reliable fisheries statistics, the working-up of trawl survey data and the supply of scientists.

Examples were given of the problems involved in the routine collection of data on catches and fishing effort, and the various causes of inaccurate and incomplete information or even inflated figures. It was suggested that the routine annual collection of these data should be replaced, in some cases, by intensive studies of specific fisheries at longer intervals. However, it was generally agreed that even with intensive studies, it is still necessary to have annual information on the amount of fish removed by fishing from the various fisheries. Also, in many fisheries, data on the fishing effort or the catch per unit of fishing are extremely useful. It was stressed that it is essential that data on effort are related to the catch generated by the effort in question, and that effort data for which this requirement is not met are useless for stock assessment purposes.

Concerning the use of catch and effort data, it was further pointed out that changes in the size, power and efficiency of fishing units and changes in the area of fishing and in fishing strategy are all capable of substantially changing the species composition and size of the catch. Therefore, a comprehensive knowledge of the practical aspects of the fisheries is extremely important.

It was suggested that an important reason for poor statistics is that there is often no direct user of the data collected. However, the more important aspect of this problem is that there should be ready communication between those using the data and those collecting it. It was suggested that, as the fisheries laboratories are the main users of the data, the group responsible for collecting catch and effort data and the research laboratory should be under the direction of the same or closely associated Directors, thus facilitating two-way communication. This is the case in India and in the USA.

With regard to the availability of survey data in the countries of Southeast Asia, it was reported that a start has been made in the Philippines to locate and analyze the large quantity of unused raw data obtained from past research-vessel exploratory trawling. This work is being conducted by a Philippine biologist working at ICLARM (as a part of a training program) and it was agreed that where large amounts of raw data are necessary to reach conclusions such work is much cheaper and more worthwhile than organizing new research to get more data that again might not be used. It is important to reduce these avoidable losses of data.

In Thailand and Indonesia, attempts are being made to computerize the large quantity of hand-recorded survey data now available, but this is making slow progress. While most countries want to work up their own data they welcome assistance in doing this. In fact, a lot of joint working up of data has been done through regional South China Sea Programme workshops and there also are evaluations of the resources by visiting scientists.

Turning to the supply of fisheries scientists in Southeast Asian countries the participants agreed that the problem appears to be primarily one of inadequate numbers of research leaders with adequate ability, training and experience rather than a shortage of fisheries biologists *per se*. In some countries, a major problem is the low salaries of government employees which makes it impossible for the government laboratories to recruit and retain qualified scientists, especially when competing against universities and the private sector.

Studying Single-Species Dynamics in a Tropical Multispecies Context*

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Abstract

Some methods available for the study of the population dynamics of tropical fish are reviewed; emphasis is given to questions of growth, mortality and recruitment, and to relatively new approaches, such as ageing by means of daily otolith structures, detailed analysis of length-frequency data and to comparative studies.

A package of methods is discussed which is based on a set of 3 new, simple computer programs written in BASIC for the analysis of length-frequency data (ELEFAN I, II and III).

Introduction

This paper is a discussion of methods for the investigation of the major aspects of the population dynamics of single-species tropical stocks, both freshwater and marine. The reason for the presentation of this contribution at a workshop devoted to the theory and management of tropical multispecies stocks is compelling: fishery biologists modeling the dynamics of multispecies systems will often work with single-species stocks as elements of the multispecies system. They will want to know as much as possible of the autecology and biology of single-species stocks.

On the other hand, the builders of tropical models have at their disposal much less information on the various species—even on those of commercial importance—than the model builders working in the temperate areas of the world.

There are three major reasons for this:
- there are many more species—even species of commercial importance—in tropical than in temperate systems
- much less has been published, in absolute terms and on a per-species basis on tropical than on temperate fishes
- much of the work done on tropical stocks is poorly documented and often remains unpublished (see Pauly 1979a).

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This contribution is addressed to the use of simple and rapid methods, and parameter estimates obtained from comparative methods.

Also, emphasis is given to methods which can be used to reduce and interpret previously published, but underutilized data (such as length-frequency data) and to methods in which certain biological features of tropical fishes, such as their short life cycles or their prolonged spawning seasons are turned from a liability to an asset.

Russel's axiom (Russel 1931) is still the best method of identifying, in qualitative terms, the elements that determine the yield of a fishery. This axiom states that four factors determine the dynamics of a closed population, namely:

- Recruitment of fishes into the usable stock   (R)
- Growth of fishes that are part of the usable stock   (G)
- Capture by fishing   (C)
- Natural death (mainly by predation)   (M)

Thus, we have

$$B_2 = B_1 + (R + G) - (M + C) \qquad \ldots 1)$$

where B_1 and B_2 are the stock sizes at the beginning and the end, respectively, of the time period to which the increments (R and G) and the decrements (M and C) apply. (See also Fig. 1.)

The four explicit items of Russel's axiom will be used to structure this contribution, which also covers another, implicit term of this axiom, namely the intrinsic rate of increase (r_m) of populations, corresponding to R (G − M)/B.

Fish Growth

THE GENERALIZED VON BERTALANFFY GROWTH FORMULA

The model most commonly used in fishery biology to express the growth of fishes is the von Bertalanffy Growth Formula (VBGF) which has, for growth in length the form

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

and

$$W_t = W_\infty (1 - e^{-K(t - t_0)})^3 \qquad \ldots 3)$$

for growth in weight, where L_∞ and W_∞ are asymptotic sizes, or the mean sizes the fish would reach if they were to grow indefinitely, where K is a growth constant, and where t_0 is the "age" the fish would have at length or weight zero if they had always grown according to the equation, while L_t and W_t are the predicted sizes at age t. Both equations can be derived from Pütter's (1920) continuity relationship

$$\frac{dw}{dt} = Hw^d - kw^m \qquad \ldots 4)$$

which states that the growth rate of fish may be conceived as the difference between two processes with opposite tendencies, one building up body substances (anabolism), the other breaking down body substances (catabolism), both processes being proportional to some power (d, m) of body weight (w). Equation (4) can be integrated in two ways:

- either by setting d = 2/3, m = 1 and by assuming that weight growth is isometric. This leads to what will be called the "special VBGF" (equations 2 and 3) called here "special" because they refer to the special case of d = 2/3 and m = 1)
- or by allowing d and m to take a wide range of values. This leads to what will be called here the "generalized VBGF".
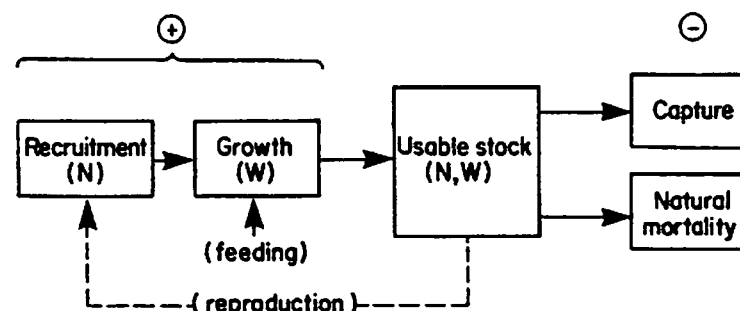

Fig. 1. Main factors investigated in stock-assessment: recruitment, growth (positive factors), capture and natural mortality (negative factors) and stock size. (N refers to numbers, W to weight). Feeding and reproduction, although also contributing to stock dynamics, are generally not considered in single-species stock assessment. Modified from Ricker (1975).

The integration of the special VBGF is well-documented (von Bertalanffy 1934, 1938, 1951; Beverton and Holt 1957; Gulland 1969), while the integration of the generalized VBGF was discussed in detail in Pauly (1979b). Here, only the definitions used in the course of that integration are presented, together with those equations pertaining to important properties of the generalized VBGF.

The substances needed for anabolism have to enter into the body across some surface (S) that increases with fish length (L) according to the relationship

$$S = p \cdot L^a \qquad \ldots 5a)$$

where a is a power that has a range of values discussed below and p is a proportionality constant.

Catabolism, on the other hand, which occurs in all cells of the fish body, may be considered directly proportional to weight (W), which is itself related to length (L) by the relationship

$$W = q \cdot L^b \qquad \ldots 5b)$$

where q is a proportionality constant and b is a power whose range of

possible values lies between 2.5 and 3.5 (Carlander 1969) and b > a. Other definitions used in the course of the integration are

$$K = \frac{k}{3} \qquad \dots 6)$$

and

$$D = b - a \qquad \dots 7)$$

with the integration of expression (4) resulting for weight growth in

$$W_t^D = W_\infty^D (1 - e^{-KD \; 3/b \; (t - t_o)})^b \qquad \dots 8a)$$

which can be simplified, when b = 3 to

$$W_t = W_\infty (1 - e^{-KD \; (t - t_o)})^{1/D} \qquad \dots 8b)$$

For lengths, the generalized VBGF has the form

$$L_t^D = L_\infty^D (1 - e^{-KD \; (t - t_o)}) \qquad \dots 9a)$$

or

$$L_t = L_\infty (1 - e^{KD \; (t - t_o)})^{1/D} \qquad \dots 9b)$$

It will be noted that these versions of the generalized VBGF (expressions (7) to (9) reduce to the corresponding form of the special VBGF (expression (2) and (3)) when D = 1, i.e., when a = 2 and b = 3.

A major difference between the special and generalized VBGF for length is that the latter has an inflexion point whose position on the time axis (t_i) is given by

$$t_i = t_o - \frac{\log_e D}{K \cdot D} \qquad \dots 10)$$

Thus, t_i moves toward t_o when D comes close to 1, with no inflexion point left point when D = 1.

Von Bertalanffy proposed his equations (expressions (2) and (3)) on the assumption that d = 2/3 generally holds true ("2/3 law of metabolism") and that the anabolism of fishes ought to be proportional to their metabolic rate (that is, to oxygen consumption). He also demonstrated that metabolism is indeed proportional to 2/3 of the weight of his experimental guppies, then assumed his "2/3 law of metabolism" applied to all fishes.

Actually, it can be demonstrated that the "2/3 law of metabolism" does not apply to all fishes—in fact, it seems to strictly apply only in the case of the very guppies which von Bertalanffy investigated. In other fishes (in fishes capable of reaching larger sizes), the power linking weight and metabolism (or that linking weight and gill surface area, which is equivalent) is generally close to 0.8, with values of up to 0.9 in tuna and presumably other large, active fishes (Muir 1969; Pauly 1981 and see Fig. 2).

Thus, to qualify as a "physiological" formula, the VBGF has to be used in conjunction with values of "d" in equation (4) ranging between 0.5 (as reported for small cyprinidontids by Winberg 1961) and 0.9 and higher (but always < 1).

The generalized VBGF has a number of properties which make it superior to the special VBGF. Among those, two may be listed here:
— fitting the generalized VBGF to a set of size-at-age data generates asymptotic size values that closely correspond to the largest fish reported from a given stock (Pauly 1981; Gaschütz et al. 1980), which demonstrates that values of L_{max} or W_{max} can generally be used as preliminary estimates of asymptotic size (Fig. 3).
— the values of K estimated from growth data on the basis of the generalized VBGF correspond more closely to the catabolism of fishes than the values of K generated by fitting the special VBGF (Pauly 1981).
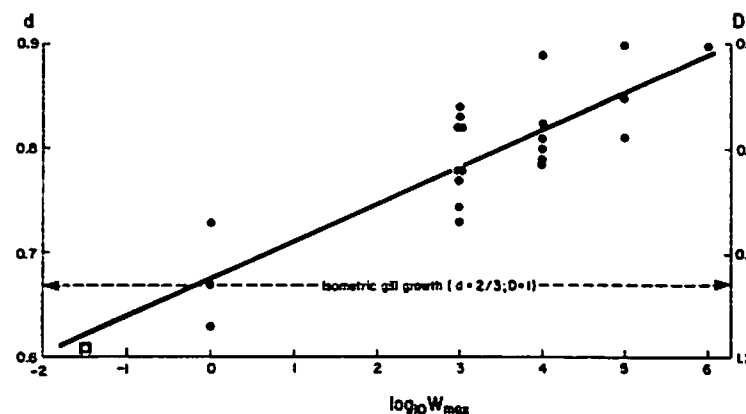

Fig. 2. Values of the power of weight (d) in proportion to which the oxygen consumption or the gill surface of fishes increase, plotted against the maximum weight commonly reached in various species of fishes (in grams). Low values of d (≈ 2/3) to cyprinodonts, high values (0.85 to 0.90) to tuna; intermediate values refer to various fishes such as salmonids, cyprinids, tilapias, cods and others. Based on Table V in Pauly (1981). The relationship between D and d is D = 3(1 — d). [The open square in the lower left corner refers to the Philippine dwarf goby *Mistichthys luzonensis*, is based on data in Te Winkel (1935) and was added subsequently to computing the regression line, which is based on the dots only.]

Fitting the generalized VBGF to a set of growth data is as easy as fitting the special VBGF because reasonable estimates of D can be obtained independently of growth data from the relationship (in Fig. 2):

$$D \approx 3 \cdot [1 - (0.6742 + 0.03574 \log W_{max})] \qquad \dots 11)$$

which was established by Pauly (1981) on the basis of data on the metabolism and/or the gill surface area and the maximum weight reached by a number of

fishes. Thus, once D has been estimated, L_∞ and K can be estimated by means of a Ford-Walford Plot, i.e., a plot of L_{t+1}^D on L_t^D or

$$L_{t+1}^D = \text{intercept} + \text{slope} \cdot L_t^D \qquad \ldots 12)$$

where

$$L_\infty = (\frac{\text{intercept}}{1 - \text{slope}})^{1/D} \qquad \ldots 13)$$

and

$$K = \frac{\log_e \text{slope}}{D} \qquad \ldots 14)$$

A simple, versatile computer program written in BASIC was presented by Gaschütz et al. (1980) which can be used to fit any type of size-at-age data with the generalized VBGF, including seasonally oscillating length growth data as discussed below. In the following, references to growth curves pertain to the generalized VBGF unless otherwise noted.
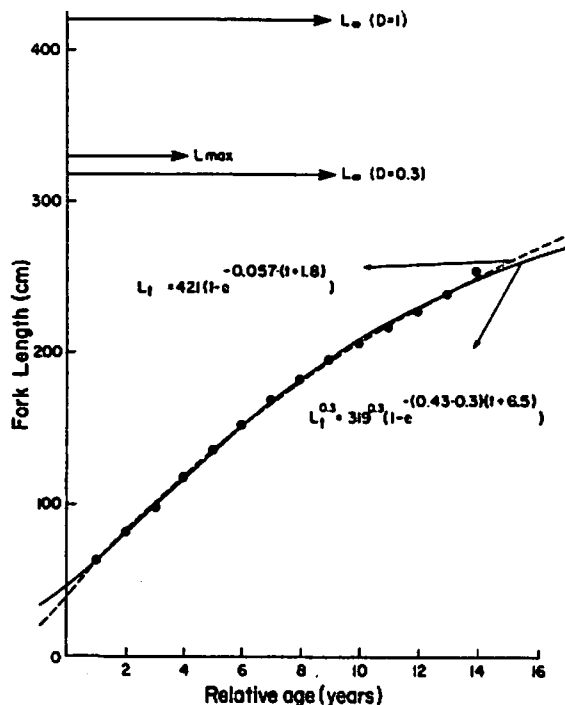

Fig. 3. Sella's (1929) length-at-age data on bluefin tuna (*Thunnus thynnus*) fitted with both the special and the generalized VBGF. Note that $L_\infty \approx L_{max}$ when using the generalized VBGF. The L_{max} value stems from Tiews (1963) and the value of d = 0.9 (hence D = 0.3) stems from Muir (1969) (see text).

SEASONALLY OSCILLATING GROWTH

While the various versions of the VBGF assume constant environmental conditions, it has been demonstrated by many authors that fish live in an environment with seasonally oscillating features (temperature, food availability) and that, therefore their growth also oscillates seasonally (Ursin 1963; Pitcher and MacDonald 1973; Lockwood 1974; Daget and Ecoutin 1976; Cloern and Nichols 1978). A versatile model suited to expressing the seasonally oscillating length growth of fishes was presented by Pauly and Gaschütz (1979) which is based on the VBGF and becomes, in its generalized form

$$L_t = L_\infty (1 - e^{-[KD(t - t_o) + C\frac{KD}{2\pi} \sin 2\pi (t - t_o)]})^{1/D} \qquad \ldots 15)$$

where L_∞, K, D, t_o, L_t and t are parameters as defined above, while the new parameters C and t_s refer to the intensity of the (sinusoid) growth oscillations of the model and to the onset of the first oscillation with regard to t = 0, respectively. It is a property of the parameter C that it takes a value of 1 when the growth rate (dL/dt) has exactly one zero value per year (generally in the coldest month of the year), a value of zero when the fluctuations are nil, in which case equation (15) reduces to equation (9), and intermediate values when the seasonal oscillations are sufficient to reduce, but not to halt growth in length (Fig. 4).

In Table 1 growth parameters are presented for 10 fishes the length-at-age data of which were fitted with equation (15) by means of the computer program presented by Gaschütz et al. (1980). Table 1 also contains estimates of the temperature range ΔT (= difference between the highest and lowest average mean monthly temperature to which the fish are exposed in the course of a year) for the 10 fish (stocks) in question.

As may be seen from Fig. 5, the values of C for the various fish (stocks) strongly correlate with ΔT, suggesting that

— seasonal length growth oscillations are caused by temperature fluctuations or by another environmental parameter which itself correlates with temperature (e.g., food availability, or foraging behavior, or both).

— slight seasonal fluctuations of temperature (or of correlated parameters) such as occur in the tropics are sufficient to generate seasonally oscillating growth curves, and a seasonally oscillating growth model should be used to fit growth data pertaining to intervals of less than one year (e.g., when fitting growth data obtained by reading daily otolith structures or when analyzing length-frequency data sampled at less than yearly intervals, see below).

A model similar to the one used here to simulate the seasonally oscillating length growth of fish was developed by Shul'man (1974) to depict the seasonally oscillating growth in weight of Black Sea fishes. Shul'man's approach seems particularly suitable for incorporation in seasonally oscillating metabolic models of fish growth in the tropics.

Table 1. Parameters of seasonally oscillating growth curves in 10 fish (stocks) arranged in order of increasing annual range of water temperature (ΔT).

No.	Species	Area	L_∞	K	t_o	t_s	C	ΔT (°C)[b]	Source of growth data
					Growth parameters[a]				
1	*Pseudotolithus elongatus*	Sierra Leone	52.0	0.366	−0.098	−0.132	0.40	3*	Longhurst (1963, Fig. 10)
2	*Tilapia nigra* (untagged)	Kenyan ponds	28.2	1.95	−0.151	−0.010	0.20	4	Van Someren and Whitehead (1960, Fig. 1)
3	*Tilapia nigra* (tagged)	Kenyan ponds	27.9	1.64	−0.253	−0.005	0.45	4	Van Someren and Whitehead (1960, Fig. 1)
4	*Macrorhamphosus scolopax*	Meteor Bank	20.0	0.462	−0.507	0.482	0.90	4*	Ehrich (1976, Table 3)
5	*Hemirhamphus brasiliensis*	Florida	32.5	0.587	−1.024	0.253	0.69	6*	Berkeley and Houde (1978, Fig. 5)
6	*Trisopterus esmarki*	North Sea	17.8	1.06	−0.179	0.189	1.04	7*	Gordon (1977, Fig. 6)
7	*Salmo trutta*	Scottish river	22.2	0.411	−0.294	−0.005	1.24	10	Egglishaw (1970, Fig. 5)
8	*Salmo salar*	Baltic Sea	14	0.324	−0.101	−0.242	1.14	12*	Thurow (1973, Table 1)
9	*Tilapia nigra* ♂)	open-air aquarium	16.9	1.24	−1.24	0.427	1.25	13	Cridland (1965, Fig. 1)
10	*Tilapia nigra* ♀	(Uganda)	16.5	0.956	−1.54	0.449	1.42	13	Cridland (1965, Fig. 1)

[a] All values refer to D = 1.
[b] The temperature data were obtained either from the paper that also gave the growth data, or from an oceanographic atlas (*).

AGING OF TROPICAL FISHES

Aging by means of markings on skeletal structures

The standard techniques for aging fishes by means of markings on their scales, otoliths or other hard structures are documented by vast amount of literature, much too large to be reviewed here. Mohr (1927, 1930, 1934) gave a comprehensive bibliography of the earlier literature, which was also reviewed by Graham (1928). Bibliographies of the more recent literature on fish growth are given in Menon (1950), Bagenal (1974) and Pauly (1978). Brothers (1980) reviewed and assessed methods that are particularly well-suited for use in the tropics, namely, aging by means of daily otolith structures and analysis of length-frequency data.

While the methods reviewed by Brothers (1980) for the analysis of length-frequency data are rather conventional ("Petersen method" and "modal class
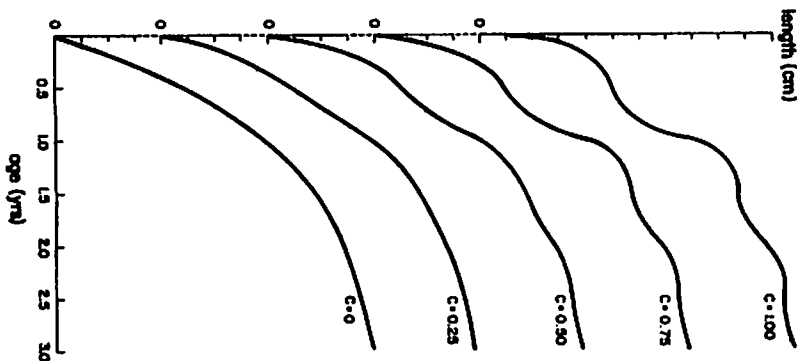

Fig. 4. Seasonally oscillating growth curves based on equation 15, with L_∞ = 25 cm, K = 1, t_o = 0, t_s = 0 and D = 1, with values of C ranging from 0 to 1.

progression analysis", see below), his review of aging by means of daily otolith structures (rings) leads to the conclusions that:

— reading daily otolith rings in tropical fishes, at least in relatively short-lived ones, is as easy as reading annual rings in temperate fishes, although it may be more time consuming,

— the overwhelming majority of commercially important tropical fish families display daily otolith rings, and

— there is no reason why aging by means of daily otolith rings should not become a standard technique for use in the tropics, especially for the validation of growth data obtained from analysis of length frequencies.

Authors reporting work conducted on daily growth rings in tropical and other fish are, among others: Brothers (1980), Brothers et al. (1976), Worthmann (1980), Gjøsaeter and Beck (1980), Methot and Kramer (1979), Le Guen (1976), Panella (1971, 1974), Steffensen (1980), Ralston (1976), Struhsaker and Uchiyama (1976) and Taubert and Cable (1977).
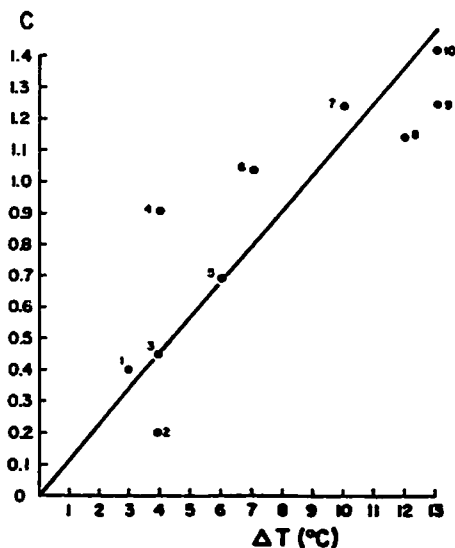

Fig. 5. Relationship between the values of the parameter C in seasonally oscillating growth curves, and the difference between the highest and lowest mean monthly temperatures to which the fishes were exposed (ΔT). Based on data in Table 1. Note that ΔT values of 2 to 3°C, such as occur in the tropics still can generate growth oscillation (see also Fig. 4).

While there is a large body of literature relating to possible reasons why annual growth checks are produced on scales, otolith and bones (and cartilage in elasmobranchs) (see e.g., Chugonova 1959 or Bagenal 1974 and references therein), few attempts have been made to explain the occurrence of marked daily structures on fish otoliths. Panella (1974) writes for example, that "whether rhythmic growth is related to diurnal migratory behavior, rhythmic feeding, or activity and rest is difficult to say."

An explanation for rhythmic growth may be provided by the hypothesis proposed earlier (Pauly 1979b, 1981) that anabolism in fishes is essentially limited by oxygen availability to the tissues (see above derivation of the generalized VBGF). This hypothesis would suggest that fish, which can store little oxygen, can be either active (e.g., feeding, escaping predators, defending territories, etc.) and diverting all available oxygen to these activities, or resting, in which case they can only then divert oxygen to anabolism. The diurnal changes in activity patterns would thus be sufficient to generate "pulses" of anabolism, the latter activity being, it must be emphasized, quite distinct from the incorporation of food into the metabolic pool (Iles 1974).

Growth as estimated from length-frequency data

The methods conventionally used for the analysis of length-frequency data have been introduced by Petersen (1892) and can be reduced to two basic techniques:

— the "Petersen Method" (sensu stricto), that is the attribution of relative ages to the peaks a length-frequency sample, and

— the "Modal Class Progression Analysis" (George and Banerji 1964), that is the linking up of the peaks of length-frequency samples sequentially arranged in time by means of growth segments.

With the first method, the problem consists of identifying those peaks representing broods spawned at known or assumed time intervals. The method generally involves the separation of the length-frequency samples into normally or otherwise distributed subsets by graphical methods, such as those proposed by Harding (1949), Cassie (1954), Tanaka (1956), or by means of computer programs such as NORMSEP (Abrahamson 1971) or ENORMSEP (Yong and Skillman 1971).

The "modal class progression analysis", on the other hand, has its major problems in the identification of those peaks which should be connected (by growth lines) with each other (Pauly 1978).

Both methods are highly subjective, and an attempt was made only recently to combine them into one single, "integrated" method which to a certain extent improves the reliability of growth estimates based on the analysis of length-frequency data (Pauly 1980a).

However, the need for a rapid, yet reliable and objective method for the analysis of length-frequency data led to a radically new approach in the analysis of length-frequency data, and such an approach was presented in Pauly and David (1981).

Briefly, this new method (called Electronic Length-Frequency Analysis or ELEFAN I) is based on the following steps:

— objective identification (definition) of the peaks and the troughs separating peaks of a (set of) length-frequency sample(s)

— attribution to the peaks of a certain number of positive "points"

— attribution to troughs separating the peaks of a certain number of negative "points"

— iterative identification of those growth parameters generating a growth curve which, by passing through most peaks and avoiding most troughs, accumulates the highest number of "points" and thus best explains the specific structure of a (set of) length-frequency sample(s).

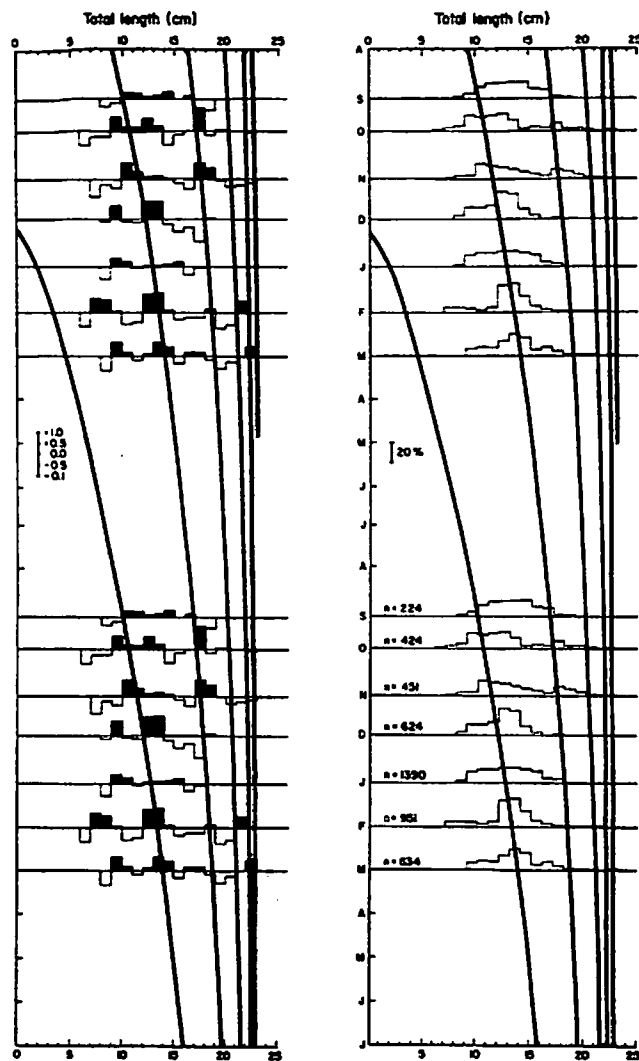The procedure is illustrated in Fig. 6.

Fig. 6. Estimation of growth parameters by means of ELEFAN I. A) Showing a "restructured" length-frequency sample, where peaks have become positive points (black) and troughs have become negative points (white). These "points" are computed and used internally by ELEFAN I to identify the growth curve which passes through the largest number of positive points, and avoids negative points as much as possible. B) Showing the original length-frequency data, with superimposed growth curve. The curve, which was traced in a purely objective fashion "explains" 62% of the peaks in the length-frequency data (as defined by ELEFAN I).

Given the assumptions that the sample(s) used represent(s) the population investigated, and that the growth of the fish in question conforms to the VBGF, (seasonalized or not), the method can be used to derive growth parameters that are reproducible (i.e., any worker will get the same result from the same set of data). Moreover, an estimator is given of the proportion of the peaks in a (set of) sample(s) that are "explained" by the growth parameters obtained at the end of the iteration process. This estimator is the ratio of a sum called "Explained Sum of Peaks", or ESP, referring to the number of "points" explained by a given growth curve, divided by another sum called "Available Sum of Peaks", or ASP, which refers to the total number of points "available" in a (set of) length-frequency samples). (See Pauly et al. 1980 for details). The method which can be readily implemented on microcomputers, is fast, reliable, and objective. Ideally, the results (growth parameter estimates) should be checked against the results obtained by reading daily structures of the otoliths of a few fishes, which would also serve to obtain estimates of t_o (which is not estimated by ELEFAN I), by solving equation (9) or (15) for this parameter.

Mortality

TOTAL MORTALITY

A basic equation used in fishery biology for expressing the mortality of fish is

$$N_t = N_o e^{-zt} \qquad \dots 16)$$

where N_o and N_t are fish numbers at time zero and t, respectively and where Z is the total mortality affecting the stock. Also, we have

$$Z = F + M \qquad \dots 17)$$

which states that total mortality is the sum of fishing mortality (F) plus natural mortality (M). A major task of fishery biologists working on a specific stock is the splitting up of Z into its component parts, F and M; this will be discussed further below, after methods for estimating Z have been briefly reviewed.

One of the simplest methods to assess total mortality is to estimate Z from the mean size is the catch, as suggested by Beverton and Holt (1956). The method was discussed in Pauly (1980a) and Munro (this vol.).

Another method of estimating Z is to construct catch curves, i.e., plots of the natural logarithm of fish numbers against their age, where Z is the slope, with sign changed, of the "descending" part of the curve (Ricker 1975).

Where fishes both are relatively long-lived and can be aged by means of annual rings on scales, otoliths or bones, catch curves can be constructed and interpreted quite straightforwardly, e.g., as described by Robson and Chapman (1961), or Ricker (1975).

Presented here are the three steps of a method which allow for the derivation of catch curves from length-frequency data, as generally collected from tropical fishes:

Table 2. Showing how to construct a catch curve from a length-frequency sample of *Sillago sihama* from Manila Bay (data from Ziegler 1979).

Class limits, in cm Lower	Upper[b]	Mid-range	N[a]	t_1[c]	t_2[c]	Δt	$N/\Delta t$	% ($N/\Delta t$)	$\log_e$ (% $N/\Delta t$)	Mean relative age (years)[d]
6	7	6.5	0.893	0.421	0.505	0.084	10.6	0.207	−1.58	0.462
7	8	7.5	7.60	0.505	0.595	0.090	84.4	1.66	0.504	0.549
8	9	8.5	21.1	0.595	0.690	0.095	222	4.31	1.46	0.641
9	10	9.5	56.5	0.690	0.792	0.102	554	10.8	2.38	0.740
10	11	10.5	75.6	0.792	0.902	0.110	687	13.4	2.59	0.846
11	12	11.5	81.6	0.902	1.021	0.119	686	13.3	2.59	0.960
12	13	12.5	122	1.021	1.151	0.130	938	18.2	2.90	1.08
13	14	13.5	121	1.151	1.294	0.143	846	16.4	2.80	1.22
14	15	14.5	79.5	1.294	1.453	0.159	500	9.73	2.28	1.37
15	16	15.5	45.9	1.453	1.632	0.179	386	5.00	1.61	1.54
16	17	16.5	32.5	1.632	1.836	0.204	159	3.09	1.13	1.73
17	18	17.5	29.2	1.836	2.075	0.239	122	2.38	0.867	1.95
18	19	18.5	14.6	2.075	2.361	0.286	51.0	0.992	−0.008	2.21
19	20	19.5	7.37	2.361	2.720	0.359	20.5	0.399	−0.918	2.53
20	21	20.5	3.49	2.720	3.201	0.481	7.26	0.141	−1.96	2.94
21	22	21.5	1.09	3.201	3.931	0.730	1.49	0.029	−3.54	3.52
22	23	22.5	1.05	3.931	5.500	1.569	0.699	0.013	−4.35	4.51

[a] The sample was obtained by adding up several samples in which frequencies were expressed in %. This procedure reduces the effects of seasonal recruitment pulses on the catch curve.

[b] The upper class limits, obviously should read 6.999, 7.999, 8.999, etc., but are rounded up for computing t_2 (see below).

[c] t_1 and t_2 are the relative ages corresponding to the lower and upper class limit, respectively, and are computed from:

$$t_{1,2} = \{\log_e [1-(L_{t_{1,2}}/L_\infty)^{1/D}]\}/-KD$$

with $L_\infty = 23.5$, $K = 0.70$ and $D = 1$.

[d] Mean relative age is the relative age corresponding to the class mid-range.

Pooling of length-frequency data. Since the overall age structure of a population in short-lived fishes is essentially determined by "pulses" of recruitment, a first step should be to attempt to smooth out the recruitment pulses by pooling data obtained at regular intervals during a period of one year. Also, to prevent a larger sample from unduly affecting the total sample, the various samples should be converted to percentage length-frequency samples prior to adding to obtain a single, overall sample (see also Munro, this vol.).

Construction of catch curve proper. Since the growth in length of fish is not linear, and generally slows down as length increases, there is a tendency for older size groups to contain more age groups than younger size groups. As suggested by J. Gulland (pers. comm.), this can be compensated for by dividing the number of fish in each size group (e.g., cm-class) by the time it takes the fish to grow through a size group (Δt). The catch curve equation thus becomes

$$\log_e (N/\Delta t) = a + bt \qquad ....18)$$

where t is the age corresponding to midlength of each length class, $b = -Z$, N = the number of fish in each length class and Δt = the time needed for the fish to grow through a length class. (See Table 2 and Fig. 7 for an example).

Identification of biased data points. The conversion of length-frequency samples to a catch curve by means of growth parameter values can involve fishes the individual lengths of which are very close to L_∞, in which cases unrealistically high "ages" are generated. Thus, it is imperative that a scattergram be drawn of the points to use for the computation of Z, in order to select for points really belonging to the descending part of the curve, and contained within a reasonable age-span (Fig. 7).

A versatile program, called ELEFAN II and written in BASIC is available from the author which performs the tasks outlined in 1) to 3), thus allowing for values of Z to be obtained from length-frequency data (Pauly et al. 1981). This program, which requires a (set of) representative length-frequency samples) and a pair of growth parameters (L_∞ and K) can be run with the length-frequency data also used in ELEFAN I for the estimation of L_∞ and K, thus allowing for growth and mortality parameters to be estimated from the same set of data. The construction of catch curves from length-frequency data can also be done with "pencil and paper" methods, as outlined by Pauly (1980a).

Another method of estimating Z from catch data akin to the use of a catch curve is the construction of a "pseudo-catch curve" (Pauly 1980b). This method is based on the interrelationships between body size and water depth on one hand, and catch rates and water depth on the other hand. The method is particularly suited to the derivation of estimates of Z from data that were gathered for purposes other than straightforward estimation of Z.

A completely different set of methods for the estimation of Z, F and M has been reviewed in Gulland (1969), Ricker (1975), Jones (1977) and elsewhere which involves the tagging and recapture of fish. Tagging programs,
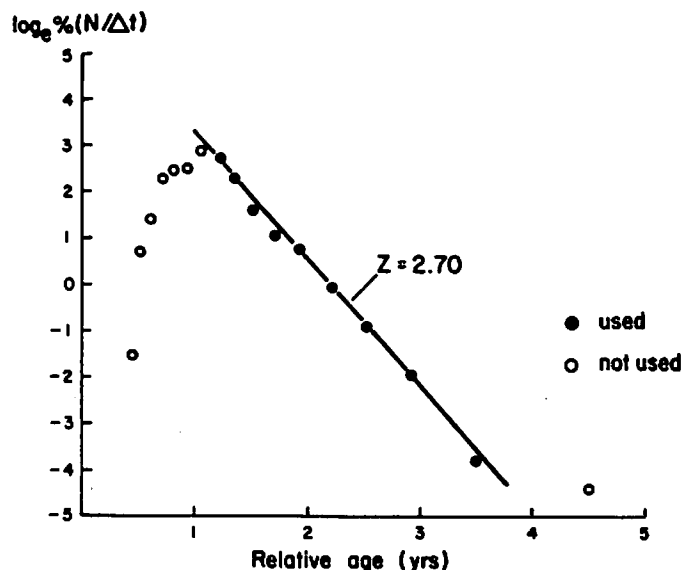
$\log_e \% (N/\Delta t)$

Fig. 7. A length-converted catch curve. Based on length-frequency data in Fig. 6B and on growth parameters (L_∞ = 23.5, K = 0.7 and D = 1) as estimated by means of ELEFAN I. The term "relative age" refers to the fact that t_o is set equal to zero when converting length to age. Note that for the computation of Z, one point, too far to the right was omitted, along with the ascending part of the curve. See also Table 2 and text.

which can provide mortality estimates in addition to estimates of growth, migrations, and data on stock size and identity have been conducted in conjunction with many tropical stocks. Table 3 summarizes the results of studies conducted in the tropics and subtropics. Tagging/recapture programs are generally quite costly (e.g., because of the need to advertise the program widely, in order to obtain a sufficiently large number of returns). It needs to be established whether tagging programs for more than a few key species should be conducted in multispecies stock investigations.

NATURAL MORTALITY

Natural mortality (M) is a parameter that is generally extremely difficult to estimate, and typically, natural mortality estimates of tropical fish have been obtained from estimates of total mortality in stocks known, or assumed to be unfished (e.g., Thompson and Munro 1978; Weber and Jothy 1977; Pauly and Martosubroto 1980). In a few cases, however, it has been possible to obtain time series of values of Z from the same stock, and to plot these against their corresponding values of effort, with M being obtained from the intercept of the line fitted to these data. Ricker (1975) gives the rationale of the method, which also provides an estimate of the catchability coefficient (q) of the gear in question (see Fig. 8 for an example from the tropics).

Tropical multispecies stocks are often exploited, while time series of Z and effort are generally unavailable, for which reasons M most often cannot be estimated by any of the conventional methods.

Following an earlier attempt by Beverton and Holt (1959) and others to identify predictors of M based on comparative studies, a compilation was undertaken of 175 estimates of M, ranging from freshwater to marine and from polar to tropical fishes. It was then shown (Pauly 1980c) that M can be predicted from a knowledge of the growth parameters of a given stock, and of its mean environmental temperature (e.g., as estimated from an oceanographic atlas), the empirical relationship linking these being

$$\log_{10} M = 0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$$
$$\ldots . 19)$$

where M is the exponential rate of natural mortality, on a yearly basis, L_∞ the asymptotic length of the fish in the stock, in cm, K their growth coefficient (on a yearly basis) and T the mean environmental temperature for the stock in question, in °C. The equation has a multiple correlation coefficient of R = 0.847, which is significant (with 171 degrees of freedom, only 0.275 is needed for significance at P = 0.01). (L_∞ and K of equation (19) refer to D = 1).

As discussed in Pauly (1980c), where the data used for the derivation of this equation are documented, the equation produces reasonable estimates of M in most stocks, the only exceptions as far as the tropics are concerned being those values of M pertaining to Clupeidae and possibly to other strongly schooling fishes, for which mortality is slightly over-estimated by the equation. Thus, in such cases, multiplying estimates of M obtained from equation (19) by a factor of 0.8 or so might be appropriate.

The values of M obtained by means of equation (19) are "reasonable" in the sense that they cannot be very different from the true values, as opposed e.g.. to estimates based on a plot of Z on effort, which at times can produce completely erroneous values of M, including negative ones (Ricker 1975 p. 174). On the other hand, it is known that the natural mortality of fishes varies with age (Boiko 1964) and most probably also with predator abundance (Pauly 1980d, 1982; Munro, this vol., Jones, this vol.). The estimates of M provided by equation (19) should thus be considered as first approximations pertaining to the exploited phase of a population, under average conditions only.

FISHING MORTALITY

Of the various methods used to estimate fishing mortality, four may be listed here:
  — tagging/recapture studies
  — subtraction of M from Z
  — swept-area method in the case of trawlable demersal stocks
  — Virtual Population Analysis (VPA) or Cohort Analysis
Tagging/recapture studies are not discussed further in this paper, and the reader is referred to the reviews mentioned above and to the references listed in Table 3.

Table 3. Selected tagging-recapture or marking studies conducted on tropical and subtropical fishes.[a]

Species	Family	Area	Main results	References
Trianodon obesus	*Carcharhinidae*	Johnston Island, Central Pacific	growth data, movements	Randall (1977)
Galeorhinus australis	*Carcharhinidae*	South-East Australian Waters	growth parameters, M&F	Grant et al. (1979)
Various shark spp.	—	Eastern Central Pacific	growth data, movements	Kato and Carvallo (1967)
Beryx splendens	*Berycidae*	Japan	growth parameters	Ikenouye and Masazawa (1968)
Priacanthus tayenus	*Priacanthidae*	Gulf of Thailand	growth data, movements	Chomjurai and Bunag (1970)
Chrysophrys auratus	*Sparidae*	South-East Australian Waters	growth parameters	Sanders and Powell (1979)
Pagrus major	*Sparidae*	Japan	population size, M&F	Kato and Yamada (1976)
Tilapia esculenta	*Chichlidae*	Lake Victoria (Uganda)	growth parameters, by sex	Garrod (1968)
Amphiprion spp.	*Pomacentridae*	Eniwetok Atoll, Pacific	growth data, behavior	Allen (1975)
Acanthurus triostegus	*Acanthuridae*	Hawaii	growth data, movements	Randall (1961)
Balistes capriscus	*Balistidae*	Togo Shelf, West Africa	F, movements	Beck (1974)
Rastrelliger neglectus	*Scombridae*	Gulf of Thailand	M&F, growth parameters	Hongskul (1974)
Scomber australasicus	*Scombridae*	North of Taiwan	movements, growth data	Chang and Wu (1977)
Thunnus albacares	*Scombridae*	Eastern Central Pacific	migrations	Bayliff (1979)
Istiophorus platypterus	*Istiophoridae*	off Eastern Florida	tagging mortality	Jolley and Irby (1979)
Various teleostean spp.	—	Florida, U.S.A.	new tagging method	Threeher and Gronell (1978)
Various telacostean spp.	—	Virgin Island, Caribbean	behavior, growth data	Randall (1962, 1968)

[a] This list is not exhaustive and is presented only for illustrative purposes, and to give an entry into the literature.

The detailed analysis of length-frequency data, as outlined above, based either on the programs ELEFAN I and ELEFAN II, or on "paper and pencil methods" (Pauly 1980a) provides estimates of growth parameters and of Z, while the growth parameters, combined with an estimated value of mean environmental temperature can be used to provide an estimate of M from equation (19), which is then subtracted from Z to obtain F.

This method allows for a quick assessment of whether a stock is over-fished or not, based on the assumption that the value of F which optimizes yield should be similar to M, or

$$E_{opt} \approx \frac{F}{F + M} \approx 0.5 \qquad \ldots 20)$$

where E_{opt} is the exploitation rate which optimizes the yield from a given stock (Gulland 1971).

Another method of estimating fishing mortality in trawl fisheries is the "swept area method", as treated in Gulland (1969). The method can be summarized in one equation, namely

$$F = \frac{a \cdot X_1}{A} \qquad \ldots 21)$$

where "a" is the total area "swept" by the combined effects of all gears of a fleet (of trawlers), A is the total area inhabited by the stock in question, and X_1 is the escapement factor, i.e., the fraction of the fish in the path of the gear that are actually retained by the net.
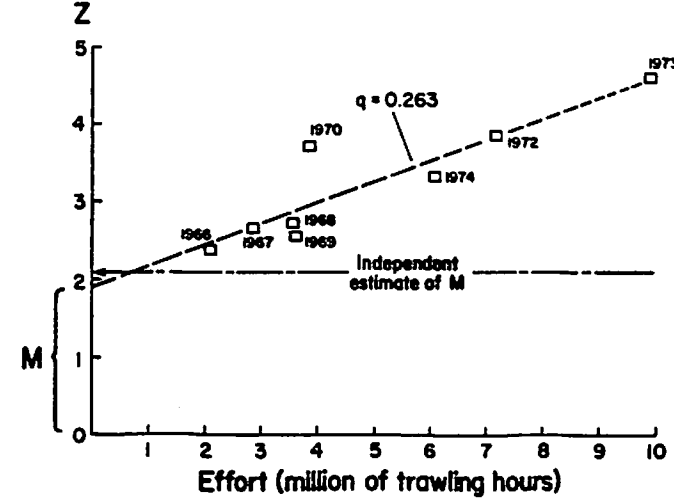

Fig. 8. Example of a plot of total mortality on effort for a tropical stock (*Selaroides leptolepis*, Gulf of Thailand). Note that estimated M (intercept) corresponds closely with value of M estimated independently, from equation (19). [The values of Z and f stem from Pauly (1980d).]

Values for the escapement factor ranging between 1 and 0.4 have been proposed and used by various authors working in tropical multispecies stocks (Isarankura 1971; Saeger et al. 1976; SCSP 1978; Gulland 1979): these estimates are commonly based on assumptions of various kinds. Pauly (1980d) demonstrated that, for the Gulf of Thailand trawl fishery, values of F obtained independently i.e., by estimating Z from mean sizes in the catch in 6 species of fish, and M by means of an empirical equation similar to equation (19) could, on the average, be made equal to values of F obtained from equation (20) by setting $X_1 = 0.5$ (and $X_2 = 0.5$, see below).

The area "swept" by the gear during one unit of effort (a') is estimated from

$$a' = t \cdot v \cdot h \cdot X_2 \qquad \dots 22)$$

where t is the time spent trawling, v the velocity of the trawler over ground when trawling, h is the length of the trawl's head rope and X_2 a fraction expressing the width of the area swept by the gear divided by the head rope length. Values of X_2 ranging between 0.4 and 0.66 are commonly used in Southeast Asian waters, 0.5 probably being the best guess (Pauly 1980d; see above for X_1).

Wheeler and Ommaney (1953) have attempted to adapt the swept-area method to handlining for large coral fishes. (See also Gulland 1979).

Virtual Population Analysis (VPA) and the related method of cohort analysis which can be used to estimate F from catch-at-age data have recently been reviewed by Jones (1981), who also suggested a version of cohort analysis suitable for use with catch-at-length data (Jones 1974, 1981). More recently, Pauly (in prep.) suggested a simple version of VPA analysis suitable for use with catch-at-length data. Table 4 puts in context the four related methods that are available for the estimation of fishing mortality from catch data.

As opposed to VPA and cohort analysis run with catch-at-age data, the methods developed to date for the analysis of catch-at-length data do not

Table 4. Showing some properties of 4 methods[a] for the analysis of sequential catch data.

Data required	Solution	Iterative, but precise[e]	Direct, but approximate	Remarks
catch-at-age data		Virtual Population Analysis Murphy (1965) Gulland (1965)	Pope's cohort analysis (1972)	single cohorts can be followed
catch-at-length data		Pauly (in prep.)	Jones' length cohort analysis (1974)	single cohorts cannot be followed; equilibrium conditions must be assumed or generated by averaging

[a]Simple programs, implemented on HP 67/97 programmable calculators are available from the author for all four of these methods.

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allow for the fate of single cohorts to be investigated, i.e., length "cohort analysis provides estimates of the *average* number attaining each length during a year, as well as the *average* numbers present in a length group at any particular moment." (Jones 1981) [emphasis added, DP].

With this problem in mind, Pope et al. (in prep.) have developed a BASIC program (ELEFAN III) which allows for the use of catch-at-length data in VPA. In this program, the growth parameters of the stock in question (e.g., as obtained from ELEFAN I) are used in conjunction with the catch data arranged sequentially in time to define, in a first step, series of cohorts "sliced" from the catch-at-length data. Then VPA's are run for each of these (arbitrary) cohorts, which leads to the identification of recruitment peaks, i.e., which allow for the definition of "real" cohorts, composed of fish recruited at approximately the same time. The program then allows, in a final step, for running VPA's on whichever cohorts have been identified as "real", the crucial advantage of this approach over the two length-structured models in Table 4 being that an equilibrium situation need not occur, i.e., the decay of single cohorts can be followed over time. The program, it may be mentioned, can accommodate seasonally oscillating growth in length, and may thus be used also with temperate fishes.

Stock Size, Production and Intrinsic Rate of Increase

ESTIMATING STOCK SIZE

A plethora of methods are available to estimate the stock size of fish, a partial list being:
— tagging/recapture methods (see above)
— acoustic methods
— egg and larval surveys
— swept-area method
— VPA and cohort analysis
— De Lury's method
— interrelationship between catch, fishing mortality and standing stock

Acoustic methods are not reviewed here, and the reader is referred to Forbes and Nakken (1972).

Egg and larval survey, in the tropics, generally cannot be used to estimate (spawning) stock size because of the extremely short development time of most eggs (most often less than 10 hours, see Delsman 1972), which renders quasi-synoptic surveys of the spawning grounds extremely difficult to conduct.

The swept area method, which was discussed above in connection with the estimation of F can obviously also be used to estimate stock sizes (B), i.e.,

$$B = \frac{(\overline{c/f}) \cdot A}{a' \cdot X_1} \qquad \dots 23)$$

where $\overline{c/f}$ is the mean catch-per-effort obtained during a survey (or within one stratum of a survey), and A, a' and X_1 are defined as in equation 21 and 22).

VPA and cohort analysis (including the versions for use with catch-at-length data) can be used to estimate absolute population sizes; in fact this

Table 5. Successive sample sizes of reef eels *(Kaupichthys hyoproroides)* from an isolated Bahamian patch reef.[a]

Samples	No. of fish collected	Effort[b]
A	5	1
B	4	1
C	3	1
D + E	1	2

[a] Based on data in Smith (1973, Table 5, Station 1).
[b] The unit effort is "11 fluid ounces of emulsified rotenone applied from a plastic squeeze bottle."

is one of the reasons why the methods have become so popular. The reader is thus referred to the discussion of these methods, presented above in conjunction with the estimation of fishing mortality.

The two last methods for stock size estimation seem particularly suited for use in coral reef fish populations. The first of these is De Lury's method of plotting catch-per-effort on cumulative effort in such cases where the reduction of a population by fishing is so rapid that the effects of recruitment or natural mortality can be neglected.

In such cases, e.g., when sampling is done with repeated rotenone applications, the plot yields estimates of initial population generally higher than those obtained by simply adding up all sampled individuals (i.e., by assuming that all fish were removed). An example of this approach is given in Table 5 and Fig. 9.
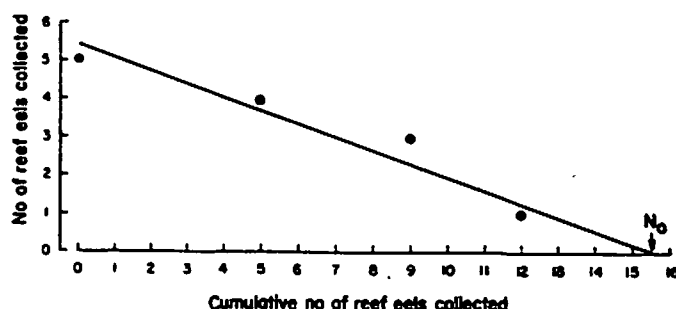

Fig. 9. Example of a DeLury plot from tropical waters: successive catches and cumulative catches of reef eels in a Bahamian reef patch. Based on data in Table 5. See Ricker (1975) for details on the method.

As documented by various authors (see reviews by Ehrlich 1975, Goldman and Talbot 1976, Russel et al. 1978) coral reef fish communities are extremely difficult to sample quantitatively. Thus, in reef stock assessment, emphasis should possibly be given to sampling catches and performing detailed analysis of these data to obtain estimates of F by means of one of the methods outlined above, and to estimate mean standing stock size (B̄) from the relationship

$$\overline{B} = \frac{C}{F} \qquad \dots 24)$$

where C is the annual catch from the reef in question, and F the estimated fish mortality. This equation, incidentally, was used by Sekharan (1974) to estimate the standing stock of mackerels *(Rastrelliger kanagurta)* and sardines *(Sardinella longiceps)* of the West Coast of India.

PRODUCTION

Production (P) is defined as "the total elaboration of fish tissue during any time interval Δt, including what is formed by individuals that do not survive to the end of Δt" (Ivlev 1966).

Allen (1971) has shown that production, in equilibrium situations, can be estimated from

$$P = Z \cdot \overline{B} \qquad \dots 25)$$

where $\overline{B}$ is the mean annual standing stock and Z is the total mortality, as estimated by one of the methods outlined above. (Other, more sophisticated methods are available to estimate production, see Chapman 1978 a, b).

Equation (26) shows that production can be also defined as the sum of the catch plus the weight of all fish that died of natural causes or

$$P = (F \cdot \overline{B}) + (M \cdot \overline{B}) \qquad \dots 26)$$

Regrettably, little information is available on the production of tropical marine fishes; what little data there are on tropical fish production stems from freshwater systems (Durand 1978; Welcomme 1979). Thus, it remains to demonstrate that production can be turned into a concept useful for tropical marine stock assessment, e.g., for comparative studies of various systems (see Marten and Polovina, this vol.).

INTRINSIC RATE OF INCREASE

The intrinsic rate of increase (r_m) of a population or stock is a parameter which only ecologists use explicitly (see e.g., Odum 1971, or Ricklefs 1973). However, this parameter is implicit in the parabolic surplus-yield or Schaefer model (Schaefer 1954, 1957) i.e.,

$$MSY = \frac{r_m \cdot B_\infty}{4} \qquad \dots 27)$$

where Maximal Sustainable Yield is defined as the product of the intrinsic rate of increase of a population, times the carrying capacity of its habitat (B_∞) divided by 4 (see also Ricker 1975, p. 315).

Thus, when an estimate is available of the virgin biomass of a given population (B_v, or B_o in Gulland 1971) and when it is legitimate to set $B_\infty \approx B_v$ (it is *not* always the case, see Pauly 1979a or May et al. 1979), all that is needed to obtain a preliminary estimate of MSY is a value of the intrinsic rate of increase (r_m) of the population.

Blueweiss et al. (1978) partly based on earlier data in Fenchel (1974) and Smith (1954) have shown that r_m, in animals and various small organisms is closely related to "adult" body size, and presented a log/log plot of r_m against mean adult body weight ($\overline{w}$) spanning 22 orders of magnitude (!)

and ranging from virus (T-phage) to deers (Fig. 10). Blueweiss et al. (1978) also suggest that the product of r_m and $\overline{w}$ "is an estimate of the maximum possible rate of production" which seems to be a point worth investigating further in future production studies.

As the data used by Blueweiss et al. (1978) contained only two fish (Blueweiss pers. comm.) namely *Gadus morhua* and *Sardinops caerula* (No. 11 and 12 respectively on Fig. 10), 6 new fish stocks have been added onto their graph as well as 4 estimates of r_m and $\overline{w}$ pertaining to whales, which extends the graph to a span of 24 orders of magnitude (Fig. 10). The data used and mode of computation of the r_m and $\overline{w}$ values are presented in Table 6. Quite clearly, r_m and $\overline{w}$ values are strongly correlated; this pertains both to the data pairs of Blueweiss et al. (1978) as well as to the 10 new pairs added here. In fact, there was no need to recompute the regression equation presented by Blueweiss et al. (1978) which states, when r_m is expressed on a daily basis, that

$$r_m = 0.025 \cdot \overline{w}^{-0.26} \qquad \dots 28)$$

($r^2 = 0.90$). Combining equation (27) and (28) and converting to the year as time unit we obtain

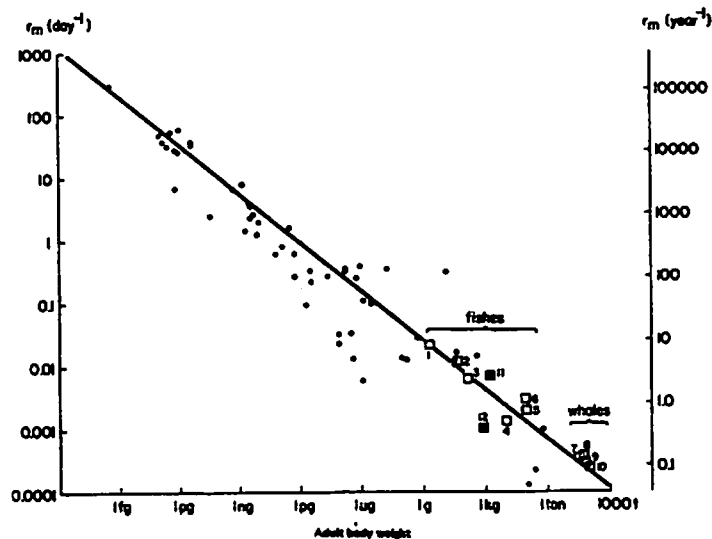$$MSY \approx 2.3 \cdot \overline{w}^{-0.26} \cdot B_v \qquad \dots 29)$$

Fig. 10. Relationship between the intrinsic rate of increase of various organisms (mainly animals) and their adult body weight. Modified from Blueweiss et al. (1978) and Blueweiss (pers. comm.). The open squares were added from Table 6, which is based on r_m values that were readily available, and not on values selected for their good fit to the line.

Table 6. Estimates of the intrinsic rate of increase (r_m) obtained from fished stocks[a], as compared with those obtained from mean adult weight ($\overline{w}$)[b] and the empirical plot of r_m on $\overline{w}$ given by Blueweiss et al. (1978).

No.	Species	B_∞ or N_∞		MSY (per year)	r_m	$\overline{w}$		$\hat{r}_m$
1	*Lebistes reticulatus*	32	g	63.3	7.91	2	g	7.62
2	*Tilapia mossambica*	10	kg	11.25	4.50	50	g	3.30
3	*Saurida undosquamis*[c]	—		—	2.30	170	g	2.40
4	*Gadus morhua*	6,800	t	85.0	0.500	10	kg	0.83
5	*Hippoglossus hippoglossus*	156	million lb	28.6	0.723	90	kg	0.47
6	*Thunnus obesus*	300	thousand tonnes	82.5	1.10	90	kg	0.47
7	Humpback whale	95	thousand indiv.	3.0	0.126	35	t	0.100
8	Sei whale	150	thousand indiv.	5.0	0.133	50	t	0.091
9	Fin whale	375	thousand indiv.	10.0	0.107	70	t	0.083
10	Blue whale	150	thousand indiv.	3.5	0.093	100	t	0.076

[a]Calculations are based on the equation $r_m = (MSY \cdot 4 / B_\infty \text{ or } N_\infty)$, and B_∞ (or N_∞) and MSY data given in Silliman and Gutsell (1958), Silliman (1975), Garrod (1977, Fig. 39), Rothschild and Suda (1977, p. 323 and Fig. 68), Allen and Chapman (1977, Table 55), for all stocks except no. 3.

[b]"Adult body size" ($\overline{w}$) is not defined in Blueweiss et al. (1978). The definition used here is $\overline{w} = W_m + W_{max}/2$, where W_m is the mean weight at first maturity of the $\math9$ and W_{max} the maximum weight reached by the oldest $\math9\math9$ of a stock. The W_m and W_{max} values stem from, or were computed from data in Norman and Fraser (1963), Schubert (1953), Mathiesen and Olsen (1968), Garrod (1977), Silliman and Gutsell (1958), Silliman (1975) and Gosline and Brock (1965).

[c]The value of r_m in *S. undosquamis* was estimated from a logistic population growth curve based on Fig. 5B in Ben-Yami and Glaser (1974).

which can be used to obtain first approximations of MSY when virgin stock size and mean weight ($\overline{w}$, in g) of the adult of that stock are known, $\overline{w}$ being defined as the mean of the weight at first maturity (W_m) and the maximum weight of the fish in the stock (W_{max}).

The results obtained by means of this equation generally compare well with those obtained using Gulland's (1971) widely-used relationship

$$MSY \approx \frac{1}{2} \cdot M \cdot B_v \qquad \dots 30)$$

An application of equation (29) follows:

Thompson and Munro (1978) gave the following data for the Caribbean grouper *Epinephelus guttatus*: natural mortality $= 0.68$; TL_{max}, in cm $= 53.7$ (corresponding to $W_{max} = 2,324$ g); approximate weight at first maturity $= 243$ g. From these data, "adult body weight" ($\overline{w}$) as defined above was estimated to be 1,284 g, which, when inserted into equation (29) and assuming virgin stock (B_v) of one arbitrary unit, provides an MSY estimate of 0.36 per year. Equation (30), on the other hand, used in conjunction with $M = 0.68$ and the same virgin stock size of one arbitrary unit gives $MSY = 0.34$, which is very close to the first estimate.

Obviously, the advantage of equation (29) over equation (30) is that no estimate of natural mortality is required, which makes the application of equation (29) to little-investigated stocks rather easy. In practice, however, the best procedure will be to use both equations whenever possible because two independent estimates are always better than one.

Recruitment

ESTABLISHMENT OF STOCK-RECRUITMENT RELATIONSHIPS

Although recruitment is an extremely important parameter, its estimation and the establishment of "stock-recruitment relationships" are extremely difficult. This is true particularly for pelagic stocks which are both more difficult to sample quantitatively and which generally display greater year-to-year variability in abundance than demersal stocks (see contributions in Parrish 1973).

Very little work has been done on the stock-recruitment relationships of tropical fishes (but see Murphy, this vol. and contributions in Saville

Table 7. Data for the establishment of a stock-recruitment relationship in the false trevally *Lactarius lactarius* from the Gulf of Thailand (adapted from Pauly 1980d).

Year	Virgin stock	1963	1966	1967	1968	1969	1970	1971	1972
Fishing mortality[a]	0	0.22	0.64	0.87	1.09	1.12	1.18	1.92	2.22
Yield-per-recruit[a]	—	3.37	5.81	6.21	6.39	6.26	6.37	5.55	5.17
Spawning stock[b]	2,660	2,087	1,277	4.22	444	191	39.3	37.8	4.00
Recruits (millions)	—	239	292	128	202	903	15.5	55.5	6.90

[a] In grams.
[b] In thousand tonnes.

$$R = 0.886 \, P e^{-0.001067 \, P}$$
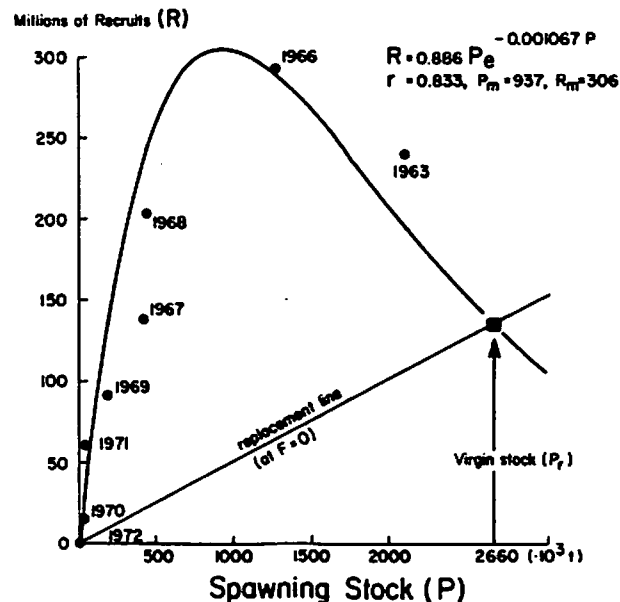$$r = 0.833, \quad P_m = 937, \quad R_m = 306$$

Fig. 11. Stock-recruitment relationship in the false trevally *Lactarius lactarius* from the Gulf of Thailand (from Pauly 1980d).

1980, and Sharp 1980) one of the main reasons for this being the lack of data that could be used for this purpose.

This has prompted several authors to use very indirect measures of recruitment (see e.g., Munro, this vol., or Pauly 1980d, 1982). The method used by the latter author involves the following steps:
a) estimation of growth and natural mortality parameters, using one of the methods above
b) computation of yield-per-recruit for each level of fishing mortality (i.e., for each year)
c) division of the calculated yield-per-recruit into the catch to obtain recruit numbers
d) plotting of estimated recruit numbers on parental stock or on predator stock or both.

The main drawbacks of the methods are steps (b) and (c) which violate important assumptions of the yield-per-recruit model of Beverton and Holt (1957), such as the assumption of an equilibrium situation in which a certain level of F has been operating long enough for the multi-aged population to have stabilized. Thus, when using this method to derive recruitment estimates, a bias is introduced in computing the yield-per-recruit. The magnitude of this bias increases with the inter-year changes in F, and with the life span of the fish in question.

Many tropical fishes, however, have short life spans and high rates of natural mortality (Qasim 1973b; Banerji and Krishnan 1973; Pauly 1980c). For these reasons, the biomass of a cohort generally peaks a few months after hatching, which results, when fishing is constant over the year, in a year's catch roughly corresponding to the actual yield-per-recruit for that year multiplied by the number of recruits produced in that year, to the exclusion of the remnants of older cohorts. This would then justify the operation described above.

Table 7 and Fig. 11, adapted from Pauly (1980d) shows results obtained by applying this approach to the false trevally, *Lactarius lactarius* from the Gulf of Thailand.

Murphy (this vol.) discusses some of the problems associated with this method and suggests an alternative explanation to some results obtained by applying it.

RECRUITMENT PATTERNS

In addition to the numbers of recruits produced within a given time interval (e.g., a year) an important aspect of recruitment is its structure within that interval, i.e., whether recruitment is discrete or continuous. Tropical fishes are reported by many authors to have very protracted spawning seasons (e.g., Qasim 1973a; Weber 1976; Nzioka 1979; Goldman 1980), but the question has rarely been asked whether this protracted spawning season is in actuality matched by a correspondingly long "recruitment season" (see Sharp 1980 for the concept of recruitment "windows", open during only brief periods of the year).

Clearly, recruitment even in tropical fishes must oscillate seasonally, since year-round recruitment would generate size frequency distributions lacking peaks and troughs. Conversely, by projecting a set of length-frequency
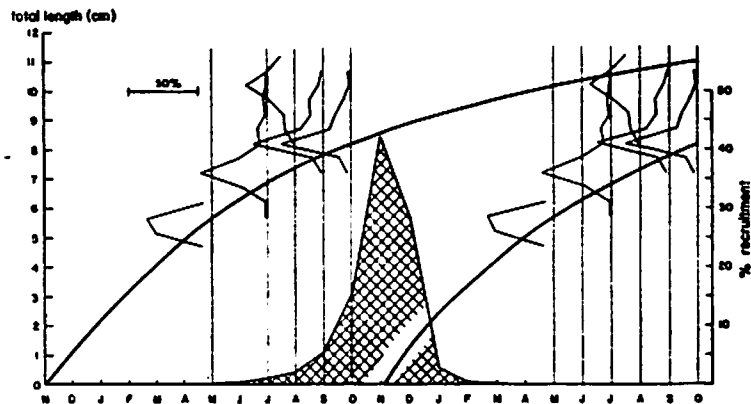
total length (cm)

Fig. 12. Recruitment pattern in *Leiognathus bindus*. Note that the time scale implies that $t_o = 0$, which most certainly doesn't apply. Thus, only the *shape* of the recruitment pattern is considered, not its position on the time axis. The growth parameters used for projecting the length-frequency data are $L_\infty = 12.2$ cm, K = 1.3 and D = 1 (ESP/ASP = 0.804) as estimated by means of ELEFAN I from data in Balan (1967).

data backward onto the time axis (by means of growth parameters) down to zero length, one can obtain a frequency distribution reflecting the "pattern of recruitment" of a stock (see Fig. 12). A procedure generating such "patterns of recruitment" has been incorporated into the ELEFAN II program. One first result obtained with this new approach is that, although it seems continuous (i.e., occurring over the whole year), recruitment to the stocks hitherto investigated is often distributed normally, with one or two peaks per year. The position of the peak(s) when adjusted to real time by means of a value of t_o thus indicates the time(s) of the year when recruitment is most intense, and this should generally correspond to the "peak" spawning season(s).

A standard deviation can be calculated for recruitment patterns, which is related to the width of the annual recruitment "window". Therefore, the standard deviation of recruitment patterns can be used to classify these according to the recruitment strategy they express (Fig. 13). However, the standard deviations of recruitment patterns are also related to the longevity of the investigated fishes, i.e., to the degree of blurring that occurs because the individual fishes, as they grow older, increasingly deviate from their predicted length for age. This effect can be easily countered by plotting the standard deviations of fishes with one single, very distinct spawning season (open dots in Fig. 14) against their estimated longevity. The resulting regression line (dotted in Fig. 14) is then shifted upward and used to separate fishes with one recruitment season (fish nos. 1-6, 11 in Figs. 13 and 14) from those with two recruitment seasons (fish nos. 8, 10, 12-14 in Figs. 13 and 14), leaving one fish (no. 9) with an undefined status. This analysis is very preliminary and will be expanded and validated when more data on recruitment patterns become available.
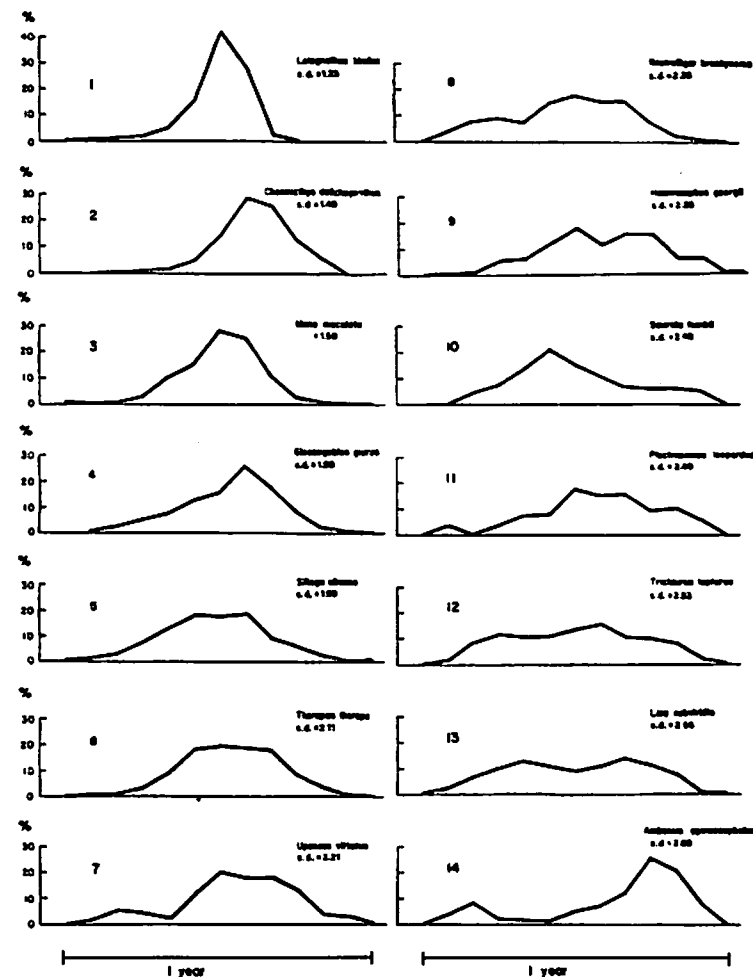
Fig. 13. Recruitment patterns in 14 stocks of fishes whose growth parameters were estimated by means of ELEFAN I. Note increase in standard deviation from *Leiognathus bindus* (s.d. = 1.25) to *Ambassis gymnocephalus* (s.d. = 2.89), with corresponding shift from 1 to 2 recruitment seasons. Source of length-frequency data: Balan 1967 (1), Goeden 1978 (11), Tamura and Honma 1977 (2), Marques 1960 (4) and Ziegler 1979 (3, 5, 6, 7, 8, 9, 10, 12, 13, 14).
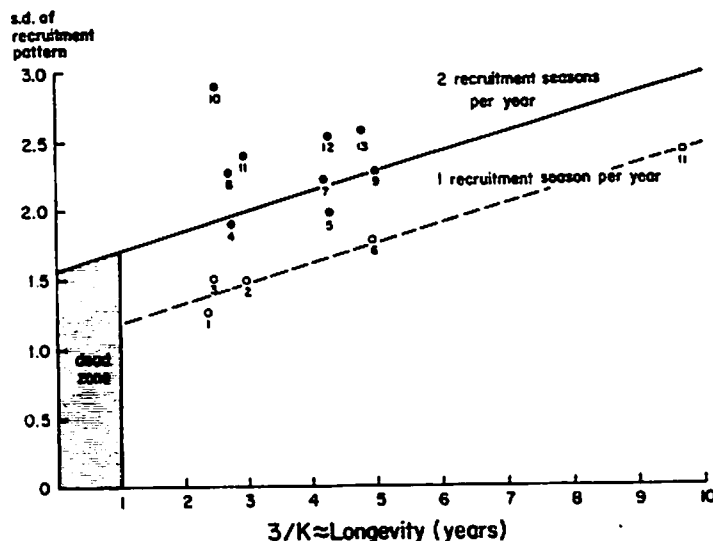
Fig. 14. Showing the relationship between the standard deviation of recruitment patterns and longevity (as estimated by dividing 3 by K of the special VBGF, see Pauly 1980c). The dotted line was fitted to points pertaining to fishes with 1 well-defined recruitment season, and the line's slope used to separate the 14 stocks of Fig. 13 into 2 groups with different recruitment strategies.

The study of recruitment patterns, such as briefly sketched here seems very promising. Most probably, recruitment patterns will, among other things, allow for a quantitative estimation of the relative impact of various environmental factors affecting the recruitment of tropical fish. Particularly, it will become possible, by comparing the relative intensity of recruitment of major vs. minor recruitment peaks (when two occur per year) to quantify the effects of the two monsoons which for a long time have been suspected to be major determinants of fish spawning and recruitment (Weber 1976).

Summary

— Methods used for investigating the population dynamics of tropical stocks should concentrate on growth, mortality, stock size and recruitment. They should be cheap and rapid, yet produce reliable results.

— Aging of fish by means of skeletal structures should concentrate on "annuli" only when large (i.e., long-lived) fishes are investigated. In fishes with short life span (i.e., in fishes that remain small) aging should be done by using daily otolith structures. As this method is very tedious, it should be used mainly to validate and complement growth estimates based on the analysis of length-frequencies.

— The von Bertalanffy Growth Formula may be used for modelling the growth of tropical fish, but workers should be aware of the assumptions involved in the derivation of the formula's two versions, and of season-

ally oscillating growth patterns, which may occur even in the tropics.

— Length-frequency data can be used to reliably estimate the values of the growth and mortality parameters of well-sampled populations. The work can be considerably facilitated by using new computer programs designed for these purposes (ELEFAN I and II). The second of these programs can also be used to generate "patterns of recruitment".

— When combined with catch data, length-frequency data can be used to generate catch-at-length data which can be used for Cohort or Virtual Population Analysis, to which several new approaches are available.

Acknowledgments

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Discussion of Dr. Pauly's Paper

The discussion concentrated around five points: clarification concerning the generalized VBGF, the reliability of growth parameter estimates based on ELEFAN I, the relationships relating r_m and body weight, recruitment patterns and the relationships between single-species and community dynamics.

Concerning ELEFAN I, Mr. Jones pointed out that in fish which can grow to an old age, there is a real danger of peaks overlapping each other to the point of being indistinguishable. Dr. Pauly fully agreed with this and pointed out that the method in general should not be used in conjunction with fishes known to reach ages beyond 4 to 5 years, unless the available length frequency samples are extraordinarily well-structured. Several participants suggested statistical and mathematical techniques suitable for improving ELEFAN I.

Concerning the relationship between r_m and body weight (Table 5 and Fig. 11 in Pauly's paper), Dr. Sainsbury pointed out that the identity of estimates of r_m based on numbers and with that of estimates based on biomass has never been demonstrated, and suggested that considering these estimates to be equal is "at best sloppy and at worst completely wrong." Concerning this same relationship Dr. Gulland and Dr. Marten pointed out that the scatter of the points is, for any range of body weights too large for the relationship to be of much help. Pauly held to the usefulness of the relationship, despite its shortcomings.

The relationship between single-species and community dynamics was discussed, especially by Dr. Marten. He suggested that there are systems (e.g.,

Lake Victoria) in which single-species investigations lead to results that are
not confirmed when the dynamics of the overall stock is investigated. A case
in point is that small fishes in Lake Victoria were assumed to have higher
turnover rates than larger fishes (and hence could be expected to withstand
heavy fishing) yet collapsed rather rapidly when exploitation increased. It
was suggested, however, that this might have been due to the stock having
been maintained "fully exploited" prior to the onset of any fishery.

Estimation of Biological and Fishery Parameters
in Coral Reef Fisheries

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Abstract

The problems of parameter estimation in coral reef fisheries are discussed
and the methods used by the author and co-workers to investigate the fisheries
biology of coral reef fishes in Jamaican waters are evaluated. It is concluded
that the systematic analysis of length-frequency data offers the best oppor-
tunities for producing usable estimates of fishery parameters. Daily growth
rings in otoliths appear to offer excellent opportunities for determining ages
of coral reef fishes and should be more extensively used.

Attention is drawn to the possibilities of attempting to derive fishery para-
meters from easily obtainable statistics such as mean weights of individuals
in catches, catch compositions in multispecies fisheries, catch-per-effort
indices and to the use of gross measures such as coastal population densities
or numbers of boats per unit area of shelf in order to make progress in the
assessment of tropical multispecies stocks.

Introduction

Our knowledge of the fishery biology of coral reef fishes stems primarily
from three major studies: those of Bardach and co-workers in Bermuda
(1957, 1958), Randall in the U.S. Virgin Islands (1962 and 1963) and Munro
and co-workers (1973-1980) in Jamaica. Additionally, Nagelkerken (1979)
has undertaken a major study of the small grouper, *Epinephelus (= Petrome-
topon) cruentatum* around Curaçao. For the Indo-Pacific region I am aware
of no large-scale studies which have yet been completed. The contributions
by Goeden (1978) and Lebeau and Cueff (1975) appear to be among the
few studies of any of the larger species of Indo-Pacific reef fishes.

The reasons for the paucity of data are extremely simple. Coral reefs
are inhabited by an enormous diversity of harvestable animals, principally

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