

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

Daniel Pauly

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

## Abstract

The features of short-lived fishes 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 fishes and squids to quantitative differences, and, hence, to render squids amenable to the kind of comparative studies which, for fish, have rendered preliminary stock assessments possible even when data are scarce.

## Introduction

This invited paper which deals 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, the commercially-important short-lived species occur predominantly in tropical waters, where relatively little research in population dynamics is conducted. Thus, many stock-assessment specialists, who rely predominantly on virtual population analysis (VPA), found themselves conceptually and methodologically unprepared when they were confronted in the mid-1970's with having to assess the newly-exploited squid stocks and to derive management measures for them. Indeed, investigations of short-lived species, such as the squids, require a return to the basic concept of Russell (1931) which states that

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

or that future biomass ( $B_2$ ) of a stock with no emigration or immigration is a function of its original biomass ( $B_1$ ), plus weight of recruits ( $R^*$ ) and growth of the recruited animals ( $G^*$ ), minus the catch ( $Y$ ) and the weight of animals dying of natural causes ( $M^*$ ). Equation (1) is an obvious basis for this contribution, which is structured as a review of methods to measure or predict each of the parameters in populations of short-lived animals, particularly squids.

## Growth

What appear to be successful attempts to age squids by means of daily rings in their statoliths have been reported by Spratt (1978) for *Loligo opalescens* and by Kristensen (1980) for *Gonatus fabricii*. A theory exists (Lutz and Rhoads, 1977) which seeks to explain

the origin and nature of these rings, with the implication that they should be as ubiquitous in molluscs as daily rings are in the otoliths of fishes. Indeed, this theory could, with suitable generalization, also explain the occurrence of daily rings in fish otoliths, since the basic mechanisms in both fishes and molluscs involve short-term anaerobiosis during periods of activity (Pauly, 1981, 1982a).

Ageing of squids by means of daily rings in statoliths appears to involve too much work, even in short-lived forms, to become a routinely-applied method, especially if the generalization that squid growth rate is extremely variable within populations proves to be true (Caddy, 1983). This obviously leads, for the lack of a better alternative, to often murky methodologies that are used to infer growth rates and growth curves from size (especially length) frequencies. Many researchers, involved in studying fish, squid and 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 representing the results as "growth" rates (Fig. 1).

As far as research on squid growth is concerned, the chief result of this belief has been growth parameters that are often mutually inconsistent and represent an array of contradictory statements about the growth of squids, which is perceived to be "linear", "exponential", "asymptotic" or "oscillating" (Fig. 2) (see also tables 6 and 7 of Lange and Sissenwine, 1983). Until recently, similar confusion was characteristic of shrimps, but, 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 LeReste, 1981). This can be

\* ICLARM Contribution No. 207.

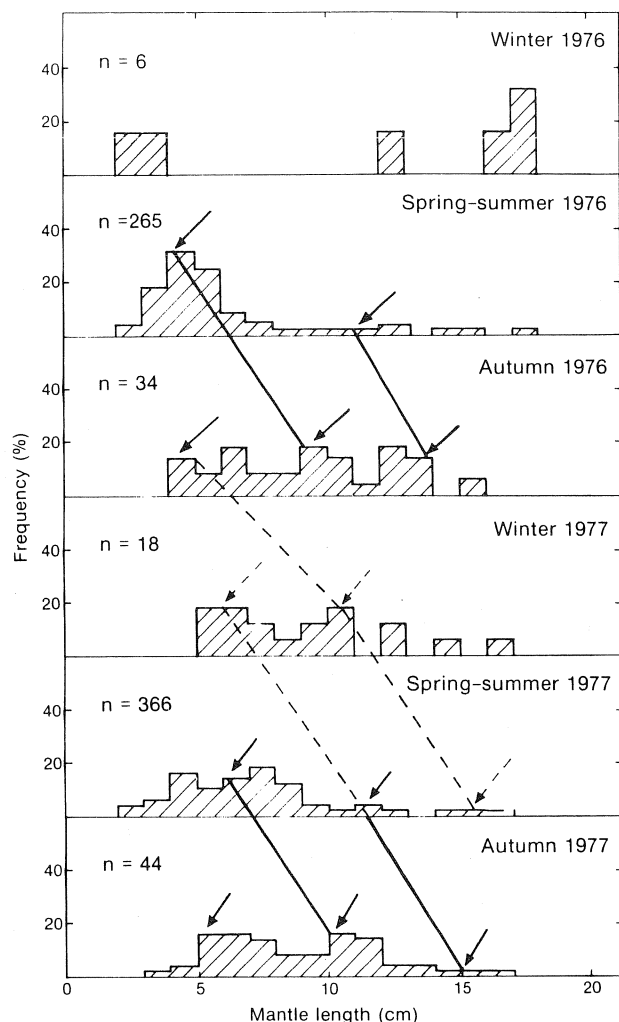


Fig. 1. Original legend to this graph, redrawn from Hixon *et al.* (1981) reads as follows: "Size frequency distribution of ... females of *Loligo pealei* obtained from six seasonal collections in 1976 and 1977. Mean lengths of well defined modes designated by a solid arrow. Dashed arrows indicate less certain mean modal lengths estimated by the probability paper method. Lines drawn between successive modes depict increases in mantle length between successive seasons. 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.

expressed by a modified von Bertalanffy model of the form

$$L_t = L_{\infty} \left\{ 1 - e^{-\left( K(t-t_0) + \frac{CK}{2\pi} \sin 2\pi(t-t_0) \right)} \right\} \quad (2)$$

where  $L_t$  is length (cm) at age  $t$ ,  $L_{\infty}$  is asymptotic length,  $K$  and  $t_0$  are the same constants as in the normal von Bertalanffy model,  $C$  is a constant expressing the amplitude of the growth oscillations, and  $t_s$  is the onset

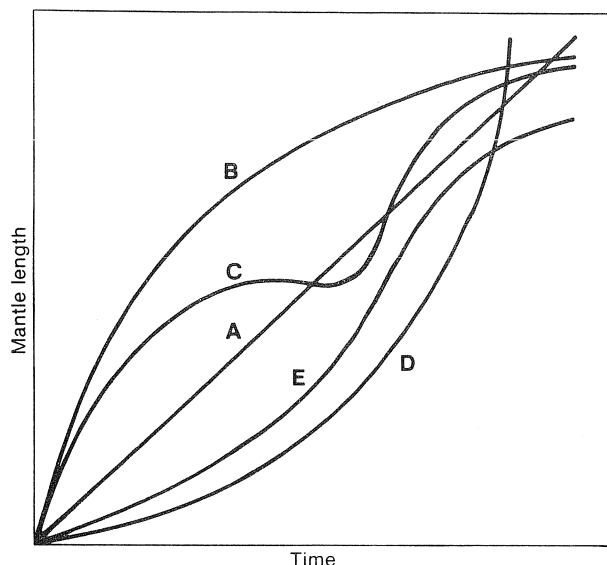


Fig. 2. Growth curves for five loliginid species (after Hixon, MS 1980). A, linear growth of *Loligo opalescens* (Fields, 1965); B, asymptotic growth of *L. pealei* (Verrill, 1881); C, cyclic growth of *L. vulgaris* (Tinbergen and Verwey, 1945); D, exponential growth of *L. vulgaris* (Mangold, 1963)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

of sinusoid oscillations with respect to  $t = 0$ . Thus, the key hypothesis here is that, within populations, what appear to be differences in growth characteristics are artefacts due to changes in birthdate (Fig. 3). 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 that are exposed to seasonal temperature oscillations (Fig. 4).

Another advantage of using a standard growth model, such as the above-mentioned seasonalized von Bertalanffy growth equation, to express the results of growth studies is that it offers the possibility of conducting comparative studies among various populations of the same squid species, among various squid species (see Table 1) and between squids and fishes (Fig. 5), and hence to use the information available for some species within a given genus or family to infer the growth performance of species for which data are not available.

One approach, which works rather well for fishes and shrimps, is to rely on the within-group constancy of the parameter  $\phi$ , which is defined in base 10 logarithms as

$$\phi = \log K + 2/3 \log W_{\infty} \quad (3)$$

where  $W_{\infty}$  is the asymptotic whole weight (g) corresponding to  $L_{\infty}$  in equation (2), and the growth coefficient ( $K$ ) is expressed on an annual basis (Pauly,

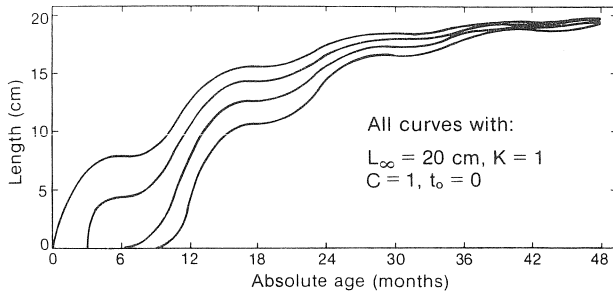


Fig. 3. Four growth curves drawn from a seasonally oscillating version of the von Bertalanffy growth function with the same set of parameters ( $L_\infty$ ,  $K$ ,  $C$ ,  $t_0$ ) and different values of  $t_0$ . (Note that these curves closely duplicate a variety of shapes assumed representative of squid growth. Subjective length-frequency analysis, which must rely on the well-separated, younger age-groups, will necessarily overemphasize the apparent differences in growth and miss the underlying overall growth pattern modified by temperature-induced oscillations.)

1980b; Munro and Pauly, 1983; Pauly and Munro, 1984).

For practical purposes, the use of equation (3) consists of estimating a mean value of  $\phi$  for a given group of species from available  $W_\infty$  and  $K$  pairs of values for the group, and relying on  $\phi$  to obtain preliminary estimates of  $K$  for species (or stocks), for which growth data are not available, from the formula

$$\log K = \phi - 2/3 \log(W_\infty) \quad (4)$$

where ( $W_\infty$ ) is an estimated value of the asymptotic weight which is derived from maximum weight ( $W_{\max}$ ) for a given stock (e.g. Roper *et al.*, 1984) by the relationship

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

This 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, and the systematic application of consistent, objective methods for length-frequency analysis (Fig. 6), could alleviate rapidly the present dearth of knowledge on the growth of squids and help researchers obtain a "feel" for the growth performance of squids similar to that which biologists now have for fishes.

### Estimation of Mortality and Biomass

Estimating mortalities of short-lived animals is usually problematic, especially when individual animals are difficult to age. One approach, which is becoming increasingly popular in studies of fishes and

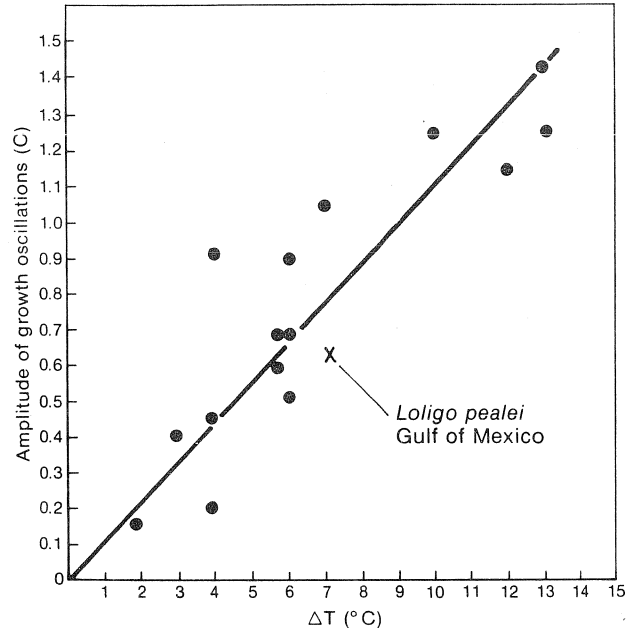


Fig. 4. Relationship between amplitude of seasonal growth oscillations for fishes and squids, as expressed by parameter  $C$  of equation (2) and the difference between highest and lowest monthly water temperature in the course of 1 year ( $\Delta T$ ), as adapted from Pauly *et al.* (1984). (Note that  $C = 0.65$  for *L. pealei*, derived in Fig. 6, matches with the appropriate value of  $\Delta T = 7.2^\circ\text{C}$  (from Rivas, 1968) and fits into the general pattern for fishes and shrimps.)

shrimps, is the use of "length-converted catch curves", which are based on length-frequency data whereby lengths are converted to their corresponding (relative) ages by means of a set of growth parameters ( $L_\infty$  and  $K$ , with a simple correction for non-linearity of growth). Total mortality ( $Z$ ) is estimated from the descending right limb of the curve (Fig. 7A). Length-converted catch curves, as in the case of standard age-based catch curves, are based on the assumption that all cohorts in the available data experience the same total mortality (Ricker, 1975; Pauly, 1984). This assumption is probably not fully applicable in the majority of cases. However, estimating mortality for each cohort separately will often be too demanding of data from the squid stocks, and the pooling of cohorts will usually be the only approach toward obtaining reasonable estimates of mortality.

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

1. Obtain periodic (e.g. monthly) length-frequency samples, preferably over a period of 1 year, such that a cumulative sample can be derived. This sample should, as far as possible, be representative of the average length composition of the stock, such that seasonal pulses are evened out.

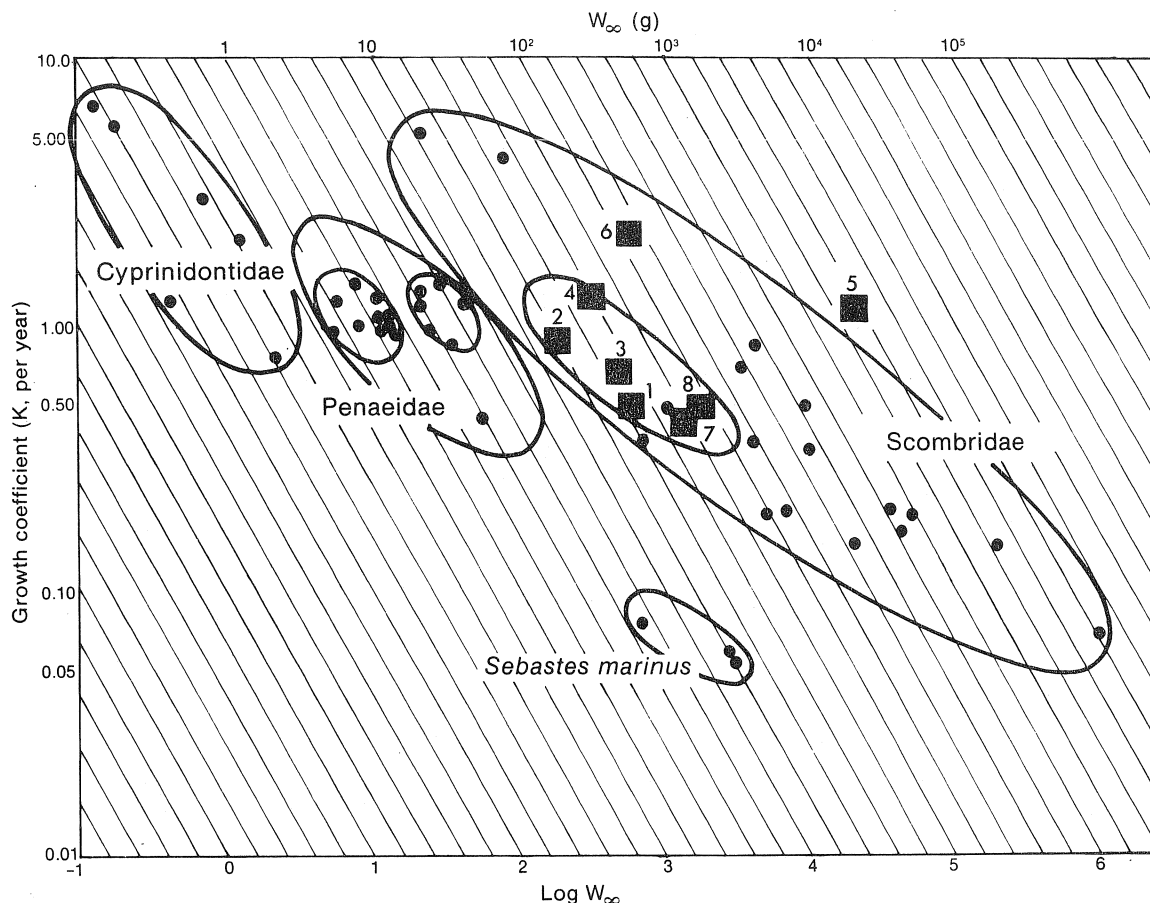


Fig. 5. Comparison of growth performance of squids (No. 1-8 from Table 1) with that of a family of fast-growing fishes (Scombridae, tunas and mackerels), a family of short-lived fishes (Cyprinodontidae, guppies), a long-lived redfish (*Sebastes marinus*), and a family of shrimps (Penaeidae) by means of an auximetric grid. (The fish growth data were documented by Pauly (1980b) and the shrimp data by Pauly *et al.* (1984). The grid indicates that squids are as fast-growing as their pelagic competitors, but the growth parameters for data sets 5 and 6 in Table 1 are probably erroneous.)

2. Estimate the "relative" age ( $t'_i$ ) that corresponds to the lower class limit of each length class ( $L_i$ ) from the relationship

$$t'_i = -\ln(1-L_i/L_\infty)/K \quad (6)$$

where  $\ln$  refers to natural logarithms. Here,  $t'_i$  is called "relative", because, with  $Z$  being estimated from the slope of the catch curve,  $t_0$  can be assumed to be zero. Also, seasonal growth oscillations need not be considered because an "average" sample is analyzed.

3. Plot the cumulated number of squid in each length class ( $N_i$ ) against the corresponding  $t'_i$  value (see Fig. 7, A-C) and estimate (when possible)  $Z$  from the descending (linear) right limb of the catch curve, i.e. from the slope of

$$\ln N_i = a + bt'_i \quad (7)$$

which can be turned into an estimate of  $Z$  by the relationship

$$|b| + K = Z \quad (8)$$

When parameter  $K$  of the von Bertalanffy growth equation is not known, relative age can be defined as  $t'_i = (\text{age} - t_0) K$ , i.e. by setting  $K = 1$  in equation (6). In this case, the slope of the catch curve yields an estimate of  $(Z/K) - 1$  (see Fig. 7B, and Pauly, 1984).

Equations (7) and (8) provide estimates of  $Z$  which are extremely close (within less than 1%) to the true values of  $Z$ , as was ascertained from analysis of constructed data (Pauly, 1984; P. Sparre, Danish Institute of Fisheries, Charlottenlund, pers. comm.). The method has been shown to yield remarkably straight catch curves in a large number of fish and shrimp stocks (Pauly and Ingles, 1981; Pauly, 1982a; Ingles and Pauly, 1984; Pauly *et al.*, 1984).

This approach was applied to a number of squid samples during the preparation of this paper, and it led, in many cases, to catch curves that were not linear (e.g. Fig. 7C), thus apparently confirming the view of Juanico (1983) that "squids are not fish and that few

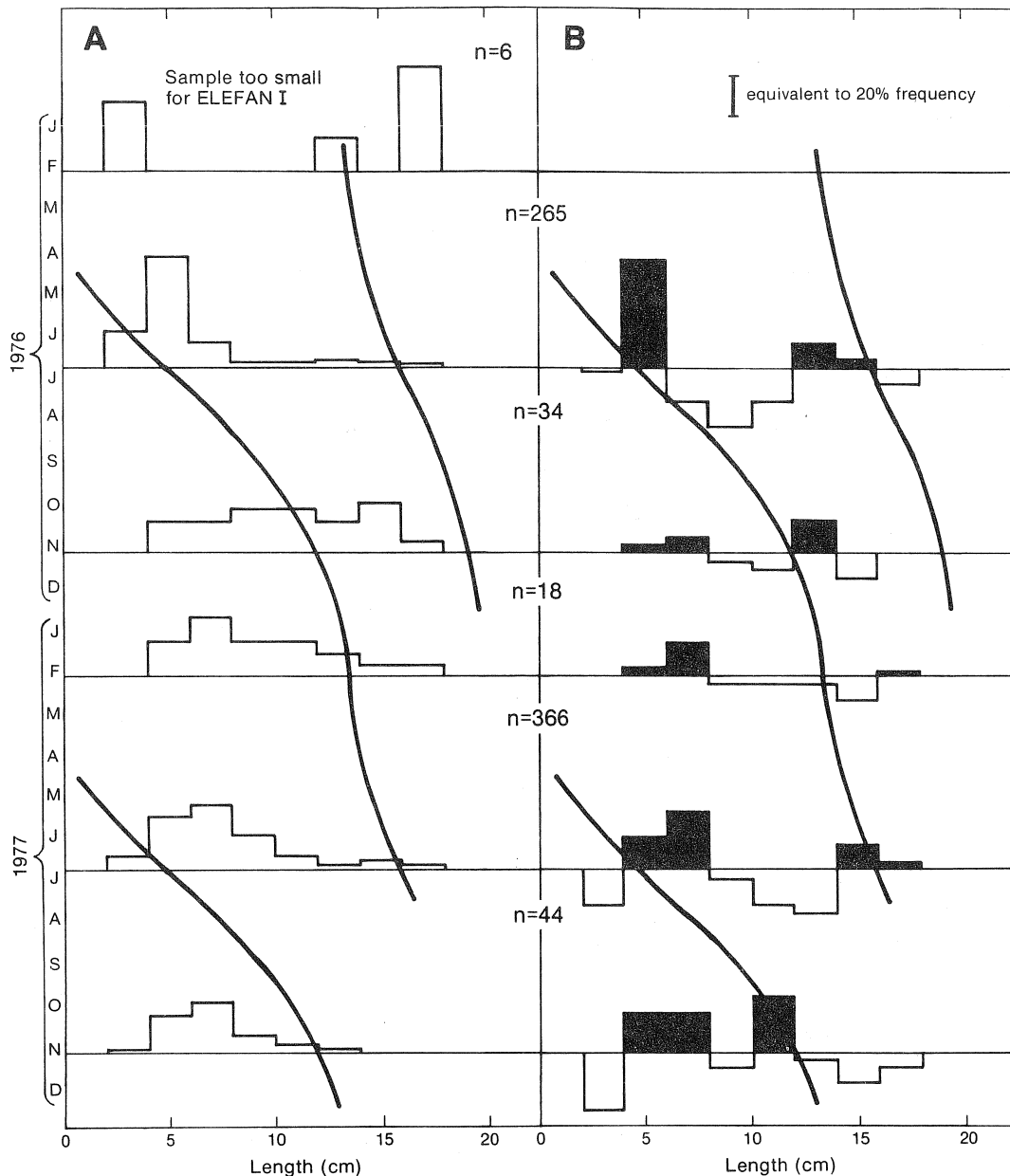


Fig. 6. Reanalyzed length-frequency data of Fig. 1 (*Loligo pealei* females from Gulf of Mexico), with (A) regrouping of data into smaller number of length classes; and (B) restructuring of samples, as performed by ELEFAN I program, to identify seasonally-oscillating growth curves that best explain the data. (The resultant growth curve has the parameters  $L_{\infty} = 21.5$ ,  $K = 0.285$  and  $C = 0.65$ .)

principles of fish biology apply to these molluscs". More interestingly, however, these catch curves, simple as they are, may, if applied widely, help to resolve whether the high postspawning mortalities that are 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, or are a peculiar feature of the few species that have been investigated to date. This latter viewpoint seems to be favored by Voss (1983).

During the application of catch-curve methods, especially good care must be taken to ensure the representativeness of the samples that are used. In the particular case of squids, this implies that the samples must not be biased by massive immigration from the sampling area, e.g. as reported for *Illex illecebrosus* by Hurley and Waldron (MS 1978) and Caddy (1983), or by highly selective gears. Rigorous experiments with jiggers and other gears (except trawls) that are used to catch squids seem not to have been performed, thus

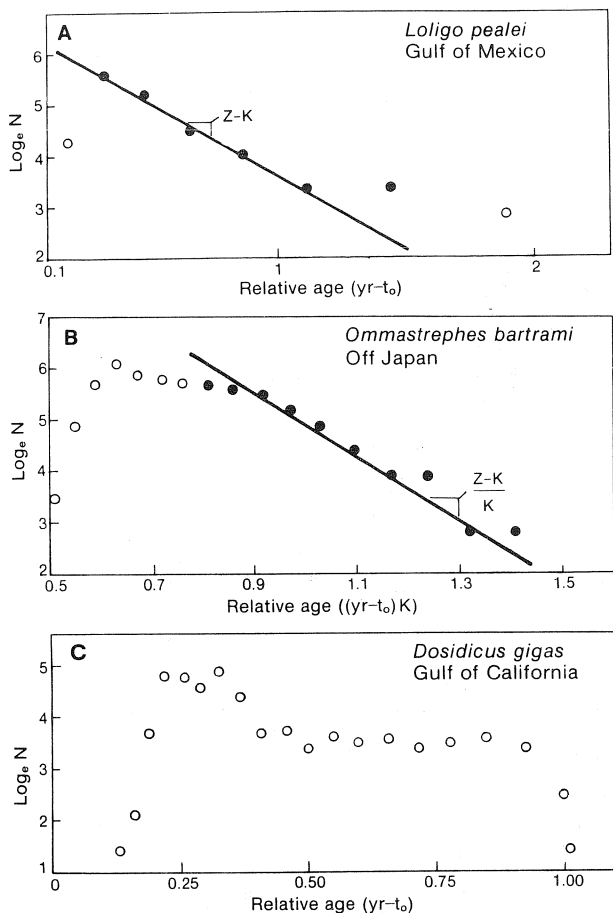


Fig. 7. Examples of length-converted catch curves for squids: **A**, *Loligo pealei*, based on data in Fig. 1, with successive samples first transformed to percentages and then weighted by the square root of sample size prior to addition by length class to obtain an annual average sample, more or less representative of the population, with conversion to relative ages by the  $L_\infty$  and  $K$  values in Fig. 6; **B**, *Ommastrephes bartrami*, based on length-frequency data in fig. 9 of Araya (1983), with  $L_\infty = 45$  cm as suggested by Roper *et al.* (1984); and **C**, *Dosidicus gigas*, based on length-frequency data of Ehrhardt *et al.* (1983) and on  $L_\infty$  and  $K$  values in Table 1. (Note lack of evidence for postspawning mortality in **B** and marked increase in this parameter in **C**.)

leaving open, for the time being, the interpretation of estimates of apparent total mortality which are derived from length-converted catch curves.

Pauly (1984) reported 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 without the benefit of selection experiments. The method, which has been field-tested (i.e. shown to provide estimates similar to those obtained from selection experiments) with fishes, has yet to be applied to squids. If it is assumed that the central part of a length-converted catch curve for squid 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 for estimating ( $F$ ), namely (i) from the ratio of catch and biomass when the latter can be estimated, and (ii) from the difference between  $Z$  and  $M$ , when  $Z$  can be estimated from a catch curve and a plausible estimate of  $M$  can be derived from comparative life-history studies.

The first method, which can be applied profitably when the sampling gear is a trawl, involves estimating the biomass ( $B$ ) by the swept-area method (Gulland, 1969) and then estimating  $F$  from the ratio

$$F = Y/B \quad (9)$$

where  $Y$  is the catch in weight from the stock. An alternative to this is to relate the area swept by all gears of the commercial fleet ( $a'$ ) during a certain period of time and the total area of occurrence of the stock ( $A$ ), whereby

$$F = a'/A \quad (10)$$

Applications of these methods to squid were reported by Lange and Sissenwine (1980) and by Sato and Hatanaka (1983).

The potential pitfalls in the use of equations (9) and (10) are numerous. They range from the generally unknown and probably changing catchabilities of squids to the seasonal contraction and expansion of their area of occurrence ( $A$ ), together with the problems associated with conducting a suitably-weighted stratified-random survey to quantify a biomass that is changing rapidly during the course of the survey. These and associated problems cannot be discussed here, and there seems to be no alternative but to apply judiciously the best standard approaches (Gulland, 1983). However, the data that are needed to obtain reasonable estimates of  $F$  from equations (9) and (10) will often not be available. In such cases, it will be necessary to rely on the opposite approach, namely, that of subtracting an approximate value of  $M$  from  $Z$ , when both are obtained independently.

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

$$\log M = -0.2107 - 0.0824 \log W_\infty + 0.6757 \log K + 0.4627 \log T \quad (11)$$

where  $K$  (annual rate) and  $W_\infty$  (whole weight in grams) are defined as above and  $T$  is the mean annual water temperature ( $^{\circ}\text{C}$ ). The equivalent relationship based on length (Pauly, 1980a) has been widely applied and found by several researchers to provide reasonable

TABLE 1. Some estimates of growth parameters for squids, with corresponding values of  $\phi$  and M computed from equations (3) and (10) respectively, and approximate mean environmental temperatures. (L is mantle length (cm),  $W_{\infty}$  is whole weight (g), and K is expressed on an annual basis.)

| Species (sex)                                 | Area (temperature) <sup>a</sup> | $L_{\infty}$ | $W_{\infty}$ | K    | $\phi^b$ | M    | Remarks  |
|---|---------------------------------|--------------|--------------|------|----------|------|--|
| 1. <i>Loligo pealei</i>                       | Off New England (14.5° C)       | 38.3         | 680          | 0.59 | 1.66     | 0.87 | $L_{\infty}$ and K from Ikeda and Nagasaki (MS 1975); conversion of $L_{\infty}$ to $W_{\infty}$ based on Lange and Johnson (1981).  |
| 2. <i>Loligo pealei</i>                       | Gulf of Mexico (24° C)          | 23           | 207          | 0.95 | 1.52     | 0.64 | See Fig. 6; conversion of $L_{\infty}$ to $W_{\infty}$ based on Lange and Johnson (1981).  |
| 3. <i>Illex illecebrosus</i> (♀)              | Off Eastern Canada (9° C)       | 29.4         | 500          | 0.65 | 1.61     | 0.76 | $L_{\infty}$ and K from Lange and Sissenwine (1983), citing Amaratunga (1980) which I have not seen, with $L_{\infty}$ corrected from 2.94 for females and 2.39 for males to those shown here.   |
| 4. <i>Illex illecebrosus</i> (♂)              | Off Eastern 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 | $L_{\infty}$ and K from Au (MS 1975); conversion of $L_{\infty}$ 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 | $L_{\infty}$ , $W_{\infty}$ and K computed from data of Ehrhardt <i>et al.</i> (1983).   |
| 7. <i>O. borealijaponica</i> (♀) <sup>c</sup> | East of Hokkaido (8° C)         | 40           | 1,575        | 0.47 | 1.80     | 0.53 | $L_{\infty}$ , $W_{\infty}$ and K computed from data of Okutani and Murata (1983), using the method of Gaschütz <i>et al.</i> (MS 1980), which also provided estimates of C (equation 2) of 1.40 for females and 4.3 for males, both indicating a long period (winter) of no growth. |
| 8. <i>O. borealijaponica</i> (♂) <sup>c</sup> | East of Hokkaido (8° C)         | 35           | 1,600        | 0.48 | 1.82     | 0.53 |  |

<sup>a</sup> Sea-surface temperatures from Anon. (1944) except for Gulf of Mexico value from Rivas (1968).

<sup>b</sup> Values of  $\phi$  appear to be mutually consistent for data sets 1 and 2, sets 3 and 4, and sets 7 and 8, whereas the lack of consistency in data sets 5 and 6 indicate erroneous growth parameters (see also Fig. 5), which may be attributed largely to the subjectivity of methods used in tracing growth curves and to the effect of seasonal growth oscillations.

<sup>c</sup> Genus is *Onychoteuthis*.

estimates of M for fish as diverse as Pacific skipjack tuna (Kleiber *et al.*, 1983), Arabian myctophids (Sanders and Bouhlel, 1982), and West African demersal fishes (Longhurst, 1983).

The predictive relationship (equation 11) should also provide reasonable first estimates of M for squids, because fish and squid usually share the same habitat, resources and predators and they are not likely to differ widely in interrelationships between their vital parameters (see Fig. 5). This reasoning, which was also applied to shrimps by Pauly *et al.* (1984) was justified *post hoc* by the fact that the resultant M-values were well within the range of values considered to be reasonable (S. Garcia, FAO, pers. comm.). The M-values in Table 1 were derived from equation (11). When growth parameters ( $L_{\infty}$  or  $W_{\infty}$ , and K) and estimates of F and M are available, yield-per-recruit analyses can be conducted quite straightforwardly (Beverton and Holt, 1966; Ehrhardt *et al.*, 1983), and first steps toward fishing management can be proposed.

## Recruitment

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

Predicting recruitment in stocks that have been exploited for only a few years is doubly difficult when the conventional approach is relied upon (i.e. accumulation of one point per year until enough points become available, from which a single "stock-recruitment curve" of some sort can be derived). For short-lived fishes and shrimps, detailed examination of length-frequency data reveals that recruitment is pulsed and that two pulses (of unequal strength) are generated every year (Fig. 8A) (Pauly and Navaluna, 1983; Pauly *et al.*, 1984). This may also be the general case in squid stocks (see Fig. 8B), although relatively

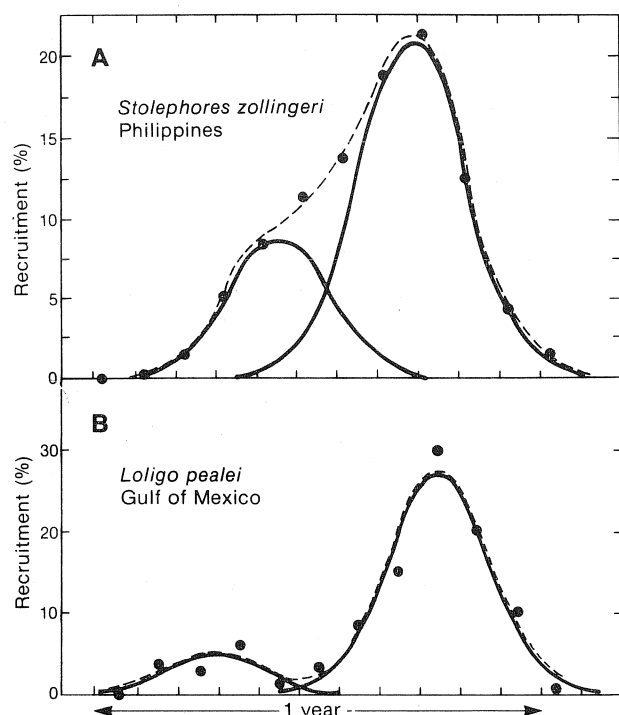


Fig. 8. Recruitment patterns obtained by projecting length-frequency data onto the time axis with growth parameters  $L_{\infty}$  and  $K$  and the ELEFAN II program: **A**, a very short-lived ( $t_{max} \sim 1$  yr) anchovy from Manila Bay in the Philippines (Pauly and Navaluna, 1983); and **B**, *Loligo pealei* from the Gulf of Mexico based on data in Fig. 1 and growth parameters estimated in Fig. 6. (Note indication of two recruitment pulses per year in both cases, although little importance can be placed on this point in the case of *L. pealei* due to small sample size.)

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 in the giant squid (*Dosidicus gigas*) but relied on a subjective method of analysis (i.e. tracing

growth curves by eye). An objective method, which utilized all of the available data at one time, was used to derive recruitment patterns of the type illustrated in Fig. 8.

More elaborate approaches to obtain estimates of recruitment in short-lived fishes and invertebrates are length-structured cohort analyses (Jones and van Zalinge, 1981), two forms of which are incorporated in the ELEFAN III program (written in BASIC and available from the author) and which were applied to the Peruvian anchoveta stock by Pauly and Tsukayama (1983). These methods, which require fairly detailed catch composition data (e.g. monthly) over a period of at least 4–5 years offer real possibility of increasing markedly the number of data "points" for stock-recruitment studies. The statistical problems that must be considered when such approaches are used cannot be discussed here, but all of them can be solved with the use of 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, is estimation of their annual absolute recruitment. This approach is straightforward because annual catch is the product of yield-per-recruit and the number of recruits. After performing a yield-per-recruit analysis, absolute recruitment ( $R$ ) is estimated from

$$R = \text{annual catch/yield-per-recruit} \quad (12)$$

Such estimates of recruitment can then be plotted against any variable or combination of variables which are thought to impact on recruitment, e.g. parent stock size, predator biomass, and the like. This approach is illustrated here by using data from the inshore waters of the Gulf of Thailand to a depth of 50 m. This relatively well-monitored fishery, which accounts for approximately 800,000 tons of fish and invertebrates

TABLE 2. Vital statistics for a generalized loliginid squid that were used in the yield-per-recruit analysis of the cephalopod stock in the Gulf of Thailand.

| Parameter                    | Symbol       | Value   | Remarks   |
|------------------------------|--------------|---------|---|
| Asymptotic weight            | $W_{\infty}$ | 150 g   | See Table 1 and Fig. 5.   |
| Annual growth rate           | $K$          | 1       | Yearly  |
| Age at zero length           | $t_0$        | 0 yr    | Assumed   |
| Selection factor             | SF           | 2.1     | From Amaratunga <i>et al.</i> (1979)  |
| Mean length at first capture | $L_c$        | 5.25 cm | SF $\times$ mesh size   |
| Mean weight at first capture | $W_c$        | 2.1 g   | Based on length-weight relationship of Lange and Johnson (1981)                         |
| Mean age at first capture    | $t_c$        | 0.28 yr | Equal mean age at recruitment to fishery ( $t_r$ )                                      |
| Mean age at first maturity   |              | 1 yr    |   |
| Mean relative fecundity      |              | 400/g   | Number of eggs per gram based on loliginid fecundity data of Roper <i>et al.</i> (1984) |



TABLE 3. Selected information for the demersal stock and fishery in the Gulf of Thailand, 1961-80. (Data from Boonjool and Pramokchutima, MS 1982, complemented with information by Sakurai, 1974.)

| Year | Total standing stock <sup>a</sup><br>(000 tons) | Fishing mortality <sup>b</sup><br>(F) | Cephalopod catch<br>(000 tons) |
|------|---|---------------------------------------|--------------------------------|
| 1961 | 624   | 0.17                                  | 3.33                           |
| 1962 | 621   | 0.21                                  | 4.03                           |
| 1963 | 618   | 0.32                                  | 6.00                           |
| 1964 | 604   | 0.53                                  | 9.12                           |
| 1965 | 471   | 0.72                                  | 12.2                           |
| 1966 | 353   | 1.03                                  | 15.4                           |
| 1967 | 307   | 1.42                                  | 18.5                           |
| 1968 | 204   | 2.52                                  | 23.8                           |
| 1969 | 275   | 1.89                                  | 29.1                           |
| 1970 | 258   | 2.05                                  | 34.4                           |
| 1971 | 176   | 3.46                                  | 39.7                           |
| 1972 | 168   | 4.39                                  | 45.0                           |
| 1973 | 139   | 5.98                                  | 51.0                           |
| 1974 | 155   | 3.90                                  | 48.4                           |
| 1975 | 125   | 6.02                                  | 53.5                           |
| 1976 | 152   | 5.18                                  | 58.2                           |
| 1977 | 125   | 6.78                                  | 76.9                           |
| 1978 | 139   | 5.86                                  | 71.3                           |
| 1979 | 137   | 6.08                                  | 66.4                           |
| 1980 | 127   | 6.28                                  | 61.4                           |

<sup>a</sup> Based on the swept-area method.

<sup>b</sup> Based on annual estimates of total catch and equation (9); estimates are assumed to apply to cephalopod component of multi-species stock.

per year, also catches 60,000–70,000 tons of cephalopods, most of which (80%) consists of loliginids (*Loligo chinensis* = *L. formosana*, *L. duvauceli* and *L. uyii* = *L. tagoi*) (Chotiyaputta, 1982; Roper *et al.*, 1984, for synonyms). The exercise was performed by using vital statistics for a “generalized loliginid squid” (Table 2). It must be realized that those values are not “averages” or “best estimates” of any kind, but are rather “possible” values for use in the illustrative example. They also represent the minimum set of data that must be available for any stock to enable application of the method. Table 3 presents the catch data for cephalopods and the corresponding fishing mortality, as well as the estimated biomasses of all fish and invertebrates in the Gulf of Thailand, representing the biomass of all predators (and possibly competitors) of cephalopod prerecruits. The estimated standing stock values for cephalopods in Table 3 were reduced by a fraction (*m*), corresponding to the fraction of cephalopods older than 1 year in the stock. This fraction, which is a function of *F*, was obtained from

$$m = \frac{e^{-Zr_3} \left\{ \frac{1}{Z} - \frac{3e^{-Kr_2}}{Z+K} + \frac{3e^{-2Kr_2}}{Z+2K} - \frac{e^{-3Kr_2}}{Z+3K} \right\}}{\frac{1}{Z} - \frac{3e^{-Kr_1}}{Z+K} + \frac{3e^{-2Kr_1}}{Z+2K} - \frac{e^{-3Kr_1}}{Z+3K}} \quad (13)$$

where  $r_1 = t_c - t_o$ ,  $r_2 = t_m - t_o$ , and  $r_3 = t_m - t_c$ .

Results of the computations, including derivation of the prerecruit mortality index ( $-\ln R/S$ ) are summar-

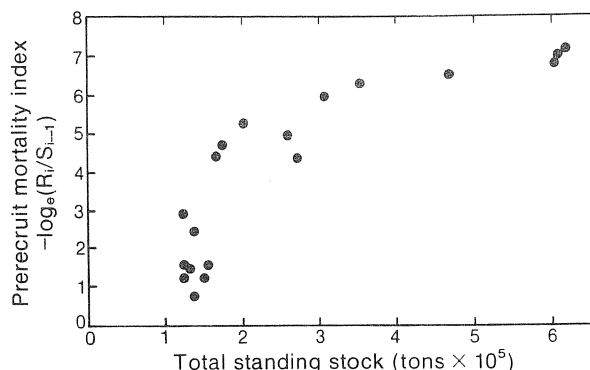


Fig. 9. Relationship between estimated prerecruit mortality of cephalopods in the Gulf of Thailand and total fish biomass in the Gulf's inshore waters, 1961-80.

ized in Table 4. There was a marked decline in prerecruit mortality with decrease in total demersal standing stock (Fig. 9). This decline, which corresponds to a change of one order of magnitude (from 7% to about 0.7%) in the daily prerecruit mortality, 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).

## Discussion and Conclusions

Juanico (1983) stated that squids differ markedly from fishes with regard to the major features of their population dynamics. This view should not remain as a matter of opinion but be seen as a hypothesis which can be tested by deliberately applying to squids those methods and models which have been applied successfully to fishes and shrimps.

To model the growth of squids, a seasonally-oscillating version of the von Bertalanffy growth equation is proposed, along with an objective method (ELEFAN I program) for fitting it to length-frequency data, which should (i) allow for comparative studies of growth performance in different species of squids (and thus for inferring growth parameters in little-known species), and (ii) help resolve whether growth patterns differ markedly between fishes and squids when account is taken of seasonal growth oscillations. This latter point seems to be particularly important in view of statements by various researchers who reported high variation in growth of individual squids (and squid cohorts) and expressed doubts about the applicability of a single growth model (Caddy, 1983, and references therein). However, studies of feeding and food conversion in *I. illecebrosus* (O'Dor *et al.*, 1980) do not indicate results that are vastly different from those in similar studies on fishes (e.g. Pandian, 1970). It may

TABLE 4. Step-by-step approach to computation of prerecruit mortality index ( $-\ln R_t/S_{t-1}$ ) for cephalopods in the Gulf of Thailand, following the method of Pauly (1980b, 1982b) except for the feature that recruitment is divided by egg production of the preceding year, as suggested by Murphy (1982), Garcia (1983) and Bayley (1984).

| Year | Cephalopod biomass <sup>a</sup><br>(000 tons) | Fraction mature <sup>b</sup> | S = eggs spawned <sup>c</sup><br>(10 <sup>9</sup> ) | Y/R <sup>d</sup><br>(g) | Recruits <sup>e</sup><br>(10 <sup>9</sup> ) | Prerecruit mortality index |
|------|---|------------------------------|---|-------------------------|---|----------------------------|
| 1961 | 19.6  | 0.575                        | 2,250   | 1.86                    | 1.79  | —                          |
| 1962 | 19.2  | 0.566                        | 2,170   | 2.22                    | 1.82  | 7.12                       |
| 1963 | 18.2  | 0.542                        | 2,040   | 3.05                    | 1.97  | 7.00                       |
| 1964 | 17.2  | 0.497                        | 1,710   | 4.23                    | 2.16  | 6.85                       |
| 1965 | 16.9  | 0.458                        | 1,550   | 4.94                    | 2.43  | 6.56                       |
| 1966 | 14.9  | 0.398                        | 1,190   | 5.64                    | 2.73  | 6.34                       |
| 1967 | 13.0  | 0.330                        | 858   | 6.04                    | 3.06  | 5.96                       |
| 1968 | 9.44  | 0.187                        | 353   | 6.01                    | 3.96  | 5.38                       |
| 1969 | 15.4  | 0.261                        | 804   | 6.15                    | 4.73  | 4.31                       |
| 1970 | 16.8  | 0.240                        | 806   | 6.13                    | 5.61  | 4.97                       |
| 1971 | 11.5  | 0.110                        | 253   | 5.63                    | 7.05  | 4.74                       |
| 1972 | 10.2  | 0.063                        | 128   | 5.24                    | 8.59  | 3.38                       |
| 1973 | 8.53  | 0.024                        | 40.9  | 4.68                    | 10.9  | 2.46                       |
| 1974 | 12.4  | 0.085                        | 211   | 5.44                    | 8.90  | 1.53                       |
| 1975 | 8.89  | 0.023                        | 40.9  | 4.66                    | 11.5  | 2.91                       |
| 1976 | 11.2  | 0.039                        | 87.4  | 4.94                    | 11.8  | 1.24                       |
| 1977 | 11.3  | 0.014                        | 31.6  | 4.45                    | 17.3  | 1.62                       |
| 1978 | 12.2  | 0.026                        | 63.4  | 4.71                    | 15.1  | 0.74                       |
| 1979 | 10.9  | 0.222                        | 48.0  | 4.65                    | 14.3  | 1.49                       |
| 1980 | 9.78  | 0.020                        | 39.1  | 4.59                    | 13.4  | 1.28                       |

<sup>a</sup> Obtained by using catch, F-values in Table 3, and the relationship  $B = Y/F$ .

<sup>b</sup> Derived from equation (13) with vital statistics in Table 2 and F-values in Table 3.

<sup>c</sup>  $S = \text{biomass} \times \text{fraction mature} \times \text{relative fecundity} \times 0.5$ .

<sup>d</sup> Conventional Y/R analysis, using vital statistics in Table 2 and F-values in Table 3.

<sup>e</sup> Obtained by applying equation (11).

also be mentioned that the cannibalism of *I. illecebrosus* and other squids, at least under conditions of food scarcity (O'Dor *et al.*, 1980) should have the tendency to reduce the variability in growth rates of surviving squids and, at the same time, to increase the variability in mortality (Mohn, 1982). The study of squid mortalities could be greatly accelerated by the systematic application of length-converted catch curves. However, rigorous selection experiments, notably for jigging gear, will have to be conducted if definitive conclusions (e.g. on postspawning mortality) are to be drawn from the shape of the catch curves.

Natural mortality in squids (prior to postspawning) should be similar to those of fishes with matching growth parameters. If so, it should be possible to obtain reasonable estimates of  $M$  from the empirical equations given above, and this will help to test and/or substantiate estimates of  $M$  based on even simpler methods, e.g. from the assumed life expectancy of the squids under consideration (Au, MS 1975).

With regard to recruitment studies, the short life-span of squids can be quite readily turned from a liability into an asset. Two lines of thought were noted to illustrate this: one makes use of within-year recruitment fluctuations to provide inferences on between-year fluctuations, and the other relies on the lack of overlap between cohorts to provide mutually inde-

pendent estimates of recruitment from annual catches and a few ancillary data. Such independent estimates of recruitment can be used to test hypotheses on the trophic and other interactions that link squids to their biotic and abiotic environments. This approach helps to bridge the gap between "population dynamics" and the "ecological" studies that Caddy (1983) wrote about.

Finally, it is suggested that nothing can be gained by emphasizing the differences between squids and fishes and by inferring that methods which have been developed to study fishes will not work when they are applied to squids. Rather, "fish" models of known properties should be applied systematically to squids and the "deviations" from such model studied in detail, because it is these deviations that will indicate how squids are different from fishes.

### Acknowledgements

I thank Lourdes "Deng" Palomares for her assistance in preparing this manuscript and Chan Eng Heng for useful references on Southeast Asian squids. My thanks also go to Anne Lange, Northeast Fisheries Center, Woods Hole, Mass., for presenting (in my absence) an earlier version of this paper at the NAFO Special Session on Squids in September 1984.

## References

- AMARATUNGA, T. MS 1980. Growth and maturation patterns of the short-finned squid (*Illex illecebrosus*) on the Scotian Shelf. *NAFO SCR Doc.*, No. 30, Serial No. N062, 17 p.
- AMARATUNGA, T., S. KAWAHARA, and H. KONO. MS 1979. Mesh selection of the short-finned squid, *Illex illecebrosus*, on the Scotian Shelf using a bottom trawl: a joint Canada-Japan 1978 research program. *ICNAF Res. Doc.*, No. 35, Serial No. 5361, 29 p.
- ANON. 1944. World atlas of sea surface temperatures. U.S. Navy Hydrographic Office, Washington, H. O. No. 235.
- ARAYA, H. 1983. Fishery, biology and stock assessment of *Ommastrephes bartramii* in the North Pacific Ocean. *Mem. Nat. Mus. Vict.*, **44**: 269-283.
- AU, D. W. K. MS 1975. Considerations of squid (*Loligo* and *Illex*) population dynamics and recommendations for rational exploitation. *ICNAF Res. Doc.*, No. 61, Serial No. 3543, 13 p.
- BAYLEY, P. 1984. Comment: prerecruit mortality in Gulf of Thailand shrimp stocks. *Trans. Amer. Fish. Soc.*, **113**: 403-404.
- BEVERTON, R. J. H., and S. J. HOLT. 1959. A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics. *CIBA Colloquia on Ageing*, **5**: 142-180.
1966. Manual of methods for fish stock assessment. Part II. Tables of yield functions. *FAO Fish. Tech. Pap.*, **38**(Rev. 1): 1-67.
- BOONJUBOL, M., and S. PRAMOKCHUTIMA. 1982. Demersal trawling in the Gulf of Thailand. *Thai Fish. Rep. Bangkok*, **9**: 23 p. (in Thai). (Available in English as ICLARM Transl. No. 6.)
- CADDY, J. F. 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In *Advances in assessment of world cephalopod resources* (p. 416-452), J. F. Caddy (ed.), *FAO Fish. Tech. Pap.*, **231**: 452 p.
- CHATFIELD, C. 1975. The analysis of time series: theory and practice. Chapman and Hall, London, England, 263 p.
- CHOTIYAPUTTA, C. 1982. Squid fisheries of Thailand. *FAO Fish. Rep.*, **275**: 124-134.
- EHRHARDT, N. M., P. S. JACQUEMIN, F. GARCIA, G. CONZALEZ, J. M. LOPEZ, B. ORTIZ, and A. SOLIS. 1983. On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. In *Advances in assessment of world cephalopod resources* (p. 306-340), J. F. Caddy (ed.), *FAO Fish. Tech. Pap.*, **231**: 452 p.
- FIELDS, W. G. 1965. The structure, development, food relations, reproduction and life history of the squid, *Loligo opalescens* Berry. *Fish. Bull. Calif. Dept. Fish Game*, **131**: 1-108.
- GARCIA, S. 1983. The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretations? *Océanogr. Trop.*, **18**: 25-48.
- GARCIA, D., and L. LeRESTE. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. *FAO Fish. Tech. Pap.*, **203**: 1-215.
- GASCHÜTZ, G., D. PAULY, and N. DAVID. MS 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. *ICES C. M. Doc.*, No. D:6, 14 p.
- GULLAND, J. A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. *FAO Man. Fish. Sci.*, **4**: 1-154.
1983. Fish stock assessment: a manual of basic methods. FAO/Wiley Ser. Food and Agric., Vol. 1, John Wiley and Sons, New York, 223 p.
- HIXON, R. F. MS 1980. Growth, reproductive biology, distribution and abundance of three species of loliginid squids (Myopsida, Cephalopoda) in the northwestern Gulf of Mexico. Ph.D. Thesis, Univ. of Miami, Florida, 234 p.
- HIXON, R. F., R. T. HANLON, and W. H. HULET. 1981. Growth and maximum size of the long-finned squid *Loligo pealei* in the northwestern Gulf of Mexico. *J. Shellfish Res.*, **1**: 181-185.
- HURLEY, G. V., and D. E. WALDRON. MS 1978. Population estimates for squid (*Illex illecebrosus*) in ICNAF Subarea 4 from the international fishery in 1977. *ICNAF Res. Doc.*, No. 61, Serial No. 5229, 10 p.
- IKEDA, I., and F. NAGASAKI. MS 1975. Stock assessment of *Loligo* in ICNAF Subarea 5 and Statistical Area 6. *ICNAF Res. Doc.*, No. 44, Serial No. 3523, 5 p.
- INGLES, J., and D. PAULY. 1984. An atlas of the growth, mortality and recruitment of Philippine fishes. *ICLARM Tech. Rep.*, **13**: 127 p.
- JONES, R., and N. P. van ZALINGE. 1981. Estimate of mortality rate and population size for shrimps in Kuwait waters. *Kuwait Bull. Mar. Sci.*, **2**: 273-288.
- JUANICO, M. 1983. Squid maturity scales for population analysis. In *Advances in assessment of world cephalopod resources* (p. 341-378), J. F. Caddy (ed.), *FAO Fish. Tech. Pap.*, **231**: 452 p.
- KLEIBER, P., A. W. ARGUE, and R. E. KEARNEY. 1983. Assessment of skipjack (*Katsuwonus pelamis*) resources in the Central and Western Pacific by estimating standing stock and components of population turnover from tagging data. *Tech. Rep.*, *New Caledonia, Tuna and Billfish Assess. Progr. S. Pac. Comm.*, **8**: 38 p.
- KRISTENSEN, T. K. 1980. Periodic growth rings in cephalopod statoliths. *Dana*, **1**: 39-52.
- LANGE, A. M. T., and K. L. JOHNSON. 1981. Dorsal mantle length-total weight relationship of squids *Loligo pealei* and *Illex illecebrosus* from the Atlantic coast of the United States. *NOAA Tech. Rep. NMFS Circ.*, **745**: 17 p.
- LANGE, A. M. T., and M. P. SISENWIN. 1980. Biological considerations relevant to the management of squid (*Loligo pealei* and *Illex illecebrosus*) of the Northwest Atlantic. *Mar. Fish. Rev.*, **42**(7-8): 23-28.
1983. Squid resources of the Northwest Atlantic. In *Advances in assessment of world cephalopod resources* (p. 21-54), J. F. Caddy (ed.), *FAO Fish. Tech. Pap.*, **231**: 452 p.
- LARKIN, P. A., and W. GAZEY. 1982. Applications of ecological simulation models to management of tropical multispecies fisheries. In *Theory and management of tropical fisheries* (p. 123-140), D. Pauly and G. I. Murphy (ed.), *ICLARM Conf. Proc.*, **9**: 360 p.
- LONGHURST, A. 1983. Benthic pelagic coupling and export of organic carbon from a tropical Atlantic continental shelf — Sierra Leone. *Estuarine Coast. Shelf Sci.*, **17**: 261-285.
- LUTZ, R. A., and D. C. RHOADS. 1977. Anaerobiosis and a theory of growth line formation. *Science*, **198**: 1222-1227.
- MANGOLD, K. 1963. Biologie des cephalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu*, **13**(suppl.): 1-285.
- MOHN, R. K. 1982. Yield-per-recruit analysis of short-finned squid on the Scotian Shelf by simulation. *NAFO Sci. Coun. Studies*, **3**: 39-45.
- MUNRO, J. L., and D. PAULY. 1983. A simple method for comparing the growth of fish and invertebrates. *Fishbyte*, **1**(1): 5-6.
- MURPHY, G. I. 1982. Recruitment of tropical fishes. In *Theory and management of tropical fisheries* (p. 141-148), D. Pauly and G. I. Murphy (ed.), *ICLARM Conf. Proc.*, **9**: 360 p.
- O'DOR, R. K., R. D. DÜRWARD, E. VESSEY, and T. AMARATUNGA. 1980. Feeding and growth in captive squid, *Illex illecebrosus*, and the influence of food availability on growth in the natural population. *ICNAF Sel. Papers*, **6**: 15-21.
- OKUTANI, T., and M. MURATA. 1983. A review of the biology of the oceanic squid, *Onychoteuthis borealijaponica*. *Mem. Nat. Mus. Vict.*, **44**: 189-195.
- PANDIAN, T. J. 1970. Intake and conversion of food in the fish *Limanda limanda* exposed to different temperatures. *Mar. Biol.*, **5**: 1-17.
- PAULY, D. 1979. Theory and management of tropical multispecies stocks: a review, with emphasis on the southeast Asian demersal fisheries. *ICLARM Stud. Rev.*, **1**: 35 p.
- 1980a. On the interrelationships between natural mortality, growth, parameters and mean environmental temperature in 175 fish stocks. *ICES J. Cons.*, **39**: 175-192.
- 1980b. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality and stock-recruitment relationships. In *Stock assessments for tropical small-scale fisheries* (p. 154-172), S. Saita and P. Roedel (ed.), Intern. Cent. Mar. Res. Dev., Univ. Rhode I., 198 p.
1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Ber. Dtsch. Wiss. Komm. Meeresforsch.*, **28**: 251-282.

- 1982a. Studying single-species dynamics in a multispecies context. In Theory and management of tropical fisheries, D. Pauly and G. I. Murphy (ed.), *ICLARM Conf. Proc.*, **9**: 360 p.
- 1982b. A method to estimate the stock-recruitment relationship of shrimps. *Trans. Amer. Fish. Soc.*, **111**: 13-20.
1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. *ICLARM Stud. Rev.*, **8**: 325 p.
- PAULY, D., and J. INGLES. 1981. Aspects of the growth and mortality of exploited coral reef fishes. *Proc. 4th Int. Coral Reef Symp., Manila*, **1**: 89-98.
- PAULY, D., and J. L. MUNRO. 1984. Once more on growth comparison in fish and invertebrates. *Fishbyte*, **2**(1): 21.
- PAULY, D., and N. A. NAVALUNA. 1983. Monsoon-induced seasonality in the recruitment of Philippine fishes. *FAO Fish. Rep.*, **291**(3): 823-833.
- PAULY, D., and I. TSUKAYAMA. 1983. On the seasonal growth, monthly recruitment and monthly biomass of the Peruvian anchoveta from 1961 to 1979. *FAO Fish. Rep.*, **291**(3): 987-1004.
- PAULY, D., J. INGLES, and R. NEAL. 1984. 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). In Penaeid shrimps — their biology and management (p. 220-234), J. A. Gulland and B. I. Rothschild (ed.), Fishing News Books, Farnham, England, 312 p.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, **191**: 1-382.
- RIVAS, L. R. 1968. Fishermen's atlas of monthly sea surface temperature for the Gulf of Mexico. *Circ. U.S. Fish. Wildl. Serv.*, **300**: 33 p.
- ROPER, C. F. E., M. J. SWEENEY, and C. E. NAUEN. 1984. An annotated and illustrated catalogue of species of interest to fisheries. FAO species catalogue, Vol. 3: cephalopods of the world.
- RUSSELL, E. S. 1931. Some theoretical considerations on the overfishing problem. *ICES J. Cons.*, **6**: 3-20.
- SAKURAI, T. 1974. Squid and cuttlefish fisheries in Thailand. *Proc. IPFC*, **15**(III): 496-511.
- SANDERS, M. J., and M. BOUHLEL. MS 1982. Preliminary estimates of some stock assessment parameters for the mesopelagic species *Benthoosema pterotum* inhabiting the western and northern Arabian Sea. *FAO/UNDP (Tech. Assist.) Rep. Fish.*, RAB77/008, 23 p.
- SATO, T., and H. HATANAKA. 1983. A review of assessment of Japanese distant-water fisheries for cephalopods. In Advances in assessment of world cephalopod resources (p. 145-180), J. F. Caddy (ed.), *FAO Fish. Tech. Pap.*, **231**: 452 p.
- SPRATT, J. D. 1978. Age and growth of the market squid, *Loligo opalescens* Berry, in Monterey Bay from statoliths. *Fish. Bull. Calif. Dept. Fish Game*, **169**: 35-44.
- SUMMERS, W. C. 1971. Age and growth of *Loligo pealei*: a population study of the common Atlantic coast squid. *Biol. Bull. Mar. Biol. Lab. Woods Hole, Mass.*, **141**: 189-201.
- TAYLOR, C. C. 1958. Cod growth and temperature. *ICES J. Cons.*, **23**: 366-370.
1959. Temperature and growth — the Pacific razor clam. *ICES J. Cons.*, **25**: 93-101.
1960. Temperature, growth and mortality — the Pacific cockle. *ICES J. Cons.*, **26**: 117-124.
- TINBERGEN, L., and J. VERWEY. 1945. Zur Biologie von *Loligo vulgaris*. *Arch. Néerl. Zool.*, **3**: 333-364.
- VERRILL, A. E. 1881. The cephalopods of the northeastern coast of American Part II. The smaller cephalopods including the squid and the octopus, with other allied forms. *Trans. Conn. Acad. Arts Sci.*, **5**: 260-446.
- VOSS, G. L. 1983. A review of cephalopod fishery biology. *Mem. Nat. Mus. Vict.*, **44**: 229-241.