

Proceedings of the Fourth International Coral Reef Symposium, Manila, 1981, Vol. 1

## ASPECTS OF THE GROWTH AND NATURAL MORTALITY OF EXPLOITED CORAL REEF FISHES

D. Pauly

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

J. Ingles

University of the Philippines, College of Fisheries, Institute of Fisheries Development and Research (IFDR),  
Diliman, Quezon City, Philippines (ICLARM Intern)

### ABSTRACT

A newly developed computer-based method for the analysis of length-frequency data (ELEFAN I & II) is applied to data on reef fishes. It is shown that the growth of reef fishes often oscillates seasonally, and that adjusting for this effect considerably increases the accuracy of growth parameter estimates. This is also confirmed by a re-analysis of tagging data from the Caribbean.

Potential causes of natural mortality in reef fishes are discussed in the light of a recently established empirical relationship between natural mortality, growth parameters and mean environmental temperature in fishes.

### INTRODUCTION

For reasons which need not be discussed here, coral reef fishes have traditionally been investigated by ecologists and ethologists rather than by fishery biologists. The result of this is that, while a large body of data is available on the ecology and behaviour of coral fishes (Sale 1980), comparatively little is known of the growth, mortality and recruitment of those fishes, i.e., of the processes which determine their exploitability.

The most notable exception to this rule is the work of Munro and co-workers (1974-1980), but this represents but a few drops in an ocean of work to do. This applies particularly to the study of growth, which in coral fishes has been particularly neglected, to the extent that growth parameters are available for only a small minority of exploited or potentially exploitable fishes (Pauly 1978).

The main purpose of this paper is to apply to coral fish data a newly developed method for the extraction of reliable growth parameter estimates from length-frequency data. Since the method in question accounts for seasonal growth oscillations, a secondary purpose of this paper is to demonstrate that — contrary to a widely-held view — growth in coral reef fishes can oscillate seasonally and be markedly reduced during the colder season and accelerated during the warm season.

Finally, a method for constructing catch curves, hence to estimate total mortality from length frequency data is briefly discussed, along with an empirical equation, applicable also to coral reef fishes,

which allows for the derivation of natural mortality estimates from values of the growth parameter and the mean environmental temperature.

### MATERIAL AND METHODS

#### MATERIAL

Since this paper is meant to show that, in general, more can be extracted from available data on coral fishes, we have here limited ourselves to re-examining previously published length-frequency and other data, with the exception of an original length-frequency data set pertaining to the serranid *Epinephelus sexfasciatus* from the Visayan Sea and kindly put at our disposal by Dr. Virginia Aprieto, College of Fisheries, University of the Philippines.

#### METHODS

##### The ELEFAN I method

The method used here to extract growth parameters from length-frequency data is described in detail in Pauly and David (1981). It is a computer-based method (we used a TRS 80 Model 1, 16K microcomputer) which has the property of providing objective estimates of growth parameters, as opposed to the commonly used "Petersen method", or the "modal class progression analysis", whose results are unavoidably tainted by subjectivism (Pauly 1980a). Put briefly, the new method (Elec-

tronic Length Frequency Analysis) does the following:

- restructures the length-frequency samples that have been entered such that "peaks" are attributed "positive points", and the "troughs" separating peaks "negative points",
- calculates from the positive points of the peaks of all samples entered a sum named "available sum of peaks" (ASP, analogous to the total variance of parametric methods),
- traces a series of growth curves starting from the bases of the peaks, and projects these curves backward and forward in time such as to hit the other samples in the data set and recording all "points" (positive and negative) "hit" by a curve,
- identifies the curve — and hence, the growth parameters — which, by passing through most peaks and avoiding most troughs, best "explains" the peaks in the sample set. This curve will have scored the highest number of points, whose sum is called the "explained sum of peaks" (ESP, analogous to the explained variance of parametric methods).

Assuming that the sample(s) used is (are) representative of the population, that the growth patterns are similar from year to year, and that the von Bertalanffy Growth Formula (VBGF) gives a reasonable representation of fish growth, the ELEFAN I method helps obtain growth parameter estimates that are completely objective, i.e., in which no subjective assumptions as to the age composition of the catch have been incorporated (Pauly and David 1981 and Pauly et al. 1980).

#### ELEFAN I and Seasonal Growth

While it is widely appreciated that the growth of fishes in temperate waters oscillates seasonally, it is often assumed — implicitly or not — that the growth of tropical and of coral reef fishes should be more or less uniform throughout the year, both because the annual average temperature is high and because the temperature difference between "winter" and "summer" is much less than in temperate waters (Table 1).

However, the ELEFAN approach allows for the identification and quantification of seasonal growth oscillations, because of the inclusion in the program of the growth equation:

$$L_t = L_\infty (1 - \exp[-K(t-t_0) + C \frac{K}{2\pi} \sin 2\pi(t-t_0)]) \quad (1)$$

which is the modified version of the VBGF presented by Pauly and Gaschütz (1979) where  $L_\infty$  is the asymptotic length,

$K$  a growth coefficient,

$t_0$  the origin of the growth curve,

$t_s$  the beginning of a growth oscillation with respect to  $t = 0$ ,

$C$  a coefficient expressing the intensity of the growth oscillations, and

$L_t$  is the length at age  $t$ .

$C$  is defined such as to generally range between 0 (when there are no growth oscillations) to unity (when the growth oscillations cause growth to halt briefly in the winter time).

At present, it is still not possible to obtain confidence intervals for parameter estimates obtained from ELEFAN I. For this reason, we have also re-analyzed sets of tagging-recapture data presented by Randall (1962) to test, using a parametric method, our contention that the growth of coral reef fish can oscillate seasonally. The method used in this context is discussed further below.

#### Seasonal Growth Oscillations and Tagging-Recapture Data

Randall (1962) presented tagging-recapture data from a variety of fish caught and released off the Virgin Islands, and concluded, on the basis of his growth rate computations that temperature had little or no influence on the growth of tagged fish.

Table 2 contains data of the type which Randall (1962) used to draw his inference, along with estimates of the mean weighted temperature encountered by the tagged fish while at large, as computed from the dates of release and recapture and the temperatures given by Randall (1962, Tables 1 and 3).

To demonstrate the effects of temperature on growth rate, it is necessary to account for the simultaneous effects of mean length and of repeated capture on growth rate. This can be done by computing correlation coefficients ("zero order" partial correlations) and then first order and second order partial correlation coefficients between all combinations of variables. Also, growth parameters may be calculated from the data such as those in Table 2 by plotting the growth increments ( $G$ ) simultaneously against mean length while at large ( $L$ ), mean temperature while at large ( $T$ ) and number of times recovered ( $N$ ) which results in a multiple linear regression of the form

$$G = a + b_L L + b_T T + b_N N \quad (2)$$

from which the parameters of the VBGF are estimated in analogy to the method of Gulland and Holt (1959) by

$$K = -b_L \quad (3)$$

Table 1. Mean monthly temperatures (°C) at three coral reef sites and in a temperate environment.

Locality	Month												$\bar{X}$	C.V. <sup>e)</sup>	$\Delta T$
	J	F	M	A	M	J	J	A	S	O	N	D			
Lameshur Bay <sup>a)</sup> Virgin Islands	27.6	27.5	27.7	28.0	28.9	29.1	29.2	29.2	29.4	29.3	29.4	27.2	28.5	3.0	1.9
Biscayne Bay <sup>b)</sup> Florida	23.3	22.2	22.2	24.4	25.0	26.9	28.1	28.9	27.8	26.9	25.3	23.9	25.4	9.1	6.7
One Tree Island <sup>c)</sup> Great Barrier Reef Australia	26.8	26.5	25.5	24.7	23.9	23.0	21.5	20.7	21.2	22.2	24.8	26.7	24.0	9.2	6.1
Western Baltic Sea <sup>d)</sup>	2	1	2	3	7	12	14	14	13	12	10	6	8	63.5	13

a) from Table 2 Randall (1962)

b) from Rivas (1968)

c) from Russel et al. (1977)

d) from Siedler and Hatje (1974)

e) (standard deviation/mean) · 100 = coefficient of variation (C.V.)

Table 2. Data on growth of tagged and recovered ocean surgeon fish (*Acanthurus bahianus*) from the Virgin Islands<sup>a)</sup>

Specimen #	Variable code and units			
	G monthly growth increment (mm)	L mean length (mm)	T mean temp. (in °C)	N times recovered in traps
1	2.87	99.5	27.48	3
2	3.69	107	28.61	2
3	2.53	113.5	27.79	2
4	2.68	115.5	29.29	9
5	3.46	138.5	28.37	1
6	5.07	132	28.89	3
7	1.72	141.5	27.55	5
8	1.25	162.5	27.99	2
9	0.97	164	27.54	6
10	0.57	171	28.00	2
11	0.82	178.5	28.30	4

a) Computed from data in Tables 2 and 3 of Randall (1962).

and

$$L_{\infty} = (a + b_T T_M) / -b_L \quad (4)$$

where  $T_M$  is the mean annual temperature, and where  $L_{\infty}$  is estimated for  $N = 0$ , i.e.,  $L_{\infty}$  is estimated independently of temperature fluctuations and of capture-related effects.

Finally, the parameter  $C$  in (1), expressing the intensity of growth oscillations can be estimated

from

$$C = \frac{b_T (T_s - T_w)}{2 [a + (b_T T_m)]} \quad (5)$$

where  $T_s$  and  $T_w$  are the highest (summer) and lowest (winter) mean monthly temperature, respectively (see Table 1).

Table 3. Data for the construction of a catch curve for the banded grouper (*Epinephelus sexfasciatus*) from the Visayan Sea, Philippines.

Class limits		Midlength SL (cm)	N <sup>a)</sup>	t <sub>1</sub> <sup>b)</sup>	t <sub>2</sub> <sup>b)</sup>	Δ t <sup>d)</sup>	Adjusted number per length class log <sub>e</sub> % (N/Δt)	Mean relative age <sup>e)</sup> (yr)
Lower	Upper							
4.000	5.999	5	5	0.272	0.423	0.151	0.233	0.346
6.000	7.999	7	29	0.423	0.587	0.164	1.67	0.504
8.000	9.999	9	114	0.587	0.767	0.180	2.83	0.675
10.000	11.999	11	161	0.767	0.964	0.197	3.22	0.863
12.000	13.999	13	143	0.964	1.183	0.213	3.05	1.07
14.000	15.999	15	118	1.183	1.430	0.247	2.64	1.30
16.000	17.999	17	61	1.430	1.713	0.283	1.98	1.57
18.000	19.999	19	50	1.713	2.043	0.330	1.65	1.87
20.000	21.999	21	32	2.043	2.440	0.397	0.868	2.23
22.000	23.999	23	17	2.441	2.939	0.498	0.0888	2.67
24.000	25.999	25	4	2.940	3.610	0.670	-1.82	3.25
26.000	27.999	27	4	3.611	4.639	1.028	-2.41	4.06

a) N values are sums of % frequencies in Fig. 4.

b) Time needed to reach lower class limit } as computed from  $t_{1/2} = \{-\log_e(1-(L_{1/2}/L_\infty))\}/K$ , with  
 c) Time needed to reach upper class limit }  $L_\infty = 30.9$  and  $K = 0.51$ .

d)  $t_2 - t_1 = \Delta t$

e) Time needed to reach class midlength, computed as in b) and c).

#### Estimation of Total Mortality From Length-Converted Catch Curves (ELEFAN II)

The standard method to obtain "catch curves", i.e., plots of the natural logarithm of the relative abundance of fishes against their age, is to obtain representative samples of fish, to age these, then to plot the natural logarithm of the numbers on the corresponding ages (Ricker 1975). However, when representative length-frequency samples and growth parameters ( $L_\infty$  and  $K$  of the normal VBGF) are available, total mortality can be estimated directly from length-converted catch curve, the major problem in this context being to account for the fact that the growth of fish is not linear, but gradually declines as fish grow larger, this effect resulting in the fishes of several year groups "piling up" in the larger length classes.

Correcting for this effect is accomplished by plotting against the relative age of the fish the natural logarithm of their number divided by the time needed to grow through each respective length class, i.e.,

$$\log_e(N/\Delta t) = a + bt \quad (6)$$

where  $N$  is the number of fish in a given length class,  $\Delta t$  the time needed to grow through that length class (as estimated from the VBGF),  $a$  the intercept of the catch curve, and  $t$  the relative age correspon-

ding to a given value of  $N$ , the slope  $b$  being, with sign changed, an estimate of the exponential rate of total mortality ( $Z$ ) (Table 3).

#### Estimation of Natural Mortality

Ricker (1975) reviewed classical methods for estimating natural mortality ( $M$ ) in exploited fish populations. These methods, however, have data requirements which often make their application to tropical fish quite difficult.

For this reason, Pauly (1980b), based on 175 sets of  $M$ ,  $L_\infty$ ,  $K$  and  $T$  (mean environmental temperature in °C) derived the empirical relationship

$$\log_{10}M = -0.0066 - 0.279 \log_{10}L_\infty + 0.6543 \log_{10}K + 0.4634 \log_{10}T \quad (7)$$

from which reasonable estimates of  $M$  can be obtained — also in coral reef fishes — given values of  $L_\infty$  (total length, in cm),  $K$  (expressed on an annual basis) and  $T$  (in °C).

#### Recruitment Patterns (ELEFAN II)

"Recruitment patterns" are obtained by projecting backward, onto the time axis the peaks and

troughs of a set of lengths-frequency samples by means of a set of growth parameters. For example, if a set of lengths-frequency data consists of fishes recruited once a year, a more or less normally distributed recruitment pattern will be produced, while a recruitment pattern displaying two distinct peaks will suggest two recruitment peaks per year. Thus, the structure of length-frequency samples can be used to corroborate evidence obtained from data on the reproductive activity of fish, e.g., as obtained by studies of their gonads.

## RESULTS

### GROWTH OF THREESpot DAMSELFISH (*EUPOMACENTRUS PLANIFRONS*)

Williams (1978) presented length-frequency data on threespot damselfish which she used to test certain hypotheses as to the social structure of this fish; also, she made preliminary estimates of the size of threespot damselfish of various ages. These estimates, however, are imprecise and cannot be used for stock assessment purposes.

By rearranging by sex and regrouping the data presented by Williams (1978, Fig. 4) into larger length classes (5 mm instead of 1 mm classes) and running them through ELEFAN I, we obtained growth parameters for both female and male threespot damselfish, as given in Figure 1. As will be noted, the "trick" here consists of using the same sample repeatedly (on the assumption that the growth patterns repeat themselves from year to year, see above).

### GROWTH, MORTALITY AND RECRUITMENT PATTERN OF BANDED GROUPER (*EPINEPHELUS SEXFASCIATUS*)

Figure 2 shows the best fitting growth curve, which explains 47% of the available peaks in the set of samples, and was obtained using ELEFAN I. Also, Figure 2 shows the catch curve and the recruitment patterns obtained using ELEFAN II. Total mortality ( $Z$ ) was estimated to be 1.95.

Natural mortality ( $M$ ), as estimated from equation (3) with  $L_{\infty} = 30.9$ ,  $K = 0.51$  and  $T = 28^{\circ}\text{C}$  is 1.14 which, subtracted from  $Z$  provides an estimate of  $F = 1.95 - 1.14 = 0.81$ .

The computed recruitment pattern in Figure 2 has the same overall shape as the "spawning pattern" obtained from the study of maturity stages in the *E. sexfasciatus* stock in question. We conclude, thus, that this fish has, in the Visayan Sea, two major spawning seasons per year, and that the length-frequency data we used reflect this feature in the form of two recruitment peaks.

### SEASONALLY OSCILLATING GROWTH OF PUFFER (*SPHOEROIDES TESTUDINEUS*)

As might be seen from Figure 3, plotting the length-frequency data at intervals proportional to the time elapsed between the various samples, and "doubling up" the sample set allows for estimation of the parameters of a long, uninterrupted growth curve which explains 66% of the available peaks and displays distinct growth oscillations ( $C = 0.70$ ), i.e., reduced growth in winter and an accelerated growth in summer.

### SEASONALLY OSCILLATING GROWTH OF CORAL TROUT (*PLECTROPOMUS LEOPARDUS*)

Figure 4 shows two samples of coral trout, adapted from Goeden (1978, Fig. 1). Prior to the analysis, the data for the October sample of Goeden (1978) were corrected for the unjustified addition of 3.7 mm to each length (Goeden 1978) and regrouped in 2 cm classes, in order to obtain a manageable number of length classes (Sokal and Rohlf 1969, p. 28).

As in the previous cases, we have an instance of seasonal growth with slower growth during the winter months, as expected (see Fig. 4).

### SEASONAL GROWTH OF OCEAN SURGEON- FISH (*ACANTHURUS BAHIANUS*)

Table 4 gives the partial correlation coefficients derived from the tagging data in Table 2. It will be noticed that while the zero order coefficient (simple correlation coefficient) between growth increment and temperature is not significant, partialing out the associated effects of length and number of recaptures increases all biologically relevant coefficients ( $r_{GL}$ ,  $r_{GT}$  and  $r_{GN}$ ) dramatically and makes 2 of them statistically significant. It will also be noted that  $r_{GT}(L, N)$ , the 2nd order partial correlation linking growth increment and temperature is significant, suggesting that temperature does influence the growth of tagged fish at large.

The following multiple linear regression was derived from the data in Table 2:

$$G = -24.8 - 0.0319L + 1.145T - 0.189N \quad (8)$$

(with  $R = 0.862$ )

from which  $K$  (on an annual basis) is obtained from

$$K = [0.0319 \cdot 12] = 0.383 \quad (9)$$

and  $L_{\infty}$  (in mm, for  $T_M = 28.5^{\circ}\text{C}$ ) from

$$L_{\infty} = [(1.145 \cdot 28.5) - 24.8] / 0.0319 = 246 \quad (10)$$

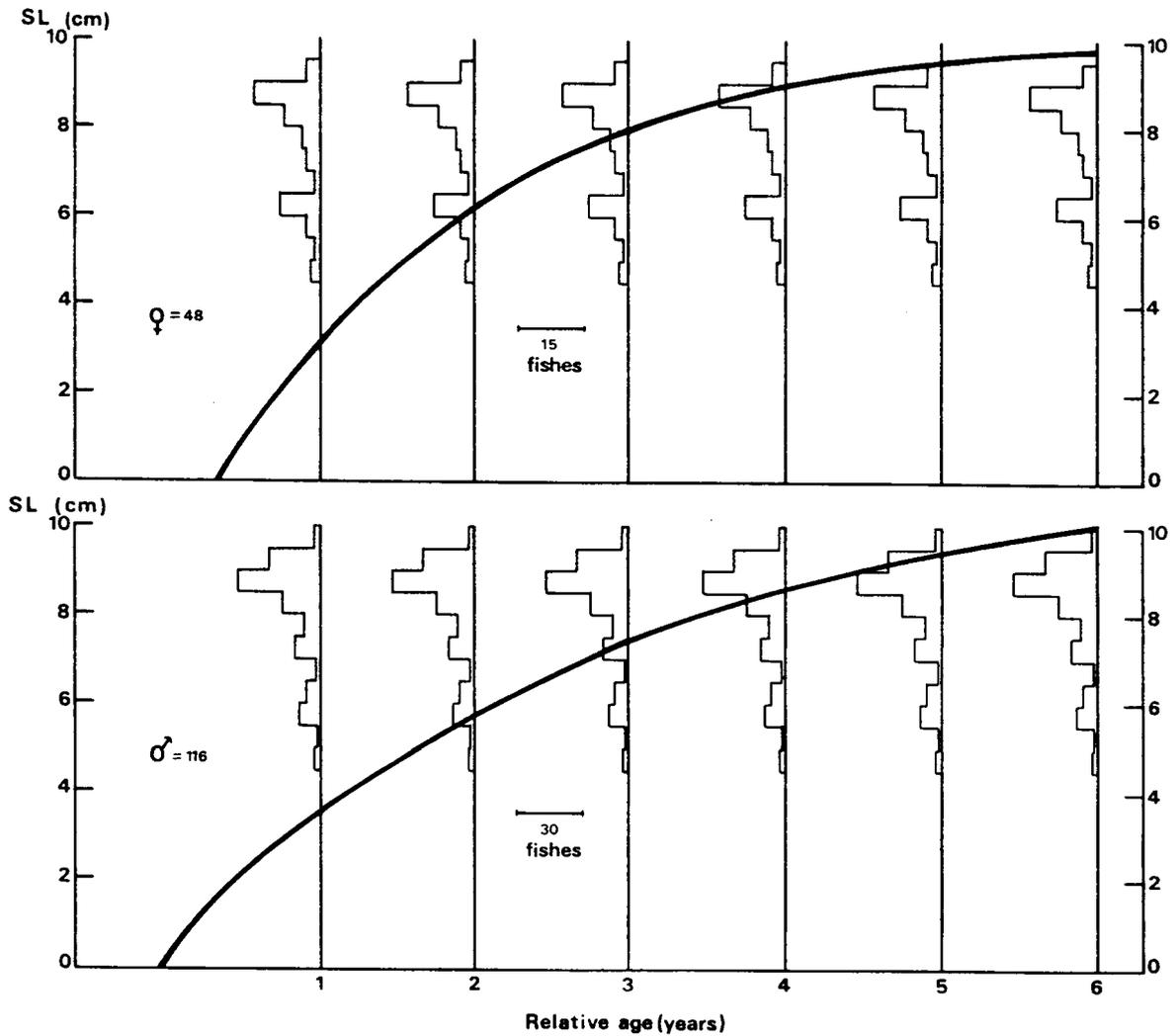


Figure 1. Growth curves of female and male threespot damselfish (*Eupomacentrus planifrons*), as derived by ELEFAN I. The growth parameters for ♀♀ are :  $L_{\infty} = 10.2$  cm,  $K = 0.58$  (ESP/ASP = 0.917), and for ♂♂ :  $L_{\infty} = 11.6$  cm,  $K = 0.33$  (ESP/ASP = 1.12). The length-frequency data are adapted from Williams (1978, Fig. 4) and consist of females + immatures, and males + immatures speargunned at Discovery Bay, Jamaica from May to July 1976.

Finally, the value of C was estimated, as suggested in equation (5) from

$$C = \frac{1.145 (29.4 - 27.5)}{2 [(28.5 \cdot 1.145) - 24.8]} = 0.14 \quad (11)$$

i.e., winter and summer growth are reduced and enhanced respectively by 14% with respect to annual average growth.

Thus, the "normal" VBGF for *A. bahianus* in the Virgin Islands is

$$L_t = 246 (1 - \exp -0.383 (t-t_0)) \quad (12)$$

while the seasonally oscillating version of the VBGF for this fish stock is

$$L_t = 246 (1 - \exp - [0.383 (t-t_0) + 0.14 \frac{0.383}{2\pi} \sin 2\pi (t-t_s)]) \quad (13)$$

with  $t_0$  and  $t_s$  remaining unknown.

## DISCUSSION

### GROWTH AND ELEFAN I

The four examples of applications of the ELEFAN I (Figs. 1 to 4) may have given the reader

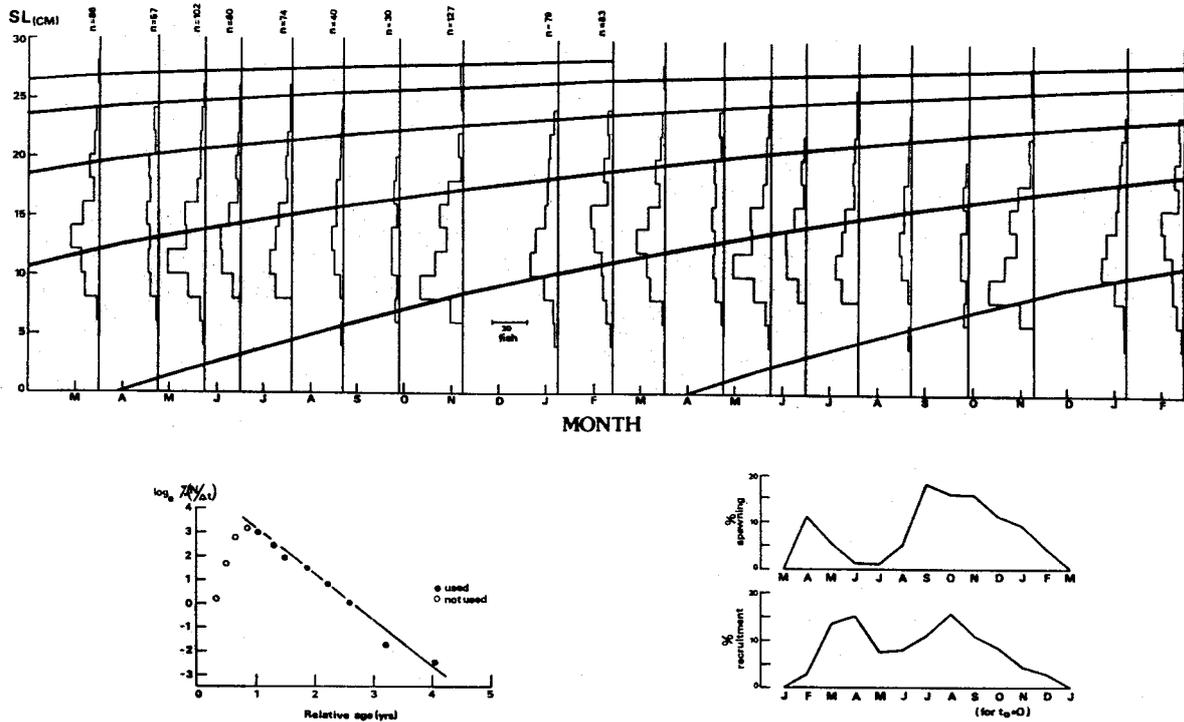


Figure 2. Application of ELEFAN I and II to length-frequency data on banded grouper (*Epinephelus sexfasciatus*) from the Visayan Sea, Philippines. Above: growth curve as estimated by ELEFAN I, with  $L_{\infty} = 30.9$  and  $K = 0.51$  ( $ESP/ASP = 0.47$ ). Below, left side: catch curve obtained from ELEFAN II (see text) and length-frequency data above, with  $Z = 1.95$ . Below, right side: recruitment pattern for banded grouper from the Visayan Sea, suggesting 2 main recruitment seasons. These results correspond with the pattern obtained by plotting mean maturity stages against time (" % spawning").

an idea of the versatility of this method. As far as tropical fishes are concerned, the method's most interesting feature is that it is used in conjunction with easy-to-obtain length-frequency data. As the damselfish and puffer examples (Figs. 1 and 2) illustrate, the method can provide reasonable results when sample sizes are quite small, which will be of importance to biologists working on relatively rare species, or in a situation (underwater natural park) where a large number of specimens cannot be sampled.

SEASONAL GROWTH OSCILLATIONS

Seasonal oscillations in the growth of fishes have been hitherto neglected in the literature, although there are suggestions that a proper understanding of the interrelationships between growth and gonad maturation cannot be achieved without taking such oscillations into account (Iles 1974, Shul'man 1974). In the tropics, seasonal growth oscillations have been well documented only in the fishes of fresh water habitats, where spectacular floods are suc-

ceeded by periods of dessication, during which growth in length is generally completely halted and growth in weight negative (Daget and Ecoutin 1976).

The models presented here for dealing with seasonal growth oscillations (ELEFAN I and equation (4)) allow, however, for the detection and quantification of even the small growth oscillations occurring in coral reef and other tropical fishes.

Considering such growth oscillations when estimating growth parameters has two aspects:

- the resulting growth parameter estimates are far more accurate than those obtained without considering such oscillations (Pauly and Gaschutz 1979 and Gaschutz et al. 1980)
- the results (e.g., the estimated values of the parameter "C") give added insight into growth processes in fish.

To illustrate this last point, we have plotted values of C obtained from a variety of fishes from different habitats (tropical to temperate) against their values of  $\Delta T$  (= difference between highest and lowest monthly temperatures of their habitat) (Fig. 5).

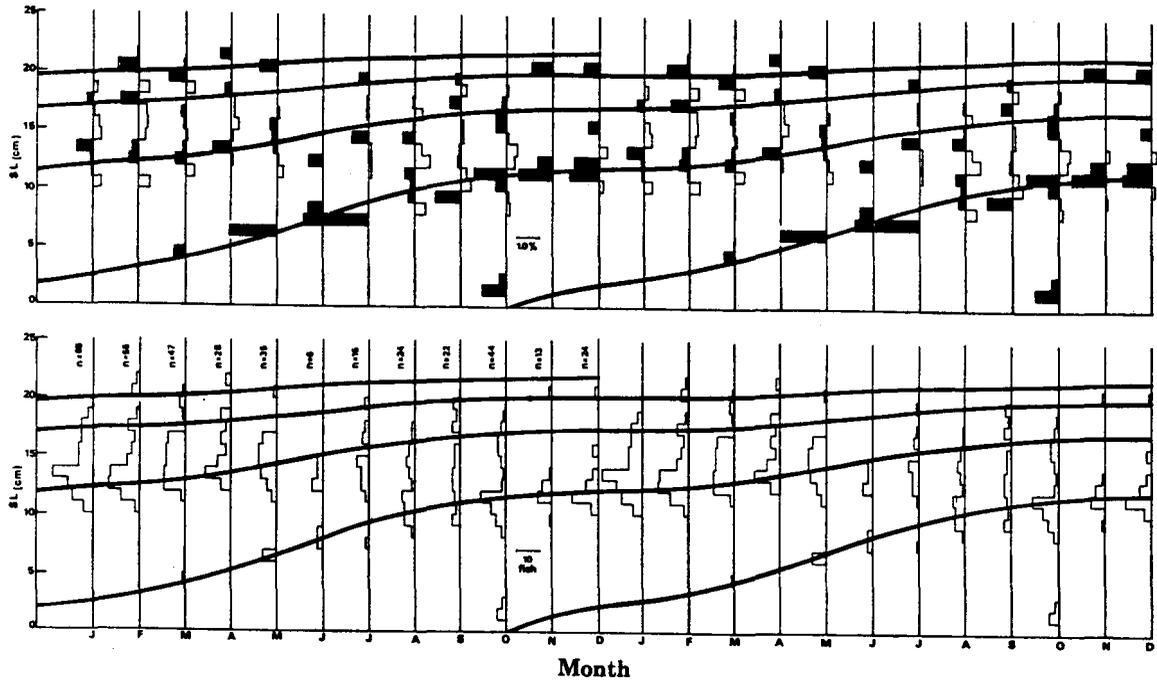


Figure 3. Seasonally oscillating growth curve in puffer *Sphoeroides testudineus* caught off Biscayne Bay, Florida. Below: the length-frequency data (from Targett 1979) used for the analysis (note "doubling up" of the data set). Above: "restructured" length-frequency data, as computed and used internally by ELEFAN I. Dark histograms represent frequencies that are part of "peaks", open histograms represent "troughs" separating peaks. The growth curve explains 66% of the peaks, i.e., ESP/ASP = 0.66.

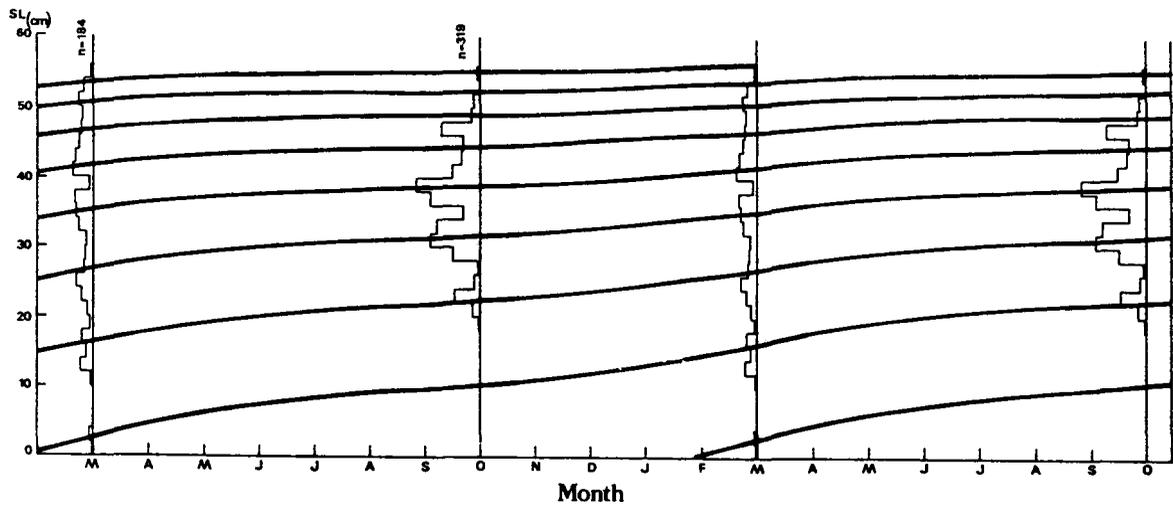


Figure 4. Seasonally oscillating growth in coral trout (*Plectropomus leopardus*) from the Great Barrier Reef. (Adapted from data in Goeden 1978). The growth parameters are  $L_{\infty} = 64.7$ ,  $K = 0.25$  and  $C = 0.5$ , with ESP/ASP = 0.63.

As may be seen, the values of C, i.e., the intensity of the growth oscillations correlate very well with the  $\Delta T$  values, suggesting that the intensity of growth oscillations in fishes are:  
 — caused solely by temperature fluctuations, or by

something (e.g., food availability) which itself correlates strongly with environmental temperature  
 — independent of the mean temperature of the habitat.

Table 4. Zero, first and second order partial correlation coefficients linking growth increment (G) to length (L), mean temperature while at large (T) and times recovered (N) in ocean surgeon fish (*Acanthurus bahianus*) from the Virgin Islands. The asterisks refer to significant coefficients ( $P=0.05$ ).

Partial correlation coefficient	$r_{GL}$	$r_{GT}$	$r_{GN}$	$r_{LT}$	$r_{LN}$	$r_{TN}$
zero order (df 9)	-0.707	0.514	-0.173	-0.187	-0.0241	0.264
first <sup>b</sup> order (df 8)	-0.725* (T)	0.550 (L)	-0.269 (L)	0.291 (G)	-0.210 (G)	0.418 (G)
second <sup>b</sup> order (df 7)	-0.722* (N)	0.589 (N)	-0.373 (T)	-0.187 (N)	0.0267 (T)	0.264 (L)
second <sup>b</sup> order (df 7)	-0.771* (T, N)	0.669* (L, N)	-0.525 (L, T)	0.427 (G, N)	-0.382 (G, T)	0.512 (G, L)

a) Calculated from data in Table 2.

b) Letter(s) in brackets refer(s) to variable partialled out (see Table 2 for code).

These properties, it will be noted, allow for growth oscillations to be predicted in fishes whose growth is not well-documented.

#### TOTAL MORTALITY

Length-converted catch curves have seldom been used for the estimation of total mortality of fishes. This is unfortunate as far as tropical and especially coral reef fishes are concerned because the information needed for the construction of catch curves is generally embedded in the length-frequency data available in a number of papers pertaining to the biology of such fishes.

#### NATURAL MORTALITY

Among the 175 independent sets of  $M$ ,  $L_{\infty}$ ,  $K$  and  $T$ -values used for the derivation of the empirical equation proposed here for estimating  $M$ , 17 sets pertained to coral reef fishes (they were obtained mainly from Munro 1974). It was found that the values predicted from the equation did not, on the average, differ significantly from the empirical values. Therefore, equation (7) should provide more or less unbiased estimates of  $M$  in coral reef fishes also.

In light of the diversity of adaptations and population interactions in coral reef and other fishes, it might be difficult to conceive of natural mortality in a given population to be mainly a function of its growth parameters and environmental temperature. Thus, Munro (1980), for example, suggested natural mortality in the Jamaican stocks he investigated was directly proportional to the biomass of their predator.

However, a model of predation which allows for natural mortality to be relatively independent of

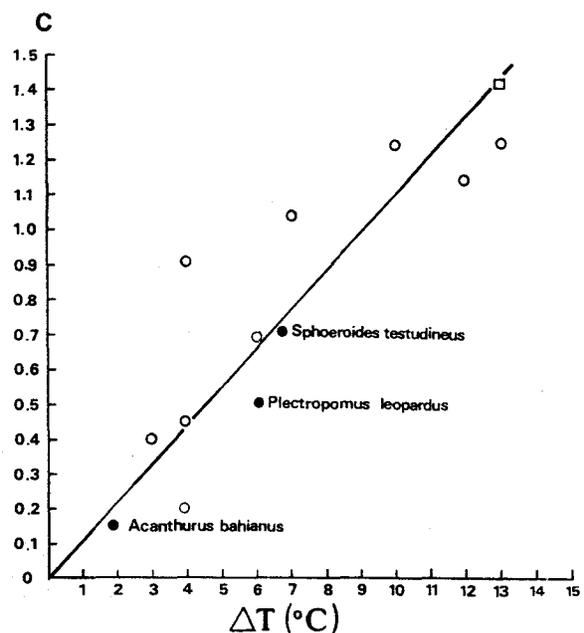


Figure 5. Relationship between the intensity of seasonal growth oscillations (as expressed by the parameter C) and the differences between highest and lowest monthly mean temperature ( $\Delta T$ ) in 13 stocks of fishes ranging from coral reef (black dots) to temperate habitats (the single square refers to Baltic Sea Salmon). The points derived here (open dots and square) are fully documented in Pauly (in press).

predator biomass and other biotic factors was recently presented by Jones (1979). In this model, the growth rates in and of a given population are viewed as factors causing, via intraspecific competition, the "displacement" of animals that are less fit (e.g., out of territories in territorial reef fishes). It is

then mainly these "displaced" animals which the predators have access to, predation often being, as Jones (1979) argues, an "agent" rather than a "cause" of natural mortality.

This effect might explain much of the relationship, in coral reef fishes, between growth and natural mortality, but more detailed investigations, e.g., of the type conducted by Potts (1980) will be necessary to actually understand how reef predators switch from less abundant to more abundant ("displaced") preys.

ICLARM Contribution No. 127.

### REFERENCES

- Daget, J. and J.M. Ecoutin. 1976. Modèles mathématiques de production applicables aux poissons tropicaux subissant un arrêt prolongé de croissance. Cah. O.R.S.T.O.M. ser. Hydrobiol. 10: 59-69.
- Gaschütz, G., D. Pauly and N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. I.C.E.S. CM 1980/D: 6 Statistics Cttee. 14 p.
- Goeden, G.B. 1978. A monograph of the coral trout, *Plectropomus leopardus* (Lacépède). Queensland Fish. Service, Res. Bull. 1: 1-42.
- Gulland, J.A. and S.J. Holt. 1959. Estimation of growth parameters for data at unequal time intervals. J. Cons. int. Explor. Mer 25(1): 47-49.
- Iles, T.D. 1974. The tactics and strategy of growth in fishes. In F.R. Harden-Jones (ed.). Sea Fisheries Research. Pp. 331-345. London: Elek Science.
- Jones, R. 1979. Predator-prey relationships with particular reference to vertebrates. Biol. Rev. 54: 73-97.
- Munro, J.L. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Scientific Report of the ODA/UWI Fisheries Ecology Research Project: 1969-1973. Part V.m. Summary of biological and ecological data pertaining to Caribbean fishes. Res. Rep. Zool. Dept. Univ. West Indies (3): 24 p.
- \_\_\_\_\_. (ed.). 1973-1980. The biology, ecology, exploitation and management of Caribbean reef fishes. Scientific Reports of the ODA/UWI Fishery Ecology Research Project, 1969-1973. Res. Rep. Zool. Dept. Univ. West Indies (3) Parts I-VI.
- \_\_\_\_\_. 1980. Stock assessment models: applicability and utility in tropical small-scale fisheries. In S. Saila and P. Roedel (eds.). Stock Assessment for Tropical Small-scale Fisheries. Pp. 35-47. Int. Cent. for Mar. Res. Development. Univ. of Rhode Island, Kingston, U.S.A.
- Pauly, D. 1978. A preliminary compilation of fish length growth parameters. Ber. Inst. f. Meereskunde (Kiel) No. 55, 200 p.
- Pauly, D. 1980a. A selection of simple methods for the assessment of tropical fish stocks. FAO Fish. Circ. No. 729 (FIRM/C 729). 54 p.
- \_\_\_\_\_. 1980b. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39(2): 175-192.
- \_\_\_\_\_. (In press). Studying single-species dynamics in a multispecies context. In D. Pauly and G.I. Murphy (eds.). Proc. of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multi-species Stocks. ICLARM Conf. Proc.
- Pauly, D. and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforsch. 28(4): 205-211.
- Pauly, D., N. David and J. Ingles. 1980. ELEFAN I: User's instructions and program listing. (mimeo) pag. var.
- \_\_\_\_\_. 1981. ELEFAN II: User's instructions and program listings (mimeo) pag. var.
- Pauly, D. and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. I.C.E.S. CM/1979/G: 24. Demersal Fish. Cttee., 26 p.
- Potts, G.W. 1980. The predatory behaviour of *Caranx melampygus* (Pisces) in the channel environment of Aldabra Atoll (Indian Ocean). J. Zool. Lond. 192: 323-350.
- Randall, J.E. 1962. Tagging reef fishes in the Virgin Islands. Proc. Gulf and Caribb. Fish. Inst. 14: 201-241.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can., (191): 382 p.
- Rivas, L.R. 1968. Fishermen's atlas of monthly sea surface temperatures for the Gulf of Mexico. U.S. Dept. Int. Fish. Wild. Serv. Circular 300, 33 p.
- Russel, B.C., G.R.V. Anderson and F.H. Talbot. 1977. Seasonality and recruitment of coral reef fishes. Aust. J. Mar. Freshwater Res. 28: 521-528.
- Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18: 367-421.
- Shul'man, G.E. 1974. Life cycles of fish; physiology and biochemistry. Isr. Progr. Sci. Transl. Wiley and Sons. 258 p.
- Siedler, G. and G. Hatje. 1974. Temperatur, Salzgehalt und Dichte. In L. Magaard and G. Rheinheimer (eds.). Meereskunde der Ostsee. Pp. 43-60. Springer Verlag. 269 p.
- Sokal, R.R. and F.J. Rohlf. 1969. Biometry. San Francisco: W.H. Freeman and Co. 776 p.
- Targett, T.E. 1979. A contribution to the biology of the puffers *Sphoeroides testudineus* and *Sphoeroides sprengleri* from Biscayne Bay, Florida. U.S. Fish. Bull. 77(1): 292-295.
- Williams, A.H. 1978. Ecology of the threespot damselfish: social organization, age structure and population stability. J. Exp. Mar. Biol. Ecol. 34: 197-213.