[d]	12·6	Ramamurthy (1965, Fig 3)
	9a	*Parapenaeus longipes* ♀ and ♂	Visayan Sea, Philippines, 1976/77	25·1	28·3	26·8[b]	3·2	Ingles (1980, Appendix IIIb)
	9b	*Parapenaeus longipes* ♀ and ♂	Visayan Sea, Philippines, 1976/77	25·1	28·3	26·8[b]	3·2	Ingles (1980, Appendix IIIb)
	10a	*Penaeus duorarum* ♂	Tortugas, Florida, 1957/58	22·8	28·6	25·6[e]	5·8	Iversen et al (1960, Appendix Table 2)
	10b	*Penaeus duorarum* ♂	Tortugas, Florida, 1957/58	22·8	28·6	25·6[e]	5·8	Iversen et al (1960, Appendix Table 2)
	11	*Penaeus kerathurus* ♀	Gulf of Cadiz, Spain, 1971/72	14·2	20·3	18·0[f]	6·1	Rodriguez (1977, Fig. 12)
	12	*Penaeus kerathurus* ♂	Gulf of Cadiz, Spain, 1971/72	14·2	20·3	18·0[f]	6·1	Rodriguez (1977, Fig. 12)
	13	*Penaeus setiferus* ♀	Off Texas, USA	16·9	28·2	22·7[e]	11·3	Anderson and Lindner (1958, Table 1)
	14	*Penaeus setiferus* ♂	Off Texas, USA	16·9	28·2	22·7[e]	11·3	Anderson and Lindner (1958, Table 1)
	15	*Trachypenaeus fulvus* ♀	Visayan Sea, Philippines, 1976/77	25·1	28·3	26·8[b]	3·2	Ingles (1980, Appendix IIIa)
	16	*Trachypenaeus fulvus* ♂	Visayan Sea, Philippines, 1976/77	25·1	28·3	26·8[b]	3·2	Ingles (1980, Appendix IIIa)

[a] Bottom temperature not available. Value of 15°C is an estimate.
[b] Actual bottom temperature, as measured by Ingles (pers. obs.).
[c] Anon. (1944).
[d] Ramamurthy (1967, Table VII).
[e] Rivas (1968).
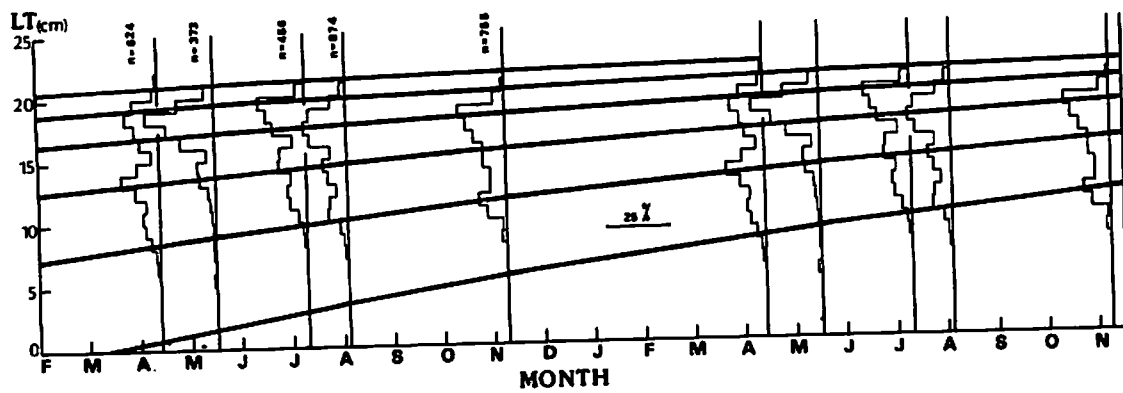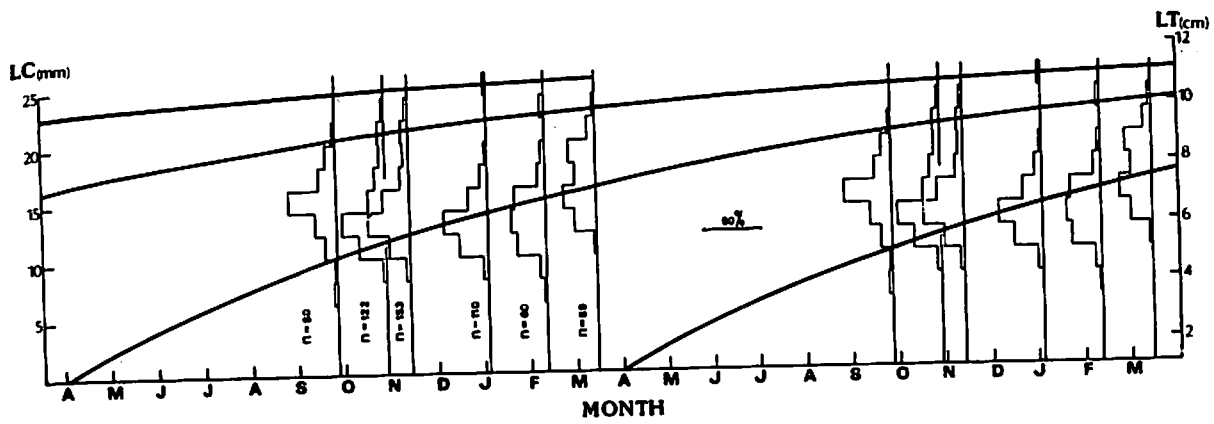[f] Rodriguez (1977, Fig 20).

Fig 8 Above: growth, catch curve and recruitment pattern of *Hymenopenaeus robustus* ♀ off Florida. Below: growth, catch curve and recruitment pattern for *Metapenaeopsis durus* ♀ and ♂ from the Visayan Sea, Philippines. See *Tables 1* to *4* for details on these stocks.

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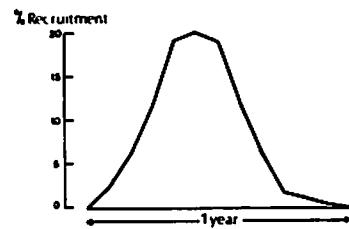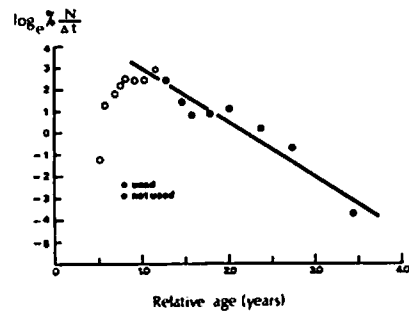
Fig 9 Above: growth, catch curve and recruitment pattern for *Penaeus duorarum* ♂ from Tortugas, Florida. Below: growth, catch curve and recruitment pattern for *Metapenaeus brevicornis* ♀ and ♂ off Kutch, India, 1960–61. See *Tables 1* to *4* for details on these stocks.
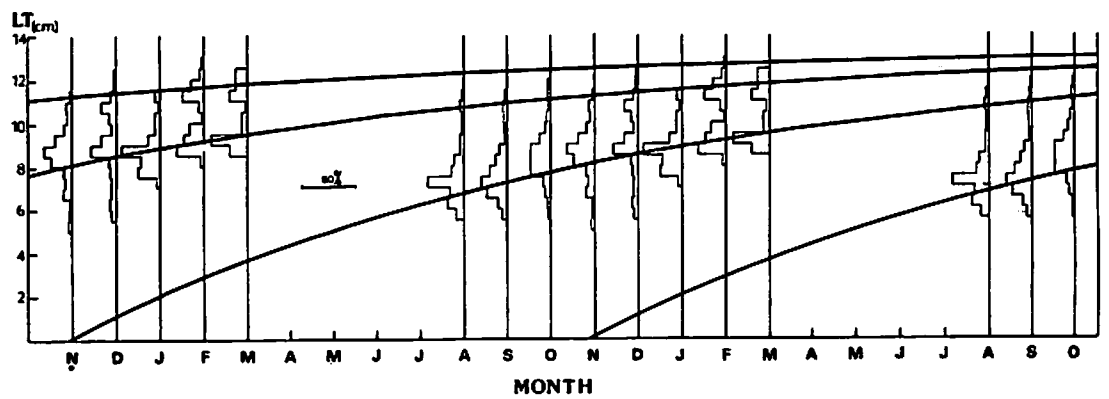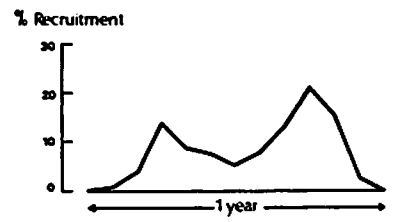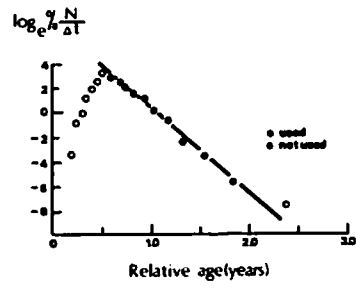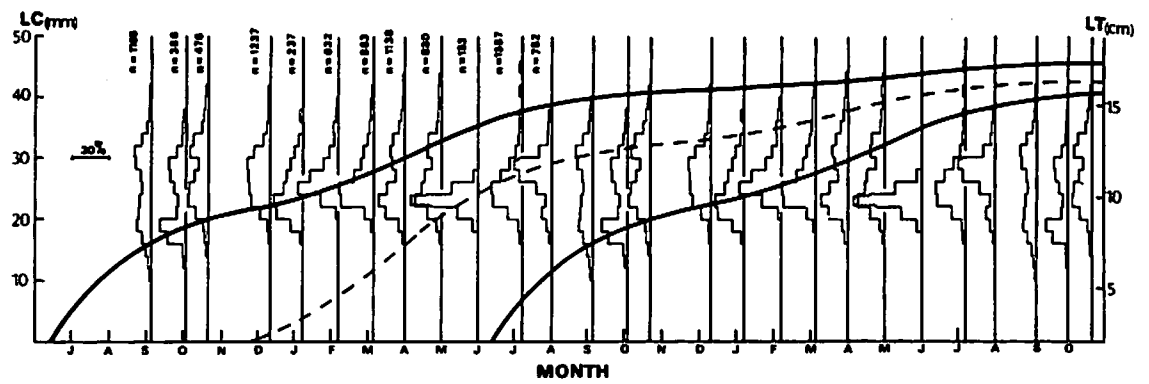
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Table 2

SUMMARY OF RESULTS PERTAINING TO THE GROWTH OF SHRIMP

Fig. No.	Stock No.	Species, sex	Growth parameters					
			L_∞	'W_∞'[a]	K	C	Winter Point	ESP/ASP[b]
8	1	Hymenopenaeus robustus ♀	24·25	114	0·39	0·10	0·4 (May)	0·531
	2	Metapenaeopsis durus ♀ and ♂	11·6	12·5	0·95	—	—	0·446
9	3	Metapenaeus brevicornis ♀ and ♂	13·3	18·8	0·93	—	—	0·465
	4	Metapenaeus brevicornis ♀ and ♂	14·25	23·1	0·90	—	—	0·490
	5	Metapenaeus affinis ♀ and ♂	17·5	42·9	1·20	—	—	0·392
	6a	Metapenaeus kutchensis ♀ and ♂	14·0	22·0	1·15	—	—	0·418
	6b	Metapenaeus kutchensis ♀ and ♂	14·0	22·0	1·2	—	—	0·209
	7	Metapenaeus kutchensis ♀ and ♂	13·5	19·7	1·05	—	—	0·456
	8	Metapenaeus kutchensis ♀ and ♂	13·75	20·8	1·10	—	—	0·328
	9a	Parapenaeus longipes ♂	10·0	8·00	1·4	—	—	0·379
	9b	Parapenaeus longipes ♀	10·25	8·62	1·15	—	—	0·251
	10a	Penaeus duorarum ♂	17·6	43·6	1·45	0·60	0·93 (Dec)	0·347
	10b	Penaeus duorarum ♂	17·6	43·6	1·2	0·54	0·87 (Nov)	0·264
	11	Penaeus kerathurus ♀	21·0	74·1	0·8	0·9	0·8 (Oct)	0·457
	12	Penaeus kerathurus ♂	18·0	46·7	0·9	0·85	0·75 (Sept)	0·566
	13	Penaeus setiferus ♀	22·5	91·1	1·25	0·61	0·11 (Feb)	0·433
	14	Penaeus setiferus ♂	19·25	61·6	1·55	0·675	0·15 (Feb)	0·476
	15	Trachypenaeus fulvus ♀	13·0	17·6	1·4	—	—	0·481
	16	Trachypenaeus fulvus ♂	11·4	11·9	1·6	—	—	0·451

[a] Computed throughout by setting $W = 0.008 \, L^3$, where L is the total length in cm, and W the weight in grams.
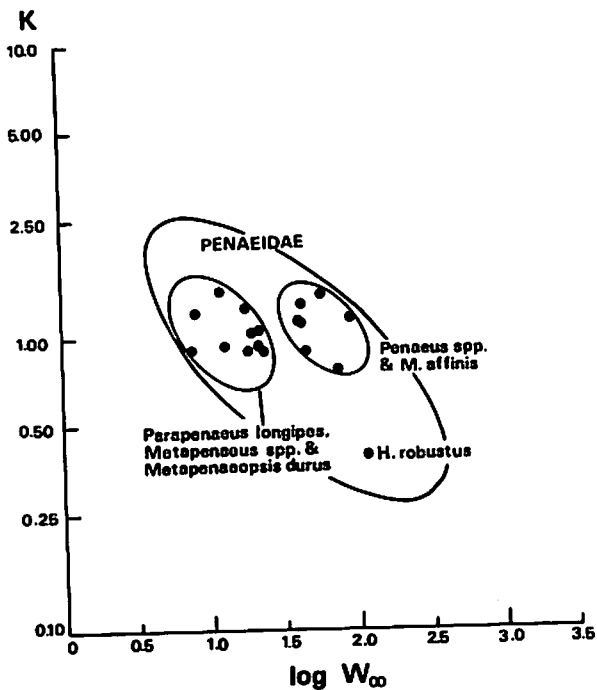[b] Explained sum of peaks/available sum of peaks; see text for definitions.

Fig 10 Comparison of growth performance of various penaeid species. The stocks with a highest value of K for a given value of W_∞ (or conversely) grow fastest (ie reach faster any given size). Note that various groups fall into ellipsoid clusters, suggesting ranges of W_∞, K, combinations possible in Penaeidae. Based on data in Table 2 and 'auximetric grid' method of Pauly (1979).

equation (1) has simply been set at zero. For all other cases, values of C and WP were estimated from the data. As might be seen, the various 'Winter Points' indeed fall within the periods where the temperature is reduced. This may also apply to Hymenopenaeus robustus (stock #1 in Tables 1 to 4) whose 'Winter Point' falls in May, and which occurs in deep water, where the annual temperature minimum probably occurs later than in shallow waters. The values of C correspond, for a given difference between highest mean monthly summer and winter temperature (ΔT), very well with values obtained from seasonally oscillating growth curves of fish (Fig 11). Thus, as in the case of fish, it appears in shrimp that the intensity of seasonal growth oscillations correlates well with the intensity of the annual temperature fluctuations.

Total mortality estimates
Table 3 gives the estimates of Z obtained from the length converted catch curves. Overall, they are similar to those obtained using Beverton and Holt's (1956) equation for the estimation of Z from mean lengths.

Selection patterns
In Fig 12, four selection patterns are presented. The limited number of examples were selected:
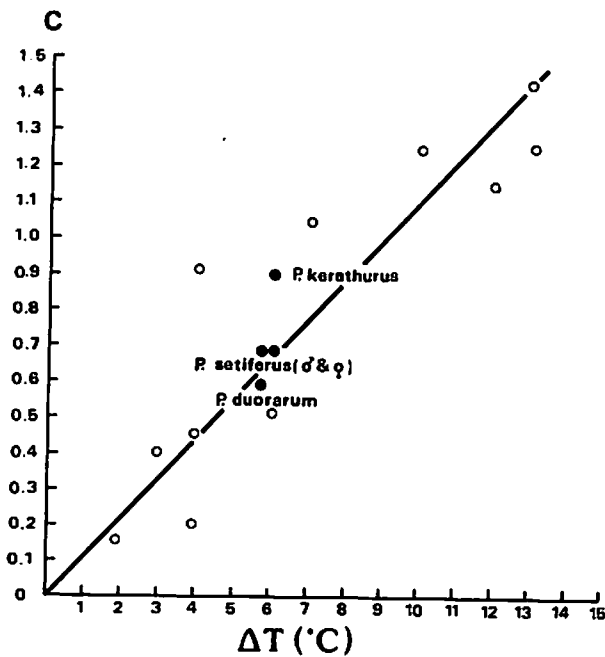
229

C

ΔT (°C)

Fig 11 Relationship between intensity of seasonal growth oscillation, as expressed by the parameter C of equation (1) and the difference between highest and lowest mean monthly water temperature in the course of one year (ΔT). Open dots pertain to fish stocks, documented in Pauly (1982) and Pauly and Ingles (1981), black dots pertain to shrimp stocks, documented in Tables 1 and 2.

– to include the females and males of a given species, in order to show that similar results are indeed obtained where similar results may be expected, and

– to include a stock with a 'knife-edge' selection pattern as well as a stock with selection occurring over a wider length range, to show that the method does not, due to some inherent bias, always generate similar recruitment patterns.

Selection patterns as defined here thus can be used to extract useful information, eg length at 50% retention, or $L_{c'}$,* from a given set of length-frequency data. They may serve as complement to selection experiments, the results of which they generally should confirm. Also, they might be used to replace selection experiments where such experiments cannot be conducted, eg, because of the costs involved in such experiments, or when analyzing old data.

Estimates of natural and fishing mortalities
Table 3, which summarizes the estimates of mortalities, shows the estimates of M obtained by

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*Footnote: The 50% retention length estimated from selection patterns may be coded $L_{c'}$ to distinguish it from a 'real' estimate of L_c, as obtained from a selection experiment.

Table 3
SUMMARY OF RESULTS PERTAINING TO THE MORTALITY OF SHRIMP

| Fig.	Stock	Species, sex	Catch curve r^2	n	Z_1	$\dot{M}$	F	E	Remarks
8	1	*Hymenopenaeus robustus* ♀	0·994	4	3·77	0·77	3·00	0·80	active fishery
	2	*Metapenaeopsis durus* ♀ and ♂	0·995	6	3·28	2·21	1·07	0·33	incidental catch in demersal fisheries
9	3	*Metapenaeus brevicornis* ♀ and ♂	0·910	8	2·46	2·03	0·43	0·18	active fishery
	4	*Metapenaeus brevicornis* ♀ and ♂	0·960	11	2·55	1·91	0·64	0·25	
10	5	*Metapenaeus affinis* ♀ and ♂	0·983	5	5·29	2·29	3·00	0·57	'no overfishing in the areas' (George 1970)
	6a	*Metapenaeus kutchensis* ♀ and ♂	0·970	4	6·49	2·33	4·16	0·64	
	6b	*Metapenaeus kutchensis* ♀ and ♂							active fishery
11	7	*Metapenaeus kutchensis* ♀ and ♂	0·999	6	3·55	2·19	1·36	0·38	
	8	*Metapenaeus kutchensis* ♀ and ♂	0·988	5	5·83	2·20	3·63	0·62	
12	9a	*Parapenaeus longipes* ♀	0·997	6	3·83	2·79	1·04	0·27	not accessible to most commercial trawlers (too deep)
	9b	*Parapenaeus longipes* ♀							
	10a	*Penaeus duorarum* ♂							
	10b	*Penaeus duorarum* ♂	0·991	10	7·07	2·40	4·67	0·66	known to be heavily fished
13	11	*Penaeus kerathurus* ♀	0·967	6	1·96	1·39	0·57	0·29	'the catch and yields decreased in an alarming
	12	*Penaeus kerathurus* ♂	0·988	4	2·76	1·57	1·19	0·43	manner in the last years' (Rodriguez 1977)
14	13	*Penaeus setiferus* ♀	0·881	6	6·71	2·03	4·68	0·70	known to be heavily fished
	14	*Penaeus setiferus* ♂	0·863	4	5·43	2·55	2·88	0·53	
15	15	*Trachypenaeus fulvus* ♀	0·981	7	4·59	2·75	1·84	0·40	active fishery
	16	*Trachypenaeus fulvus* ♂	0·834	8	5·9	3·12	2·78	0·47	

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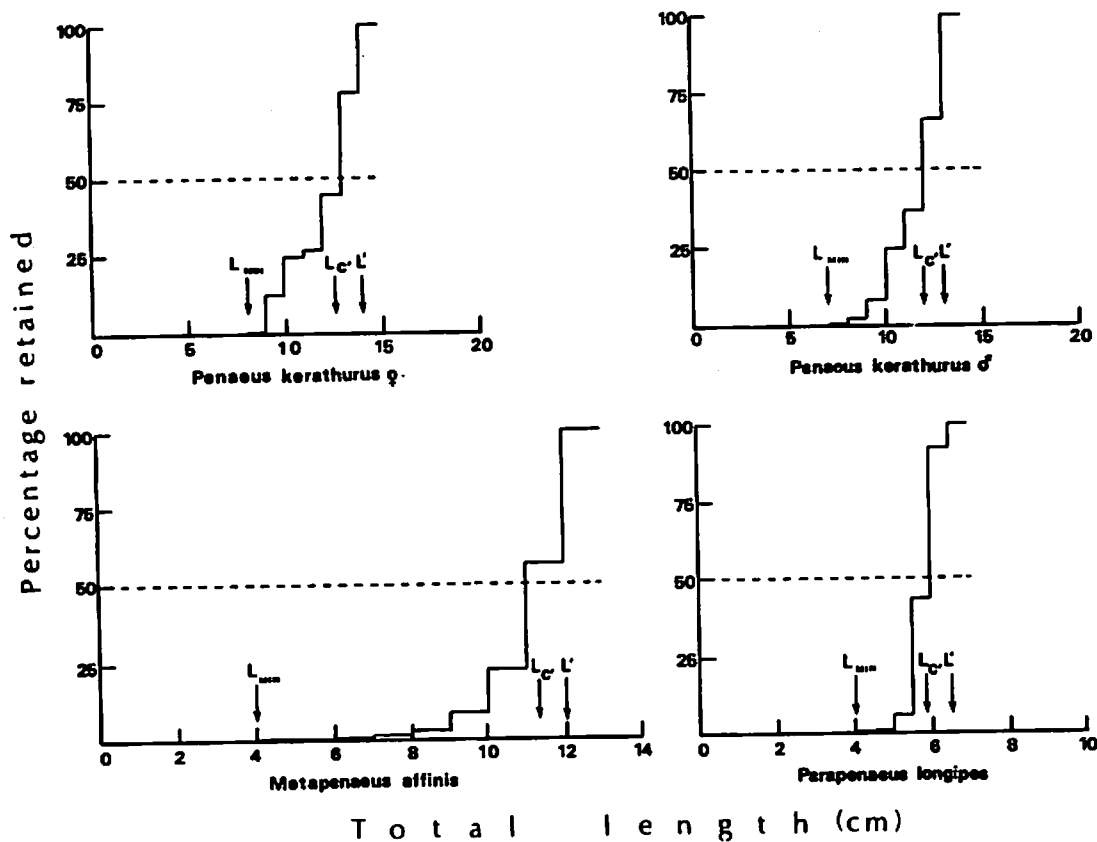
Fig 12 Four examples of 'selection patterns'. Above: showing the similarity of selection patterns in the two sexes of the same stock. Below left: a selection pattern covering a wide range of lengths. Below right: an almost 'knife-edge' selection pattern.

applying equation (9) to the growth parameter estimates of *Table 2* and the mean temperatures of *Table 1*. These values of M range from 0.77 in *Hymenopenaeus robustus* to 3.12 in male *Trachypenaeus fulvus*, a small Philippine shrimp.

When subtracted from the value of Z in *Table 3*, estimates of fishing mortality are obtained which range from 4.67 in male *Penaeus duorarum* to 0.43 in *Metapenaeus brevicornis*. Values of $E = F/Z$, are listed in *Table 3* which are complemented by brief comments gleaned from the literature as to the status of the various fisheries. There is broad agreement between the comments on the status of the fishery and the 'message' represented by a value of E ('underfishing' when $E < 0.5$; 'overfishing' when $E > 0.5$).

Recruitment patterns

The recruitment patterns obtained here fall into 3 categories:

- recruitment patterns suggestive of one recruitment event per year (or of two events, with one completely dominating the other);

- recruitment pattern suggestive of two recruitment events per year;
- recruitment patterns from which no secure inference can be drawn.

Table 4 summarizes and discusses the information extracted from the recruitment patterns here (see also *Figs 8* and *9* for examples).

Discussion

The set of methods presented here to extract growth parameters from length-frequency data (ELEFAN) is not fail safe. Given a set of highly unrepresentative length-frequency data (*eg*, as might be obtained from fishing only in the extremes of the depth range of *Penaeus* spp.) ELEFAN I will output ridiculous growth parameter values. However, when this happens, the goodness of fit values will generally be very low, suggesting themselves that the results are unreliable.

In fact, the goodness of fit values of the examples provided here (*Table 2*) are low compared with values for fish (Pauly and David 1981, Pauly and

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Stock No.	Species, sex	Structure of recruitment pattern	Biological interpretation and remarks
1	*Hymenopenaeus robustus* ♀	one normally distributed group, or two, with one much larger than the other	Probably one recruitment event per year, with smaller 'mode' reflecting only sampling variability (see *Fig 8*)
2	*Metapenaeopsis durus* ♀ and ♂	two overlapping, normally distributed groups	Two recruitment events per year, one larger than the other (see *Fig 8*)
3	*Metapenaeus brevicornis* ♀ and ♂	one normally distributed group, or two, with one much larger than the other	Pattern suggestive of one recruitment event per year. Comparison with stock No. 4 suggests some broods may fail to recruit (see *Fig 9*)
4	*Metapenaeus brevicornis* ♀ and ♂	two overlapping, normally distributed groups	Two recruitment events per year confirming George (1970) who reports 'breeding' twice a year
5	*Metapenaeus affinis* ♀ and ♂	one normally distributed group, or two, widely overlapping groups	No clear inference can be drawn; Mohamed (1967) suggests two spawning seasons, while George (1970), reviewing several papers, suggests one spawning season per year
6	*Metapenaeus kutchensis* ♀ and ♂	two readily identifiable groups	Two recruitment events per year
7	*Metapenaeus kutchensis* ♀ and ♂	two widely overlapping groups	Two recruitment events per year
8	*Metapenaeus kutchensis* ♀ and ♂	four modes in pattern, but two groups apparent	Probably two recruitment events per year
9	*Parapenaeus longipes* ♀	three modes in pattern, but two groups apparent	Probably two recruitment events per year
10	*Penaeus duorarum* ♂	Two readily identifiable groups	Two recruitment events per year (see *Fig 9*) confirming observations reported by Castello and Allen (1970)
11 12	*Penaeus kerathurus* ♀ ⎱ *Penaeus kerathurus* ♂ ⎰	one normally distributed group, or two, with one much larger than the other	⎧ Patterns equivocal, but not contradicting solid evidence ⎨ Presented by Rodriguez (1977) for one spawning/recruitment season per ⎩ year
13 14	*Penaeus setiferus* ♀ ⎱ *Penaeus setiferus* ♂ ⎰	one single, normally distributed group	⎰ One recruitment event per year, as ⎱ reported by Lindner and Cook (1970)
15 16	*Trachypenaeus fulvus* ♀ ⎱ *Trachypenaeus fulvus* ♂ ⎰	two readily identifiable groups, one stronger than the other	Two recruitment events per year

Ingles 1981). However, this is probably due to the feature that these previous demonstrations of the use of ELEFAN I were selected for their 'good fit' (the textbook syndrome), whereas availability of data was the main criterion for including the shrimp examples provided here.

To date, use of length-frequency analysis for determination of growth parameters has been of limited use with penaeids, due to extended and fluctuating recruitment and mixing of broods. Thus, it has most often been impossible to 'follow' a selected brood. The method described here is a viable alternative if a broadly representative set of samples of the population can be obtained. When this is the case, the method will be superior to mark-recapture experiments.

Deriving catch curves from length-frequency data has been done only rarely in the past, and when done, a serious bias was involved which generated erroneous results (see *Fig 5*). Correction of this bias, however, is simple, and length-converted catch curves can thus be used to obtain reasonable estimates of Z.

However, representativeness of the samples used in the analysis remains a problem, because the distribution of shrimps is correlated with size. A related problem is that samples taken in an area of very active fishing (also an area of active recruitment) may lead to an over-estimation of total mortality for the population as a whole. Thus, it is imperative that the samples used for this part of the analysis adequately represent the population for a

period of one (or more) year(s).

Given representative samples, length-converted catch curves are, most often, remarkably straight, and allow the identification of the point on the catch curve from which recruitment and selection are completed (P_1).

Only a very short comment seems appropriate concerning the concept of selection patterns as introduced here. The concept is apparently new, and there were no data available for a comparison of a selection pattern with a real selection curve, as obtained from a selection experiment, or better with a 'resultant curve', as obtained by combining a selection with a recruitment curve.

The backward projection of the catch curve as used here to generate selection patterns evidently involves a bias ($L'_c > L_c$) since fishing mortality – hence also Z – gradually decreases as one progresses from right to left on the ascending part of a catch curve. However, two factors still contribute toward making L'_c as defined here a reasonable estimator of L_c:

- among smaller shrimps, natural mortality could be higher, thus compensating (at least in part) for the reduction in fishing mortality
- both L'_c and L_c are constrained by the same values of L_{min} (smallest size caught) and L' (length at full retention, corresponding to P_1, see Figs 6, 12 and text).

The method presented here to estimate the natural mortality of shrimps is risky in that it is based on data obtained from fish stocks. However, even if shrimp differed from fish in having – for a given set of growth parameters and environmental temperature – a slightly higher or lower natural mortality, the method would still provide estimates of M that are more reasonable than many of those to be found in the literature, in which values of M, eg, for $P. duorarum$, ranging from 28·6 (Kutkuhn, 1966) to 1·04 (Berry, 1970) may be found. Also, the Z and M data in Table 3 provide indirect evidence that M in shrimp generally cannot be much lower than in fish. If they were, some of the Z values associated with low fishing intensities would have turned out to be lower than the M value estimated from equation (12).

Finally, it should be pointed out that the values of E for the various shrimp stocks, as obtained from the estimates of Z, M and F, as a whole, do not suggest anything different from what is known from the various fisheries referred to in Table 3. Thus, for example, in the case of heavily exploited stocks such as Penaeus duorarum off Tortugas, high values of E were obtained, while a relatively low value of E was obtained for Parapenaeus longipes, which occurs at depths between 40 and 200 fathoms and is therefore virtually inaccessible to the trawlers operating in the Visayan Sea area of the Philippines. Thus, the values of M obtained from equation (12) seem to provide reasonable results for shrimps as well as fish. These values allow, in conjunction with values of Z estimated from length-converted catch curve, the estimation of values of E and therefore a direct assessment of the status of a fishery.

The information obtained from recruitment patterns (Table 4) is in general agreement with studies on the reproduction of the shrimp stocks in question. It may be concluded that this method of examining recruitment patterns is a useful tool.

In summary the methodology proposed here (the application of ELEFAN I and II) for the study of shrimp stocks has the following features:

- given suitably representative length-frequency data, information is extracted which is important both for practical stock assessment purposes and for understanding the basic biology of shrimp,
- all results obtained by these methods are reproducible, ie, different authors using the same set of data will get the same results,
- the methods can be applied to both tropical and temperate shrimp stocks and implemented on cheap microcomputer, affordable even by the fishery research laboratories of developing countries, and
- the methods can be applied both to new or existing (published or unpublished) data. This permits comparative studies and the reconstruction of time series (eg, of Z, growth parameters) which should prove invaluable in understanding the dynamics of shrimp stocks.

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