



GROWTH OF SKIPJACK

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INTRODUCTION

For more than twenty years fishery biologists have assiduously investigated the problem of growth in skipjack tuna, particularly in the Pacific. The various teams of tuna specialists, national and international, have furnished more or less exhaustive accounts of the numerous studies undertaken and results published on growth. Nowhere have we found an examination in depth of these results, an examination which has now become necessary with the reawakening of interest in the biological and ecological parameters in the models of production. The variety of growth rates estimated for skipjack, ranging from simple to double, or even triple, certainly poses a problem of choice for students of population dynamics.

We therefore propose to review the principal types of work enabling estimation of growth, at the same time analyzing in detail the various hypotheses, implicit or explicit, which the authors have made, as well as the comparability of the requisite basic data.

I. AGE READING FROM HARD PART STRUCTURES (vertebrae, scales, dorsal spines, otoliths)

A. Seasonal marks (vertebrae, scales, dorsal spines)

Reading the vertebrae to estimate age in skipjack has been practised since the 1930s (Aikawa and Kato, 1938; Chi and Yang, 1973). These latter authors on the hypothesis of a single annual growth check, found the following results as derived from back-calculation:

Length of fish L_n at formation of the annulus n	L_1	L_2	L_3	L_4
Aikawa, 1937	26	34	43	54
Aikawa and Kato, 1938	27	37	46.5	55

Since then a study on the interpretation of vertebral marks has been carried out by Chi and Yang (1973). Their hypothesis of growth checks differs from the foregoing, these authors considering that two rings should form per year. The results of growth would then be as follows:

$$\begin{array}{lll} L_1 = 27.4 & L_2 = 38.4 & L_3 = 46.7 \\ L_4 = 54.7 & L_5 = 62.7 & L_6 = 67.8 \end{array}$$

With the assumed periodicities in the appearance of growth rings not having been verified irrefutably by the authors, it is difficult in the present state of knowledge to endorse or reject, without important reservations, one or other of the preceding results. Nevertheless, Chi and Yang (1973) adduce some interesting arguments in support of their thesis that two growth rings are formed per year. It is interesting to note that growth would be of the same order of magnitude on the basis of the preceding age readings if a common hypothesis is assumed for the periodicity of ring formation.

It is agreed today that demonstrating growth marks on the vertebrae of skipjack tuna is still a very difficult matter. Analysis of the growth annuli remains unreliable. Batts (1972) voices very definite reservations as to the unquestionable existence of these growth marks: "Aikawa (1937), Aikawa and Kato (1938), Yokota *et al.* (1961) and Shabotiniets (1968) made no serious attempts to validate observed growth marks as annuli. Growth marks on vertebrae of skipjack of North Carolina waters were discontinuous on the surface of the centrum and did not possess the physical appearance of annuli" (Batts, 1972).

In respect of the scales it is assumed today that with classic age reading techniques the demonstration of seasonal marks is impossible (Aikawa, 1937; Postel, 1955; Batts, 1972).

Batts (1972) has very clearly demonstrated growth annuli in dorsal spine sections. By back-calculation he has derived from these the following mean lengths-for-age for skipjack:

$$L_1 = 40.6 \text{ cm} \quad L_2 = 49.3 \text{ cm} \quad L_3 = 56.9 \text{ cm} \quad L_4 = 63.8 \text{ cm}$$

Unfortunately the periodicity of ring formation has not been established and his hypothesis can neither be validated nor invalidated. It is worth emphasizing that the mean lengths-for-age obtained by Batts correspond to within 2 or 3 cm to those obtained by Aikawa and Kato (1938) and Chi and Yang (1973).

<u>VERTEBRAE</u>	L ₁	L ₂	L ₃	L ₄	L ₅	L ₆
Chi and Yang, 1973	27.4	38.4	46.7	54.7	62.7	67.8
Aikawa and Kato, 1938	27	37	46.5	55	-	-
<u>DORSAL SPINES</u>		L ₁	L ₂	L ₃	L ₄	
Batts, 1972		40.6	49.3	56.9	63.8	

B. General remarks on the interpretation of seasonal marks in tropical environments for growth studies

We feel that it would be useful at this point to set forth some observations on the utilization of seasonal marks (on bony structures in tropical environments) for establishing key lengths-for-age.

Determination of L_n by the back-calculation method invites certain reservations.

A linear relation is assumed between the growth of the fish and the hard part examined (vertebra, scale, dorsal spine or otolith). Gheno (1975) has shown after examining thousands of scales of *Sardinella aurita* that the correlation between fork-length and size of scale is highly significant. The standard error of estimation of L_n , however, is of the order of 3 cm for a fish the maximum size of which does not exceed 30 cm. The rings on the scales used in this study were particularly sharp, regular and constant when compared, for example, with the rings formed on the vertebrae of the skipjack tuna. There is here, then, a not inconsiderable source of error. The principal difficulty, however, in interpreting seasonal marks in the tropics does not lie at this level. In point of fact the most troublesome aspect of the "annuli" of intertropical fish is essentially their heterogeneity of formation in relation to the hydrobiological conditions to which the fish are subject in the course of their existence (Poinsard and Troadec, 1966; Gheno and Le Guen, 1968; Gheno, 1975). Moreover, taking into account the extended nature of the reproductive season in the intertropical environment during the first year, 0, 1, 2, 3 and even 4 growth marks may be formed (Gheno, 1975).

Chevey (1933) has long since demonstrated the importance of variations in the surrounding environment for natural marks. He compared the same species, *Synagris japonicus*, off the coasts of Tonkin (North Vietnam) and Cochin China (the Mekong Delta area). In the north surface water temperatures are 27-28° in summer and 23-24° in winter. This difference of 3-4° is sufficient to leave its mark on the scales. In the south, where the waters remain at the same temperature throughout the year, the scales show no seasonal marks. The alternation of seasons does not always have so direct an effect. Chevey has shown that its influence on nutrition and growth in fish may be mediated by complex phenomena. Thus, the waters of the Tonle Sap in Cambodia fall in winter and rise in flood during summer. The fish inhabiting these waters feed up during the season of inundation since the lake at this time extends over an immense territory where insects overtaken by the rising flood waters perish in large numbers. The wide zones on their scales correspond to the summer season. Conversely, sea fish which frequent the mouth of the Mekong are abundantly fed in winter when the subsidiary waters from the Tonle Sap bring down enormous quantities of organic material. The wide zones on the scales here correspond to the winter season.

Monod (1950) and Daget (1952) have come to broadly analogous results for the fish of the middle Niger and Lake Debo. High and low waters correspond, in short, to what are, in essence, physiological summers and winters. In the great lakes of Africa where variations in level are scarcely perceptible and where the availability of food remains constant throughout the year, the fish, by contrast, show no recognizable growth zones on their scales (Bertin, 1958). In short, as Bertin writes, the utmost caution is necessary in reading the seasonal marks on hard part structures. No serious application of the method is possible without in depth knowledge of the environment of each species. This applies with particular force to the skipjack in which migration patterns and the hydrobioclimatic conditions of life are very poorly understood.

C. Daily growth marks on the otoliths

As a result of the meeting of the working party on otoliths at the Scripps Institute, La Jolla, California, in July 1976, it is today accepted that daily growth marks are laid down in the otoliths of tropical fish just as they are in those of the fish of temperate seas (Pannella, 1971). Le Guen (1976), utilizing results obtained from growth studies (Petersen method) of Sciaenids in the Congo, showed that the interpretation of annual marks using Moller-Christensen's method (1964) and the counting of "daily" rings using Pannella's technique are very comparable, at least insofar as immature fish are concerned. In the case of mature fish, the interpretation of the daily marks has proved difficult. Le Guen was able to discern in tropical Sciaenids marks closely resembling the "S" marks of arrested growth during spawning (spawning breaks) observed by Pannella (1973).

The count made of daily marks on the otolith of an adult Sciaenid of the Congo underestimates by up to 30% the age previously read by Poinard and Troadec (1966) on the symmetrical otolith of the same fish. It has been impossible, however, to distinguish between the biological reality and artefacts bound up with the technique of reading (Le Guen, personal communication).

Uchiyama and Struhsaker (in press) have demonstrated daily marks on the otoliths of skipjack using Pannella's technique. They appear, on the other hand, to make the implicit assumption that arrest of growth never occurs in skipjack.*

Today we know that numerous fish are subject to interruptions (long or short) in their growth (Bertin, 1938). Clark (1925) has shown that for the grunion (*Leuresthes tenuis*) of the Californian coasts, the spawning season extends from March to July and comprises successive egg-layings corresponding to the very high tides, both spring and neap. During this long reproductive period (at the very least April to June) the growth of breeding fish stops. It is not impossible that skipjack pass through phases during which their growth is nil. If so, Pannella's technique is inadequate and is not, by itself, sufficient to resolve the problem of age. There is a risk, which should not be neglected, of overestimating growth.

The growth rate obtained by Uchiyama and Struhsaker (according to Bessineton, 1973), is very rapid and very similar to that obtained by Brock (1954) from length-frequency distributions. We note that the sampling carried out by these authors ran the risk of favouring the largest individuals and introducing a bias which overestimates the "mean growth rate" of skipjack (in the sense of least squares) in the exploited phase.

D. Conclusions

The immediate value of the seasonal marks on the hard parts is the demonstration of periods of arrested, or at least markedly slowed growth.

This finding is particularly important in regard to individual growth rates of skipjack on which are based the studies of growth by tagging.

* The definitive text not having been published we make the usual reservations in respect of this interpretation of the studies of Uchiyama and Struhsaker.

The crowding of the interannular spaces on the dorsal spines with age (Batts, 1972) prompts the thought that skipjack do not escape the general rule of mean growth of exponential type even if, individually, linear phases between the checks or slackenings in growth are observed.

Study of the hard parts has attracted renewed interest since the demonstration of daily growth marks on the otoliths by Pannella (1971).

If the technique is really effective for immature fish and juveniles (Le Guen, 1976), it should allow resolution of the problem of the age of skipjack at the time of their recruitment into the fishery stock, this age at present being estimated very approximately.

Initial work on otoliths in Papua New Guinea (Figure 1) shows that skipjack of 40 to 45 cm would be about one year old. This age is probably slightly underestimated by difficulty in rendering visible the daily marks close to the nucleus (Lewis, 1976).

II. GROWTH OBSERVED FROM TAGGING STUDIES

The results obtained from examination of the hard parts have shown very distinct seasonal variations in the growth increments of these structures with the formation of more or less regular "annuli" corresponding to interruptions - or at any rate slackenings - in growth. The successions of interannular growth increments have proved to be of exponential type. Under these conditions, and even if individual growth phases of linear behaviour exist (Uchiyama and Struhsaker, in press), we have chosen to minimize the risks of error in the study of growth rate of tagged fish, by considering the increments $\frac{\Delta l}{\Delta t}$ so obtained, to be functions at one and the same time of l and of Δt .

The data employed did not allow us to take into account the season of tagging, but it will be necessary to consider this in the future if skipjack, like numerous other fish, experience "physiological summers and winters" (Bertin, 1958).

Strictly speaking, annual growth from tagging studies should be estimated only for fish which have spent a complete year at large. We will continue to speak, however, of annual growth, giving this expression the simple arithmetic value of $\frac{\Delta l}{\Delta t}$.

We have reviewed the principal tagging data available today. For the central Pacific zone, we have taken the tagging data of the Bureau of Commercial Fisheries in Hawaii in 1958 as presented by Rothschild (1966, Table 1).

For the eastern Pacific we have used the recapture data of the Inter-American Tropical Tuna Commission presented by Joseph and Calkins (1969, Annex Table 4) eliminating 43 of the data entries considered as not significant by the authors. For the western Pacific we have the recapture data from the tagging campaigns carried out in Papua New Guinea (Lewis, 1977). Also included here are the preliminary results obtained for the Atlantic (ORSTOM, 1976).

It is important to note that the first tagging cruises, carried out in Hawaii as well as near the American coasts, were designed primarily for studying migrations, and that lengths of tagged skipjack during this period are only approximated. Schaefer *et al.* (1961) indicate that the majority of skipjack were measured to the nearest 5 cm at the time of tagging and that lengths of other skipjack were estimated from the average lengths of fish belonging to the same school and fished at the same time. The measurements of skipjack tagged in Hawaii are even more inadequate, which may explain the fact that only a very small proportion of recaptures were used by Rothschild (1966).

From the measurements $L_1 = Y$ estimated at the moment of tagging and $L_2 = X$ measured to the nearest millimetre in the ten days following (assuming the increment to be nil during this short interval of time), Rothschild (1966) and Joseph and Calkins (1969) have calculated the regressions fitting the data. Rothschild (1966) used the linear regression of Y on X ($Y = a + b X$), following here the classic procedure when only the variable Y is subject to error (Ricker, 1973). Joseph and Calkins (1969) followed the method of Krutchkoff (1967) who, because of the problems of calibration, prefers the regression of X on Y ($X = a' + b' Y$).

This controversial procedure can be justified if it is assumed that the values of X are themselves also subject to error when measurements are carried out directly on certain fishing vessels, without subsequent verification by fishery scientists. In this latter case, moreover, it would be judicious to employ Teissier's linear regression (Mayrat, 1959) also known as G.M. regression (Ricker, 1973).

Joseph and Calkins (1969) have thus used the regression of X on Y to correct the measurements made at the time of tagging. Indeed, they have shown that the direct use of estimated data imparts a substantial bias. A test has demonstrated that the slope of the equation $L_2 = 66.87 + 0.872 L_1$ differs from 1 in a highly significant manner. Without correction, lengths below 52 cm would be underestimated by 5 cm on average and above 52 cm these would be overestimated by the same amount. However, the standard deviation for the calculated values of L_2 (the standard deviation from regression - Snedecor, 1956) has not been published. It is therefore not certain that the correction carried out is in reality very effective and is not offset by another error just as large.

Rothschild (1966) gives the standard deviation for the L_1 values calculated from the linear regression $L_1 = a + b L_2$. This procedure involves no estimation of the error made in the length L_2 , supposedly exact. Nevertheless it gives an idea of the scatter of the estimated values of L_1 . The 95% confidence interval about the regression estimate of L_1 is ± 5.6 cm.

The data for Papua New Guinea are of a different nature to the foregoing, as the measurements there were made with the study of both growth and migration in mind. At the time of tagging, large numbers of fish were measured to the nearest centimetre. Each tagging series was carried out on fish of very homogeneous size. A sample of fish was fished at the same time in order to estimate the average length of the school. Thus for every fish tagged, either a length L_1 measured to the nearest centimetre or a length L_1 estimated from a modal value is available. Very frequently one has both L_1 and L_1 values. The measurements carried out at tagging (L_1) or estimated (L_1) have proved to be excellent. We have tested their value by comparing the lengths at tagging and the lengths L_2 of fish recaptured during the ten

days following. The values of the lengths L_2 used for control were verified by those responsible for the tagging programme. The body of data used to verify the adequacy of the measurements appears in Table I of Annex I.

We have simply calculated the mean values of $x = L_2 - \overline{L_1}$ and $x' = L_2 - L_1$ with their confidence intervals.

The following mean values have been obtained:

$\bar{x} = + 0.509$ At a confidence level of 95%: ± 0.464 (N = 67)

$\bar{x}' = + 0.452$ At a confidence level of 95%: ± 0.654 (N = 69)

For measurements carried out to the nearest centimetre it may thus be assumed that there is practically no error of measurement at tagging, the more so as there will nonetheless be a certain amount of growth between the first and tenth days of liberty. Moreover we have verified that the use of a linear regression between the parameters L_1 and L_2 on the one hand and $\overline{L_1}$ and L_2 on the other, did not produce any improvement in the measurements, but on the contrary involved a not insignificant risk of error (Table II, Annex I).

Furthermore, having both values, measured and estimated L_1 and $\overline{L_1}$, for 423 skipjack we have calculated the mean value of $x = L_1 - \overline{L_1}$. We have found $x = 0.38 \pm 0.20$ cm at the 95% confidence level. These results confirm that tagging in Papua New Guinea has been carried out for the most part on groups of very homogeneous size class fish (Lewis, personal communication).

We have postulated that the annual growth $\frac{\Delta L}{\Delta t}$ is a function of the length L at time of tagging, as well as the time Δt spent at large. Taking into account the size of the fish at the time of tagging and after the time at large, we have regrouped the data by zones, by 5 cm size classes and for fish which had been roughly the same length of time in the sea. We were thus able to assemble data for fish which had been in the sea from two to five months, from five to twelve months and for more than a year. We purposely omitted from this study data for skipjack which had been at large for less than two months. With the errors in estimating lengths at time of tagging being often greater than the value of the increments ΔL for periods of less than two months, a not inconsiderable proportion of the values $\Delta L = L_2 - L_1$ are, and this is quite logical, mathematically negative. This can be readily verified for the eastern Pacific by examining the skipjack growth curves in Figure 9 of the Annual Report for 1959 of the IATTC (Anon., 1960). The negative increments, which are in conflict with simple logic, have everywhere had a very clear tendency to disappear from the data for a variety of reasons and without it being easy to estimate the bias thus introduced into the results.

The body of data which we have used appears in Annex I: Tables III, IV, V, VI and VII. For skipjack which were at large for two to five months and for five to twelve months we have calculated the mean annual growth increments $m = \frac{\Delta L}{\Delta t}$ for each size class. The confidence interval of the means m has been estimated by $\pm t \frac{s}{\sqrt{n}}$ (Student's t) for the small samples ($n \leq 30$). For the samples of larger size, the formula used was $m \pm \epsilon \sqrt{n}$ (Schwartz, 1963).

The collected results obtained appear in Tables 1 and 2. In the Pacific the lowest growth rates were observed in Papua New Guinea and the highest in Hawaii. Since the confidence intervals for the estimation of m largely tally, we have made test comparisons of the means, two by two, for each size class.

The comparison between two means m_a and m_b observed for $n_a \geq 30$ and $n_b \geq 30$ is based on:

$$t = \frac{m_a - m_b}{\sqrt{\frac{s_a^2 + s_b^2}{n_a + n_b}}}$$

In the case of the other samples we used Student's t test where:

$$t = \frac{m_a - m_b}{\sqrt{\frac{s_a^2}{n_a} + \frac{s_b^2}{n_b}}} \quad \text{and} \quad s^2 = \frac{\sum (m - m_a)^2 + \sum (m - m_b)^2}{n_a + n_b - 2}$$

Tables 3 and 4 present the results of the different tests. One cannot say with complete confidence that there are differences among the data groups.

The study rests, in fact, on few data in each group. The confidence intervals for m are only small for a large number of data ($n \geq 30$).

Moreover, in calculating the means and in comparing them group by group, we implicitly assumed that we were dealing with data taken at random in normal distributions. This is obviously a crude approximation. Our efforts at homogenization of the data are of limited application. For example, in the 40-45 cm group the data might fall between 40 and 41 cm in one tagging area and between 44 and 45 cm in another. Thus if the increments in the months following are significantly different, this should not cause surprise.

The length estimation errors made at time of tagging may be amply sufficient to produce significant differences. The example of skipjack tagged in Papua New Guinea and which remained in the sea for five to twelve months (Table 4) is especially instructive in this regard. Indeed, according to whether the measured length values L_1 are used or those estimated from the modal value \bar{L}_1 , the mean growths obtained are significantly different for tagged skipjack measuring between 55 and 60 cm.

This observation is particularly important when one considers the margin of error involved in skipjack length estimation for certain tagging series.

The artificiality of the divisions should also be emphasized. In our schema the increments of skipjack whose length at tagging time was estimated as 49.9 cm have not been compared with the increments of skipjack whose length at tagging was 50.1 cm. In the same way, the length increments of fish which remained five months in the sea are not directly compared with those of fish which were at large for six months.

TABLE 1. Mean value of annual growths m calculated for each 5 cm interval of length, in different areas, for a time at large of 2 to 5 months. In each interval, besides the mean m , the standard deviation s and the confidence levels 90 and 95% appear, as well as the number of available data n .

Length at tagging release	East Pacific JOSEPH and CALKINS (1969)		Papua New Guinea L_1 (measured to the nearest cm)		Papua New Guinea \bar{L}_1 : estimated from the modal value		Atlantic	
	n m s 90% 95%	n m s 90% 95%	n m s 90% 95%	n m s 90% 95%	n m s 90% 95%	n m s 90% 95%	n m s 90% 95%	n m s 90% 95%
40 - 45 cm		5 20.22 8.60 + 8.20 +10.67						1 29.4
45 - 50 cm		14 15.01 11.87 +5.62 +6.85		3 13.46 9.62 +16.23 +23.91		3 20.12 3.92 +6.61 +9.74		1 25.17
50 - 55 cm		61 17.78 9.92 +2.09 +2.49		26 7.65 8.53 +2.86 +3.45		39 8.14 9.35 +2.46 +2.93		3 15.00 18.73 +31.57 +46.52
55 - 60 cm		6 12.52 9.17 +7.54 +9.62		39 7.19 9.83 +2.59 +3.09		41 6.51 13.45 +3.46 +4.12		2 16.20 1.10 +4.91 +9.87
60 - 65 cm		1 7.18 - - -		3 5.95 2.48 +4.18 +6.16		3 3.75 9.00 +15.18 +22.36		

TABLE 2. Mean value of annual growths m calculated for each 5 cm interval of length in different areas for a time at large of 5 to 12 months. In each interval, besides the mean m , the standard deviation s and the 90 and 95% confidence limits appear, as well as the number of available data n .

Length at tagging release	East Pacific JOSEPH AND CALKINS (1969)		Hawaii ROTHSCHILD (1965)		Papua New Guinea L_1 (measured to the nearest cm)		Papua New Guinea L_1 : estimated from the modal value		Atlantic	
	n	m	n	m	n	m	n	m	n	m
35 - 40 cm			n	1						
			m	23.10						
40 - 45 cm	n	1	n	10			n	1	n	1
	m	21.82	m	23.67			m	9.82	m	18.09
	s		s	7.00						
	90%		90%	+4.06						
	95%		95%	+5.01						
45 - 50 cm	n	7	n	18	n	7	n	3	n	1
	m	11.03	m	21.97	m	11.76	m	14.69	m	19.55
	s	6.99	s	5.29	s	5.80	s	4.23		
	90%	+5.14	90%	+2.16	90%	+4.26	90%	+7.14		
	95%	+6.47	95%	+2.62	95%	+5.37	95%	+10.52		
50 - 55 cm	n	12	n	2	n	26	n	52	n	1
	m	12.46	m	14.33	m	7.98	m	6.85	m	12.01
	s	6.94	s	8.21	s	4.18	s	4.57		
	90%	+3.60	90%	+36.65	90%	+1.40	90%	+1.04		
	95%	+4.41	95%	+73.76	95%	+1.69	95%	+1.24		
55 - 60 cm	n	3	n	1	n	33	n	110	n	1
	m	15.26	m	10.43	m	3.90	m	5.28	m	0.00
	s	2.32			s	3.32	s	3.41		
	90%	+3.92			90%	+0.98	90%	+0.54		
	95%	+5.77			95%	+1.18	95%	+0.64		
60 - 65 cm					n	4	n	5		
					m	2.62	m	-1.12		
					s	2.82	s	4.22		
					90%	+3.32	90%	+4.02		
					95%	+4.48	95%	+5.23		

TABLE 3. Comparison of the means for the different intervals of length for fish which remained at large for 2 to 5 months.

S: means are significantly different
 NS: means are not significantly different
 df: degrees of freedom

Eastern Pacific - Papua New Guinea (L_1 measured)

=====

	t or ϵ	df	0.05	0.001
45 - 50 cm	/t/ = 0.21	15	NS	NS
50 - 55 cm	/t/ = 4.54	85	S	S
55 - 60 cm	/t/ = 1.25	43	NS	NS
60 - 65 cm	/t/ = 0.43	2	NS	NS

Eastern Pacific - Papua New Guinea ($\overline{L_1}$ modal value)

=====

	t or ϵ	df	0.05	0.001
45 - 50 cm	/t/ = 0.72	15	NS	NS
50 - 55 cm	/ ϵ / = 4.91	x	S	S
55 - 60 cm	/t/ = 1.05	45	NS	NS
60 - 65 cm	/t/ = 0.33	2	NS	NS

Papua New Guinea (L_1 measured) - Papua New Guinea ($\overline{L_1}$ modal value)

=====

	t or ϵ	df	0.05
45 - 50 cm	/t/ = 1.11	4	NS
50 - 55 cm	/t/ = 0.21	63	NS
55 - 60 cm	/ ϵ / = 0.26	x	NS
60 - 65 cm	/t/ = 0.41	4	NS

TABLE 3. (cont.)

Eastern Pacific - Atlantic

=====

	t or ϵ	df	0.05
40 - 45 cm	/t/ = 0.97	4	NS
45 - 50 cm	/t/ = 0.83	13	NS
50 - 55 cm	/t/ = 0.46	62	NS
55 - 60 cm	/t/ = 0.54	6	NS

Papua New Guinea (L_1 measured) - Atlantic

=====

	t or ϵ	df	0.05
45 - 50 cm	/t/ = 1.05	2	NS
50 - 55 cm	/t/ = 1.25	27	NS
55 - 60 cm	/t/ = 1.28	39	NS

Papua New Guinea ($\overline{L_1}$ modal value) - Atlantic

=====

	t or ϵ	df	0.05
45 - 50 cm	/t/ = 1.12	2	NS
50 - 55 cm	/t/ = 1.14	40	NS
55 - 60 cm	/t/ = 1.01	41	NS

TABLE 4. Comparison of the means for the different intervals of length for fish which remained at large for 5 to 12 months.

S: means are significantly different
 NS: means are not significantly different
 df: degrees of freedom

Eastern Pacific - Hawaii

	t or ε	df	0.05	0.001
40 - 45 cm	/t/ = 0.25	9	NS	NS
45 - 50 cm	/t/ = 4.25	23	S	S
50 - 55 cm	/t/ = 0.35	12	NS	NS
55 - 60 cm	/t/ = 1.80	2	NS	NS

Eastern Pacific - Papua New Guinea (L_1 measured)

	t or ε	df	0.05	0.025	0.01	0.001
45 - 50 cm	/t/ = 0.21	12	NS	NS	NS	NS
50 - 55 cm	/t/ = 2.48	36	S	S	NS	NS
55 - 60 cm	/t/ = 5.76	34	S	S	S	S

Eastern Pacific - Papua New Guinea ($\overline{L_1}$ modal value)

	t or ε	df	0.05	0.01	0.001
45 - 50 cm	/t/ = 0.83	8	NS	NS	NS
50 - 55 cm	/t/ = 3.45	62	S	S	NS
55 - 60 cm	/t/ = 5.03	111	S	S	S

Hawaii - Papua New Guinea (L_1 measured)

	t or ε	df	0.05	0.001
45 - 50 cm	/t/ = 4.22	23	S	S
50 - 55 cm	/t/ = 1.97	26	NS	NS
55 - 60 cm	/t/ = 1.94	34	NS	NS

TABLE 4. (cont.)

Hawaii - Papua New Guinea ($\overline{L_1}$ modal value)

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	t or ϵ	df	0.05	0.025
40 - 45 cm	/t/ = 1.89	9	NS	NS
45 - 50 cm	/t/ = 2.25	19	S	NS
50 - 55 cm	/t/ = 2.22	52	S	NS
55 - 60 cm	/t/ = 1.50	109	NS	NS

Papua New Guinea (L_1 measured) - Papua New Guinea ($\overline{L_1}$ modal value)

=====

	t or ϵ	df	0.05	0.025
45 - 50 cm	/t/ = 0.78	8	NS	NS
50 - 55 cm	/t/ = 1.06	76	NS	NS
55 - 60 cm	/ ϵ / = 2.08	x	S	NS
60 - 65 cm	/t/ = 1.51	7	NS	NS

The methods of analysis of the data are also involved in the various results obtained for the growth means. Thus Schaefer *et al.* (1961) have shown that in using a straight line $\Delta l = a + b \Delta t$, whether passing or not through the origin, for the regression between the increment Δl in mm and the time at liberty Δt in days, the mean increments in their size intervals differed appreciably (Table 5). If the Papua New Guinea data of Table 1 are regrouped into the same size intervals as those employed by Schaefer *et al.* (1961), the results for the fish which remained at liberty for 2 to 5 months are obtained (Table 6). The growths obtained in Tables 5 and 6 are of the same order of magnitude.

The data used by Schaefer have a 90% correspondence with those of fish which remained in the sea from 0 to 6 months. His results are thus roughly comparable to those which we have obtained for skipjack which remained for 2 to 5 months in the sea in Papua New Guinea. These results lend support to the preceding hypothesis of results not significantly different from one tagging zone to another. A global approach such as that which Schaefer *et al.* (1961) had in mind has been adopted in calculating the linear regression $\Delta l = a + b \Delta t$ for the total number of skipjack which remained in the sea for 2 to 5 months in Papua New Guinea and in the eastern Pacific (IATTC zone).

Δl being expressed in cm and Δt in days, the two following regressions have been obtained:

$$\text{Eastern zone (IATTC)} : \Delta l = 1.4683 + 0.03055 \Delta t$$

$$\text{Papua New Guinea zone} : \Delta l = -0.8049 + 0.03151 \Delta t$$

These correspond to a mean increment of 12.61 cm for the eastern Pacific and 10.69 cm for Papua New Guinea.

The two values of a are not significantly different from 0 and neither are the slopes significantly different from one another. Nevertheless, too hasty a conclusion should not be drawn as to the equality of the results because the variances s_a and s_b are very high. For fish which remained at large in Papua New Guinea for 5 to 12 months, we have obtained the following equation for the linear regression:

$$\Delta l = -0.1697 + 0.01585 \Delta t$$

which would correspond to an annual increment of 5.62 cm per annum. The variability of the increment data utilized is such that this latter line is not significantly different from the two preceding ones.

As regards skipjack at large for more than a year, our data permit no valid comparison between zones. We can merely give the results obtained in Papua New Guinea (Table 7).

The mean size at recapture of the few tagged skipjack between 55 and 60 cm and recaptured in the Papua New Guinea zone after an interval of more than two years was 62 cm.

TABLE 5. Estimation of the growth of skipjack from recapture data.

IATTC data for recaptures to 31 October 1959.

Size at tagging release	Regression of the growth increment in mm on time at large in days			Regression passing through the origin	
	N	b	Annual increment	b	Annual increment
400-499 mm	29	0.475	173 mm	0.567	207 mm
500-599 mm	82	0.290	106 mm	0.318	116 mm
600 and above	28	0.160	58 mm	0.003	1 mm
All sizes	139	0.341	124 mm	0.335	122 mm

(SCHAEFFER *et al.*, 1961)

TABLE 6. Annual increments calculated in centimetres for skipjack which remained at large for 2 to 5 months in Papua New Guinea.

Length classes	Measurements at tagging release	
	Length L_1 measured to the nearest cm	L_1 estimated from the modal value
40 - 50 cm	13.46 cm n = 3	20.12 cm n = 3
50 - 60 cm	7.37 cm n = 65	7.30 cm n = 80
> 60 cm	5.95 cm n = 3	3.75 cm n = 3

TABLE 7. Mean value of annual growths m calculated for each 5 cm interval of length for a time at large of 12 to 24 months. In each interval, besides the mean m , the standard deviation s and the 90 and 95% confidence levels appear, as well as the number of available data n .

	Papua New Guinea L_1 (measurement to the nearest cm)		Papua New Guinea \overline{L}_1 : estimated by the modal value)	
	40 - 45 cm	n m	1 5.09	
45 - 50 cm	n m s 90% 95%	2 4.69 2.66 +11.87 +23.89	n m s 90% 95%	2 5.27 2.23 +9.94 +19.99
50 - 55 cm	n m s 90% 95%	15 5.69 1.66 +0.75 +0.92	n m s 90% 95%	37 5.68 2.52 +0.68 +0.81
55 - 60 cm	n m s 90% 95%	10 5.60 3.00 +1.74 +2.15	n m s 90% 95%	16 4.34 2.22 +0.97 +1.18
> 60 cm	n m	1 3.64	n m	1 3.55

We note that of the 660 fish recaptured, about thirty had escaped from the coastal zone and had moved north of the equator dispersing along the equatorial convergence as far as longitude 172°W, which was the eastern limit of Japanese fishing activity in 1972-1974 (Figure 2). Some skipjack might quite possibly have gone even further east, since it is hard to see what ecological barrier would halt them at 172°W.

It seems that the skipjack which set out into the open ocean had a more rapid growth rate than those which remained in the coastal waters. But the data do not allow this to be stated as fact. However, this idea that there is a different rate of growth in the coastal zone as compared with the open sea is an interesting one to follow. The recapture at Hawaii of 16 skipjack tagged in open waters off California and of one skipjack tagged in open water off Japan (Table 8) lends support to the hypothesis of a more rapid growth of fish which have escaped from the coastal zone.

Japanese fishing data (Tanaka, 1976-1977) show that large quantities of skipjack of 8 to 10 kg are found in the open ocean along the equatorial convergence from 145°E to 170°E, whereas in the coastal zones of Papua New Guinea, the Philippines and Japan, the skipjack fished rarely exceed a length of 60 cm.

A very general hypothesis could be proposed that suggests there exist a number of spatio-temporal "ecological compartments", more or less favourable, and within which the biological parameters of the skipjack (growth, natural mortality, etc) would be adapted to the environmental conditions. This hypothesis has already been formulated by Kearney (1976) in a different form.

Here, the skipjack is assumed to pass more or less en masse from one compartment to another. The "coastal compartment" of Papua New Guinea could in this case be regarded as comparatively tight (for exit) since only some thirty fish out of 660 recaptured departed from it to head in the direction of the equatorial convergence without, however, crossing it. We note that any migration towards the south was not discernible during the period of the tagging programme due to the absence of fishing.

Tagging recapture data for the Pacific as a whole have not demonstrated any very important exchanges between distant geographic zones, insofar as the exploited phase of the population (or populations) is concerned.

Nevertheless, these exchanges do take place on a large scale, since fish marked on either side of the Pacific may turn up in Hawaii.

Growth seems to come to a halt in the coastal zones at around 60-65 cm and to continue to 80 cm and beyond in the zones of the open ocean such as Hawaii.

A bias may have led to underestimation of growth in Papua New Guinea. Recaptures were made essentially by pole-and-line vessels which are very selective for coastal fish. The distribution and frequency of pole-and-liners and of seiners, drawn up for a number of years at IATTC, are of interest in this connection. The seiners can take distinctly larger skipjack than the pole-and-liners. Captures of skipjack of more

TABLE 8. Recapture data for skipjack tuna tagged by IATTC, presented at the meeting of the group of experts of the IPFC at Manila, 1-2 March 1978.

Date		Days at liberty	Position		Fork-length (cm)		No. of the tag
Recapture	Tagging-release		Recapture	Tagging-release	Recapture	Tagging-release	
6-12-62	9-05-60	646	Hawaii	Baja CA	77.4		
8-22-62	4-17-60	858	Idem	Revillagigedo Is.	78.0		
4-05-63	9-22-61	561	Christmas Is.	Baja CA	70.0		
6-27-67	6-05-65	753	Hawaii	Revillagigedo Is.	81.4	45.0	
7-21-70	11-06-69	258	Idem	Clipperton Is.	70.3	66.0	
8-08-70	11-06-69	276	Idem	Idem	71.5	65.0	
9-01-76	7-06-75	422	Molokai, Hawaii	Baja Madgalena, CA	72.7	59.0	J5242
9-01-76	7-20-75	408	So. of Pearl Hbr.	Cabo San Lucas, CA	75.1	45.0	J8250
* 8-22-76	7-06-75	410	21°14'N-171°51'W	24°07'N-113°45'W	80.0	65.0	J5543
**12-09-76	5-17-76	206	Waianae, Hawaii	31°57'N-159°12'E	68.0	42.0-59.0	No I.D.
6-10-77	6-17-76	357	Kahuku, Hawaii	21°16'N-111°04'W	73.0-75.0	46.0	K4105
6-28-77	6-18-76	375	Kaneohe, Hawaii	21°07'N-111°16'W	76.0	53.0	L0263
7-26-77	10-04-76	295	Idem	25°45'N-112°47'W	72.3	44.0	L0222
7-29-77	6-17-76	407	Idem	21°16'N-111°04'W	75.0	47.0	K7250
8-19-77	6-18-76	427	Hawaii	21°07'N-111°16'W	74.9	47.0	L0047
9-14-77	6-17-76	454	Barbers Pt., Hawaii	21°16'N-111°04'W	76.0	43.0	K7182
9-20-77	6-17-76	460	Waianae, Hawaii	Idem Idem	75.2	49.0	K8615

* Recaptured by a Japanese vessel

** Tagged by Japanese fishery scientists

than 65 cm, common for the seiners, are very much rarer for the pole-and-line boats. Moreover the factor "distance from the coast" for the two types of vessel may play a part, being superimposed on the intrinsic selectivity of each type of fishing gear.

When growth curves or key lengths-for-age are being established, another possible source of error is worth pointing out. Scientists interpreting recapture data have assumed (as we have) that growth is a function of the length of the fish at the time of release. In fact, it is also a function of age. When growth is slow there is thus more risk that fish of a given size class are derived from different age groups. This risk is greater if tagging is done on relatively aged fish, the range of sizes increasing with age. If there are several possible ages for the same size, one may find several types of growth for this same size.

In Figure 3 we have drawn up the histograms of frequencies of the annual growth rates $\frac{\Delta l}{\Delta t}$ for fish of 50 to 55 cm and of 55 to 60 cm which remained at liberty for two to five months in Papua New Guinea. There would appear to be several modes in the growth rates. The small number of observations (26 and 33) does not allow any conclusion, but in future work it would be useful to study this phenomenon more closely, particularly in conjunction with counts of daily growth marks on the otoliths of recaptured fish.

In short, it can be said that the analysis of the growth data available in the approximately 45 to 60 cm range has shown slower mean growth for the skipjack of Papua New Guinea than for those of the eastern Pacific. Nevertheless, since the values obtained in the east and west are not significantly different, the results will need to be checked on the basis of more abundant and reliable data, particularly insofar as the eastern Pacific is concerned.

III. PETERSEN'S METHOD

A. General considerations

The method of length frequencies was, of course, introduced by Petersen (1892). It is worth recalling that this method consists of following the growth of some modal lengths as a function of time. "Much early work by d'Arcy Thompson and others, using Petersen's method, was later shown to be inaccurate because a succession of modes had been treated as belonging to successive year classes, when in fact they represented only dominant year classes which were separated by one or more scarce broods" (Ricker, 1958). Today some workers still use an analogous method which could be described as Petersen's method short-circuited. It consists of considering only a polymodal distribution of length frequencies and of making (generally in an implicit fashion) the hypothesis that the successive modal distributions, obtained by one of numerous methods of analysis presently available (Harding, 1949; Cassie, 1954; Partlo, 1955; Tanaka, 1956; Gheno and Le Guen, 1968; Daget and Le Guen, 1975), correspond likewise to fish of successive age classes.

Brock (1954), who was the first to study the growth of skipjack from length frequency distributions in the Pacific, used a method half-way between the Petersen and d'Arcy Thompson methods. He regrouped his

measurements by six-month periods making the (implicit) hypothesis that in each distribution the successive modal values correspond to fish of successive age classes. Unfortunately the time interval between the analysed frequency distributions definitely does not allow us to follow the progression of modes and to verify the validity of the hypothesis. There is nothing to allow us to state positively that no age class is missing from the distributions or that, on the contrary, there were several broods for the same year. Bessineton (1976), working on the growth of skipjack tuna in Tahiti, used a similar method, grouping his samples by year rather than by six-month periods. During the two years (June 1973 to July 1975) for which the sampling lasted, about 1,000 skipjack were measured each month. Bessineton (1976) noted that he had never measured fish between 70 and 75 cm. He was thus led to explicitly assume that at least one age class was not represented in the distributions. "It is necessary to note that between the last class (75 to 80 cm) and the smaller fish, there is a discontinuity in all of the samplings carried out, fish of 70 to 75 cm being completely absent from the catches for a period of one year. Fish of 57 cm of one year cannot thus be connected with those of 79 cm of the following year" (Bessineton, 1976).

The conclusions on growth differ considerably according to the various hypotheses. According to Brock (1954) skipjack reach the length of 80 cm at three years. According to Bessineton (1976), this size is reached towards the age of five years. The progression in time of the modal values used having been demonstrated by neither of the authors, *a priori* one can neither validate nor invalidate their hypotheses and their conclusions. It is nonetheless interesting that Bessineton (1976) has brought up directly, for the first time, the problem of the absence of age classes in a fishery and indirectly the problem of migrations.

A very large number of other studies based on the classic Petersen method have been carried out in the Pacific as well as in the Atlantic and Indian Oceans. Today there is a large body of length frequency distribution data available for critical study.

We have taken up certain data, published (Kawasaki, 1955a, 1955b, 1963; Diaz, 1966; Marcille and Stequert, 1976) or placed at our disposal by various laboratories (NMFS Hawaii, IATTC La Jolla, ORSTOM, ISRA Dakar). The previously unpublished frequency distributions are in Annex II.

The possible analyses of polymodal distributions into successive unimodal distributions have been carried out using the method of successive maxima (Daget and Le Guen, 1975) which does not require the hypothesis of normality of distributions but only that of symmetry in relation to the mean value.

Analysis of all the available data demonstrates three things:

- 1) Clear progressions of modes for more than a few months are extremely difficult to demonstrate. Exceptionally it is possible to have apparently acceptable mode progressions for a duration of 12 to 18 months.

- 2) The apparent mode progression may give in a single region, in different years, growths which are rapid, slow, nil and even negative.
- 3) The extremely subjective aspect of the method, as Joseph and Calkins (1969) have already emphasized, makes it an extremely questionable one.

In most cases workers fail to specify the "utilizable" part of the mode progressions used by them in the study of growth or the reasons for discarding parts of them. Marcille and Stequert (1976) clearly explained the subjective aspect of the choice made by them during a study on skipjack in the Indian Ocean. "We have therefore tried to follow a mode progression which was the most logical possible and which took no account of the actual importance of some of the modes in relation to the others. Such a method may seem seriously open to criticism since it leaves an important part to the interpretation of the biologist; we have used it, however, because from June 1974 to March 1975 no logical progression of a principal mode appeared in the total monthly samples" (Marcille and Stequert, 1976).

In working with more abundant data (Annex II) of much greater diversity of origin we have come (in the main) to the general conclusion that, with the length frequency distributions of skipjack available, the degree of reliance which can be placed on the Petersen method is not very high in view of its subjectivity.

This may be intrinsic to skipjack because of its biology (extended reproductive periods) and behaviour (migration, regrouping in schools of uniform size, catchability ...). It is certain, for example, that knowledge of the migratory patterns would allow a better interpretation of certain mode progressions. In this connection it is interesting to consider the length-frequency histograms for skipjack of the region north-west of Madagascar in the Indian Ocean (Figure 4) and to note the interpretation which Marcille and Stequert (1976) have given them.

"From June 1974 to March 1975, the modal size of catches did not progress with time, remaining always between 47 and 48 cm; a very slight regression of this mode could even be discerned. In this case, the study of growth becomes very difficult if not impossible and we are unable, moreover, to determine the number of year classes. The great constancy of the modes from June 1974 is in apparent contradiction to their rather regular evolution observed from August 1973 to May 1974; it could be explained by a continuous flux of recruitment, growth and migration, the net result of which would be an apparent mode at 47-48 cm persisting for a long period of time and creating an impression of absence of growth in the stock. Let us examine in detail the behaviour of the size histograms between July and January 1975: in July, there appears to take place a recruitment of young individuals of 38 to 43 cm, although as yet they are not very numerous; in August, these individuals are caught in greater numbers and appear to form a mode at 42-43 cm, which from October to December progressively renews the apparent mode, eventually replacing it completely. During this same period, the individuals making up the initial apparent mode are thought to leave the fishing zone as they grow. Study of the catches of the pole-and-liners during this period affords us some additional indications corroborating such a hypothesis. In June and July the c.p.u.e. is fairly low (4.5 and 3.4 tonnes/day): subsequently it increases progressively from 5.2 t/day in August to 8.1 t/day in November, as the class recruited in June-July grows and contributes to the initial

apparent mode. In the months which follow (December-January) individuals start leaving the fishery and c.p.u.e. drops to 5.3 and later to 4.2 t/day" (Marcille and Stequert, 1976).

It is certain that analogous configurations in the successions of modes may be differently interpreted in the presence or in the absence of migrations in fisheries as in those of Tahiti and Hawaii, for example (Brock, 1954; Bessineton, 1976).

B. Representativeness of the samples

The variability of results obtained by the Petersen method may also be closely related to the problem of the representativeness of the samples used. From the fish measured one is supposed to reconstitute the length frequency distributions of a stock. Le Guen (1972) has shown that sampling controls may have an essential bearing on one fundamental characteristic of the representative samples. "The essential characteristics of samples drawn from the same fish stock and which are *representative* of this fish stock will be identical frequency distributions ... There is a very convenient technique based on this principle for estimating the number n of fish to be measured in order to obtain a length frequency distribution acceptable to the biologist. One continues to measure fish until the distribution stabilizes" (Le Guen, 1972).

The Centre National d'Exploitation des Océans (CNEXO) and the Polynesian Fisheries Service (Service des Pêches de Polynésie) have been using a very interesting sampling system since 1973, for the skipjack tuna fishery in Tahiti. The fishery studied operates in what is virtually a 1^o square in which the mean annual catch is 400 tonnes of skipjack. Since the end of 1973, whenever catches have been landed at Papeete and each time that it has been possible, 50 to 100 fish have been measured from one tuna boat chosen as far as possible at random. "Thus an average of 1,000 skipjack tuna per month have been measured from the 40 to 50 tuna boats which are based at the port of Papeete and which land some 400 tonnes of skipjack per annum" (Bessineton, 1976).

Measurements of skipjack are made to the nearest cm, for want of a better method, with a tape-measure giving a length which takes into account the contour of the body between the tip of the snout and the fork of the tail ("round" length = contour length = LR) which has to be converted to the standard fork-length (LF). A conversion table (LR - LF - weight) drawn up by Bessineton (1976) is to be found in Annex II, as well as the measurements carried out from July 1973 to April 1978.

We thus possess data on a fishery which is perfectly localized and of which the rate of measurement of skipjack tuna varied from 10 to 20% from July 1973 to September 1977. This afforded an exceptional opportunity for a theoretical study of the representativeness of samples.

We firstly assumed that, with such a rate of sampling over so restricted a geographical area, the sample was necessarily representative of the 400 tonnes fished. Thus we considered that the 4,259 skipjack tuna measured from 62 landings during the first quarter of 1977 allowed the drawing up of a histogram of length frequencies representative of the total catch made during this quarter.

For each of the 62 landings, we took three random sub-samples (with the aid of an HP 97 programme) of 10, 20 and 30 fish, from which we reconstituted three new frequency distributions, comprising respectively 620, 1,141 and 1,568 individual contour lengths (LR). From the length frequency distribution observed for the 4,259 fish, taken as reference distribution, we calculated the theoretical distributions for 620, 1,141 and 1,568 skipjack. These theoretical distributions comprise respectively 38, 41 and 41 length classes (to 1 cm) with more than 5 individuals in each class. We have used the χ^2 test advocated by Snedecor (1956) to compare the three distributions reconstituted by random sampling of 10, 20 and 30 fish per ship with the corresponding theoretical distributions.

The χ^2 tests obtained for 620, 1,141 and 1,568 lengths respectively are 52.01 - 25.21 and 23.17 for 37.40 and 40 degrees of freedom.

The probability that the new distributions will be identical with that of the 4,259 fish measured will thus be:

97.5 to 99% if 30 fish are measured per ship sampled;
95 to 97.5% if 20 are measured;
and less than 10% if 10 are measured.

The conclusion, therefore, is that in the sampling in progress in Tahiti there is no need to measure 60 to 100 fish per landing as 20 to 30 measurements would suffice to sample this catch.

We accepted that the 62 landings sampled were adequately representative of the exploited stock. A second test was carried out to ascertain whether the total number of landings to be sampled could be reduced. For this we took at random 10, 20, 30, 40, 50, 55 and 60 landings and calculated as before the theoretical distributions which ought to be obtained if these distributions were identical to those obtained for 4,259 fish.

The χ^2 tests carried out on the distributions gave the following results:

Number of landings taken at random from a total of 62	Number of fish	Probability of representing the initial distribution of 4,259 skipjack
10	721	0 %
20	1,258	0 %
30	2,129	0 %
40	2,802	5 %
50	3,427	25 %
55	3,799	95 %
60	4,179	99.5%

This second test carried out on the landings of the first quarter of 1977 would tend thus to prove that although it is not necessary to measure more than 20 to 30 fish per landing to characterize the catch, it is on the other hand essential to continue to sample the largest possible number of landings.

We were thus led to study sampling strategy in greater depth. To this end we intensified sampling from October 1977 and from the end of February to the beginning of April 1978 we examined a maximum of catches landed at the port of Papeete. We succeeded in obtaining, in six weeks, 120 samples, with about twenty skipjack tuna measured on each occasion. Applying always the principle of identity of the representative distributions (Le Guen, 1972) we calculated the theoretical distributions for 40, 60 and 80 catches from the distribution obtained for the 120 catches. Random lots were drawn week by week to achieve homogenization.

The χ^2 tests carried out on the distributions obtained after five random samples gave the following results:

Number of landings taken at random from the 120 sampled	Probability of obtaining a distribution identical with that of the 2,263 lengths obtained from 120 samples					
	1st lot	2nd lot	3rd lot	4th lot	5th lot	mean
40 (33%)	5%	10%	25%	5%	5%	10%
60 (50%)	99.5%	75%	90%	95%	90%	90%
80 (66%)	99.5%	90%	99%	97.5%	95%	96%

We could have continued the drawing of lots to get a more accurate mean in each case, but this did not seem necessary for our purpose. We adopted a sampling strategy consisting of measuring 20 to 30 fish for the maximum of catches landed at Papeete. It proved necessary to sample about 50 to 60% of landings in order to feel confident that our sampling adequately represented the catch as a whole, which in turn is assumed to reflect the stock fished.

The fundamental interest of this study lies in the fact that it may account for the variability of the results obtained by the Petersen method. Indeed, once it is recognized that below a certain threshold of sampling the frequency distributions are most unlikely to represent the stock fished, one should not be surprised at results using the Petersen method with too small a sample. The set of histograms of contour length (LR) frequencies produced with the measurements from Tahiti has enabled us under apparently good conditions to follow the growth of skipjack tuna from the first age class appearing in the fishery in January-February with an average size of about 45 cm.

Assuming that we are dealing with a stable stock unaffected by the phenomena of emigration and immigration, the growth G of these recruits of 45 cm would be of the order of 15 cm per year (12 cm < G < 20 cm). Beyond 60 cm the interpretation of growth is practically impossible by the classic Petersen method.

In Figure 5 we have plotted the modal values obtained in sampling boat by boat from 1 July 1976 to 31 January 1978. There are thus from 20 to 50 different modal values for each month. The distributions obtained for the Papeete tuna boats are practically all unimodal. In Tahiti, therefore, it is easy to see the effect which any substantial reduction in the sample size would have. It is sufficient to take at random each month 1, 2 ... n

tuna boats as shown above and to draw up the histograms of the frequencies obtained with the n sub-samples taken at random. Several samplings made with a single boat from 1 February 1977 to 1 February 1978 yielded growth results ranging from 6 cm to 20 cm per year. Some random samplings with five tuna boats per month gave growth results ranging from 9 cm to 20 cm per year.

Petersen's method is much more sensitive to low sampling when the fishery is temporary and covers only three to six months of the year.

Random samplings for the Tahiti data from August to November 1977, with a single boat sampled per month have given growths ranging from -2 to +28 cm per year for skipjack tuna. In taking, at random, five of the catches landed per month, the growths obtained varied from approximately 4 cm to 20 cm per year. This result is important because numerous estimations of "annual" growth rate are obtained on the basis of data covering only three to four months of observations. It would explain the considerable variations in the growth rate estimated by us using the data for the years 1951 to 1959 published by Kawasaki (1955a, b - 1963). The Japanese tuna fisheries were very seasonal at that time. For an estimated mean growth rate of 15 cm to 16 cm per year for skipjack tuna which were initially 45 cm to 50 cm, the successive annual values ranged from 0 to 24 cm (see Table 9).

There is no question here of wanting to extrapolate the results for Tahiti to the entire assemblage of data available for the Pacific. Certainly, this limited geographical character is found within other fisheries (Hawaii; and New Zealand, for example) but fishing conditions there are very different. We simply wished to pose the general problem of the representativeness of samples which, insofar as it has not been broached, leaves a doubt hanging over the results obtained by the Petersen method.

IV. FORMULATION OF THE GROWTH RESULTS

A. General remarks on von Bertalanffy's model

The mathematical formulation most frequently used in growth studies is the von Bertalanffy model (1938). It proved convenient in population dynamics since it allowed ready integration of biological results into production models without too much tedious calculation (Beverton and Holt, 1957).

As Blanc and Laurec (1976) observe, "Another model may prove to be more efficient; thus in the case of the growth rates of juveniles, Gompertz's model is often preferable. Neither model is ever exhaustive in practice".

Today, where the use of computers enables us to escape the drudgery of tedious calculations, it is necessary to be fully aware of the limits and dangers of von Bertalanffy's model.

Too many biologists have acquired the habit of believing that where the results of their observations could be expressed in terms of mathematical formulae, these formulae remained valid beyond the limits of their observations. Numerous cases of extrapolation could be cited here in respect of growth. Knight (1968) was the first to emphasize the dangers of such extrapolations from von Bertalanffy's equation.

TABLE 9. Mode progressions taken from a study of Japanese data published for the western Pacific (Kawasaki, 1955a, b; 1963). For each year there appears:

- the month from which the mode progression can be established;
- the month in which the mode progression ends;
- the modal values (in cm) for the first and the last month;
- the estimation of growth rates expressed in cm per year ($\frac{\Delta l}{\Delta t}$)

Year Month	1951		1952		1953	1954	1955	1956	1957	1958		1959
J												
F												
M												
A												
M	45	47				43	44	46	49			
J			49	49						45	48	46
J					48							
A												
S												
O	55	55	54	52	54	51	53	53	52	45	52	50
$\frac{\Delta l}{\Delta t}$	24	19	15	9	24	19	22	17	7	0	16	12

$$l = L^{\infty} \left[1 - e^{-K(t-t_0)} \right]$$

The equation comprises three parameters L^{∞} , K , t_0 . It has become common practice to confuse L^{∞} with the maximum size of the organisms. Such a practice unfortunately is incorrect.

Take, for example, the observational data of Thompson (1948) for humans (Figure 6) and of Graham (1933) for codfish (Figure 7). "The cessation of growth being a well-known phenomenon in mammals it is hardly surprising to see that Belgians stop growing at around the age of 20 and that their maximum height lies slightly above 170 cm".

In the case of cod, the data enable us to see that there is a growth rate of approximately 14 cm per year, practically linear during the first three years with a slight curvature thereafter. But it is indeed difficult to know when growth has ended, or if it ends at all. It would be rash to state that the maximum size of the cod has the value $L^{\infty} = 132$ cm. Although the von Bertalanffy curve found gives a good fit for growth during the interval of observation, it is a mistake to assign a biological value to L^{∞} without any check being carried out to substantiate the matter (Knight, 1968).

It is, moreover, very easy to verify the dangers of extrapolation from Thompson's data. Let us suppose that only the data for growth for years 1 to 13 are available. In using Walford's method (1946) and Allen's procedure of least squares (1966), Knight (1968) found for the parameter L^{∞} the values 195 cm and 211 cm respectively.

The growth curves in both cases give a good fit for growth from years 0 to 13. Above the age of 13 the curve for growth is entirely different - a phenomenon well known to parents.

The danger of extrapolation becomes even greater when the various values of L^{∞} are used in comparative studies. One should never lose sight of the fact that the three parameters L^{∞} , K and t_0 are only simple mathematical supports to which one should not give *a priori* biological characters. These parameters are extremely sensitive to the sampling intervals and to the mathematical methods used to derive them: Walford's method (1946), that of Diaz (1966), of Tomlinson and Abramson (1961), of Abramson (1971), etc ...

"The method of least squares is the one in current use. It is well to remember that a few points markedly at variance with the model modify the result more certainly than a large number of points slightly at variance with it" (Blanc and Laurec, 1976).

In a study of the growth of the Atlantic yellowfin tuna, Le Guen (1973) has shown in numerous examples that for *identical observed growth rates* (allowing for errors of measurements) the mathematical transcription of the results could produce very considerable apparent differences if one confines oneself only to comparisons of the parameter L^{∞} , K and t_0 . This was particularly related to the problems of sampling and of mathematical methods:

- a) Different intervals of observation.
- b) More or less good comparability of the methods used entailing large confidence intervals for the estimation of the parameters. The confidence intervals of K and L^∞ to the limit 0.95 obtained by Diaz's method for the growth of yellowfin tuna in the Congo, for example, were the following:

$$0.0169 \leq K \leq 0.0729$$

(The unit of time being the month)

$$156.4 \leq L^\infty \leq 317.3 \text{ cm (Le Guen, 1973)}$$

Let us note that *within the intervals of observation* the estimations of $l = f(L^\infty, K, t_0)$ may be excellent and that as a result it is not von Bertalanffy's model that is called into question but rather its misinterpretation on the part of certain scientists.

"However well the von Bertalanffy curve may fit the code data, and in fact the fit is good, it is misleading to the reader to report any value for L^∞ at all, particularly if accompanied by an intimation that it represents the maximum size the fish can or does attain ... More important is the distorted point of view engendered by regarding L^∞ as a fact of nature rather than as a mathematical artifact of the data analysis" (Knight, 1968).

The comparison of different growth results should not, then, be made by direct comparison of the mathematical supports which are L^∞ , K and t_0 , but from the growth rates obtained in the intervals of observation whether or not one employs the formula:

$$L = L^\infty \left[1 - e^{-K(t-t_0)} \right]$$

With Blanc and Laurec (1976) we can say that "if the constraints of publication already force the research worker to structure his thoughts, the demands of the mathematical model lead him even more to be rigorous when formulating the problem or setting down his conclusions".

B. Mathematical formulation of growth rates obtained from tagging studies

Taking into account the unresolved doubts on the other methods we consider that the best method available at present for the study of the growth of skipjack tuna is that of tagging-recapture. This is all the more true because the previous objection, that the growth rates obtained by tagging recapture are slower than those obtained by the Petersen method, no longer holds true seeing that the scientific validity of the Petersen method is challenged. Moreover, Lewis (1976) has shown in Papua New Guinea that the growth ring counts in tuna of the same size, both tagged and untagged, gave virtually identical results. It would be desirable to widen the scope of these latter observations to obtain confirmation of this important finding.

Notwithstanding the foregoing reservations it is quite true that von Bertalanffy's formula remains very useful for the description of growth rates, particularly when they are based on tagging-recapture where direct comparisons are practically impossible with the data available.

The available data being inconclusive, the approach to the growth curve must be made in ignorance of age. The method most used has, until recent years, been that of instantaneous increments due to Diaz (1963) based on the formula: $\frac{d\ell}{dt} = K (L^\infty - \ell)$. It is difficult to accept that values $\frac{\Delta \ell}{\Delta t}$ and $\frac{d\ell}{dt}$ are comparable when the time that the skipjack have remained in the sea has been too long. Under these conditions it may be felt that one of the best approaches to growth rate to date has been made by Joseph and Calkins (1969) on the basis of 428 tagged fish, which had remained, on average, a short time in the sea.

Using two different mathematical treatments Joseph and Calkins (1969) found the following values for K and L^∞ :

- 1) K = 0.829 on an annual basis
 $L^\infty = 729$ mm
- 2) K = 0.431 on an annual basis
 $L^\infty = 881$ mm

Joseph and Calkins have also provided an estimation of the confidence intervals for their results, giving as the upper and lower limits the two pairs of values:

- 1) K = 0.43 - $L^\infty = 950$ mm
- 2) K = 1.39 - $L^\infty = 650$ mm

The progress achieved in research on the biology and ecology of skipjack tuna gives rise to the hope that it will soon be possible to envisage a conclusive approach to the estimation of the parameters: K, L^∞ and t_0 by assigning an age to the modal value of tagged skipjack for a group of fish of homogeneous size.

In the meantime we can make use of the first estimations of the age of young skipjack by Pannella's method. In Papua New Guinea, one-year-old skipjack were estimated to be approximately 40 to 45 cm long (Lewis, 1976). Legand's (1971) observations on the breeding period in the zone between New Caledonia and the Gilbert Islands show a very distinct maximum of the gonadosomatic indices from January to April. The first modes visible in the length frequency distributions established on the tuna boats of New Caledonia are 42 and 38 cm in the periods January-March in 1974 and 1975 (Loubens, 1976). That is also in agreement with the observations of Kishinouye (1924) who estimated that the growth rate of juvenile tuna was of the order of 4 cm per month. With K and L^∞ one can calculate t_0 knowing the age of the tuna for a given size.

In this paper our main purpose has been to compare the growth rates obtained in the Western and Eastern Pacific Ocean, without trying to estimate t_0 .

From recapture data for skipjack tuna which had remained at large from two to five months, we established the parameters K and L^∞ for Papua New Guinea fish and for those of the Eastern Pacific (IATTC area). To do so we looked for the best fit of our data to the model:

$$l_{t + \Delta t} = l_t e^{-K \Delta t} + L^\infty (1 - e^{-K \Delta t})$$

by the method of least squares (Abramson, programme BGC 4, 1971). The following results were obtained:

- 1) Papua New Guinea:
K = 0.9451 (annual basis)
L[∞] = 654.7 mm
- 2) Eastern Pacific (IATTC area):
K = 0.6371
L[∞] = 790.6 mm

The variability of the increments observed means that the results are not significantly different. Moreover in the interval of the observations (40 to 60 cm) the estimations of increments by von Bertalanffy's formula give very comparable results for Papua New Guinea and the Eastern Pacific, as the computer printouts presented in Table 10 show. The calculated growth rate is however slightly slower in the west than in the east.

CONCLUSIONS

This publication makes no claim to be exhaustive, seeking only to raise the problems connected with the use of different techniques for estimations of growth. The general impression which emerges, however, is in favour of intensive tagging-recapture of skipjack tuna which should lead to acceptable estimations of growth, provided that measurements were made with care. Moreover, the migration data obtained through tagging-recapture may be expected to result in a better understanding of the modal progression of the Petersen method. Lastly, the interpretation of daily marks on the otoliths should assist in establishing key age-lengths or at least key "age group"-lengths which are necessary for further work on population dynamics. These three techniques, closely associated, are likely to appreciably improve determination of skipjack age.

The subject of the representativeness of samples goes well beyond the scope of the present study. The degree of confidence assigned, for example, to analysis of the data used for calculations of production is directly related to the representativeness of the samples measured at the landing of catches by the tuna boats.

When the conversion of length classes to age classes can be made only on the basis of von Bertalanffy's formula for growth, the method of analysis of the data is already unreliable enough where confidence intervals for the estimations of K, L[∞] and t₀ are large. If, in addition, the length frequency distributions are not representative of the stock, the results of the various production and prediction calculations lose all credibility. A critical sampling threshold therefore needs to be determined, below which the level of sampling must not fall.

TABLE 10. Estimation of the parameters K and L_{∞} in the Eastern (IATTC) and Western Pacific (Papua New Guinea) zones from tagging data. Growths calculated by von Bertalanffy's formula for the intervals of observations.

Eastern Pacific

L_{∞} = 790.648 mm K = 0.637123 Number of increments used N = 87

Var (L_{∞}) = 204.551 Var (K) = 0.124922 Covar (L_{∞} , K) = -5.02030

Western Pacific

L_{∞} = 654.669 mm K = 0.945120 N = 83

Var (L_{∞}) = 24.1596 Var (K) = 0.249768 Covar (L_{∞} , K) = -2.37664

Growths calculated

=====

Δt (year)	<u>EASTERN PACIFIC</u>	<u>WESTERN PACIFIC</u>
	l (cm)	l (cm)
0	40.0	40.0
.1	42.4	42.3
.2	44.7	44.4
.3	46.8	46.3
.4	48.8	48.0
.5	50.7	49.6
.6	52.4	51.0
.7	54.1	52.3
.8	55.6	53.5
.9	57.0	54.6
1.0	58.4	55.6
1.1	59.7	56.5
1.2	60.9	57.3
1.3	62.0	58.0
1.4	63.1	58.7

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TABLE I. Skipjack recaptured within 10 days of tagging
(Papua New Guinea)

L_1 length measured to the nearest cm
 \overline{L}_1 length estimated from the modal value
 L_2 length measured to the nearest mm at recapture
 Δt number of days at liberty

L_1	\overline{L}_1	L_2	Δt	L_1	\overline{L}_1	L_2	Δt
58.0	54.5	57.0	2	53.0	54.4	55.0	2
54.0	54.8	53.0	7	53.0	54.2	58.0	5
57.0	56.3	57.5	9	56.0	54.6	54.0	2
55.0	56.5	57.0	3	52.0	54.6	54.5	8
52.0	53.6	53.2	8	55.0	54.6	52.0	4
53.0	54.1	53.0	7	54.0	54.5	55.0	3
54.0	55.2	56.0	3	55.0	54.8	55.0	8
51.0	55.4	54.0	5	51.0	54.8	53.0	8
55.0	56.7	54.5	2	57.0	54.8	62.0	10
54.0	55.9	53.0	5	58.0	-	60.0	10
53.0	52.6	55.0	7	56.0	56.6	59.2	5
55.0	55.6	57.8	6	55.0	55.9	55.0	10
50.0	52.6	49.0	5	55.0	55.9	55.0	2
54.0	52.6	58.0	3	55.0	55.9	57.0	3
56.0	52.3	56.0	7	58.0	55.9	57.5	5
55.0	56.4	54.5	6	48.0	52.8	48.5	10
57.0	54.5	52.0	7	55.0	52.8	55.0	0
56.0	55.8	56.0	3	52.0	52.8	51.9	9
57.0	56.8	56.5	8	49.0	52.8	49.0	7
60.0	56.8	58.0	6	53.0	52.8	50.0	10
61.0	57.6	61.0	9	55.0	52.8	50.0	10
54.0	-	54.0	6	55.0	56.5	56.0	7
54.0	55.7	54.0	0	56.0	56.5	57.0	9
57.0	52.8	58.5	0	57.0	57.4	59.0	9
-	56.0	61.0	10	57.0	54.5	57.0	3
-	54.6	55.0	2	57.0	54.3	58.2	10
-	52.0	54.0	3	63.0	59.5	62.0	10
52.0	52.6	56.0	5	51.0	50.1	52.0	6
53.0	52.6	51.0	3	55.0	54.5	56.0	4
52.0	52.6	52.0	3	55.0	54.5	56.0	10
52.0	52.6	56.0	3	49.0	56.2	47.0	8
53.0	52.6	55.0	2	53.0	-	55.0	6
53.0	52.6	53.6	3	58.0	-	58.0	10
53.0	52.6	54.0	3	59.0	-	59.0	4
54.0	54.4	56.2	2				
51.0	54.4	51.5	9				
56.0	54.4	57.0	4				
52.0	54.4	52.5	5				

TABLE II. Adjustments to be made between:

- 1) the lengths measured at time of tagging (L_1) and recapture (L_2) after ten days in Papua New Guinea;
- 2) the lengths estimated from the modal value (\bar{L}_1) and measured at recapture (L_2) after ten days in Papua New Guinea.

A - Regression of Y on X

1) $L_1 = Y, L_2 = X$

$n = 69$

$L_1 = 15.983 + 0.700 L_2 \quad r = 0.786$

$S_{yx} = 1.724$

$S_y = S_{yx} \sqrt{1 + \frac{1}{n} + \frac{x^2}{\sum x^2}}$

$S_y = 1.736$

Confidence interval for L_1 at the limit 0.10: ± 2.89

" " " 0.05: ± 3.46

2) $\bar{L}_1 = Y, L_2 = X$

$n = 67$

$\bar{L}_1 = 39.96 + 0.265 L_2 \quad r = 0.488$

$S_{yx} = 1.493$

$S_y = 1.504$

Confidence interval for \bar{L}_1 at the limit 0.10: ± 2.51

" " " 0.05: ± 3.00

TABLE II. (contd.)

B - Regression of X on Y

1) $L_1 = Y, L_2 = X$

$n = 69$

$L_2 = 6.946 + 0.883 L_1 \quad r = 0.786$

$S_{xy} = 1.937$

$S_x = 1.951$

Confidence interval for L_2 at the limit 0.10: ± 3.25

" " " 0.05: ± 3.89

2) $\overline{L_1} = Y, L_2 = X$

$n = 67$

$L_2 = 5.975 + 0.899 \overline{L_1} \quad r = 0.488$

$S_{xy} = 2.748$

$S_x = 2.768$

Confidence interval for L_2 at the limit 0.10: ± 4.61

" " " 0.05: ± 5.52

TABLE III. Data available for the Eastern Pacific (Joseph and Calkins, 1969)

L_1 : length (corrected) at tagging L_2 : length at recapture
 Δt : time at large in days Δl : increment

A - Fish which remained at large for 2 to 5 months

/ 40 \leq L_1 < 45 cm /

<u>L_1 (cm)</u>	<u>L_2 (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
43.7	49.0	77	5.3
	50.9	82	7.2
	46.2	94	2.5
	48.9	105	5.2
	49.9	140	6.2

/ 45 \leq L_1 < 50 cm /

47.0	54.1	68	7.1
	54.2	82	7.2
	50.1	88	3.1
	49.5	112	2.5
	53.8	116	6.8
	55.1	141	8.1
47.3	48.5	83	1.2
	54.4	120	7.1
49.3	48.0	65	1.3
	50.5	110	1.2
	50.8	110	1.5
	54.2	134	4.9
	56.5	137	7.2
	55.5	146	6.2

/ 50 \leq L_1 < 55 cm /

50.3	52.0	60	1.7
	56.3	61	6.0
	52.0	61	1.7
	54.2	61	3.9
	52.5	62	2.2
	51.8	64	1.5
	54.8	67	4.5
	54.8	67	4.5
	51.9	67	1.6
	56.5	70	6.2
	54.6	72	4.3
	49.4	73	-0.9
	56.3	78	6.0
	57.1	78	6.8
	52.5	78	2.2
	56.2	78	5.9
	57.2	79	6.9
	52.8	79	2.5
	56.4	79	6.1
	51.9	79	1.6

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
50.3	55.0	81	4.7
	49.3	89	-1.0
	57.0	90	6.7
	58.1	97	7.8
	58.9	99	8.6
	53.1	99	2.8
	57.2	101	6.9
	58.0	104	7.7
	58.4	110	8.1
	53.1	112	2.8
	59.6	128	9.3
	56.6	132	6.3
	56.2	137	5.9
	50.5	137	0.2
	54.9	139	4.6
	53.1	142	2.8
	56.0	146	5.7
	60.1	147	9.8
	60.0	148	9.7
	54.5	106	1.5
53.3	57.0	81	3.7
	58.8	61	5.2
53.6	56.3	61	2.7
	55.2	66	1.6
	56.2	67	2.6
	55.9	69	2.3
	55.0	69	1.4
	56.1	70	2.5
	56.9	72	3.3
	61.0	74	7.4
	58.3	77	4.7
	59.0	91	5.4
	57.0	95	3.4
	59.6	97	6.0
	55.4	99	1.8
	59.2	100	5.6
	61.2	103	7.6
	58.5	110	4.9
	57.0	123	3.4
	59.1	125	5.5
	53.4	143	-0.2
<u>/ 55 ≤ L₁ < 60 cm /</u>			
56.2	61.2	93	5.0
57.0	57.1	77	0.1
	59.1	77	2.1
	58.4	138	1.4
57.4	64.2	110	6.8
	64.1	130	6.7
<u>/ L₁ ≥ 60 cm /</u>			
60.3	62.6	117	2.3

B - Fish which remained at large for 5 to 12 months

/ 40 ≤ L₁ < 45 cm /

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
43.7	55.3	194	11.6

/ 45 ≤ L₁ < 50 cm /

47.0	57.4	208	10.4
	57.5	231	10.5
49.3	50.6	157	1.3
	50.4	158	1.1
	52.0	172	2.7
	58.0	185	8.7
	57.2	207	7.9

/ 50 ≤ L₁ < 55 cm /

50.3	51.9	151	1.6
	56.8	158	6.5
	51.8	174	1.5
	61	181	10.7
	61.5	191	11.2
	56.5	209	6.2
	62.9	218	12.6
	57.1	230	6.8
	57.0	242	6.7
53.6	57.1	173	3.5
	56.7	206	3.1
	65.7	235	12.1

/ 55 ≤ L₁ < 60 cm /

55.3	62.8	179	7.5
	64.8	162	7.8
	63.8	192	6.8

C - Fish which remained at large for more than 12 months

53.6	67.9	368	14.3
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TABLE IV. Tagging-recapture data for Hawaii (Rothschild, 1966)

L_1 : length at time of tagging L_2 : length at recapture
 Δt : time at large in days Δl : increment

A - Fish which remained at large for 5 to 12 months

/ 35 \leq L_1 < 40 cm /

<u>L_1 (cm)</u>	<u>L_2 (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
38.7	53.0	226	14.3

/ 40 \leq L_1 < 45 cm /

41.6	58.9	226	17.3
42.3	50.5	201	8.2
42.9	52.0	178	9.1
	51.6	178	8.7
43.4	61.0	183	17.6
43.9	62.5	198	18.6
44.7	66.0	324	21.3
	65.0	335	20.3
44.8	57.0	182	12.2
	54.5	204	9.7

/ 45 \leq L_1 < 50 cm /

45.3	56.3	180	11.0
	58.0	187	12.7
	58.0	189	12.7
	60.3	256	15.0
	61.4	312	16.1
	62.6	323	17.3
	64.0	358	18.7
45.8	58.7	171	12.9
	60.1	259	14.3
	61.1	260	15.3
46.3	52.2	181	5.9
	64.7	201	18.4
	62.6	308	16.3
	67.2	319	20.9
	62.4	321	16.1
46.6	60.6	175	14.0
46.7	53.1	174	6.4
49.5	63.3	191	13.8

/ 50 \leq L_1 < 55 cm /

52.0	56.6	197	4.6
52.3	66.2	252	13.9

/ 55 ≤ L₁ < 60 cm /

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
57.3	64.5	252	7.2

B - Fish which remained at large for more than 12 months

/ 40 ≤ L₁ < 45 cm /

44.77	70.5	420	25.8
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/ 45 ≤ L₁ < 50 cm /

46.3	66.9	377	20.6
	68.4	378	22.1

TABLE V. Tagging-recapture data for Papua New Guinea
(Present study)

L_1 : length of fish at time of tagging measured to the nearest cm

L_2 : length at recapture

Δt : time at large in days Δl : increment

A - Fish which remained at large for 2 to 5 months

/ 45 \leq L_1 < 50 cm /

<u>L_1 (cm)</u>	<u>L_2 (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
46.0	53.0	104	7
	48.0	97	2
49.0	51.0	88	2

/ 50 \leq L_1 < 55 cm /

51.0	49.0	70	-2
	53.4	144	2.4
	56.3	124	5.3
52.0	56.0	142	4
	53.0	94	1
	54.0	77	2
	54.0	72	2
	48.0	74	-4
	55.0	87	+3
	55.8	114	3.8
53.0	53.5	77	0.5
	56.0	141	3
	56.0	87	3
	55.0	73	2
	56.0	122	3
	55.5	127	2.5
54.0	56.0	69	2
	55.5	86	1.5
	59.0	89	5
	59.0	77	5
	56.0	70	2
	56.0	80	2
	58.0	70	4
	54.6	100	0.6
	54.0	65	0
	56.0	114	2

/ 55 \leq L_1 < 60 cm /

55.0	57.0	94	2
	58.0	85	3
	54.0	87	-1
	56.0	71	1

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
55.0	53.4	65	-1.6
	55.0	82	0
56.0	56.0	84	1
	57.0	97	1
	58.5	69	2.5
	57.6	67	1.6
	56.5	104	0.5
	57.0	93	1.0
	57.0	93	1.0
	55.0	71	-1
	56.0	150	0
	65.0	98	+9
57.0	59.0	128	+3
	57.0	139	+1
	59.0	81	+2
	59.0	67	+2
	58.0	100	+1
	64.0	96	+7
	58.5	67	1.5
	63.0	62	6
	63.0	103	6
	60.5	115	3.5
	58.0	78	1
	58.0	144	1
	57.0	70	0
58.0	58.0	76	0
	59.0	78	1
	59.0	66	1
	56.0	74	-2
	62.0	128	+4
	63.5	115	5.5
	59.0	66	3
59.0	59.0	67	0
	62.5	132	3.5
	59.0	69	0
<u>/ L₁ ≥ 60 cm /</u>			
63.0	65.0	101	+2
	64.0	118	+1
60.0	62.0	97	+2

B - Fish which remained in the sea for 5 to 12 months

/ 45 ≤ L₁ < 50 cm /

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
45.0	50.5	327	5.5
46.0	56.1	174	10.1
47.0	61.0	285	14.0
48.0	51.5	202	3.5
	56.0	244	6.0
49.0	56.0	206	7.0
	53.5	176	4.5

/ 50 ≤ L₁ < 55 cm /

50.0	58.0	272	8.0
	60.0	205	10.0
	55.0	278	5.0
	52.5	151	2.5
51.0	60.0	279	9.0
	52.0	203	1.0
	57.0	209	6.0
	55.4	177	4.4
	54.0	154	3.0
52.0	60.0	300	8.0
	55.5	173	3.5
	62.0	305	10.0
	54.5	280	2.5
	58.0	320	6.0
	54.0	211	2.0
	57.0	275	5.0
	55.0	342	3.0
	54.0	151	2.0
53.0	58.0	271	5.0
	60.8	180	7.8
	57.8	282	4.8
	61.0	236	8.0
	60.4	303	7.4
54.0	56.0	349	2.0
	56.0	212	2.0
	62.0	222	8.0

/ 55 ≤ L₁ < 60 cm /

55.0	60.0	365	5.0
	58.0	181	3.0
	59.0	186	4.0
	55.0	362	0.0
	58.0	152	3.0
	59.0	271	4.0

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
55.0	55.0	320	0.0
	58.0	158	3.0
	55.2	209	0.2
56.0	60.5	194	4.5
	59.0	294	3.0
	59.0	356	3.0
	57.0	170	1.0
	63.0	332	7.0
	55.0	249	-1.0
	60.0	259	4.0
57.0	58.0	333	1.0
	60.0	314	3.0
	64.0	269	7.0
	63.0	340	6.0
	59.0	297	2.0
	60.0	271	3.0
	61.0	282	4.0
	61.0	160	3.0
58.0	58.4	267	0.4
	62.0	208	4.0
	60.0	186	2.0
	60.5	365	2.5
	57.9	339	-0.1
	64.0	306	5.0
59.0	57.0	159	-2.0
	65.0	348	6.0
	59.0	214	0.0
<u>/ L₁ ≥ 60 cm /</u>			
60.0	62.0	274	2.0
	62.0	230	2.0
61.0	65.0	254	4.0
	60.0	336	-1.0

C - Fish which remained at large for more than 12 months

/ 40 ≤ L₁ < 45 cm /

<u>L₁ (cm)</u>	<u>L₂ (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
44.0	55.0	789	11

/ 45 ≤ L₁ < 50 cm /

46.0	53.0	389	7
49.0	52.0	390	3

/ 50 ≤ L₁ < 55 cm /

50.0	59.0	452	9
	58.0	483	8
51.0	57.0	434	6
	59.0	630	8
	60.0	607	9
52.0	58.3	533	6.3
	56.6	441	4.6
	59.0	425	7.0
	58.0	471	6.0
	61.5	578	9.5
53.0	58.0	376	5.0
	64.0	436	11.0
	58.0	514	5.0
54.0	64.0	413	10.0
	61.0	445	7.0

/ 55 ≤ L₁ < 60 cm /

55.0	67.0	393	12.0
	60.0	367	5.0
	62.0	375	7.0
56.0	63.0	394	7.0
	62.0	423	6.0
57.0	62.0	386	5.0
	57.3	386	0.3
	67.0	411	10.0
58.0	62.5	366	4.5
59.0	63.0	480	4.0

/ L₁ ≥ 60 cm /

60.0	64.0	401	4.0
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TABLE VI. Tagging-recapture data for Papua New Guinea
(Present study)

\bar{L}_1 : length of fish at time of tagging estimated from the modal value

L_2 : length of fish at recapture

Δt : time at large in days

Δl : increment

A - Fish which remained in the sea for 2 to 5 months

/ $45 \leq \bar{L}_1 < 50$ cm /

\bar{L}_1 (cm)	L_2 (cm)	Δt (days)	Δl (cm)
46.0	53.0	104	7.0
49.9	54.6	100	4.7
	57.0	139	7.1

/ $50 \leq \bar{L}_1 < 55$ cm /

50.1	53.6	113	3.5
51.4	53.4	144	2.0
51.5	54.0	77	2.5
	48.0	97	-3.5
	51.0	88	-0.5
51.7	56.0	142	4.3
51.9	55.0	78	3.1
52.3	56.0	141	3.7
52.6	54.0	72	1.4
	48.0	74	4.6
52.8	58.8	114	6.0
53.7	59.0	78	5.3
54.1	54.0	87	-0.1
	53.5	77	-0.6
54.1	59.0	77	4.9
	58.0	109	3.9
	57.0	127	2.9
	58.0	67	3.9
	60.5	77	6.4
54.2	58.0	146	3.8
	53.0	69	-1.2
	56.0	91	1.8
	54.0	77	-0.2
	56.0	122	1.8
54.3	60.0	130	5.7
	57.0	78	2.7
54.4	56.0	74	1.6
	54.0	126	-0.4
	56.0	87	1.6
	55.0	73	0.6
	55.0	87	0.6

\bar{L}_1 (cm)	L_2 (cm)	Δt (days)	Δl (cm)
54.4	54.0	65	-0.4
54.5	55.5	86	1.0
	56.0	150	1.5
	59.0	128	4.5
54.6	56.0	64	1.4
	56.0	62	1.4
54.7	53.4	65	-1.3
	58.5	110	3.8

/ 55 ≤ \bar{L}_1 < 60 cm /

55.2	58.5	69	3.3
55.4	64.0	121	8.6
55.5	59.0	67	3.5
55.5	56.3	124	0.8
55.7	59.0	66	3.3
55.9	56.5	104	0.6
55.9	56.0	70	0.1
	58.0	78	2.1
56.0	53.0	81	-3.0
	59.0	69	+3.0
	56.0	86	0.0
56.1	60.5	115	4.4
	55.0	71	-1.1
56.2	58.0	100	1.8
	60.5	139	4.3
56.3	56.0	71	-0.3
	49.0	70	-7.3
	56.0	84	-0.3
56.4	57.0	93	0.6
	56.0	114	-0.4
56.7	57.0	70	0.3
56.8	64.0	96	+7.2
57.0	65.0	98	+8.0
57.4	55.0	82	-2.4
	58.5	67	1.1
	63.0	62	5.6
57.5	63.0	103	5.5
	62.5	132	5.0
57.6	57.6	67	0.0
	62.0	66	4.4
58.0	57.0	97	-1.0
	59.0	69	+1.0
	59.0	89	+1.0
	58.0	85	0.0
	62.0	97	+4.0
58.2	58.0	76	-0.2
	59.0	67	+0.8
	57.0	93	-1.2
	60.0	65	+1.8
59.5	57.0	94	-2.5
59.9	65.0	101	5.1

/ $\bar{L}_1 \geq 60$ cm /

<u>\bar{L}_1 (cm)</u>	<u>L_2 (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
60.1	64.0	118	+3.9
60.3	62.0	128	+1.7
	58.0	144	-2.3

B - Fish which remained at large for 5 to 12 months

/ $40 \leq \bar{L}_1 < 45$ /

41.7	50.5	327	8.8
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/ $45 \leq \bar{L}_1 < 50$ cm /

46.5	61.0	285	14.5
48.8	56.1	174	7.3
49.2	56.0	244	6.8

/ $50 \leq \bar{L}_1 < 55$ cm /

50.4	57.0	282	6.6
50.7	60.0	205	9.3
	51.5	202	0.8
	55.5	173	4.8
51.0	54.0	211	3.0
	60.8	180	9.8
	56.0	349	5.0
51.3	56.5	168	5.2
51.4	57.0	209	5.6
	53.5	176	2.1
	57.0	275	5.6
51.5	54.5	280	4.0
51.6	55.0	278	3.4
51.7	56.0	206	4.3
	58.0	272	6.3
52.2	57.8	282	5.6
	59.0	297	6.8
52.3	60.0	279	7.7
	58.0	271	5.7
52.5	52.0	203	-0.5
52.6	60.0	300	7.4
	62.0	305	9.4
	57.0	170	4.4
52.8	59.0	283	6.2
	63.0	332	10.2

\bar{L}_1 (cm)	L_2 (cm)	Δt (days)	Δl (cm)
52.8	54.0	151	1.2
53.0	56.0	212	3.0
53.2	61.0	236	7.8
	60.4	303	7.2
53.6	59.0	294	5.4
54.3	57.0	189	2.7
54.4	61.0	282	6.6
54.5	55.0	342	0.5
	52.5	151	-2.0
54.6	51.0	255	-3.6
	62.0	284	7.4
	60.0	285	5.4
	57.0	324	2.4
	63.0	316	8.4
	63.0	257	8.4
	59.5	303	4.9
	59.5	314	4.9
	58.0	320	3.4
54.7	61.0	173	6.3
	61.0	301	6.3
	59.0	227	4.3
	58.0	274	3.3
	58.0	302	3.3
	58.5	300	3.8
	60.0	285	5.3
	53.5	239	-1.2
	61.0	300	6.3

/ $55 \leq \bar{L}_1 < 60$ cm /

55.0	58.0	333	3.0
	60.0	259	5.0
55.2	60.5	365	5.3
55.3	55.4	177	0.1
	60.0	168	4.7
55.4	63.0	304	7.6
	67.0	304	11.6
	55.3	195	-0.1
	61.0	303	5.6
	63.0	289	7.6
	60.0	287	4.6
	60.0	278	4.6
	59.0	358	3.6
	58.2	235	2.8
	60.0	282	4.6
	59.0	262	3.6
	60.0	324	4.6
	61.0	332	5.6
	62.0	330	6.6
	60.0	276	4.6
	61.0	232	5.6

\bar{L}_1 (cm)	L_2 (cm)	Δt (days)	Δl (cm)
55.5	63.0	301	7.5
	63.0	294	7.5
	61.0	293	5.5
	59.0	305	3.5
	58.9	184	3.4
	54.2	237	-1.3
	61.0	267	5.5
	60.0	307	4.5
	61.0	258	5.5
	60.0	273	4.5
	59.0	276	3.5
	55.2	209	-0.3
	61.0	301	5.5
	60.0	308	4.5
55.8	60.2	281	4.4
	60.2	276	4.4
	58.0	341	2.2
	63.0	310	7.2
	60.0	272	4.2
	63.0	359	7.2
55.9	61.0	160	5.1
	59.0	356	3.1
	60.0	280	4.1
	54.4	180	-1.5
	61.0	276	5.1
	61.0	323	5.1
	61.5	240	5.6
	64.0	269	8.1
	65.0	348	9.1
	60.0	314	4.1
	57.9	339	2.0
60.0	63.0	340	7.1
	53.3	175	-2.7
	61.0	265	5.0
	60.0	256	4.0
	62.0	243	6.0
	59.0	324	3.0
	61.0	240	5.0
	61.0	240	5.0
56.1	60.0	365	3.9
	59.0	284	2.9
	58.5	287	2.4
	58.0	192	1.9
	63.0	273	6.9
	62.0	272	5.9
	59.0	261	2.9
56.2	61.0	296	4.8
	60.5	320	4.3
	59.3	281	3.1
	59.0	263	2.8
	57.0	323	0.8
	65.0	361	8.8
	61.5	257	5.3

\bar{L}_1 (cm)	L_2 (cm)	Δt (days)	Δl (cm)
56.3	63.0	314	6.7
	60.5	313	4.2
	61.0	309	4.7
	57.0	180	0.7
	57.0	260	0.7
	61.0	256	4.7
	59.5	281	3.2
	61.0	268	4.7
56.4	62.0	281	5.6
	60.0	285	3.6
	57.8	273	1.4
56.5	66.0	250	9.6
	61.0	297	4.5
	61.0	262	4.5
	61.5	258	5.0
	61.5	315	5.0
	60.0	269	3.5
	58.0	181	1.5
	65.0	254	8.5
56.7	59.0	186	2.5
	58.4	267	1.7
	55.0	249	-1.7
	55.0	362	-1.7
	60.0	186	3.3
	60.0	271	3.3
	58.0	152	1.3
	59.0	271	2.3
57.1	60.0	327	2.9
	60.0	359	2.9
	57.0	286	-0.1
57.5	55.0	320	-2.5
57.6	58.0	158	0.4
	62.0	230	4.4
58.0	64.0	306	6.0
58.2	60.5	194	2.3
	62.0	304	3.8
	65.5	287	7.3

/ $\bar{L}_1 \geq 60$ cm /

60.0	55.1	230	-4.9
60.3	62.0	208	1.7
	59.0	214	-1.3
	60.0	336	-0.3
60.7	62.0	274	1.3

C - Fish which remained in the sea for more than 12 months

/ 45 ≤ \bar{L}_1 < 50 cm /

\bar{L}_1 (cm)	L_2 (cm)	Δt (days)	Δl (cm)
47.0	55.0	789	8.0
48.3	58.3	533	10.0

/ 50 ≤ \bar{L}_1 < 55 cm /

50.1	53.0	389	2.9
50.3	61.0	765	10.7
51.0	60.0	607	9.0
51.4	52.0	390	0.6
	67.0	393	15.6
	56.6	441	5.2
51.5	57.0	434	5.5
	59.0	452	7.5
51.7	59.0	630	7.3
52.3	58.0	483	5.7
52.5	59.0	425	6.5
	60.0	439	7.5
	63.0	441	10.5
	61.5	578	9.0
52.6	63.0	394	10.4
	64.0	413	11.4
	64.0	436	11.4
	61.0	445	8.4
	58.0	471	5.4
	58.0	514	5.4
52.8	62.0	423	9.2
	58.0	501	5.2
	61.0	577	8.2
53.1	61.0	665	7.9
53.9	61.0	449	7.1
54.1	61.0	393	6.9
	59.0	395	4.9
54.2	61.0	400	6.8
	47.0	408	-7.2
	62.0	455	7.8
54.4	58.0	376	3.6
54.5	57.0	438	2.5
54.6	62.0	420	7.4
	63.0	425	8.4
	61.0	622	6.4
54.7	60.0	367	5.3
	59.6	506	4.9
	63.0	539	8.3

/ $55 \leq \bar{L}_1 < 60$ cm /

<u>\bar{L}_1 (cm)</u>	<u>L_2 (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
55.3	62.0	375	6.7
55.4	59.0	570	3.6
	61.5	649	6.1
55.5	58.0	489	2.5
55.8	63.0	555	7.2
55.9	67.0	411	11.1
56.0	63.0	442	7.0
56.2	62.0	564	5.8
	62.0	686	5.8
	65.0	512	8.8
56.5	62.0	497	5.5
	65.0	607	8.5
57.2	57.3	386	0.1
57.6	62.5	386	4.9
58.0	62.5	366	4.5
58.5	63.0	480	4.5

/ $\bar{L}_1 \geq 60$ cm /

60.1	64.0	401	3.9
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TABLE VII. Tagging-recapture data from the Atlantic (ORSTOM, 1976)

L_1 : length of the fish measured to the nearest cm at tagging-release

L_2 : length of the fish at recapture

Δt : time at large in days

Δl : increment

A - Fish which remained at large for 2 to 5 months

<u>L_1 (cm)</u>	<u>L_2 (cm)</u>	<u>Δt (days)</u>	<u>Δl (cm)</u>
44.0	56.0	149	12.0
46.0	56.0	145	10.0
53.0	60.0	71	7.0
54.0	56.0	81	2.0
54.0	54.0	93	0
57.0	60.0	71	3.0
58.0	62.0	86	4.0

B - Fish which remained at large for 5 to 12 months

44.0	55.0	222	11.0
46.0	55.0	168	9.0
50.0	60.0	304	10.0
58.0	58.0	166	0.0

- The Tahiti measurements were made to the nearest cm with a tape measure giving the contour length (LR). The collected measurements are assembled in Table I. A conversion table for converting contour length (LR) to fork-length (LF) and to weight in kilogrammes is given in Table II. The author of the conversion table (Bessineton, 1976) notes that the number N of fish of 40 cm fork-length is obtained by taking the mean of the numbers of fish N' and N'' having contour lengths (LR) of 42 and 43 cm.

$$N_{40} = \frac{N' + N''}{2}$$

42 43

And also:

$$N_{59} = \frac{N' + N''}{2}$$

62 63

$$N_{78} = \frac{N' + N''}{2}$$

82 83

- Measurements from the Atlantic (Tables III and IV) are of fork-lengths (LF) to the nearest 2 cm.

For the Atlantic the proportion of fish in each length group is shown as a percentage, the total number of measurements appearing at the bottom of the table. The data have been grouped by quarters.

TABLE I. Monthly measurements at Papeete, Tahiti

1 9 7 3

LR cm	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	TOTAL
32							1						1
3										3			3
4							2		8	18			28
5							1			5			6
6							4		6	56			66
7							5			8			13
8							12		42	65	10		129
9							2	1	1	7	1		12
40							27	27	29	62	1		146
1							10	20	41	36	4	1	112
2							5	18	43	49	14	1	130
3							10	22	42	60	18	4	156
4							6	23	49	70	18	4	170
5							18	33	74	116	16	24	281
6							7	14	37	99	16	52	225
7							7	37	97	163	16	69	389
8							5	6	47	90	4	61	213
9							10	30	68	147	12	26	293
50							5	15	69	107	8	8	212
1							5	14	82	180	22	16	319
2							6	46	91	137	35	33	348
3							3	39	89	216	25	43	415
4							5	21	60	255	22	38	401
5							7	22	79	335	82	37	562
6							2	38	46	116	136	58	396
7							12	16	83	166	165	107	549
8							2	2	3	106	131	120	363
9							8	6	26	57	112	87	296
60							5	1		28	101	55	190
1							1	3		32	90	18	144
2							4	2		32	49	3	90
3							2	2			18	2	24
4							3	3	6	2	9	3	26
5							1		3		2	3	9
6							6		21	7	1	4	39
7									3			3	7
8							6	3	15			3	27
9									8			2	10
70							1		7			1	9
1									10				10
2							3						3
3							2		5				7
4							1	3	16				20
5							3		17				20
6							7	5	17			1	30
7								2	13			1	16
8							5	1	20			2	28
9							5	3	12			2	22
80							16	2	6				24
1								1					1
2								3					3
3													
4													
5													
6								1					1
7													
8													
9													
90													
1													
							258	485	1391	2830	1139	892	6994

1 9 7 4

LR cm	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	TOTAL
32													19
3					19								30
4					30								28
5					28								70
6					54							16	174
7					72	3				43		56	237
8					66	5			7	75	12	63	218
9					50	4			6	103	25	49	378
40			7	7	27	16		2	9	74	13	63	438
1		1	32	30	46	21		8	10	89	28	113	451
2	1	2	65	89	47	48		5	14	116	24	27	448
3	2	1	71	63	28	46		11	29	72	28	100	541
4	3	4	100	46	24	42		14	39	88	30	58	607
5	3	5	127	34	34	67	5	20	47	108	22	69	865
6	1	21	126	65	37	85	5	39	57	66	26	79	772
7	4	51	184	90	44	119	10	24	55	79	51	154	727
8	4	76	153	84	49	109	8	23	55	92	58	61	604
9	9	82	100	78	42	77	5	32	57	64	66	115	612
50	11	83	82	76	30	71	5	26	60	49	75	36	605
1	21	99	48	85	8	96	19	16	55	47	71	45	513
2	27	139	22	113	2	68	13	16	65	28	65	47	425
3	24	90	9	83	18	38	19	25	72	44	56	35	370
4	25	58	9	42	30	20	25	29	70	37	63	17	379
5	39	47	6	5	24	15	19	49	47	16	54	49	506
6	76	63	13		20	11	38	64	44	12	38		399
7	157	79	15		19	7	48	80	45	8	28	20	409
8	120	45	14		13	4	42	83	49	3	15	11	345
9	83	27	5		17	6	89	77	66	11	16	12	403
60	74	14			12	5	55	75	74	5	18	13	318
1	131	14					77	58	79	11	26	7	223
2	82	2					67	42	83	7	11	24	162
3	37	1					29	19	76	17	29	15	110
4	19						15	16	54	8	22	28	66
5	4						14	5	41	9	37		42
6	1						8		25	11	21		14
7	1								8		33		13
8		1							5		8		9
9									4		10		7
70									8		5		9
1									2		7		7
2					1				1		7		12
3					6				1				17
4			1		9				2				32
5			4		5				5				31
6		3	4		7								32
7		12	13		9								31
8		6	16		9								32
9		8	7		10							7	33
80		4	5		17							7	15
1		4	2		3							6	5
2		4	1										2
3		2											
4													
5													
6													
7													
8													
9													
90													
1													
	961	1048	1237	990	957	983	615	858	1426	1392	1098	1402	12967

1 9 7 5

LR cm	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	TOTAL
32													
3													
4													
5									4				4
6	55								3				58
7	46								13				59
8	91	18	7						22	19			157
9	35	27	13						27	27	31		160
40	114	59	21					27	39	47	52		359
1	127	47	36					14	41	47	69		381
2	78	47	44						43	68	67		347
3	96	50	40						47	62	84		379
4	32	43	26					1	48	51	76	10	287
5	64	49	29		7		16	6	36	34	71	10	322
6	33	48	43	4	15	1	16	5	37	26	37	12	277
7	71	60	53	12	22	1	12	20	36	20	25	10	342
8	36	50	46	19	24	1	9	15	14	6	33	19	272
9	41	41	45	40	53	19	11	19	12	4	24	22	331
50		46	40	49	68	30		9	4		14	10	270
1	8	51	31	60	83	44					9	8	294
2		33	7	56	91	59					10	10	266
3		28		61	83	71	3				12	9	267
4	1	9		48	83	101	7					9	258
5	3	10		30	67	78	8						196
6	9	5		27	76	94	4						215
7	5			10	37	83						13	148
8	3			3	31	55						11	103
9	28			30	15	51						19	143
60	48	36	13	71	4	18					10	43	243
1	29	50	12	72						9	33	65	270
2	68	53	10	75		9				32	36	76	359
3	45	53	4	80	3	16			10	111	33	63	418
4	28	57	6	72	19	18		6	9	103	46	67	431
5	9	41	3	46	41	18			12	121	39	55	385
6	9	12		12	39	16		25	15	116	12	31	287
7	12	11		8	33	18		21	8	94	12	12	229
8				7	36	9		42	7	74	9		184
9					29	10		3	4	46	8		100
70					27			1	3	14			45
1					4			6	7	11			28
2					3								3
3													
4	10							15					25
5	10		12					30					52
6	10	8	11					30					59
7	17	23	34			1		7					82
8	26	18	69	25		7		9					154
9	34	18	64	29		9				3	10		167
80	13	18	76	26		17				5	8		168
1	12		53	30		19	4			4	13		135
2			15	28		19	4			4	15		85
3			9			10	3				12		34
4						7					10		17
5						1							1
6						1							1
7													
8													
9													
90													
1						1							1
	1356	1119	872	1030	993	912	102	311	501	1158	920	584	9858

1 9 7 6

LR cm	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	TOTAL
32													
3													
4													
5													
6													
7								4					4
8					9			17					26
9	10		11	10	12			17	16				76
40	65	11	11	21	21			28	21				178
1	85	12	12	22	24			27	20				202
2	134	22	11	33	44			36	20				300
3	141	46	34	34	55	7		34	26				377
4	142	67	46	46	67	11	9	33	28				449
5	119	76	88	67	83	22	12	27	46			41	581
6	77	80	86	90	77	41	17	34	44	14		70	630
7	41	104	113	107	82	75	51	44	63	45	8	113	846
8	22	105	114	122	99	92	47	39	66	58	19	137	920
9	10	97	126	126	89	153	44	42	90	94	35	154	1060
50		71	92	121	90	146	48	46	87	128	48	165	1042
1		47	93	101	84	135	46	42	101	137	59	167	1012
2		34	90	101	89	115	46	24	101	142	73	171	986
3		35	56	80	79	88	43	24	85	146	90	111	837
4		21	35	58	69	55	46	24	77	139	87	91	702
5		21	11	46	47	43	36	9	65	118	86	46	528
6		22	9	21	20	33	25		51	85	70	28	364
7		24		10	11	21	22		41	49	62	10	250
8		23	11			10	21		19	18	31		133
9		23	11	41		11	12		9	11	33		151
60		11	20	45	11		41	33	8		15		184
1	22	23	54	57	22	12	74	65	13		18		360
2	45	34	70	56	34	35	96	75	34		35	9	523
3	44	34	79	58	35	46	90	79	47	11	39	10	572
4	42	34	80	56	41	46	72	55	41	20	46	11	544
5	46	36	69	58	32	45	56	33	45	24	51	10	505
6	42	35	56	33	33	23	23	20	36	27	43	11	382
7	11	34	48	11	35	24		16	36	31	52	11	309
8		17	11	11	35	16		12	29	25	51	9	216
9			12		23	11		2	21	14	19	9	111
70			11		20	12			5	11	13		72
1					12					8	10		30
2											9		9
3													
4													
5		12											12
6		22									9		31
7		34	10								11		55
8		35	11								9		55
9		35	12								8		55
80		23	11								18		52
1		23	12								24		59
2		22	11								28		61
3			11								33	8	52
4			9								44	8	61
5											35	11	46
6											37	21	58
7											43	25	68
8											35	23	58
9											28	23	51
90											17	10	27
1													
	1098	1405	1657	1642	1484	1328	977	941	1391	1355	1481	1513	16272

1 9 7 7

LR cm	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	TOTAL
32													
3													
4													
5													
6													
7		10							9				19
8		21	9						10				40
9		27	19	9	10				20				85
40		52	21	36	11				43				163
1		73	40	40	9	14	11		45	6			238
2		68	39	41	19	34	9	11	62	13			296
3		78	63	41	31	65	11	20	80	24		22	435
4		104	94	51	39	94	16	30	109	41	42	78	698
5		85	89	52	50	102	9	50	146	83	56	132	854
6	8	68	70	59	68	122	11	66	166	94	118	140	990
7	47	59	56	42	63	133	29	101	147	136	134	139	1086
8	78	39	59	38	65	142	40	111	172	128	170	132	1174
9	108	31	44	48	85	121	57	115	157	127	179	113	1185
50	128	25	41	52	70	104	59	116	143	123	181	99	1142
1	149	43	16	40	63	95	52	80	98	117	156	82	991
2	147	29	20	39	48	71	49	73	68	97	153	46	840
3	175	22	17	29	40	50	31	57	50	87	111	30	699
4	158	22	11	21	21	20	20	26	29	57	93	9	487
5	120	19	10	17	19	21	21	20	19	49	51	7	372
6	91	21	11	8	9	11	10	9		30	20		220
7	71	20	11							20	5		127
8	50	15	9							9			83
9	23					7							30
60		10			8	10	9						37
1		18	10		27	11	20						86
2	20	41	11		26	10	27						135
3	19	37	11	10	36	11	44						168
4	20	43	9	31	41	10	48						202
5	20	42	11	41	52	9	52						227
6	22	42	10	51	48		38						211
7	20	35	9	49	62		16						191
8	20	31	9	53	50								163
9	19	17		34	41								111
70	15	15	7	40	40								87
1			11	41	28								80
2			10	26	19								55
3			11	22	11								44
4			11	11	9								31
5			9	8									17
6			11	10									21
7			10	20									30
8				22									22
9				19									19
80				24								11	35
1		9		28							9	10	46
2	10	11	20	25	7								83
3	10	9	44	20	11								94
4	11	11	59	25	11								117
5	10	10	65	18	10								113
6	11	11	58	11	10								101
7	10	10	63	11	3								97
8		9	48	10									67
9			52	11									63
90			38	9									47
1													
	1575	1328	1356	1343	1270	1267	689	885	1573	1241	1469	1059	15055

TABLE II. Conversion table
LR - LF - weight drawn up
by Bessineton (1976)

LF in cm	LR in cm	Weight in kg
35	37	
36	38	0.7
37	39	0.8
38	40	0.8
39	41	0.9
40	42	1.0
40	43	-
41	44	1.1
42	45	1.2
43	46	1.2
44	47	1.3
45	48	1.4
46	49	1.5
47	50	1.6
48	51	1.8
49	52	1.9
50	53	2.0
51	54	2.2
52	55	2.3
53	56	2.5
54	57	2.6
55	58	2.8
56	59	3.0
57	60	3.2
58	61	3.4
59	62	3.6
59	63	-
60	64	3.8
61	65	4.0
62	66	4.3
63	67	4.5
64	68	4.8
65	69	5.0
66	70	5.3
67	71	5.6
68	72	6.0
69	73	6.3
70	74	6.6
71	75	6.9
72	76	7.3
73	77	7.6
77	78	8.0
75	79	8.3
76	80	8.7
77	81	9.1
78	82	9.5
78	83	-
79	84	9.9
80	85	10.3
81	86	10.7
82	87	11.2
83	88	11.6
84	89	12.0
85	90	12.5

ANNOBON REGION - ATLANTIC (SOUTH)

TABLE III. Frequency distribution of fork lengths (LF) in cm, with proportion in each length group shown as a percentage per quarter (1968 - 1975)

LF cm	1/68	2/68	3/68	4/68	1/69	2/69	3/69	4/69
31	0.07			0.05			0.15	0.17
3	-			-			0.04	0.28
5	-	0.24		0.10			0.11	0.68
7	1.09	0.32	0.04	0.31			0.11	0.23
9	1.46	0.57	0.08	0.84		0.35	0.57	1.08
41	6.12	2.83	0.36	1.52		0.35	1.51	1.25
3	9.18	3.31	1.78	2.47	0.16	0.70	4.46	1.36
5	10.12	8.41	7.84	3.41	1.27	2.10	6.65	2.38
7	18.72	13.02	19.17	8.66	3.02	3.86	9.71	4.76
9	18.21	18.43	19.61	12.18	38.35	8.77	14.28	12.41
51	9.91	14.07	9.90	14.43	36.35	11.22	15.22	15.01
3	10.05	16.25	11.28	14.75	15.24	15.08	18.47	22.78
5	7.36	10.91	9.70	14.33	3.65	28.07	14.13	22.44
7	2.26	4.68	7.08	10.71	0.63	14.73	7.14	6.68
9	2.33	4.04	5.78	7.14	0.79	9.82	4.42	4.02
61	1.46	1.29	4.25	3.83	0.31	4.21	2.53	2.77
3	0.58	1.13	1.13	2.15	-	0.35	0.45	1.08
5	0.66	0.32	0.52	1.52	0.16	0.35	0.04	0.22
7	0.15		0.32	0.94	0.18			0.28
9	0.22	0.16	0.08	0.31				0.06
71	0.07		0.04	0.10				-
3			0.93	0.05				0.06
5			0.08	0.16				
Total number measured	1373	1237	2473	1905	630	285	2647	1765

TABLE III. (contd)

LF cm	1/73	2/73	3/73	4/73	1/74	2/74	3/74	4/74	1/75	2/75	3/75	4/75
31		0.43	0.03					0.04		0.07	0.08	0.14
3		1.14	0.24					0.25		-	0.28	0.19
5		5.32	0.71		0.07	0.44	0.10	1.40	0.25	-	0.54	1.28
7		5.85	1.65	4.35	0.28	0.85	0.47	3.33	1.02	1.88	0.90	2.94
9	2.97	7.46	4.21	9.14	1.41	3.11	2.03	4.92	3.32	4.37	2.28	7.50
41	11.49	10.02	9.33	22.94	4.37	7.26	5.53	9.01	9.72	7.92	6.11	9.94
3	32.05	13.59	14.32	25.55	22.88	12.42	9.32	13.97	15.68	10.21	10.96	15.83
5	25.64	13.22	13.75	17.45	36.16	24.11	15.20	13.92	19.80	11.28	15.76	17.15
7	11.82	9.84	11.12	11.25	17.31	18.62	19.57	15.00	12.69	11.55	11.65	13.00
9	9.50	10.90	10.18	6.16	6.63	12.81	17.66	12.23	7.55	10.61	12.37	8.64
51	4.88	6.59	10.48	0.47	2.91	6.66	13.19	8.83	7.85	10.48	12.42	4.85
3	0.84	4.81	6.91	0.50	2.63	2.43	6.47	8.87	11.32	9.27	9.06	5.33
5	0.70	3.28	9.06	0.97	3.52	2.92	4.26	5.88	9.04	6.58	6.85	5.31
7	0.08	2.35	4.51	0.47	1.09	2.18	1.78	1.17	1.15	2.35	3.05	2.53
9	0.03	1.64	1.48	0.20	0.46	2.51	1.58	0.57	0.22	2.28	3.00	1.83
61		1.56	1.18	0.17	0.20	1.53	0.92	0.21	0.22	2.41	2.08	1.13
3		1.16	0.74	0.20	0.04	0.93	1.00	0.12	0.16	2.22	1.28	0.55
5		0.53	0.10	0.17	0.02	0.54	0.53	0.02	-	3.09	0.72	0.43
7		0.26				0.22	0.12	0.25	-	2.42	0.62	0.70
9		0.05				0.11	0.14	-	-	0.81	-	0.55
71						0.11	0.14	-	-	0.20	-	0.07
3						0.03	0.02	0.02	-	-	-	-
5						0.19	-	-	-	-	-	0.07
Total number measured	3569	3781	2968	2986	5396	3662	5119	5648	3641	1489	3897	4145

CAPE VERDE REGION - ATLANTIC (NORTH)

TABLE IV. Frequency distribution of fork lengths (LF) in cm.
 Proportion in each length group shown as a percentage
 per quarter (1968 - 1975)

LF cm	1968				1969				1970				1971			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
31																
3				0.10				0.06				0.04				
5				0.63				0.61			0.26	0.26				
7			2.10	3.07			2.04	3.05		0.09	1.18	2.19	0.27	2.31	0.08	0.39
9			2.58	6.13			2.52	6.09		1.52	3.48	7.61	0.82	3.47	2.54	2.35
41			7.40	8.66			7.39	8.64	1.85	3.92	10.36	10.70	1.37	8.38	15.56	8.23
3			19.85	13.57	2.14	2.27	19.81	13.57	6.17	11.32	24.91	13.24	1.09	13.72	22.63	15.12
5	0.76	0.01	20.44	18.10	7.49	7.53	20.44	18.11	11.73	13.64	23.86	17.33	2.19	12.86	15.37	18.51
7	0.76	0.01	12.26	15.71	16.04	16.19	12.26	15.73	23.46	15.24	11.60	12.90	8.74	13.58	8.90	11.07
9	7.85	0.08	9.15	11.72	18.18	18.04	9.12	11.74	17.28	15.86	7.02	11.70	23.50	17.20	9.20	9.27
51	23.29	23.30	7.85	7.15	17.64	17.61	7.86	7.15	7.41	15.95	4.98	12.99	31.42	11.99	12.72	9.20
3	34.68	34.67	7.32	3.35	14.97	14.77	7.39	3.38	4.32	13.90	6.49	7.35	19.67	8.67	9.45	10.75
5	26.08	26.02	7.32	4.86	15.50	15.76	7.39	4.86	7.41	7.04	4.59	3.44	10.38	6.21	3.41	11.82
7	6.58	0.07	2.37	3.70	5.35	5.11	2.36	2.22	5.56	0.89	0.59	0.17	0.27	1.45	0.14	2.66
9			1.08	2.19	2.14	1.99	1.10	0.94	6.17	0.36			0.27	0.15		0.55
61			0.16	0.92	0.53	0.43	0.16	0.06	5.56	0.18		0.04				0.04
3			0.16	0.10			0.14	0.16								0.02
5							0.14		0.62							
Total Nb. of skipjack measured	395	1099	1859	2055	187	704	636	1805	162	1121	1525	2325	366	692	3663	5067

TABLE IV. (contd)

LF cm	1 9 7 2				1 9 7 3				1 9 7 4				1 9 7 5			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
31		0.13	0.40			0.05					0.16					
3							0.07	0.50	0.14							
5		0.27	0.98	0.18		0.36		0.75	1.28				1.16			
7	0.34	1.35	4.88	2.38		0.41	0.51	3.75	7.41	0.22		0.46	2.31		0.26	
9	2.87	4.71	2.84	6.68		1.94	2.99	9.04	12.13	0.74	0.45	1.50	2.31		1.23	1.08
41	3.72	8.88	14.96	8.35		4.51	10.08	16.54	31.38	2.54	2.16	8.75	8.75	0.11	3.66	4.28
3	12.16	7.67	23.22	5.48	4.20	10.20	16.03	24.08	31.09	5.53	5.47	13.66	5.20	2.87	9.33	4.82
5	13.51	9.69	0.09	8.68	11.89	15.43	19.46	18.79	8.84	12.05	11.18	19.95	20.23	6.56	23.28	9.64
7	15.88	15.75	1.95	8.33	13.29	14.89	6.49	9.04	4.71	12.57	12.33	22.69	16.18	8.40	20.85	17.70
9	10.98	20.72	19.49	11.00	15.38	15.83	8.06	4.00	1.85	19.86	9.55	12.55	16.18	12.47	11.90	23.06
51	14.19	17.22	3.46	12.83	10.49	12.18	10.49	4.50	0.29	24.22	15.88	7.00	7.51	17.78	8.92	17.70
3	13.01	9.28	13.63	17.25	16.08	9.61	11.56	6.26	0.57	15.74	21.60	3.90	7.51	18.48	8.26	8.56
5	10.47	3.63	10.83	14.93	22.38	7.85	10.70	2.50	0.14	5.38	19.30	6.12	8.67	13.44	8.38	3.74
7	2.03	0.27	2.93	2.73	6.29	3.29	3.08	0.25	0.14	0.92	1.60	2.05	2.31	11.92	2.72	1.08
9	0.84	0.27	0.27	1.28		3.02	0.42			0.22	0.20	0.73	5.20	7.97	0.80	
61		0.13	0.04	0.06		0.41	0.07				0.09	0.17	5.20	0.70	0.40	
3												0.31			0.15	
5																
Total nb. of skipjack measured	592	743	2252	5089	143	2216	4516	3597	701	2713	6930	4055	173	1845	4235	2406

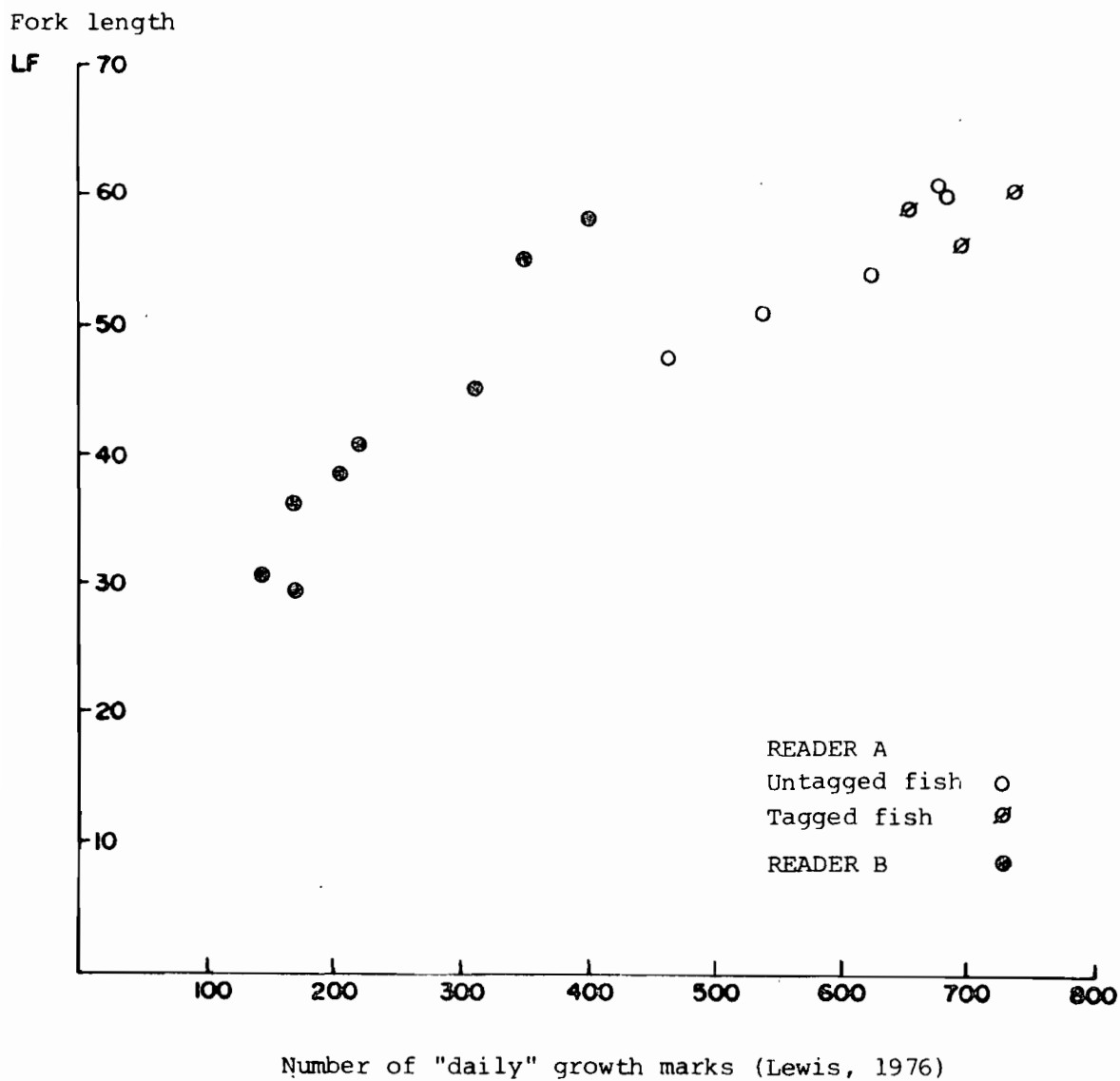
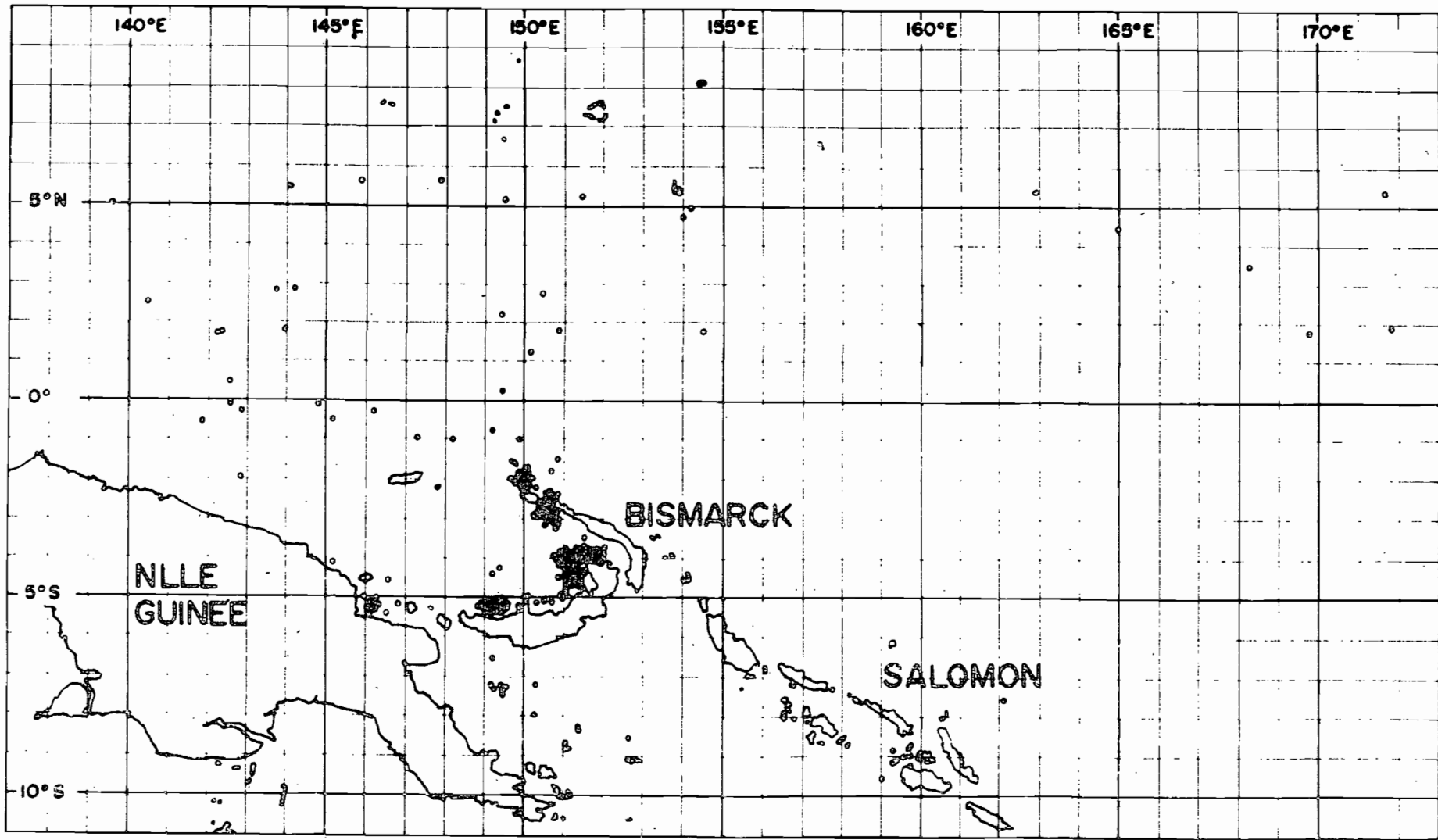


Fig. 1 - Results of counting daily growth marks on the otoliths of skipjack in Papua New Guinea by two "readers".



Recapture points of tagged skipjack tuna in Papua New Guinea 1972-1974 (from Lewis, 1976)

Fig. 2

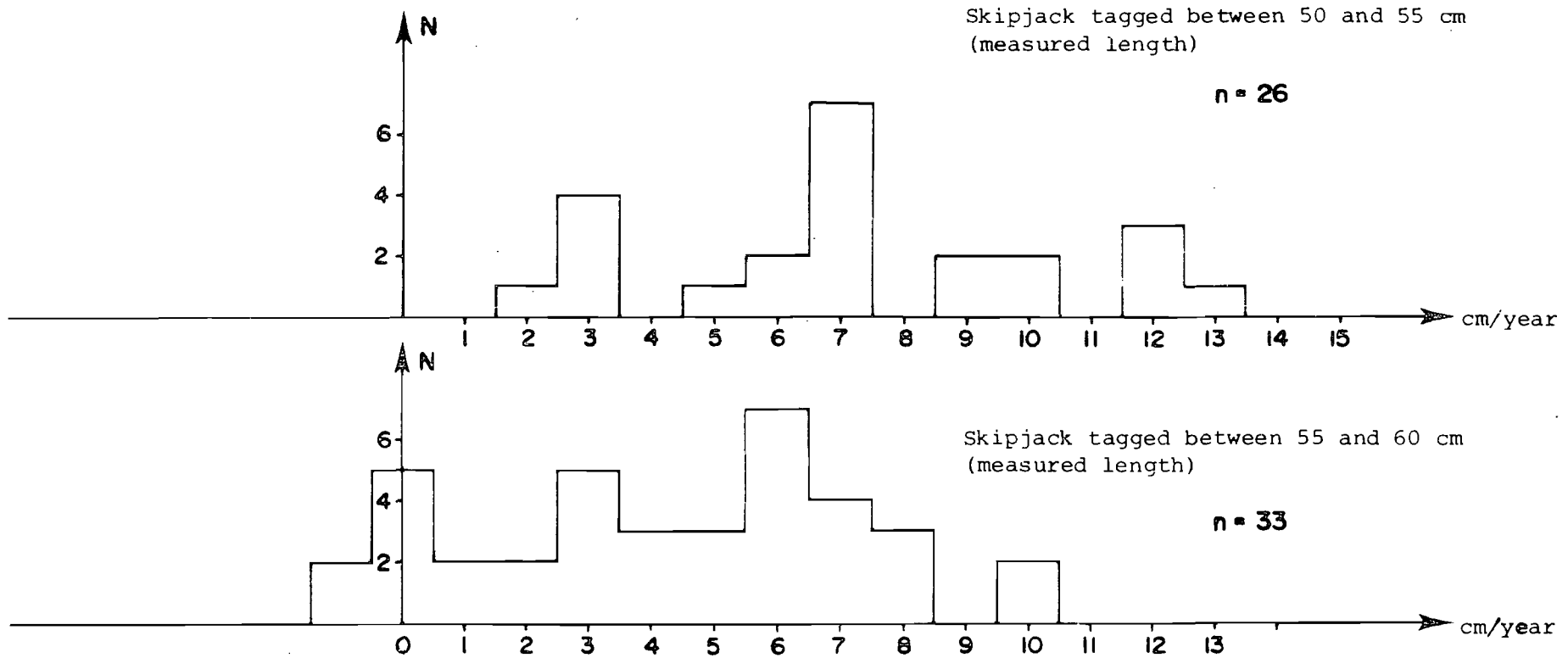


Fig. 3 - Frequency distributions of annual increments $\frac{\Delta l}{\Delta t}$ expressed in cm for skipjack tuna tagged

in Papua New Guinea and at large for 5 to 12 months.

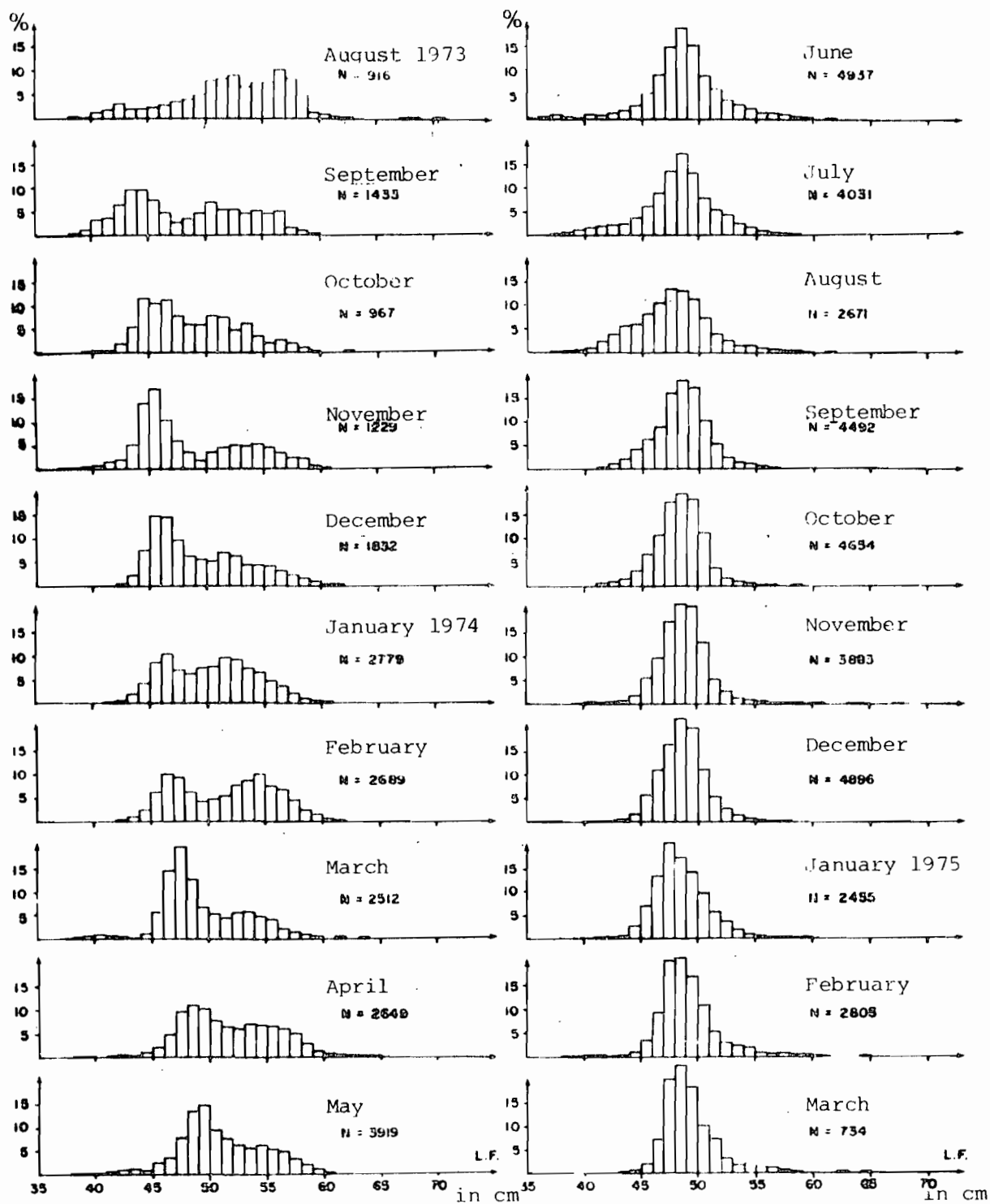


Fig. 4 - Monthly histograms of skipjack size frequencies - Nosybe (Madagascar), Indian Ocean. (Marcille and Stequert, 1976)

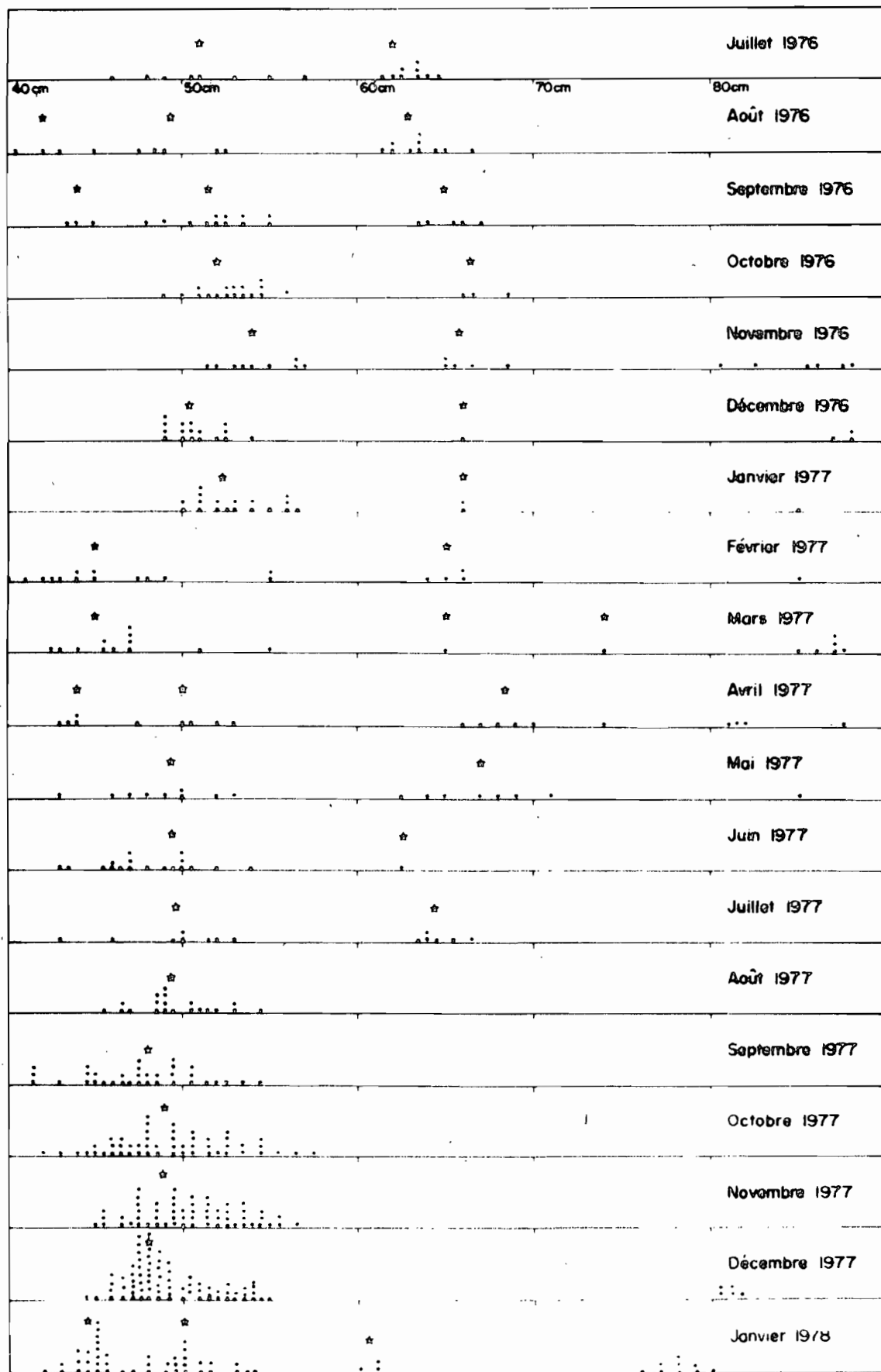


Fig. 5 - Points represent the modal values obtained for each landing sampled. Asterisks represent the position of the modal values obtained for the whole of the measurements made in one month.

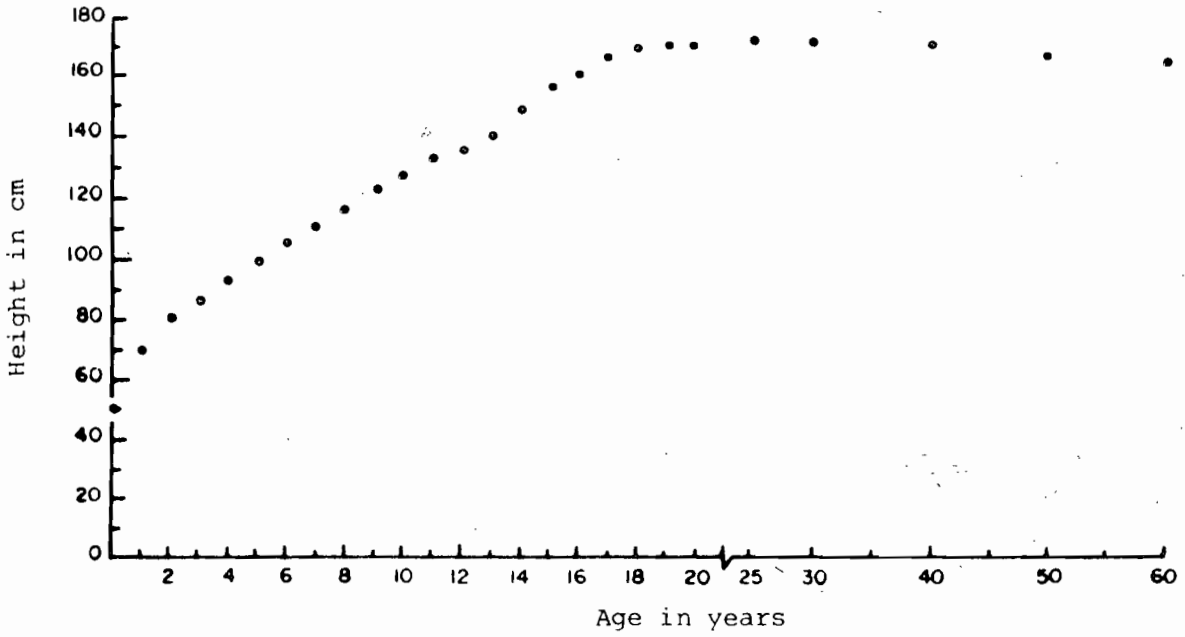


Fig. 6 - Growth of Belgians (men). Thompson (1948)

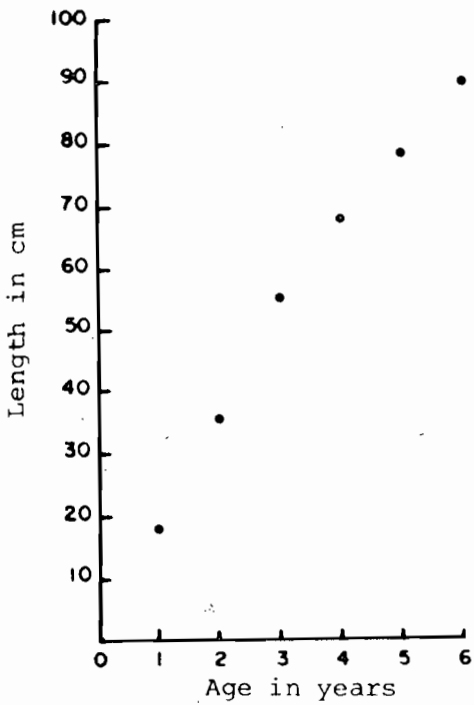


Fig. 7 - Growth of cod.
Graham (1933)

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