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The Population Dynamics of Short-lived Species, with Emphasis on Squids*

by

Daniel Pauly

International Center for Living Aquatic Resources Management
MCC P. O. Box 1501, Makati, Metro Manila, Philippines

Abstract

The features of short-lived fish and invertebrates relevant to their population dynamics and exploitation are reviewed, with emphasis on methodological approaches which could lead to improved management of squid stocks.

Several models are presented which offer the possibility of reducing what presently appear to be qualitative differences in the population dynamics of fish and squids to quantitative differences, and hence to render squids amenable to the kind of comparative studies which in fish have rendered preliminary stock assessments possible even when data are scarce.

Introduction

This invited paper dealing with the population dynamics of short lived species touches upon a subject which has not received much attention in the fisheries literature.

The major reason for this is that, as far as fishes are concerned, commercially important short-lived species occur predominantly in the tropics, where relatively little research in population dynamics is conducted.

As a result many stock assessment specialists, who rely predominantly on VPA-oriented methodologies have found themselves conceptually and methodologically unprepared when confronted, in the mid-seventies, with having to assess newly "discovered" squid stocks and to derive management measures for them.

Indeed, the short life span of most squids forces us - as does working with short-lived fish - to return to the basics of our field, i.e. to Russel's axiom (1931) which states that

$$B_2 = B_1 + (R^* + G^*) - (Y + M^*) \quad \dots 1)$$

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or that future biomass (B_2) in a stock with no emigration nor immigration is a function of its original biomass (B_1), plus recruitment in weight (R^*) and growth of the recruited animals (G^*), minus the catch (Y) and the weight of those animals dying of natural causes (M^*).

Equation (1) offers an obvious structure for the rest of this contribution, and I shall thus review our ability to measure or predict each of these factors in populations of short-lived animals, particularly squids.

Growth

What appear to be successful attempts to age squids by means of daily rings on their statoliths have been reported by Spratt (1978) and Kristensen (1980), working on Loligo opalescens and Gonatus fabricii, respectively. A theory exists (Lutz and Rhoads 1977) which seeks to explain the origin and nature of these rings, and which suggests that they should be as ubiquitous in mollusks as daily rings are in the otoliths of fishes. Indeed, this theory could, suitably generalized, also explain the occurrence of daily rings in fish otoliths, since the basic mechanisms involved in both fish and molluscs involve short term anaerobiosis during periods of activity (Pauly 1981, 1982a).

Aging of squids by means of daily rings appears to involve too much work however - even in short-lived forms - to become a method routinely applied, especially if the generalization proves true that squid growth rate are extremely variable within populations (Caddy 1983).

This obviously takes us - for lack of a better alternative - into the often murky methodologies used to infer growth rates and growth curves from size-frequency, particularly length-frequency data. Many authors working on fish, squids or other invertebrates unfortunately believe that inferring growth from length-frequency data simply consists of visually identifying "broods" from polymodal length-frequency distributions, tracing by eye whatever lines one feels like tracing and reprinting the results as "growth" rates (see Fig. 1 for a noteworthy example).

As far as research on squid growth is concerned, the chief result of this belief has been growth parameters that are often mutually inconsistent (see Table 1 and Fig. 5) and an array of contradictory statements about the growth of squids, which is perceived to be "linear", "exponential", "asymptotic", or "oscillating" (see Fig. 2 and Table 6 and 7 in Lange and Sissenwine 1983).

Similar confusion was until recently characteristic of shrimps - yet upon close examination, many of these seemingly conflicting growth patterns could be resolved in a basic growth pattern of the asymptotic type - as in fish - with superimposed seasonal growth oscillations (Garcia and Le Reste 1981). This can be expressed by a modified von Bertalanffy model of the form

$$L_t = L_{\infty} (1 - \exp -(K(t-t_0) + \frac{CK}{2\pi} \sin 2\pi(t-t_s))) \quad \dots 2)$$

where

L_t is the length at age t ,

L_{∞} is the asymptotic length,

K and t_0 are the same constants as in the normal von Bertalanffy growth formula (VBGF)

and

C and t_s are additional parameters,

with C expressing the amplitude of the growth oscillations, and

t_s the onset of a sinusoid oscillations with regard to $t = 0$.

Thus, my contention is here that, within populations, what appears to be difference in growth characteristics are artefacts due to changes in birthdate (see Fig. 3).

I believe that such interpretation should be considered if only because it offers the possibility of explaining what appear to be specific (and hence hard to study) characteristics of squids as a general feature of aquatic poikilotherms exposed to seasonal temperature oscillations (see Fig. 4).

Another advantage of using a standard growth model, such (e.g.) as the seasonalized VBGF suggested above, to express the results of growth studies is that it offers the possibility of conducting comparative studies between various populations of the same squid species, between various squid species and between squids and fish (see Table 1 and Fig. 5), and hence to use knowledge available on the various species or in a given genus or family to infer the growth performance of species for which growth data are not available.

One approach, which works rather well in fish and shrimps is for example to rely on the within-group constancy of the parameter ϕ , defined by

$$\phi = \log_{10} K + 2/3 \log_{10} W_{\infty} \quad \dots 3)$$

in which W_{∞} is the asymptotic live weight (in grams) corresponding to L_{∞} in equation (2) and K is expressed on an annual basis (Pauly 1980b, Munro and Pauly 1983, Pauly and Munro 1984).

For practical purposes, using equation (3) consists of estimating for a given group a mean value of ϕ , using the W_{∞} and K pairs available from that group, then relying on ϕ to obtain preliminary estimates of K for species or stock for which growth data are not available, using

$$\log_{10} K = \phi - 2/3 \log_{10} W_{(\infty)} \quad \dots 4)$$

where $W_{(\infty)}$ is a set value of the asymptotic weight, obtained from the maximum weight (W_{\max}) reported from a given stock (e.g. in Roper et al. 1984) and the relationship

$$W_{\max}/0.86 = W_{\infty} \quad \dots 5)$$

which is based on an assumed cubic length-weight relationship and the observation that organisms with asymptotic growth often reach about 95% of their asymptotic length (Taylor 1958, 1959, 1960; Pauly 1984).

These simple rules, plus systematic application of consistent, objective methods for length-frequency analysis (see e.g. Fig. 6) could, I believe, alleviate rapidly the present dearth of knowledge on the growth of squids, and help practitioners obtain a "feel" for the growth performance of squids similar to that which fish biologists now have.

Biomass and Mortality (total, natural and fishing)

Estimating mortalities in short-lived animals is usually rather problematic, especially when the animals in question are difficult to age individually.

One approach which is becoming increasingly popular in short-lived fish and shrimps is to use "length-converted catch curves", i.e. catch curves based on length-frequency data in which the length are converted to their corresponding (relative) ages by means of a set of growth parameters (L_{∞} and K , with a simple correction for non-linearity of growth), and where Z is estimated from the descending, right arm of the curve (Fig. 7A).

The steps toward the construction of length-converted catch curves such as shown in Fig. 7 are as follows:

- 1) Obtain periodic (e.g. monthly) length-frequency samples over a period, preferably one year, such that a cumulative sample as far as possible representative of the average length-frequency composition in the stock can be derived (i.e. such that seasonal pulses of recruitment are evened out).
- 2) Estimate the relative age (t_i') corresponding to the lower class limit of each length class (L_i) using

$$t_i' = -\log_e (1 - L_i/L_{\infty})/K \quad \dots 5)$$

Here, t_i' is called "relative" age because, Z being estimated from the slope of the catch curve, t_0 can be assumed zero (note also that seasonal growth oscillations need not be considered either because an "average" sample is analyzed).

- 3) Plot the cumulated number of squids in each length class (N_i) against the corresponding t_i' value (see Fig. 7A-C), and estimate (when possible) Z from the descending, straight, right arm of the catch curve, i.e. from the slope of

$$\log N_i = a + bt' \quad \dots 6)$$

which can be turned into an estimate of Z through

$$\{b\} + K = Z \quad \dots 7)$$

When the parameter K of the VBGF is not known, relative age can be estimated as $(\text{yrs} - t_0) \cdot K$ (i.e. by setting $K = 1$ in equation 5), in which case the slope of the catch curve yields an estimate of $(Z/K) - 1$ (Pauly 1984, and see Fig. 7B).

Equation (6) and (7) provide estimates of Z which are extremely close (within less than 1%) to the true values of Z , as was ascertained using constructed data (P. Sparre, Charlottenlund, pers. comm., Pauly 1984). The method has been shown to yield remarkably straight catch curves in a large number of fish and shrimp stocks (Pauly 1982a, Pauly and Ingles 1981, Ingles and Pauly 1984, Pauly et al. 1984).

I have applied this approach to a number of squid samples while preparing this contribution, and have obtained, in many cases, catch curves that are not straight (see Fig. 7c for an example), thus apparently confirming, at first sight, the view of Juanico (1983) that "squids are not fish and that few principles of fish biology apply to these molluscs".

More interestingly however, these catch curves, simple as they are, may, if applied widely, help resolve whether the high post-spawning mortalities reported for squids are ubiquitous in the group, as is apparently assumed by those workers who let their experimental animals starve after they have spawned (see Voss 1983) or are a peculiar feature of the few species investigated to date, which seems to be the viewpoint favored by Voss (1983).

Before we rejoice at having found a method which reflects the variable mortality patterns of squids, we must realize, however, that catch curves rest among other things on the assumptions that the length-frequency data used for their construction are representative of the population investigated.

Yet, rigorous experiments for jig and other gears (other than trawls) used to catch squids seem not to have been performed, thus leaving open, for the time being, the interpretation of estimates of apparent total mortality derived from length-converted catch curves.

Pauly (1984) presented a simple method which can be used to estimate probabilities of capture and mean length at first capture (L_{50} , or L_C) directly from a length-converted catch curve, i.e. without selection experiments. The method, which has been field-tested (i.e. shown to provide estimates similar to those obtained from selection experiments) with fish, has yet to be applied to squids.

If it is assumed that the central part of a length-converted catch curve for squids can generally be used to obtain reasonable estimates of Z , the question still remains of how to separate total mortality into its constituent parts, M and F .

Two basic approaches are available, namely (i) that of estimating for a given squid stock, the biomass, from which F , given the catch, can be estimated, or (ii) using comparative life-history studies, to estimate a plausible M , subtract it from Z to estimate F .

The first method, which may be applied profitably when the sampling gear is a trawl, involves estimating biomass (B) using the swept area method (Gulland 1969), then estimating F from

$$F = Y/B \quad \dots 8)$$

where Y is the catch from the stock in question; an alternative of this is to relate the area swept by all the gears of the commercial fleet (a') during a certain period and the total area of occurrence of the stock A, i.e.

$$F = a'/A \quad \dots 9)$$

Applications of this methodology to squids may be found in Lange and Sissenwine (1980), and in Sato and Hatanaka (1983).

The potential pitfalls in the use of equation (8) and (9) are numerous; they range from the generally unknown and probably changing catchability of squids to the seasonal contraction and expansion of their area of occurrence (A), not to mention the problems associated with conducting a suitably weighted stratified random survey to quantify a biomass that is changing rapidly during the very course of the survey. These and associated problems cannot be discussed here, and there seem to be no alternatives but to apply judiciously the best standard approaches (Gulland 1983).

The data needed to obtain reasonable estimates of F using equations (8) or (9) will often not be available, however. In such cases, it will be necessary to rely on the opposite approach, that of subtracting from Z an approximate value of M, obtained independently.

Methods to obtain independent estimates of M from comparative studies have been derived by a number of authors, starting with Beverton and Holt (1959). One such approach, which is based on growth parameters and independent estimates of M in 175 fish stocks is that of Pauly (1980a) who derived the predictive relationship

$$\log_{10} M = -0.2107 - 0.0824 \log_{10} W_{\infty} + 0.6757 \log_{10} K + 0.4627 \log_{10} T \quad \dots 10)$$

where K (annual) and W_{∞} (live weight in grams) are defined as above and T is the mean annual water temperature, in °C.

The equivalent relationship based on length, also presented in Pauly (1980a) has been widely applied, and found by a number of authors to provide reasonable estimates of M in fish as diverse as Pacific skipjack tuna (Kleiber et al. 1983), Arabian Sea myctophids (Sanders and Bouhlef 1982) or West African demersals (Longhurst 1983).

The relationship in (10) should also provide reasonable first estimates of M in squids, if only for the reason that fish and squids usually share the same habitat, resources and predators, and that therefore, they are not likely to differ widely in the interrelationships between their vital parameters (see also Fig. 5). This reasoning, which

was also applied to shrimps by Pauly et al. (1984) was justified post hoc by the fact that the method yielded M values for shrimps well within the range of values considered to be reasonable (S. Garcia, FAO, pers. comm.). Table 1 includes values of M for squids obtained from equation (10).

When growth parameters (L_{∞} or W_{∞} and K) and estimates of F and M are available yield-per-recruit analysis can be conducted quite straightforwardly (Beverton and Holt 1966, Ehrhardt et al. 1983) and first steps toward fishing management proposed.

Recruitment

The real problem with squids and other short-lived exploited organisms is not the estimation of growth, mortality or biomass, however, but the prediction of recruitment, a problem of minor importance in stocks of long-lived fishes in which annual recruitment usually contributes a small part to the overall stock biomass.

Predicting recruitment in stocks that have been exploited a few years only is doubly difficult when the conventional approach is relied upon, i.e. accumulating one point per year until enough points have become available for a single "stock-recruitment curve" of some sort to be forced onto them. In short-lived fish and shrimps, detailed examination of length-frequency data reveals that recruitment is pulsed, and that generally two pulses (of unequal strength) are generated every year (Pauly and Navaluna 1983, Pauly et al. 1984, and see Fig. 8A)

I strongly suspect this to also be the general case in many squid stocks, (see Fig. 8B) although relatively few sets of squid length-frequency data have been examined. Moreover, a generalized bimodal recruitment would be at variance with some of the accounts in the literature, notably that of Ehrhardt et al. (1983) who claim to have detected five distinct pulses of recruitment per year, but relied on a subjective method of analysis, i.e. tracing growth curves by eye (whereas an objective method, utilizing the whole available sample set in one time was used to derive the recruitment patterns of the type illustrated in Fig. 8).

More elaborate approaches to obtain estimates of recruitment in short-lived fish and invertebrates are length-cohort analysis (Jones 1981, Jones and van Zalinge 1981), and length-structured VPA, two forms of which are incorporated in the ELEFAN III program (written in BASIC and available from the author) and which was applied to the Peruvian anchoveta by Pauly and Tsukayama (1983). These methods, which require fairly detailed catch composition data (e.g. on a monthly basis) over a period of time covering at least 4-5 years offer the real possibility of increasing markedly the number of "points" available for stock recruitment studies. I cannot elaborate here on the statistical problems that must be considered when such approaches are used; all of these can be solved using the appropriate statistical techniques, e.g. time series analysis (Chatfield 1975).

Another aspect of the population dynamics of short-lived animals

which should be discussed explicitly, finally is the fact that the estimation of their annual absolute recruitment is quite straightforward: the annual catch being the product of yield-per-recruit times the number of recruits, estimating recruitment is essentially a question of performing a yield-per-recruit analysis, then estimating absolute recruitment, (R) from

$$R = \text{annual catch/yield per recruit} \quad \dots 11)$$

Estimates of recruitment obtained in this fashion can then be plotted against any variable or combination of variables thought to impact on recruitment, such e.g., as parent stock size, predator biomass and the like.

This approach shall be illustrated here using data from the inshore waters of the Gulf of Thailand (down to 50 m). The relatively well-monitored demersal fishery, which catches approximately 800000 tons of fish and invertebrates per year now also catches 60,000 - 70,000 tons of cephalopods, most of which (80%) consists of squids of the genus Loligo, i.e. L. chinensis (= L. formosana), L. duvauceli and L. uyii (= L. taqoi) (Chotiyaputta 1982, and see Roper et al, 1984 for synonym).

This exercise will be performed by using the vital statistics of a "generalized loliginid squid", as follows:

W_{∞} = 150 g (See Table 1 and Fig. 5)
 K = 1 per year (see Table 1 and Fig. 5)
 t_0 = 0 (assumed)
 M = 2 (based on equation (10) and $T = 30^{\circ}\text{C}$)
 Selection factor (S.F.) = 2.1 (from Amatarunga et. al. 1979)
 Mean length at first capture (L_c) = S.F. x mesh size = 5.25 cm
 Mean weight at first capture (W_c) = 2.1 g (based on L/W relationship in Lange and Johnson 1981)
 Mean age at first capture (t_c) = mean age at recruitment to fishery (t_r) = 0.28 yr.
 Mean age at first maturity = 1 yr.
 Mean relative fecundity = 400 egg/g female (based on loliginid fecundity data in Roper et. al. 1983)

It must be realized that these values are not "averages", or "best estimates" of any kind; they are, rather possible values for use in the illustrative example below. They also represent the minimum data set that must be available from any stock for the method to be applicable.

Table 2 presents the cephalopod catch data and the corresponding fishing mortality, as well as the estimated biomasses of all fish and invertebrates in the Gulf representing here the biomass of all predators (and possibly competitors) of cephalopod prerecruits (see below).

The estimated cephalopod standing stock values in Table 3 were reduced by a fraction (m), corresponding to the fraction of cephalopods >

1 yr in the stock. This fraction, which is a function of F was obtained from

$$m = \frac{e^{-Zr_3} \left(\frac{1}{Z} - \frac{3e^{-Kr_2}}{Z+K} + \frac{3e^{-2Kr_2}}{Z+2K} - \frac{e^{-3Kr_2}}{Z+3K} \right)}{\left(\frac{1}{Z} - \frac{3e^{-Kr_1}}{Z+K} + \frac{3e^{-2Kr_1}}{Z+2K} - \frac{e^{-3Kr_1}}{Z+3K} \right)} \dots 12)$$

Table 3 summarizes the results of all further computations, down to the derivation of the prerecruit mortality indices $(-\log_e R/S)$, which, as might be seen from Fig. 9 declined markedly with total demersal standing stock.

This decline, which corresponds to a change of one order of magnitude of the daily prerecruit mortality (from about 7% to about 0.7%) confirms that the "squid outburst" in the Gulf of Thailand was due to a release of predatory control on cephalopod eggs and prerecruits, as suggested earlier by Pauly (1979) and by some runs of the "Gulf of Thailand model" of Larkin and Gazey (1982, see particularly p. 137).

Conclusions and Summary

Whether, as stated by Juanico (1983), squids differ markedly from fish with regards to the major features of their population dynamics, or not should not remain a matter of opinion. Rather, Juanico's view may be seen as a hypothesis which can be tested by deliberately applying to squids those methods and models which have been most successfully been applied to fish and shrimps.

To model the growth of squids, a seasonally oscillating version of the von Bertalanffy growth formula is proposed - along with an objective method (the ELEFAN I program) for fitting it to length-frequency data which should (a) help resolve whether growth patterns differ markedly between fish and squids when account is taken of seasonal growth oscillations and (b) allow for comparative studies of growth performance in different species of squids, and thus for inferring growth parameters in little-known species.

The study of squid mortalities could be greatly accelerated by the systematic application of length-converted catch curves. However, rigorous selection experiments, notably on jigs, will have to be conducted if definitive conclusions, e.g. on post-spawning mortalities are to be drawn from the shape of such curves.

Natural mortalities, in squids (prior to post-spawning mortality) should be similar to those of fishes with matching growth parameters. If so, it will be possible to obtain reasonable estimates of M from the empirical equation given above.

With regards to recruitment studies, the short life-span of squids can be quite straight-forwardly turned from a liability into an asset. Two lines of thoughts are presented which illustrate this: one makes use of within-year recruitment fluctuations to infer on between year fluctuations; the other relies on the lack of overlap between cohorts to

provide mutually independent estimates of recruitment from annual catch estimates and a few ancillary data.

Such independent estimates of recruitment can be used to test hypotheses on the trophic and other interactions linking squids and their biotic and abiotic environment. This approach thus helps bridge the gap between "population dynamics" and the "ecological" studies which Caddy (1983) wrote about.

It is my impression, finally, that nothing can be gained by emphasizing the differences between squids and fish, and - if only by inference - by suggesting that methods developed to study fish will not work when applied to squids. Rather, "fish models" of known properties should be applied systematically to squids, and the "deviation" from such models studied in detail, because it is these deviations which will tell us how squids are different from fish.

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Table 1. Some estimates of growth parameters of squids^a, with corresponding values of ϕ and M computed from equations (3) and (10), respectively, and approximate mean environmental temperatures (in brackets).^b

#	Species	Area	L _∞ ML (cm) ^c	W _∞ live weight (g)	K per year	ϕ	M	Remarks
1	<i>Loligo pealei</i>	Off New England (14.5°C)	38.3	680	0.59	1.66	0.868	L _∞ and K from Ikeda and Nagesaki (1975), conversion of L _∞ to W _∞ based on Lange and Johnson (1981)
2	<i>Loligo pealei</i> ♀	Gulf of Mexico (24°C)	23	207	0.96	1.62	0.638	See Fig. 6; conversion of L _∞ to W _∞ based on Lange and Johnson (1981)
3	<i>Illex illecebrosus</i> ♀	Off Canada (9°C)	29.4	500	0.65	1.61	0.762	^d From Lange and Sissenwine (1983), citing Amarutunga (1980), which I have not seen. (Lange and Sissenwine (1983) give L _∞ = "2.39" and "2.94" for males and females, respectively; this should presumably read as corrected here)
4	<i>Illex illecebrosus</i> ♂	Off Canada (9°C)	23.9	290	1.08	1.68	1.12	
5	<i>Illex illecebrosus</i>	Northwest Atlantic (12°C)	32.0	600	2.5	2.25	2.13	L _∞ and K from Au (1975); conversion of L _∞ to W _∞ based on Lange and Johnson (1981)
6	<i>Dosidicus gigas</i>	Gulf of California (21.5°C)	96	22,000	1.2	4.42	1.26	L _∞ , W _∞ and K computed from Ehrhardt et al. (1983)
7	<i>Onychoteuthis borealijaponica</i> ♀	East of Hokkaido (8°C)	40	1,575	0.47	1.80	0.527	^d L _∞ , W _∞ and K values computed from data in Okutani and Murata (1983), using set values of L _∞ and the method of Gaschütz et al. (1980), which also provided estimates of C (see equation 2) of 1.40 (♀) and 4.3 (♂), both suggestive of a long (winter) period with no growth
8	<i>Onychoteuthis borealijaponica</i> ♂	East of Hokkaido (8°C)	35	1,600	0.48	1.82	0.534	

^aSeveral of the sets of growth parameters included here are manifestly erroneous, as shown either by their lack of consistency with other estimates (as expressed by the ϕ values) and/or by their position on an auximetric grid (Fig. 5). This can be largely attributed to the subjectivity of the methods used for tracing growth curves, and to the effects of seasonal growth oscillations (see text and Fig. 3).

^bSea surface temperatures taken from Anon. (1944) except for Gulf of Mexico, taken from Rivas (1968).

^cML = mantle length.

^dThe frames enclose values of ϕ that appear to be mutually consistent (see also Fig. 5).

Table 2. Selected information on the Gulf of Thailand demersal stock and fishery, 1961 to 1980.^a

Year	Total standing stock (tons x 10 ³) ^b	Fishery mortality ^c	Cephalopod catch (tons x 10 ³)	Year	Total standing stock (tons x 10 ³) ^b	Fishery mortality ^c	Cephalopod catch (tons x 10 ³)
61	624	0.17	3.33	71	176	3.46	39.7
62	621	0.21	4.03	72	168	4.39	45.0
63	618	0.32	6.00	73	139	5.98	51.0
64	604	0.53	9.12	74	155	3.90	48.4
65	471	0.72	12.2	75	125	6.02	53.5
66	353	1.03	15.4	76	152	5.18	58.2
67	307	1.42	18.5	77	125	6.78	76.9
68	204	2.52	23.8	78	139	5.86	71.3
69	275	1.89	29.1	79	137	6.08	66.4
70	258	2.05	34.4	80	127	6.28	61.4

^aBased on data in Boonjubil and Pramokchutima (1982), complemented with information in Sakurai (1974).

^bBased on the swept-area method.

^cBased on annual estimates of total catch from the Gulf and equation (8); these estimates of F are also assumed to apply to the cephalopods component of the multispecies stock.

Table 3. Showing step-by-step approach to computation of a prerecruitment mortality index ($-\log_e R/S$) in Gulf of Thailand cephalopods.^a

Year	Cephalopod biomass (tons x 10 ³) ^b	Fraction mature ^c	S = eggs spawned (x 10 ⁹) ^d	Y/R (grams) ^e	Recruits (x 10 ⁹) ^f	Mortality index $-\log_e (R_i/S_{i-1})$
61	19.6	0.575	2,250	1.86	1.79	—
62	19.2	0.566	2,170	2.22	1.82	7.12
63	18.2	0.542	2,040	3.05	1.97	7.00
64	17.2	0.497	1,710	4.23	2.16	6.85
65	16.9	0.458	1,550	4.94	2.43	6.56
66	14.9	0.398	1,190	5.64	2.73	6.34
67	13.0	0.330	858	6.04	3.06	5.96
68	9.44	0.187	353	6.01	3.96	5.38
69	15.4	0.261	804	6.15	4.73	4.31
70	16.8	0.240	806	6.13	5.61	4.97
71	11.5	0.110	253	5.63	7.05	4.74
72	10.2	0.063	128	5.24	8.59	3.38
73	8.53	0.024	40.9	4.68	10.9	2.46
74	12.4	0.085	211	5.44	8.90	1.53
75	8.89	0.023	40.9	4.66	11.5	2.91
76	11.2	0.039	87.4	4.94	11.8	1.24
77	11.3	0.014	31.6	4.45	17.3	1.62
78	12.2	0.026	63.4	4.71	15.1	0.74
79	10.9	0.022	48.0	4.65	14.3	1.49
80	9.78	0.020	39.1	4.59	13.4	1.28

^aThis approach follows essentially the method outlined in Pauly (1980b, 1982b), except for the feature that recruitment is divided by the egg production of the *preceding* year, as suggested by Murphy (1982), Garcia (1983) and Bayley (1984).

^bObtained using catch and F estimates in Table 2, and the relationship $B = Y/F$.

^cDerived from equation (12), F values in Table 2 and vital statistics in text.

^dObtained by performing: Biomass x fraction mature x relative fecundity x 0.5 (= fraction of ♀♀ in stock).

^eConventional Y/R analysis, using vital statistics in text and F values in Table 2.

^fObtained by applying equation (11).

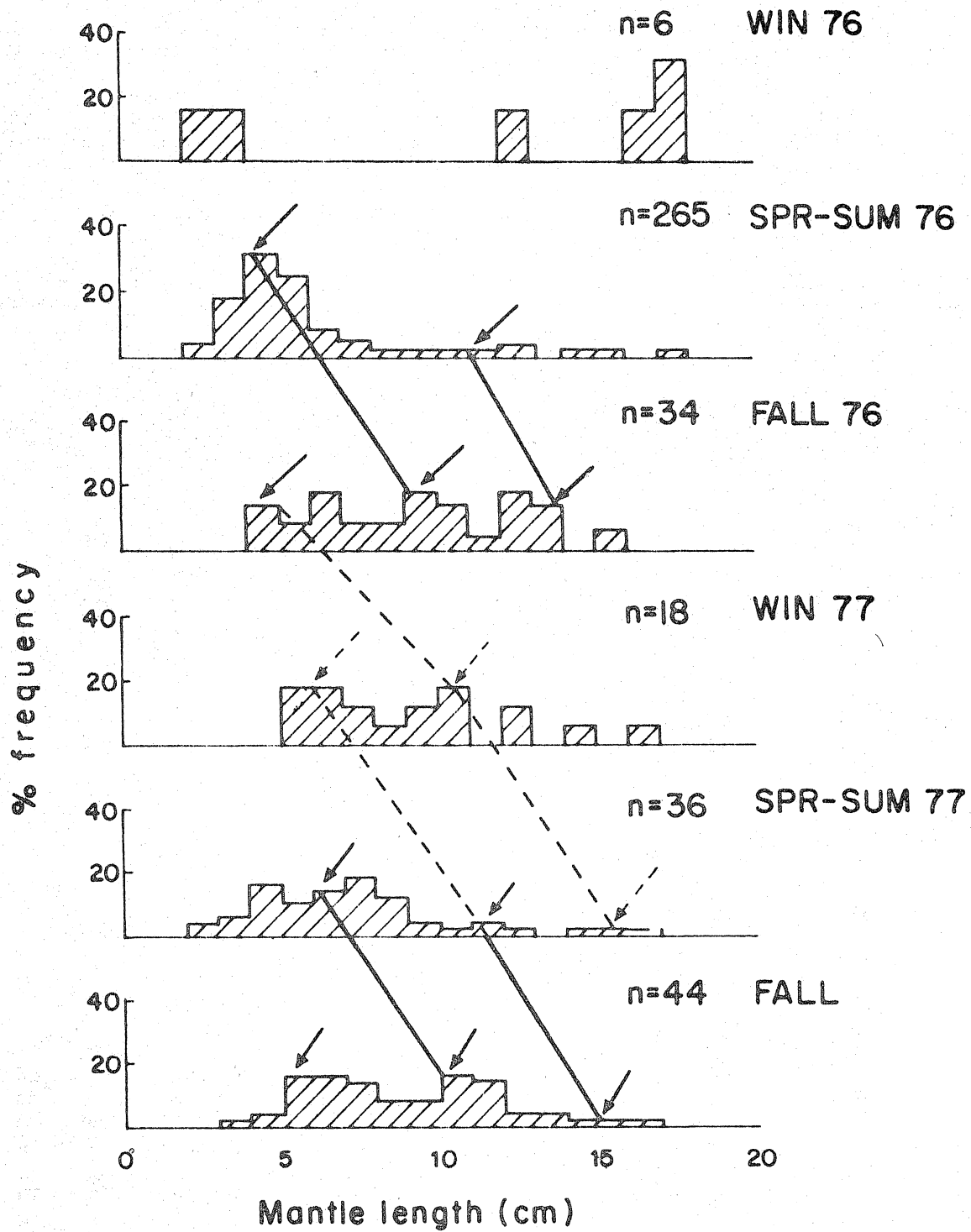


Fig. 1. Original legend to this graph, redrawn from Hixon et al. (1981) read as follows: "Size frequency distribution females of *Loligo pealei* obtained from six seasonal collections in 1976 and 1977. Mean lengths of well defined modes designated by a solid arrow. Dashed arrows indicate less certain mean modal lengths estimated by the probability paper method. Lines drawn between modes depict increases in mantle length between successive season. Solid lines indicate growth between well defined modes; dashed lines designate growth based on less certain modes." Note lack of explicit criteria in selection of modes linked by assumed growth (see also Fig. 6), and erroneous tracing of lines, which should link the *bases* of the modal classes considered, rather than their peaks.

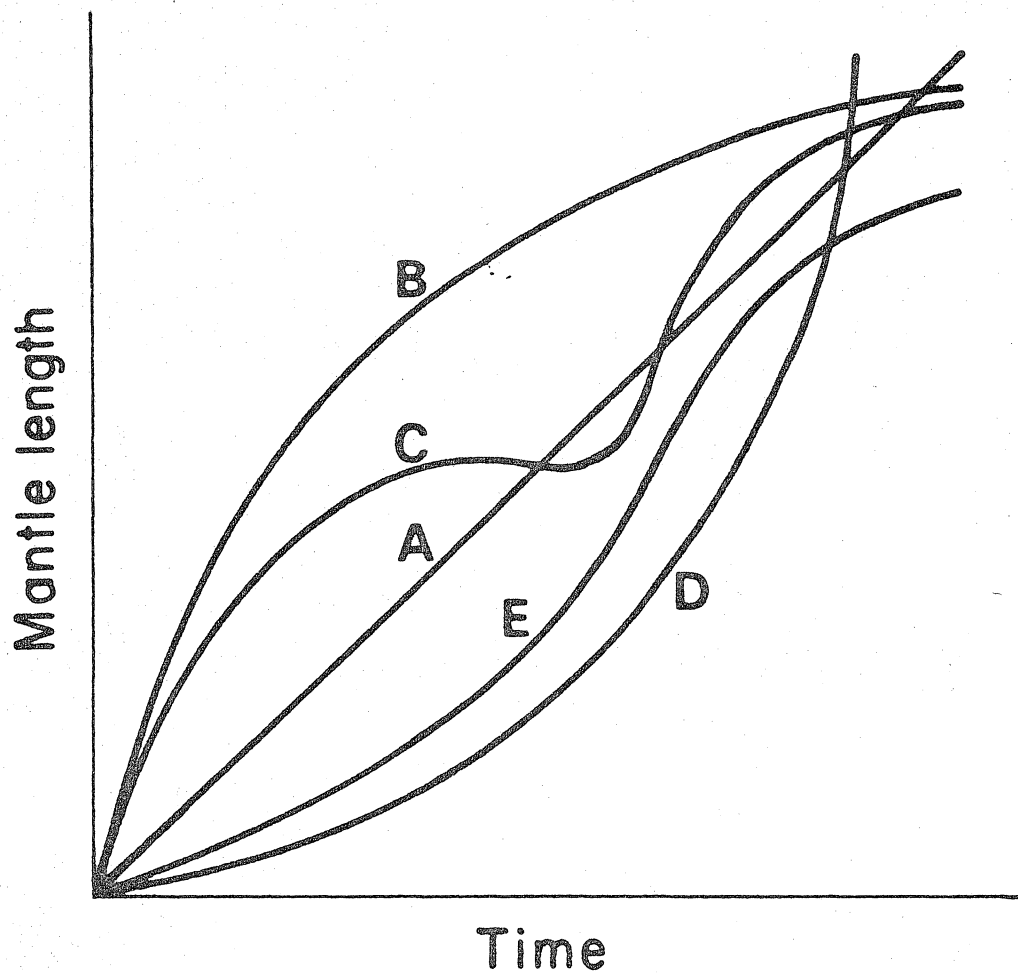


Fig. 2. Growth curves for five loliginid species (after Hixon 1980). A = linear growth (*Loligo opalescens*, Fields 1965), B = asymptotic growth (*L. pealei*, Verrill 1881), C = cyclic growth (*L. vulgaris*, Tinbergen & Verwey 1945), D = exponential growth (*L. vulgaris*, Mangold-Wirz 1963; *L. pealei*, Summers 1971), E = sigmoid growth (*L. pealei*, *L. plei*, *Lolliguncula brevis*, Hixon 1980).

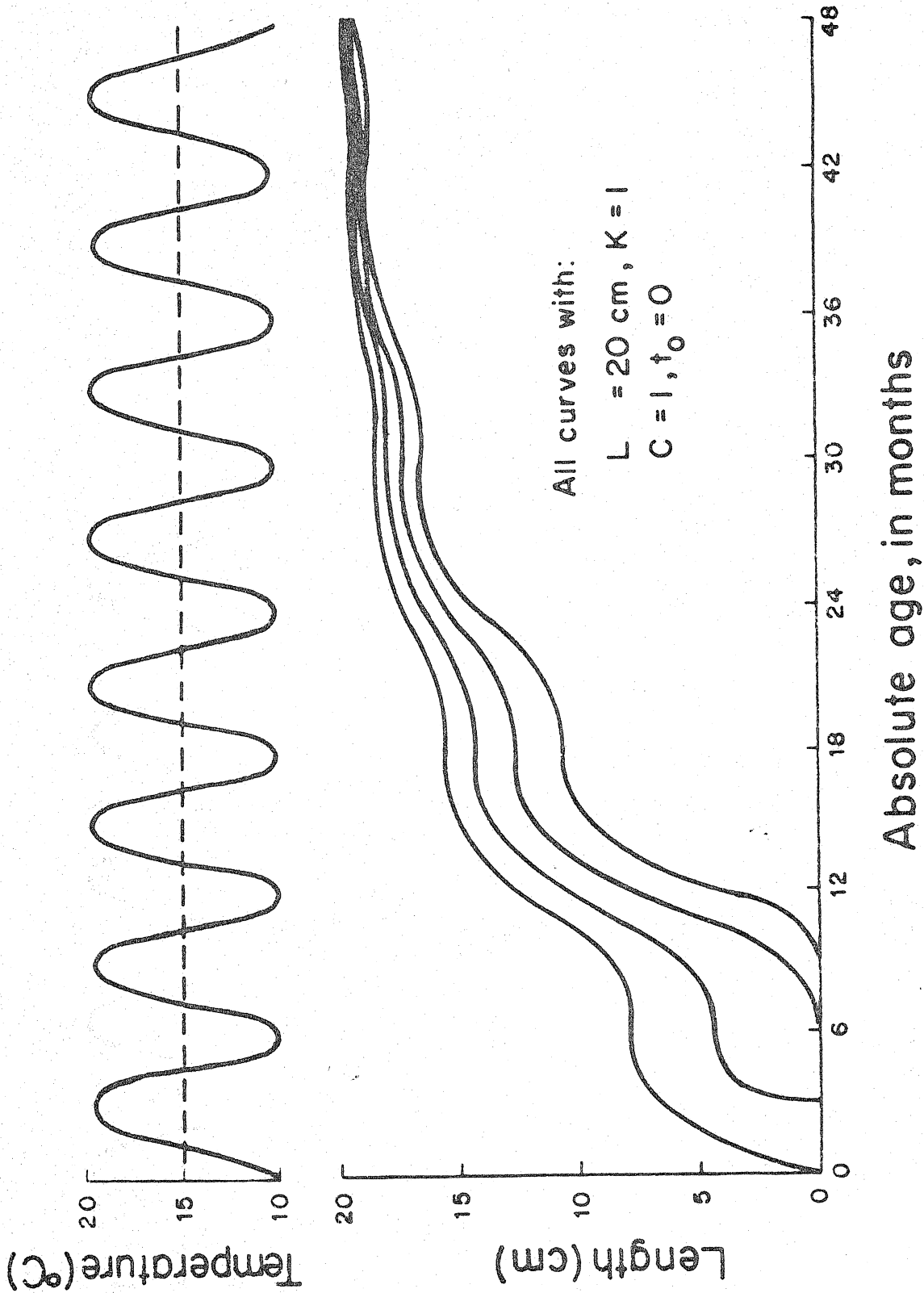


Fig. 3. Four growth curves drawn using equation (2), a seasonally oscillating version of the von Bertalanffy Growth Function, and the same set of parameter values (L_{∞} , K , C and t_0). The curves, which differ only in their value of t_0 , closely duplicate the variety of shapes assumed representative of squid growth (see also Fig. 2). Note also that "paper and pencil" length-frequency analysis, which must rely on the well-separated, younger age groups, will necessarily overemphasize the apparent difference in growth, and miss the underlying overall growth pattern modified by the temperature-induced oscillations. (See also Figs. 4, 6 and text)

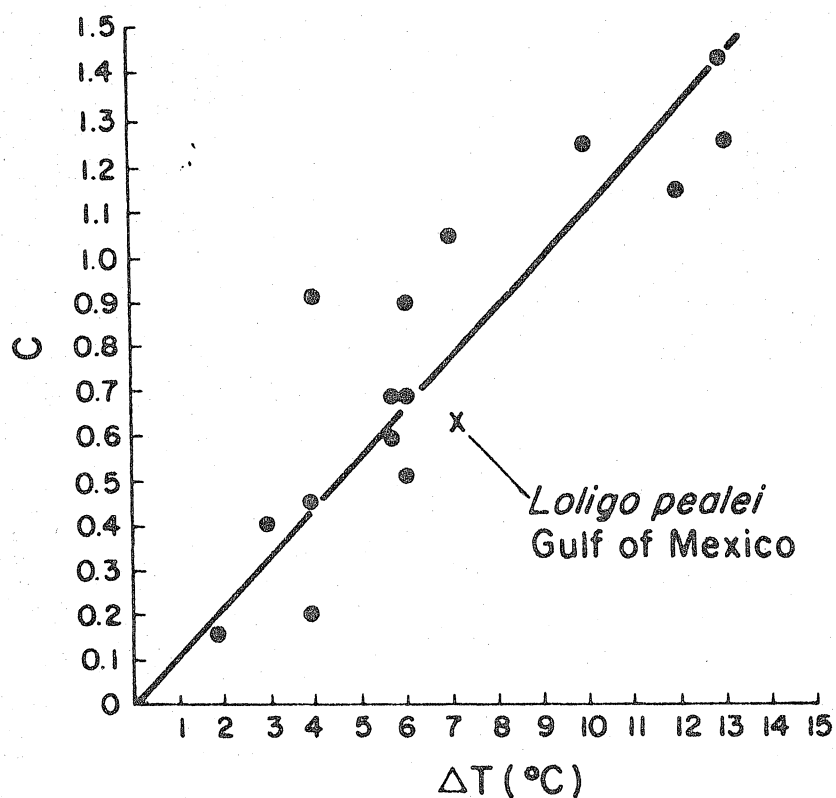


Fig. 4. Relationship between intensity of seasonal growth oscillation, of fish and shrimps as expressed by the parameter C of equation (1) and the difference between highest and lowest mean monthly water temperature in the course of one year (ΔT). (Adapted from Pauly et al. 1984). Note that value of $C = 0.65$ for *Loligo pealei*, derived in Fig. 6, matched with the appropriate value of $\Delta T = 7.2^{\circ}\text{C}$ (from Rivas 1968) fits into the general pattern, suggesting that growth oscillations, in squids, can be explained, as in fish and shrimps by the temperature oscillations of their habitats.

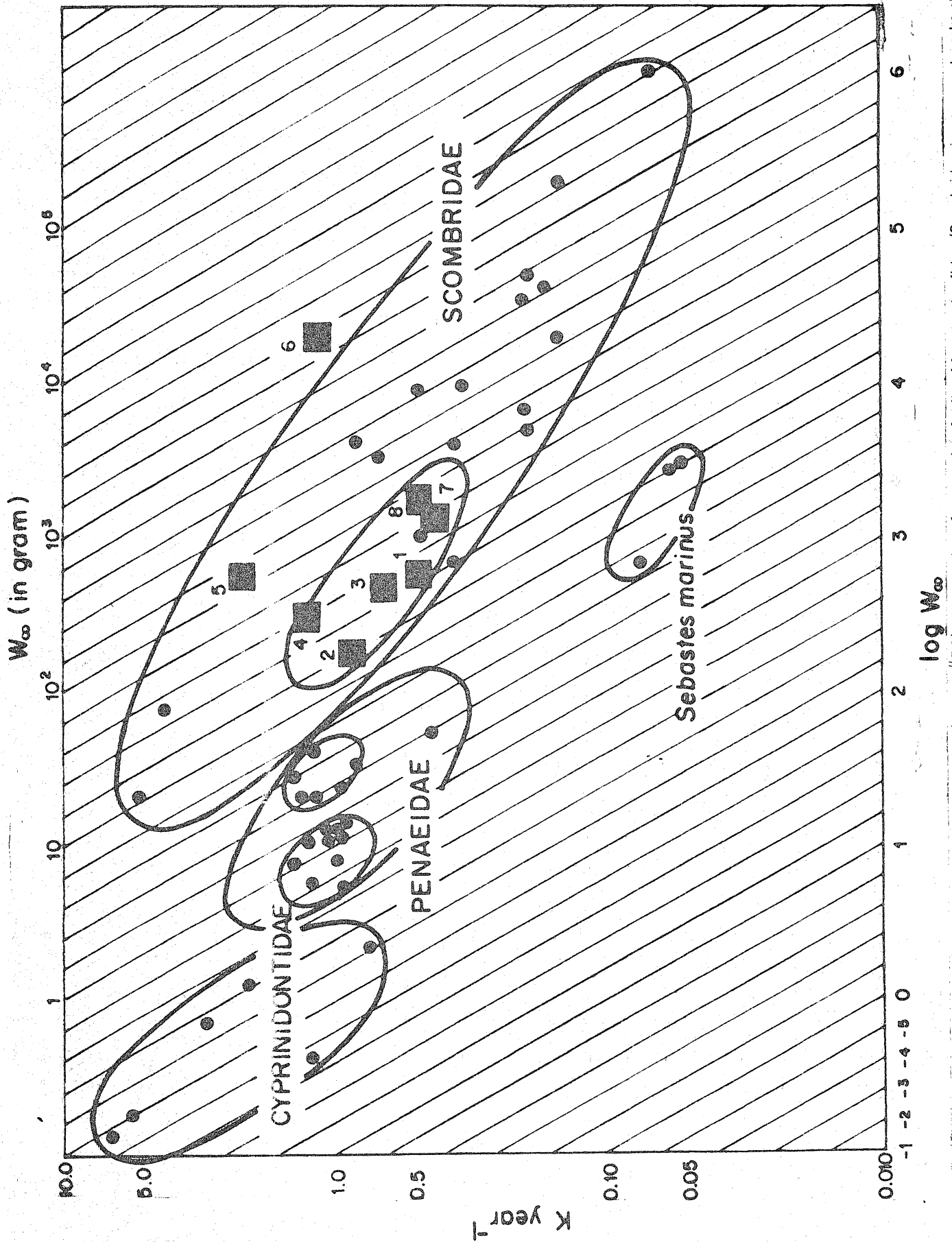


Fig. 5. Comparison of the growth performance of the squids in Table 1 (squares #7-8) with growth performance in a family of fast-growing fishes (Scombridae, i.e., tuna and mackerels), a family of extremely short-lived fishes (Cyprinodontidae, i.e., guppies) and another group of invertebrates (several genera of penaeid shrimps) by means of an auximetric grid *sensu* Pauly (1980b). Note also low growth performance of the very long-lived redfish (*Sebastes marinus*). The grid leads to the (tentative) conclusion that squids are as fast growing as their pelagic competitors, but that two sets of growth parameters (#5 and 6) are probably erroneous. The fish growth parameters used here are documented in Pauly (1980b); the shrimp data are from Pauly et al. (1984).

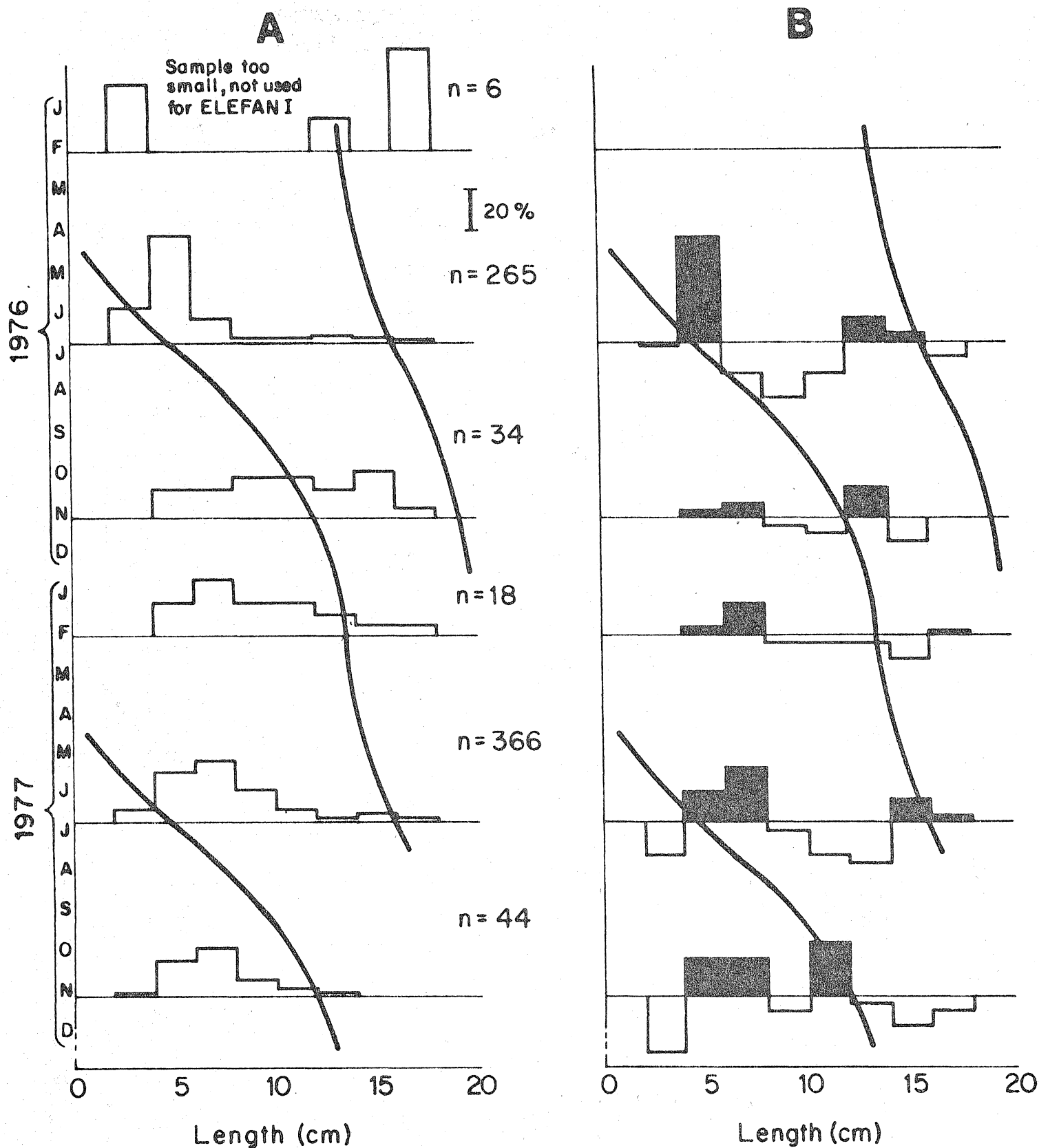


Fig. 6. Length-frequency data of Fig. 1 (*Loligo pealei* ♀) reanalyzed using the ELEFAN I program. Note in (A) regrouping of L/F data into a smaller number of length-classes and (B) restructuring of L/F samples, as performed by the ELEFAN I program to identify seasonally oscillating growth curves best explaining data at hand. This growth curve has the parameter values $L_{\infty} = 21.5$, $K = 0.285$, $WP = 0.05$ and $C = 0.5$ (see also Figs. 4, 5, 9 and Table 1).

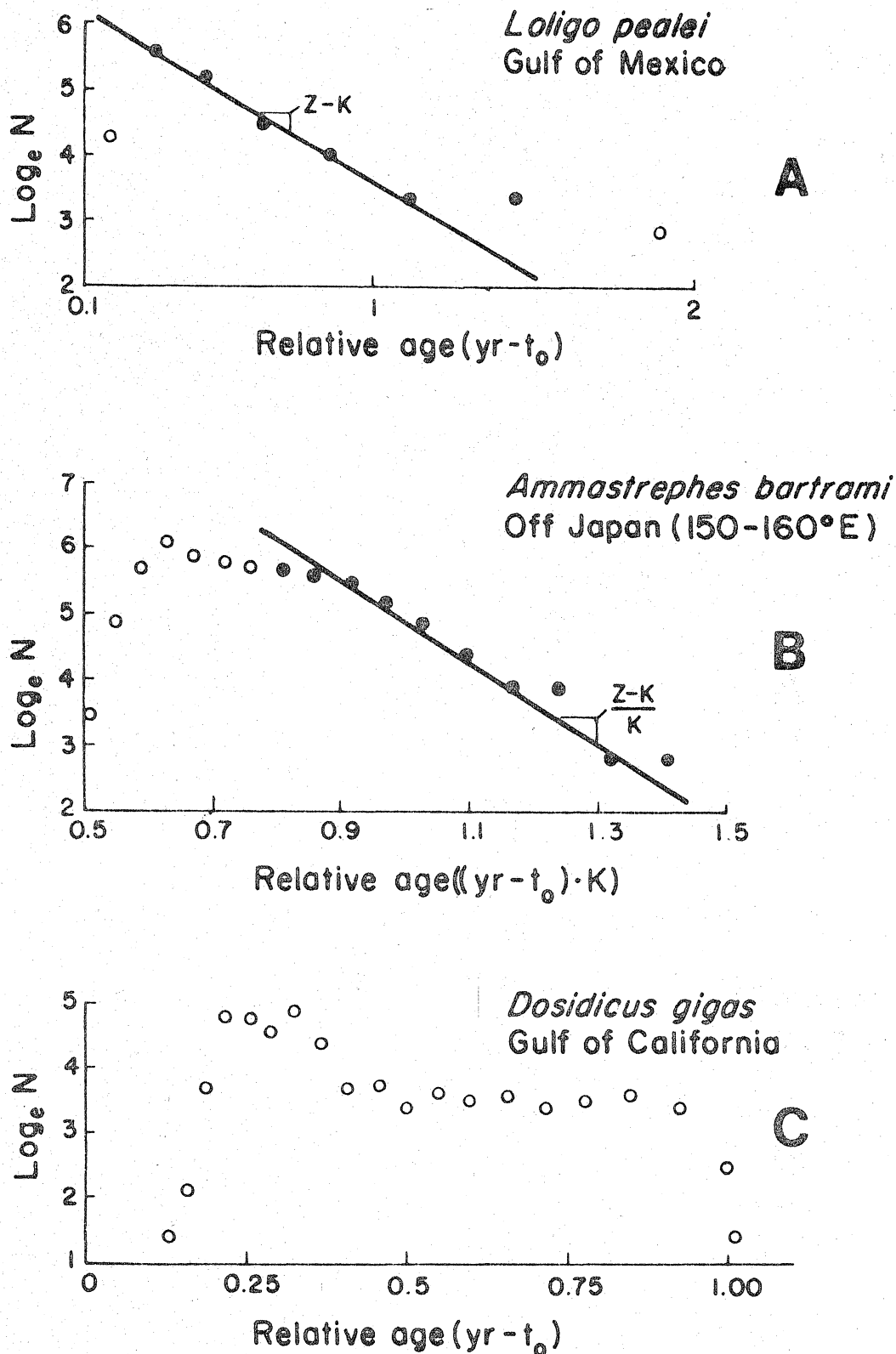


Fig. 7. Examples of length-converted catch curves for squids. A: *Loligo pealei*, based on data in Fig. 1, with successive samples first transformed into percent samples then weighted by the square root of sample size prior to addition by length class, to obtain an annual average sample, more or less representative of the population as a whole (see Pauly 1984). The slope of the catch curve is $b = -1.82$, and hence $Z = 2.82$. The values of L_∞ and K used for the conversion to relative ages are given in Fig. 6. B: *Ammastrephes bartrami*, based on 1979 length-frequency data ($n = 3233$) in Fig. 9 of Araya (1983); note lack of evidence for a large increase of mortality associated with spawning (but see Araya 1983, p. 278). The values of L_∞ used here was 45 cm, as suggested in Roper et al. (1984). C: *Dosidicus gigas*, based on length-frequency data in Fig. 7 (below) and growth parameters $L_\infty = 9.6$ cm and $K = 1.2$ from Ehrhardt et al. (1983). Note shape of curve, suggestive of marked post spawning mortality (but see text).

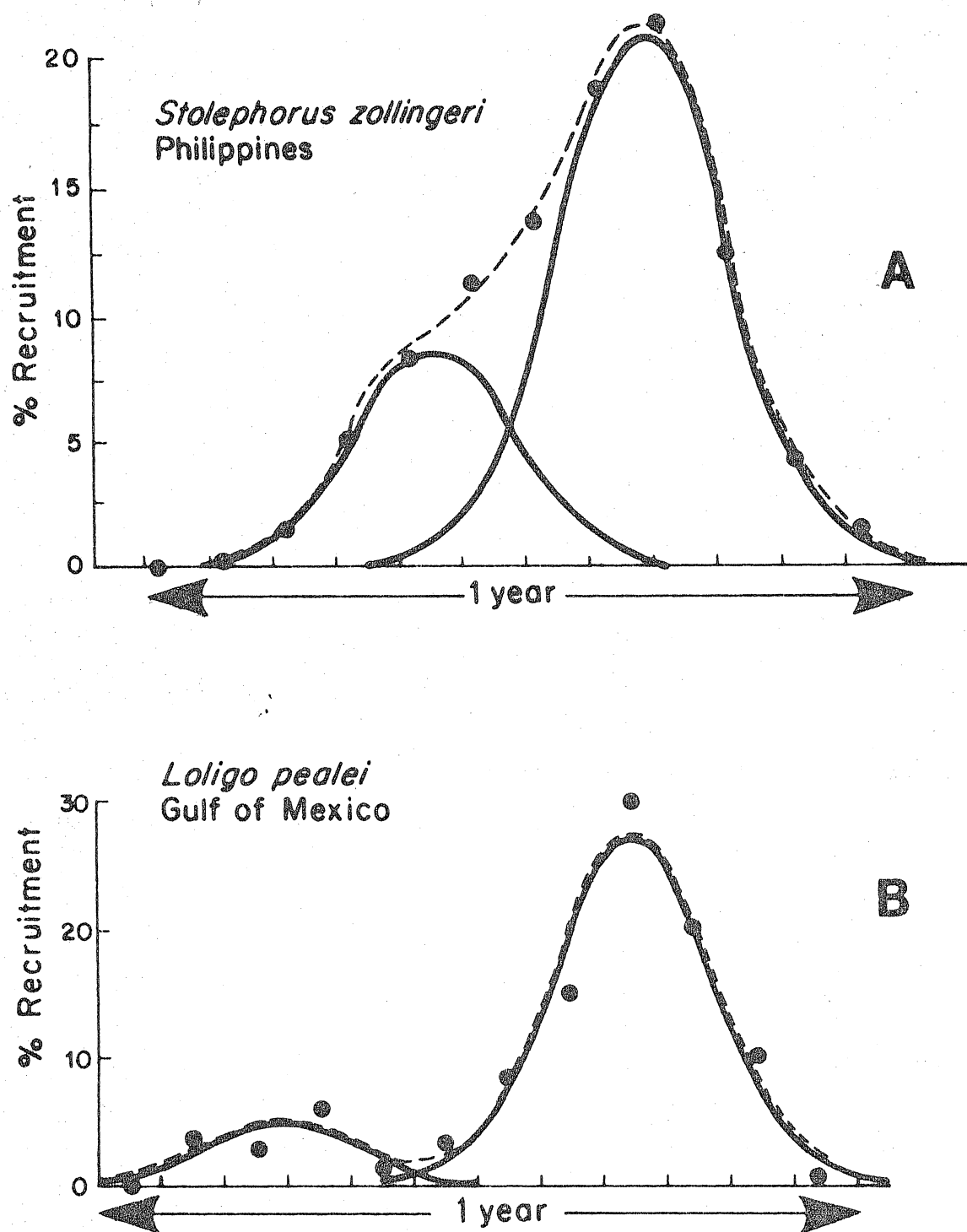


Fig. 8. Recruitment patterns, obtained by projecting a set of length-frequency data onto the time axis, using growth parameters L_{∞} and K and the ELEFAN II program (Pauly 1982). A: recruitment pattern of a very short-lived anchovy ($t_{max} \approx 1$ year) from Manila Bay, Philippines (from Pauly and Navaluna 1983) and B: recruitment pattern for *Loligo pealei* from the Gulf of Mexico (based on length-frequency data in Fig. 1 and growth parameters estimated in Fig. 6). Note suggestion of two recruitment pulses per year in both cases (the small sample size in the case of *L. pealei* should preclude attaching too much importance to this finding, however).

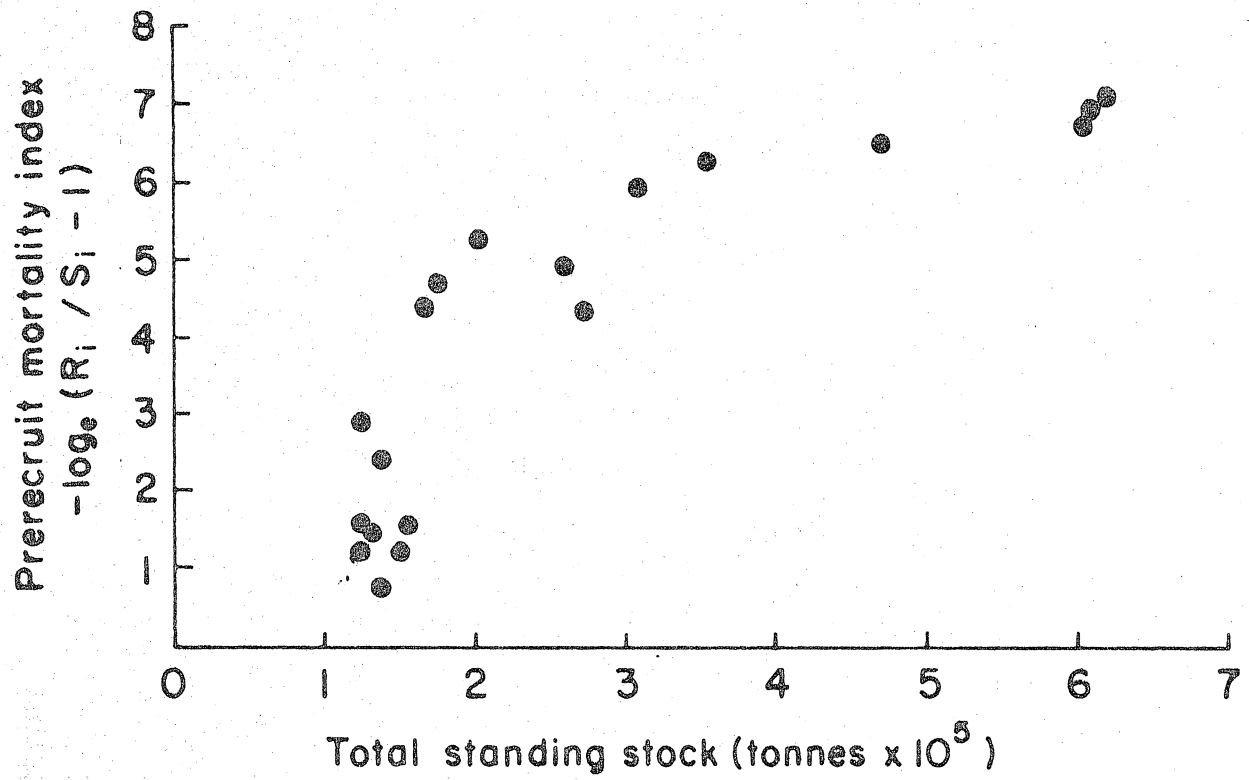


Fig. 9. Relationship of estimated prerecruit mortality in Gulf of Thailand cephalopods to total fish biomass in the Gulf's inshore waters, 1961-1980.