

STUDY OF THE GROWTH OF YELLOWFIN TUNA (*THUNNUS ALBACARES*) IN THE WESTERN INDIAN OCEAN BASED ON LENGTH FREQUENCY DATA.

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ABSTRACT

Several studies have been made on age and growth of yellowfin tuna from the three oceans. The main techniques used have been length frequency analysis, tagging experiments and direct ageing from the calcified structures. However, few studies have been made in the Indian Ocean and results are still open to debate. It is not clear if yellowfin tuna follows a classical Von Bertalanffy model or a two step growth pattern with a low rate in the young ages and a sudden increase in the intermediate ages, leading to a common growth trend that can be described by the Von Bertalanffy growth curve. The marked seasonality of gonad index (GI) in the Indian Ocean explains the existence of yearly cohorts and allows following the modal progressions of these cohorts in the fishery. This analysis is based on length frequency samples mainly from purse seiners (PS) operating in the western Indian Ocean and also from Oman and Iran drifting gillnets. Considering the difficulty to fit correctly the younger and older stages of a same cohort because of a lack of data between 70 and 90 cm FL, each cohort was followed under 2 hypotheses, (a) using only PS data and (b) using also sizes taken in Oman and Iran data. In both methods, growths appear to follow a two stanzas growth pattern. Growth rates results are significantly different considering the two methods. Taking into account only the PS data, results are quite similar to those obtained in previous length frequency analysis (Marsac and Lablache, 1985; Marsac, 1991). The addition of Omani and Iranian data are leading to slower growth rates which are well-matching with others studies based on calcified structures reading (Stéquert *et al.*, 1995) and from tagging experiments (Yesaki and Waheed, 1992).

These two models are in competition and it is quite difficult to determine which can be the more realistic one even if the migratory based model seems to fit more properly others techniques results. Moreover, this model is based on a migration route of yellowfin from Seychelles to Arabian sea areas which has to be confirmed.

INTRODUCTION

Yellowfin tuna, *Thunnus albacares*, is one of the most valuable of tropical tunas. In the Indian Ocean, the amount of landings reveals yellowfin being in second in importance in term of weight of catch only to skipjack (*Katsuwonus pelamis*). Despite this economic value, there are still lacks of knowledge about yellowfin biology, notably about its growth.

Several studies have been conducted on the age and growth of yellowfin tuna in the tropical oceans, but only a few age and growth studies have been conducted in the Indian Ocean, and the results are still open to debate.

There are presently two main hypotheses concerning yellowfin tuna growth:

- The first one, based on the analysis of length frequency distributions (Marcille and Stequert, 1976; Anderson, 1988) or seasonal growth marks on calcified structures (Huang *et al.*, 1973) suggests that growth follows a Von Bertalanffy model (Von Bertalanffy, 1938) with growth rates between 2.9 and 3.4 cm per month for individuals between 60 and 70 cm.
- The second growth model, also based on length frequency analysis, suggests a two growth stanzas model in which a slow period occurs for young fish (1.5 cm per month for fork length [LF] below 60 cm) followed by a faster period for larger fish with FL upper

than 60 cm (Marsac and Lablache, 1985; Marsac, 1991). Similar two stanzas models are presently obtained and used in the Atlantic and in the eastern and western Pacific.

The present study is based on length data analysis and its main goal is a revision of yellowfin tuna growth pattern in the Indian Ocean, based on a longer data series than previous length frequency analysis (Marsac and Lablache, 1985 ; Marsac, 1991) and new data from Oman and Iran drifting gillnets.

MATERIALS AND METHODS

Source of data

The data used in this study came mainly from the international purse seine fleet operating in the Western Indian Ocean. The size data used are the raw size data of the samples processed without strata substitution or extrapolation. One important point is to notice that all small yellowfin have been measured in fork length (sizes smaller than about 80cm). On the opposite, large yellowfin have been measured in predorsal length and later converted in fork length. In this conversion, each class of predorsal length is converted into a normal distribution of fork length based on the observed variability of fork length in each class of predorsal length. This conversion tend to introduce a smoothing in the subsequent fork length distribution. The importance of these catches shows that the samples analysed

are well representative of the PS landing. The temporal spectra of these data extends from 1983 to 2001, but only data from 1987 have been analysed. Its range of sizes extends from 30 to 180 cm FL. Nevertheless, considering the difficulty to distinct the modes of the older cohorts which are grouped, only the sizes smaller than 144 cm FL have been analysed. It comprises a part of the size range exploited by the artisanal fishery (smaller fish) and by the longline fishery (bigger fish). Therefore, these samples represent the bulk of yellowfin sizes exploited in the Indian Ocean.

In order to complete previous data, monthly sizes of catches from Oman and Iran drifting gillnets have been taken into account. The size spectra of Oman and Iran data respectively extends from 1987 to 1994 and from April 2000 to March 2001.

All data were collected on a monthly basis.

Method of analysis

Most gonad analyses conducted on yellowfin tuna in the Indian Ocean show one protracted spawning season of intense sexual activity in the period November to February (IPTP, 1992). Those studies, based on the simultaneous observation of the macroscopic characters of gonads, of the diameter of oocytes and the evaluation of gonad index permit to distinguish different phases in the sexual cycle of yellowfin tuna that is, maturation of gonad from October to December and spawning from December to April. A secondary reproductive period may also exist in July-August in the eastern part of the Indian Ocean between the Seychelles and the Chagos Islands (Hassani and Stéquert, 1991). Such results allows to distinguish a clearly modal distribution of fishes population beyond its recruitment about 35 cm FL.

In order to follow modal evolution of population cohorts, the data have been analysed on a monthly basis which gives a good picture of the progression of the modes. The length frequency samples of purse seiners from 1989 to 2001 were weighted to the quantity of the species in question in the fish tank. Other data were not weighted. Data of all the zones covered by the seiners have been merged for this analysis.

The separation of the modes from the length frequency data was carried out using the Bhattacharya method (1967).

RESULTS

Modal progression

The evolution of the sizes class of the modes such identified can be followed from the successive histograms for the time scale examined. The time evolution of the different modes identified in the analysis can be followed, showing the modal progression and therefore the apparent growth of the different length groups constituting the population (Fig.1).

According to the relative difficulty to fit correctly the younger and older stages of a same cohort because of a lack of data between 70 and 90 cm FL, determination of the yearly cohorts are difficult. In fact, there are two ways to

discriminate population cohorts (a) when only PS data are used or (b) when Oman and Iran sizes are added (Fig.2).

The growth patterns of the identified cohorts were compared on the basis of a birth in December or in January. The early recruits at about 35 cm FL, taken in May and June, would represent a cohort born in the very beginning of the year. (Fig. 3)

Whatever the way selected to discriminate the population cohorts, previous superposition show similar distributions of yearly cohorts. However, several major observations can be made :

There is an inter-annual variability in the modes positions,

The growth pattern seems to follow a two growth stanzas model in which a slow period occurs for young fish until about 60 cm, followed by a fast growth from this same length.

These results suggest a two stanzas growth pattern like all previous length frequency analysis. Nevertheless, considering the way analysed, growth rate results are significantly different.

Growth models

Several growth models have been developed and fitted to the apparent modal progression in order to describe the relationship between fish size and age. Among the most used models, five of them (Von Bertalanffy (1938), Von Bertalanffy generalized (Pauly, 1979), Gompertz (1935, *in* Ricker, 1975), Richards (1959) and Gascuel (1992)) were tested. The selected candidate models were chosen because of their shape of the desired curve (with two stanzas) and biological assumptions upon which they are derived. The equations of these models are summarized in Table 1.

Estimation of the growth parameters

Because of a growth pattern following a two stanzas model, it will be improper to fit a growth curve using the von Bertalanffy model on all the length range, bearing in mind that the growth of the yellowfin is in two phases. L_{∞} and K will therefore be estimated from the length groups having a slower growth rate (*i.e.* those above 60 cm FL). According to the specific progression applied there, no biological meaning can be given to the parameter t_0 .

Other models will be fitted on the whole length range.

The estimation of the parameters were calculated using a Newton regression procedure and are summarized in Table 2.

Growth models corresponding to these parameters are shown on figure 4.

Models adjustment

Results of the models adjustment are different considering the data used in the analysed.

In the first case, taking into account only the PS data, the adjustment of each model shows high correlation coefficient (Table 2,a). Nevertheless, analysis of residuals after fitting the models shows particular trend of underestimation of smallest fork length and overestimation beyond 50 to 100

cm FL, except for the composite model. This five parameters composite model is the only one that fit correctly the whole data.

The equation of the selected best model is also :

$$FL_t = 37 + 12.t + [136.34 - (37 + 12.t)] \cdot [1 - \exp(-2.25.t)]^{137.46}$$

In the second case, considering the addition of Omanese and Iranese data to the PS data, the adjustment of each model shows an high correlation coefficient (Table 2,b). The residuals analysis results in a best distribution, centered around zero and without trend, for two models which best fit the data: Richards and Gascuel models (Fig. 5).

Taking into account the equivalent fitting of the two selected models, preference can be given to the more parsimonious (i.e. the model that fits data acceptably with the fewest number of parameters). The Akaike information criterion (AIC) has been used to determine the most parsimonious model because of the two models are not hierarchical (Akaike, 1973). AIC results suggest Richards model as the most parsimonious [$AIC_{Richards} (4.51) < AIC_{Gascuel} (6.31)$].

Nevertheless, the Gascuel composite model is considered as a better one than the Richards four parameters model, because it appears to be more realistic according to its slower decrease of the growth rates in the older studied age. Moreover, it allows an easier comparison with the other PS data set results.

The equation of the selected best model is also:

$$FL_t = 34.8 + 15.3.t + [152.1 - (34.8 + 15.3.t)] \cdot [1 - \exp(-0.84.t)]^{17.76}$$

Growth rates

In order to compare with previous studies, monthly growth rates have been estimated in several size intervals from the selected models (Table 2).

DISCUSSION

The results obtained with the two different data set seems to confirm the hypothesis of a differential growth between small and large yellowfin, with an acceleration of growth above 60 cm FL, like suggested in previous studies based on length frequency analysis.

However, several factors and bias could affect the growth rate estimated in the present study. The growth curves resulting from length frequency analyses are affected by a combination of uncertainties from recruitment process, mortality, sampling and biases in sizes due to the gear selectivity, etc. This potential bias includes the selectivity of the gear and the limited number of individuals sampled in certain months of Oman and Iran data. However the main source of uncertainty is probably the subjectivity involved in the process of separating the modes (Bhattacharya method) and linking them. In the larger length groups, the spread of modes observed may sometimes be due to differing growth rates between males and females.

Considering the data of Oman and Iran gillnets catches, the evolution of the sizes class of the modes identified can be clearly followed from the successive histograms for the time scale examined and appears to be quite similar to those obtained from PS fishery. Gillnet selectivity seems to not

affect significantly A consistent apparent modal progression is visible in the Omanese monthly catches, and this fact do suggest that the selectivity of the fishing gear, the gillnets, is not a introducing a major bias. Moreover, the size extent and the time scale of these data match with PS data. In this context, the hypothesis of a yearly migration of juvenile and pre-adult yellowfin between the western and the north western part of the Indian Ocean seems to be interesting.

Additional information obtained from tagging may also be useful in order to distinguish between the two previous growth models. Limited tagging experiments on tropical tunas could indicate that stocks exploited in the western part of the Indian Ocean belong to a single stock (Cayré and Rancharrun, 1990). However, few reports suggest a northward movement of yellowfin tuna off Comoros Islands migratory route (Cayré and Rancharrun, 1990 ; Sivasubramaniam, 1970) and a seasonal movements of intermediate size yellowfin in the northern Arabian sea (Losse, 1970 ; Imad, 1987). Sizes taken by the Omanese and Iranese gillnets fisheries are then particularly interesting, notably because of their intermediate length frequency, sizes which are missing in the other fisheries and areas.

The growth rates found by various authors in and outside the Indian Ocean are summarised in table 4.

Previous studies based on length frequency analysis suggest a two stanzas growth model with an initial slow rate of young recruits at about 1,3 cm.month⁻¹ (Marsac and Lablache, 1985 ; Anderson, 1988 ; Marsac, 1991; Firoozi and Carrara, 1992). Such results are equivalent to those obtained with the two hypothesis models of this study. Considering the fast growth rate of older stage, results are quite different. The fast growth rate of 4.8 cm.month⁻¹ obtained with the PS data seems to be a bit high comparatively to other studies (higher growth rates obtained are respectively 4.0 and 3.9 cm.month⁻¹ in Marsac, 1991 and Firoozi and Carrara, 1992). Results obtained with the migration hypothesis show a fast growth rate of 2.5 cm.month⁻¹ which matches with the growth rate obtained on female in Firoozi and Carrara, 1992 and the lowest growth rate obtained by Yesaki, 1991.

Comparatively and using methods based on otolith microstructure, growth rates beyond 65 cm FL of the migration hypothesis model are relatively similar to those obtained in previous studies in Pacific Ocean (Uchiyama and Strushaker, 1981 ; Wild, 1986) and Indian Ocean (Stéquert *et al.*, 1995). Considering Indian Ocean results, the mean difference also concerns the estimation of absolute age (Fig.6). This can be explained by a possible underestimation of the absolute age of older fishes due to the difficulty to read the micro-increments of otoliths. In the opposite, results are obviously dissimilar for younger fishes and particularly about growth rates increment. As a result, the two methods are providing results which are in contradiction concerning the general growth pattern. This growth patterns divergence seems to be due to an unknown bias in one of the methods used in the growth and age studies.

Biological and physiological considerations can be used in order to infirm or to validate the two stanzas growth pattern.

It has been observed that larger individuals have a relatively lower metabolic rate than small individuals. For yellowfin tuna in particular, the development of the gas bladder likely reduces drastically the energy requirement which is required to swim. Yellowfin tuna has a gas bladder which grows allometrically, becoming progressively larger as the fish increases. Until it attains about 50-60 cm, the fish has no gas in the bladder. After this size, their weights in water increase more slowly than their lifting areas and “large yellowfin can swim at slower speeds even in a absolute units ($\text{cm}\cdot\text{s}^{-1}$)” (Magnuson, 1973). Moreover, the development of the gas bladder associated with the increase in size also corresponds to a change in behaviour (the fish moving deeper) and consequently in an extension of the habitat with potentially different biotic and abiotic conditions (Lehodey and Leroy, 1999).

Other techniques based on calcified structures such as reading age of spines, vertebrae and scales of yellowfin tuna in the Indian Ocean do not help in determining which model is the most valuable. Vertebrae reading suggests a growth rate of about 1.1 to 2.9 $\text{cm}\cdot\text{month}^{-1}$ (Romanov and Korotkova, 1988) according to the migration hypothesis, while scale reading gave a higher growth rate of about 3.4 $\text{cm}\cdot\text{month}^{-1}$ (Huang et al., 1973) which match better with the PS data analysis.

Tagging offers another independent means of estimating growth rates. Nevertheless, few tagging experiments have been conducted on yellowfin in the area. In a tagging experiment carried out in the south-west of Seychelles Islands and in the Mozambique channel (Cayré and Ramcharrun, 1990), three individuals (FL = 67, 73 and 67 cm) were recaptured after a liberty at sea of 252, 411 and 613 days. Their mean growth rate was of 2.3 $\text{cm}\cdot\text{month}^{-1}$. Another interesting experiment was carried out in the

Maldives with more recoveries (69 individuals > 30 liberty days) (Yesaki and Waheed, 1992). Using PLOTREC software (Fonteneau and Nordstrom, 2000) in order to plot the apparent growth of recovered fishes of the two previous tagging experiments in association with the theoretical growth curves obtained with length frequency analysis suggests a better fit with the migration hypothesis growth curve (Fig.7).

CONCLUSION

This study based on length frequency analysis shows the difficulty of such analysis, due to the difficulty to identify and to follow over time the modes in the size distributions. Nevertheless, the present analysis suggest a two stanzas growth model with a slow growth rate (1.0 to 1.3 $\text{cm}\cdot\text{month}^{-1}$) up to around 60 cm FL, followed by a more rapid growth. Growth rates beyond 60 cm FL are more subjects to uncertainty and debate in a range between 2.5 to 4.8 $\text{cm}\cdot\text{month}^{-1}$. Effectively, similar results can be found in previous studies based on different methods for each model.

Moreover, the migration hypothesis of yellowfin tuna in the western and north western parts of the Indian Ocean has to be confirmed in order to valid the slower growth rate model. In this way, it should be necessary to valid the main hypothesis of a migratory route from Seychelles to Arabian sea areas by tagging experiments. Calcified structures studies and mainly tagging experiments in the Indian Ocean will be required to obtain a fully validated growth curves covering all the sizes and ages taken by the fisheries, which is unlikely to be resolved by further length frequency studies. This uncertainty is probably worst for large fishes taken at sizes at which the modes can never be identified nor followed.

REFERENCES

- ANDERSON, R.C., 1988. Growth and migration of juvenile yellowfin tuna (*Thunnus albacares*) in the central Indian Ocean. *Coll. Vol. Work Doc.*, IPTP, TWS/88/21 : 28-39.
- BERTALANFFY, L. VON., 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.*, 10 (2) : 181-213.
- BHATTACHARYA, C.G., 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics.*, 23 : 115-135.
- CAYRÉ, P. AND RANCHARRUN, B., 1990. Results of the tagging operations conducted within the Regional Tuna Project (Indian Ocean Commission) in 1988 and 1989. *FAO/IPTP/TRW/90/61* : 63-85.
- FIROOZI, A. AND CARRARA, G., 1992. An analysis of length-frequencies of *Thunnus albacares* in Iranian waters. *Coll. Vol. Work Doc.*, IPTP, TWS/92 : 95-102.
- FONTENEAU, A., unpublished. A comparative study of yellowfin tuna in the eastern Pacific and in the eastern Atlantic. IATTC. Internal report 22, 71p.
- FONTENEAU, A. AND NORDSTROM, V., 2000. PLOTREC, a graphic software for plotting the apparent growth of recovered fishes in association with theoretical growth curves. WPTT-00-21
- GASCUEL, D., FONTENEAU, A., CAPISANO, C., 1992. Modélisation d'une croissance en deux stances chez l'albacore (*Thunnus albacares*). *Aquat. Living Resour.*, 1992, 5 : 155-172
- HASSANI, S. AND STÉQUERT, B., 1991. Sexual maturity, spawning and fecundity of the yellowfin tuna (*Thunnus albacares*) of the western Indian Ocean. *Coll. Vol. Work Doc.*, IPTP, TWS/90/68 : 91-107.
- HUANG, C.C., SUN, L., YANG, R.T., 1973. Age, growth and population structure of Indian yellowfin tuna. *J. Fish. Soc. Taiwan* 2 : 16-30.
- IMAD, A., 1987. Some observations on the tuna fishery of Pakistan. *Work. Pap. Presented at IPTP Workshop on Small Tunas, Seerfish and Billfish*. Dec. 1987. Colombo.
- LEHODEY, P. AND LEROY, B., 1999. Age and growth of yellowfin tuna (*Thunnus albacares*) from the western and central Pacific Ocean as indicated by daily growth increments and tagging data. *SCTB12, 16-23 June 1999, Tahiti, Work. Pap. YFT-2*, 21p.
- LOOSE, G.F., 1970. The tuna fishery of the Gulf of Aden. Fishery Survey of Somalia. *Tech. Rep.* 1. Fao, Rome
- MARCILLE, J. AND STÉQUERT, B., 1976. Etude préliminaire de la croissance du listao (*Katsuwonus pelamis*) dans l'ouest de l'océan Indien. *Cah. ORSTOM (Sér. Océanogr.)*, 14 (2) : 139-151
- MARSAC, F. AND LABLACHE, G., 1985. Preliminary study of the growth of yellowfin estimated from purse seine data in the Western Indian Ocean. *Coll. Vol. Work Doc.*, IPTP, TWS/85/22 : 91-110.
- MARSAC F., 1991. Growth of Indian Ocean Yellowfin Tuna estimated from size frequencies data collected on french purse seiners. *Coll. Vol. Work Doc.*, IPTP, TWS/91/17 : 35-39.
- PAULY, D., 1979. Gill size and temperature as governing factors in fish growth : a generalization of Von Bertalanffy's growth formula. *Ber. Inst. Meeresk. Christian-Albrechts Univ. Kiel.*, 63 : 156 p.
- RICHARDS, F.J., 1959. A flexible growth function for empirical use. *J. Exp. Bot.*, 10 : 290-300.
- RICKER W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, 191 : 382p.
- ROMANOV, E.V. AND KOROTKOVA, L.P., 1988. Age and growth rates of yellowfin tuna *Thunnus albacares* (Bonaterre 1788)(Pisces, Scombridae) in the north-western part of the Indian Ocean, determined by counting the rings of vertebrae. *Coll. Vol. Work Doc.*, IPTP, TWS/88/38 : 68-73.
- SIVASUBRAMANIAM, K., 1970. Surface and subsurface fisheries for young and immature yellowfin tuna (*Thunnus albacares*) around Ceylon. *Bull. Fish. Res. Stn. Ceylon* 21 : 113-122.
- STÉQUERT, B., PANFILI, J., DEAN, J.M., 1995. Age and growth of yellowfin tuna, *Thunnus albacares*, from the western Indian Ocean, based on otolith microstructure. *Fish. Bull.* 94 : 124-134.
- UCHIYAMA, J.H. AND STRUHSACKER, P., 1981. Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. *Fish. Bull.*, 79 : 151-162.
- WILD, A., 1986. Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. *IATTC Bull.* 18 (6) : 423-482.
- YAMANAKA, S.H., 1990. Age growth and spawning of yellowfin tuna in the southern Philippines. *Coll. Vol. Work Doc.*, IPTP, TWS/90/21 : 1-87
- YESAKI, M., 1991. Population parameter estimates of Indian Ocean yellowfin tuna based on length data. *Coll. Vol. Work Doc.*, IPTP, TWS/91
- YESAKI, M. AND WAHEED, A., 1992. Results of the tuna tagging program conducted in the Maldives during 1990. *FAO/IPTP/92/WP/24* : 18p.

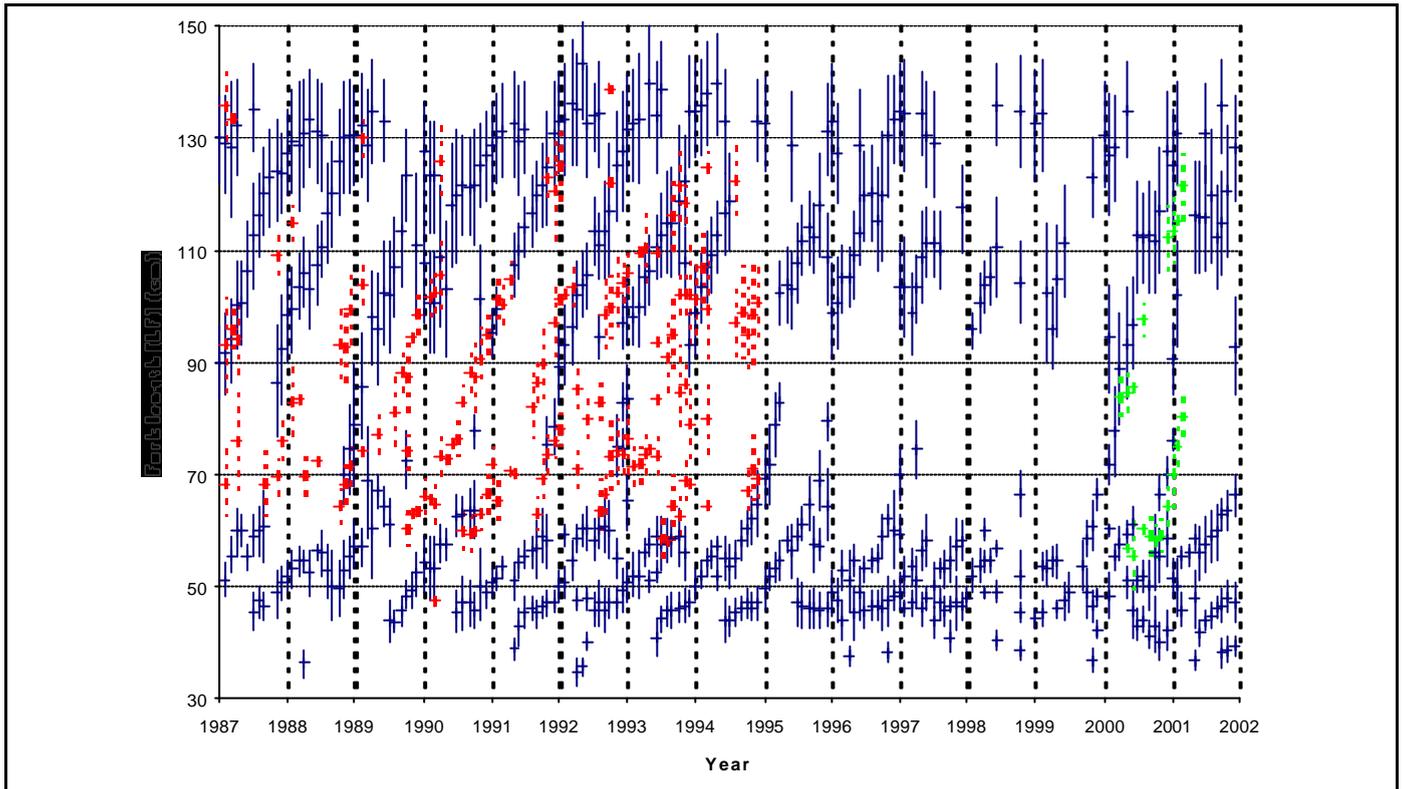


Figure 1: Mode positions identified in the size frequencies data from catches 1987-2001.

Each mode is identified by a horizontal bar corresponding to its mean fork length and by a vertical line corresponding to ± 1 standard deviation. Full and dashed lines respectively correspond to international purse seiners fleet, Omanese and Iranese gillnet data.

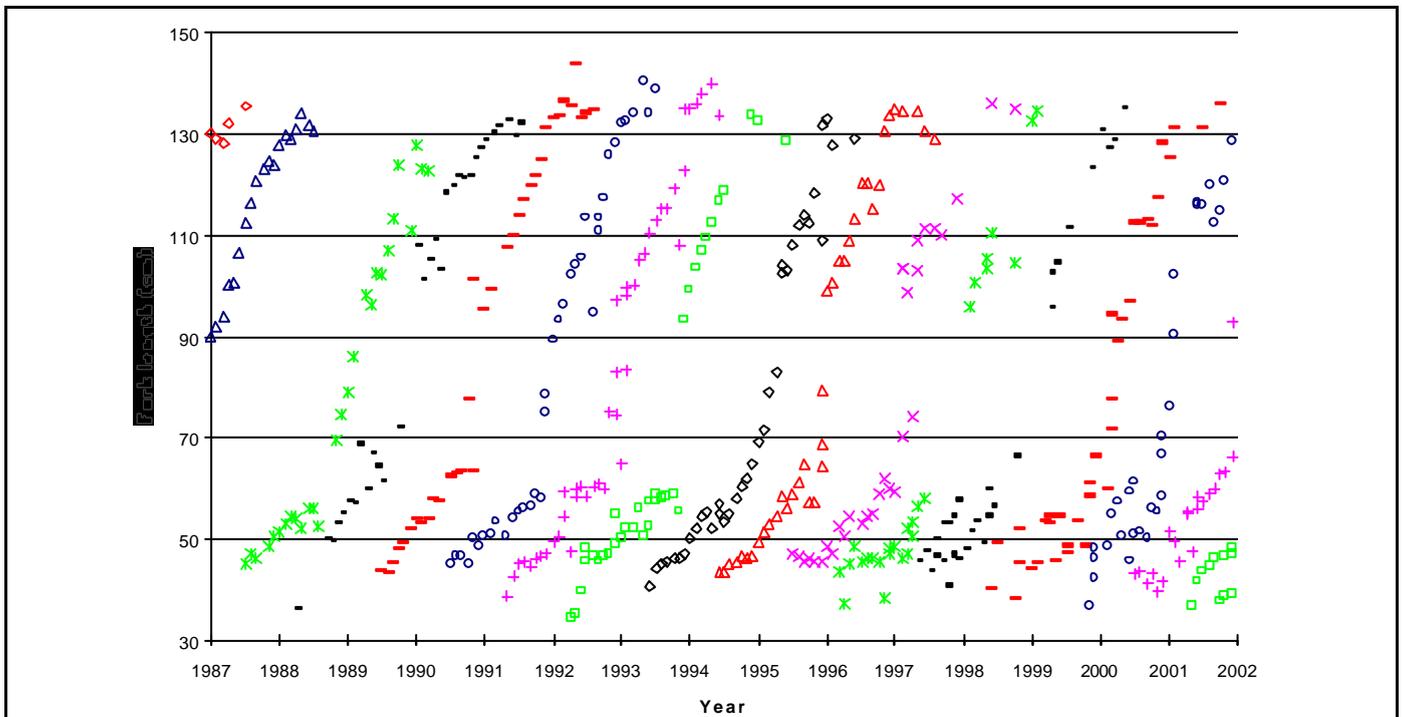


Figure 2, a: Population cohorts identified in the size frequencies data from purse seine catches 1987-2001.

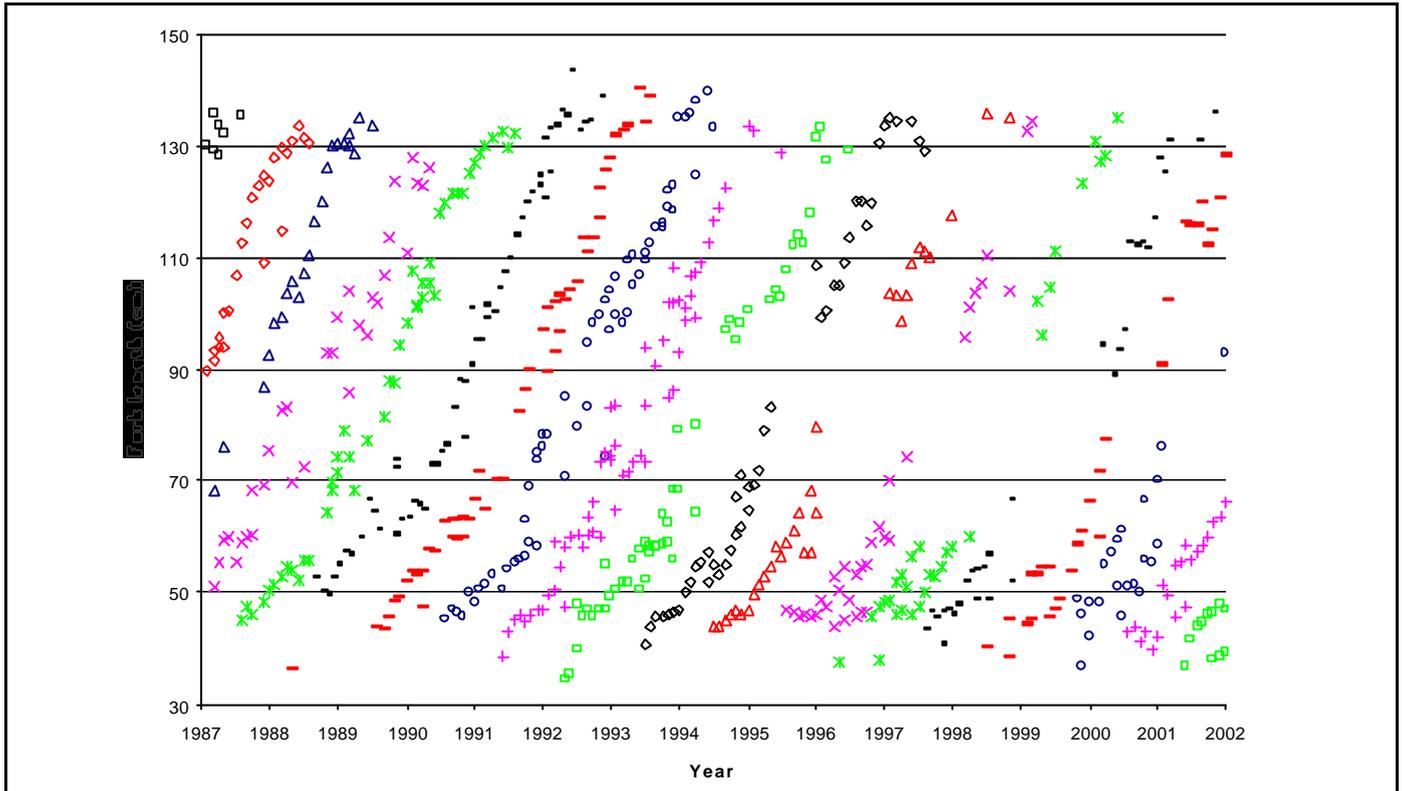


Figure 2,b: Population cohorts identified in the size frequencies data from PS and Omanese and Iranese gillnet catches 1987-2001.

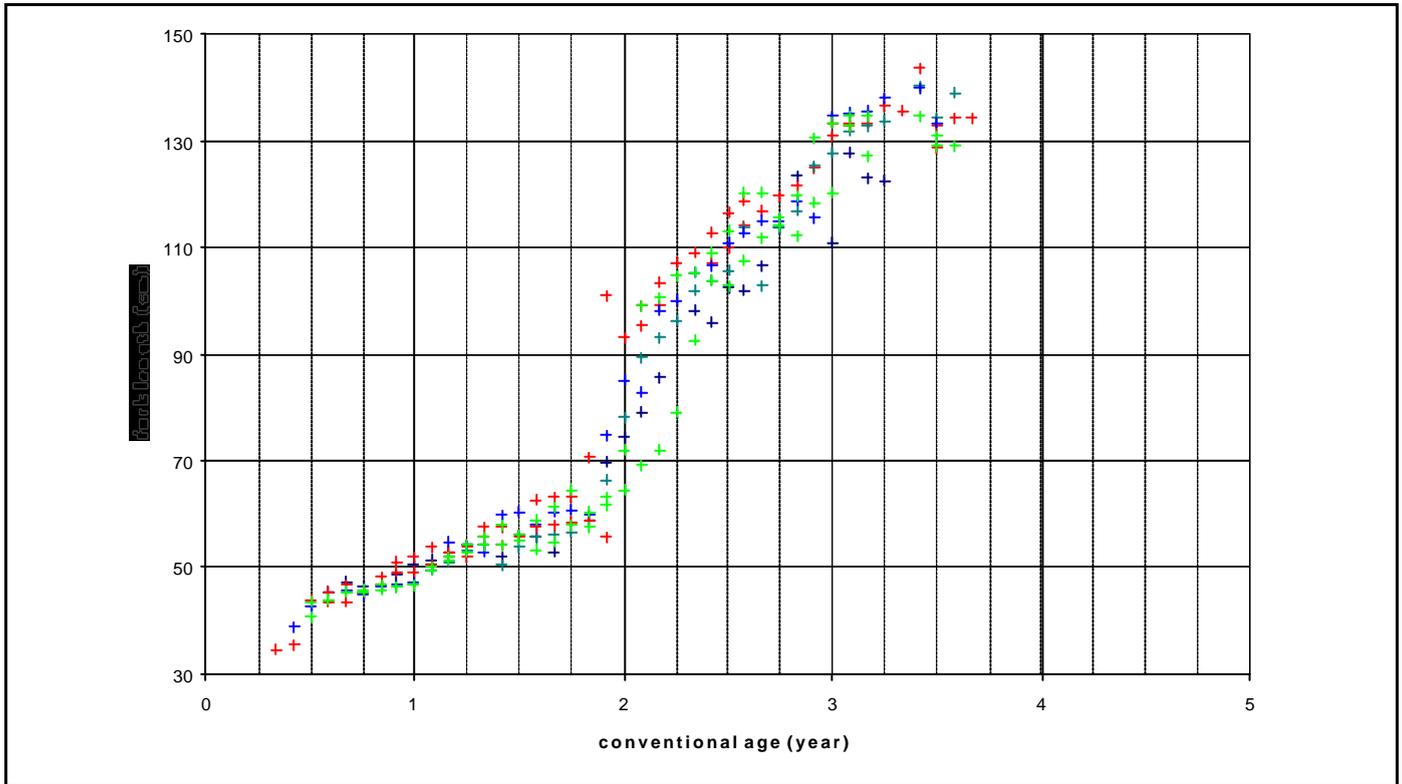


Figure 3,a: Modes superposition of seven well-identified cohorts from purse seine data catches 1987-2001.

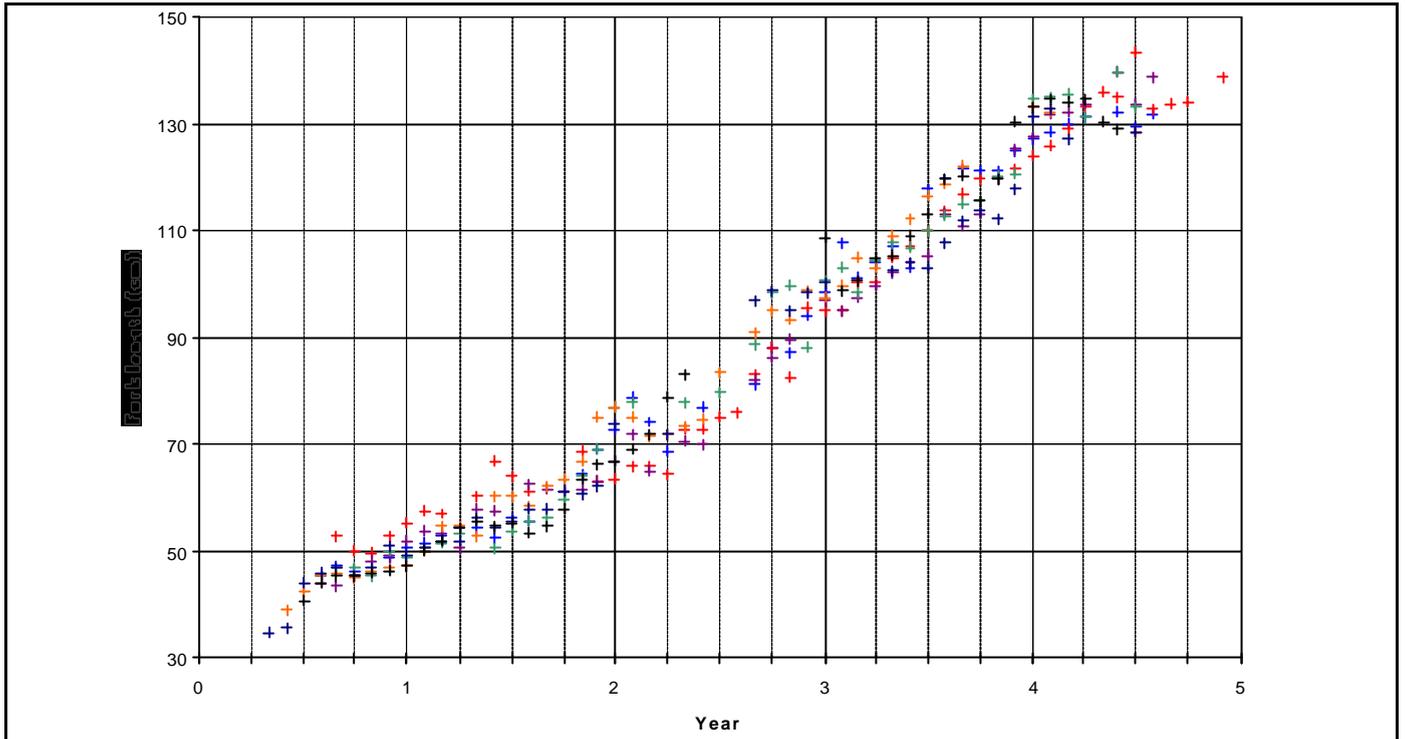


Figure 3,b: Modes superposition of seven well-identified cohorts from purse seine, Omanese and Iranese gillnet catches 1987-2001.

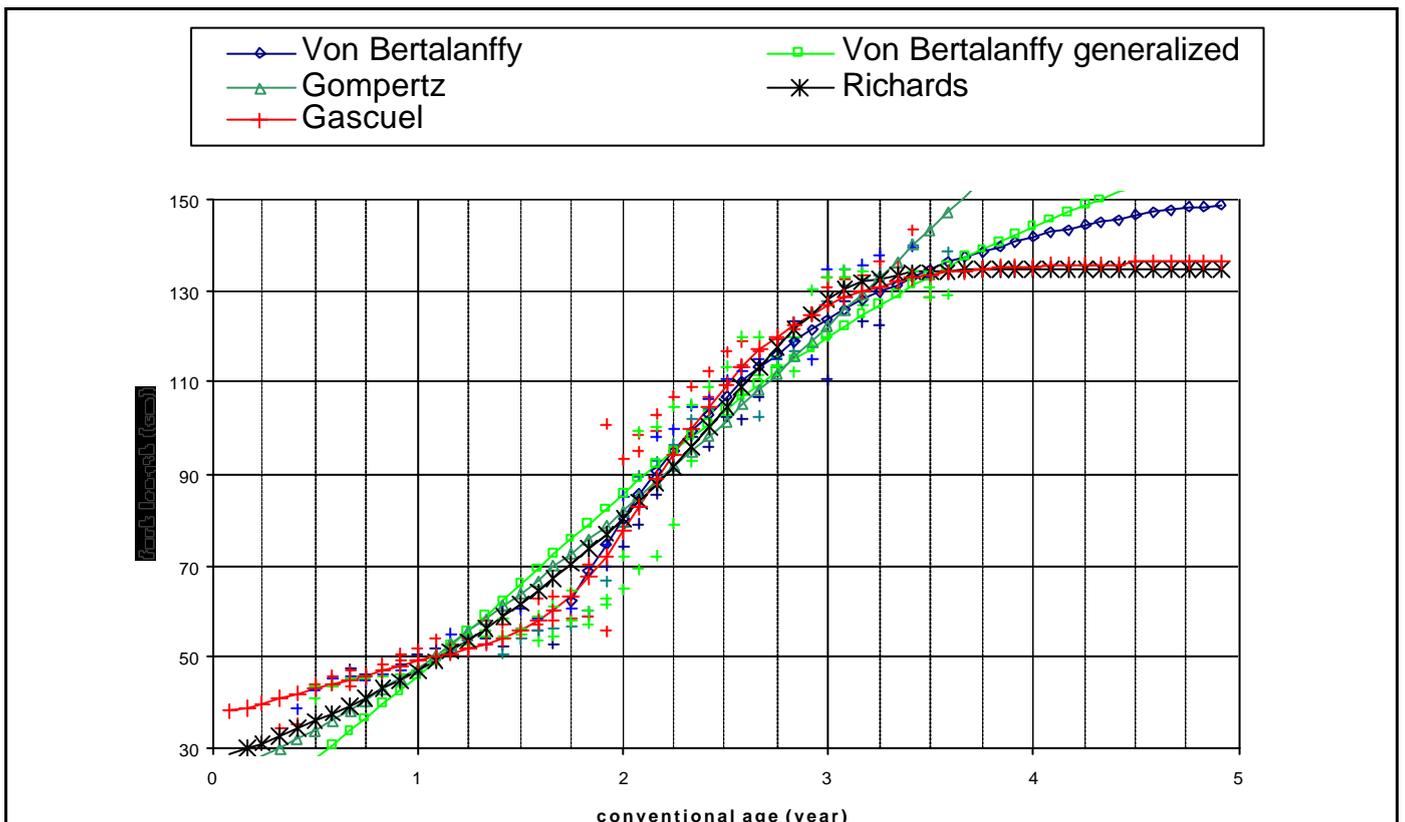


Figure 4,a: Yellowfin growth modelling in the Western Indian Ocean according to PS data

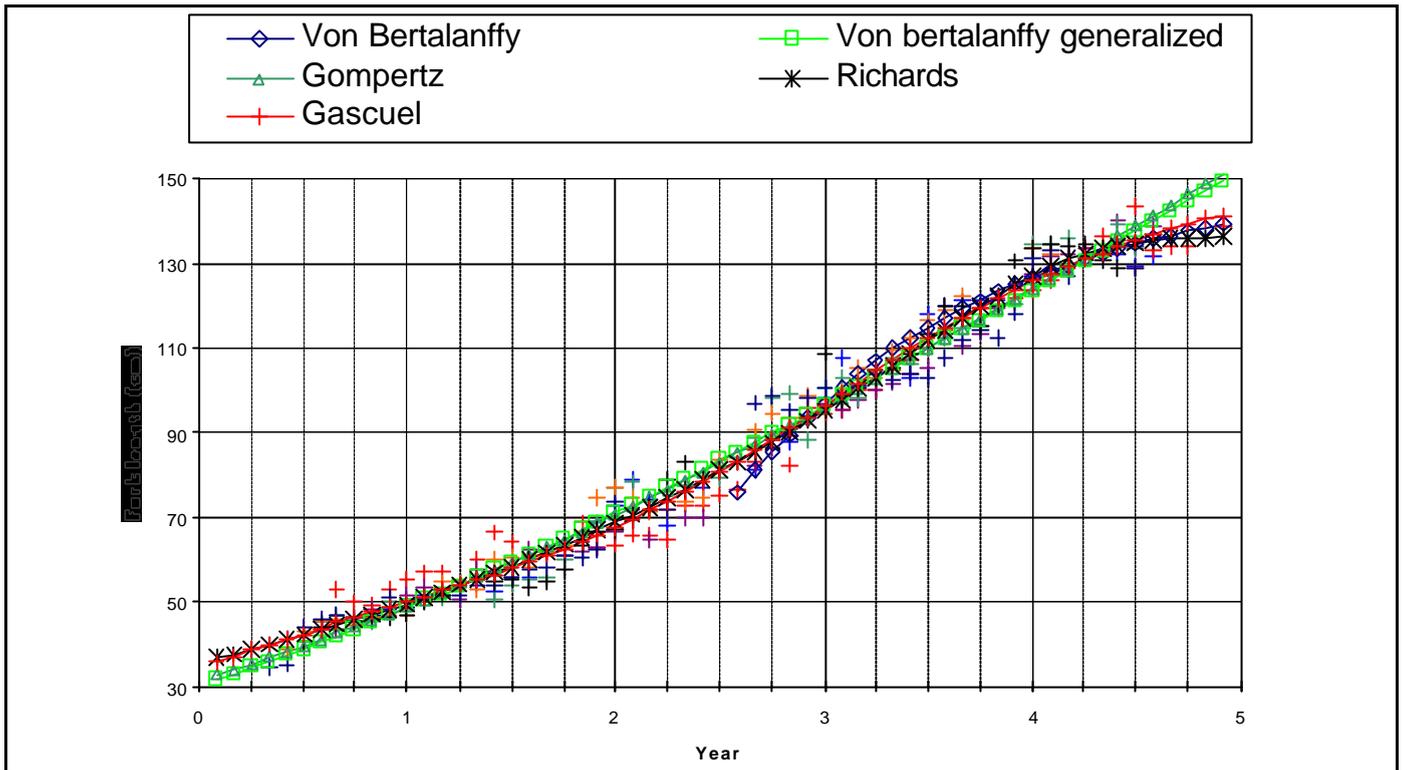


Figure 4,b : Yellowfin growth modelling in the Western Indian Ocean according to all the data

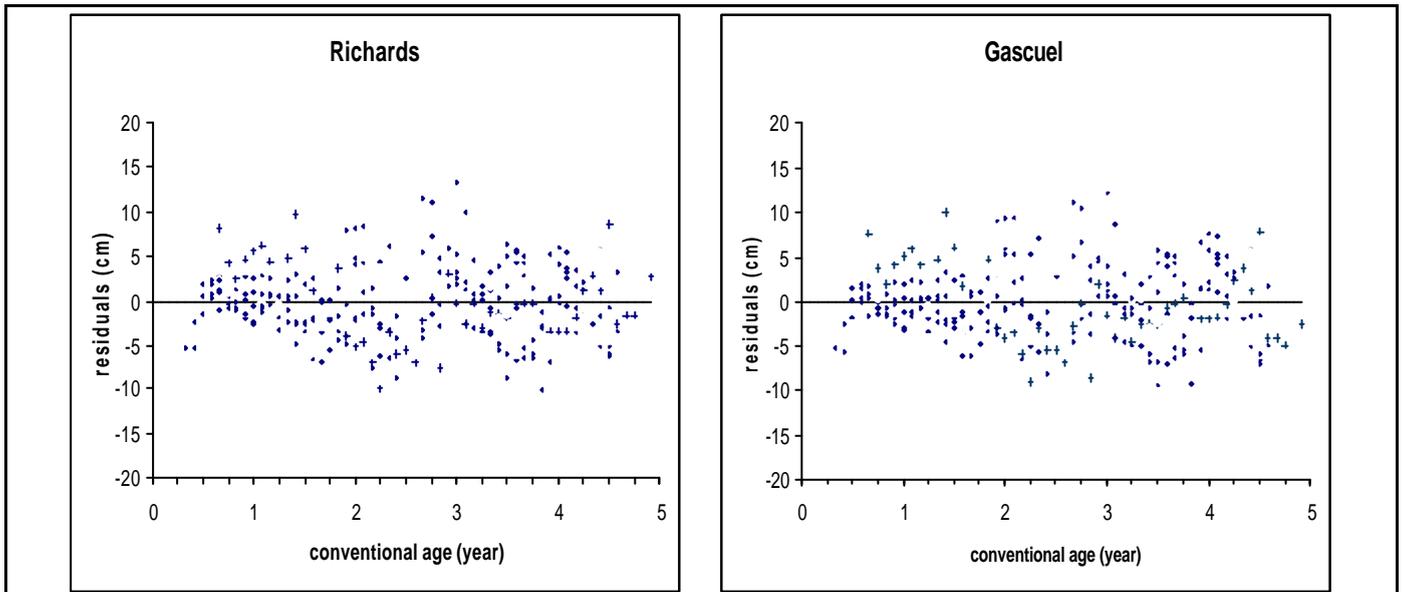


Figure 5 : Residuals analysis about Richards and Gascuel growth models

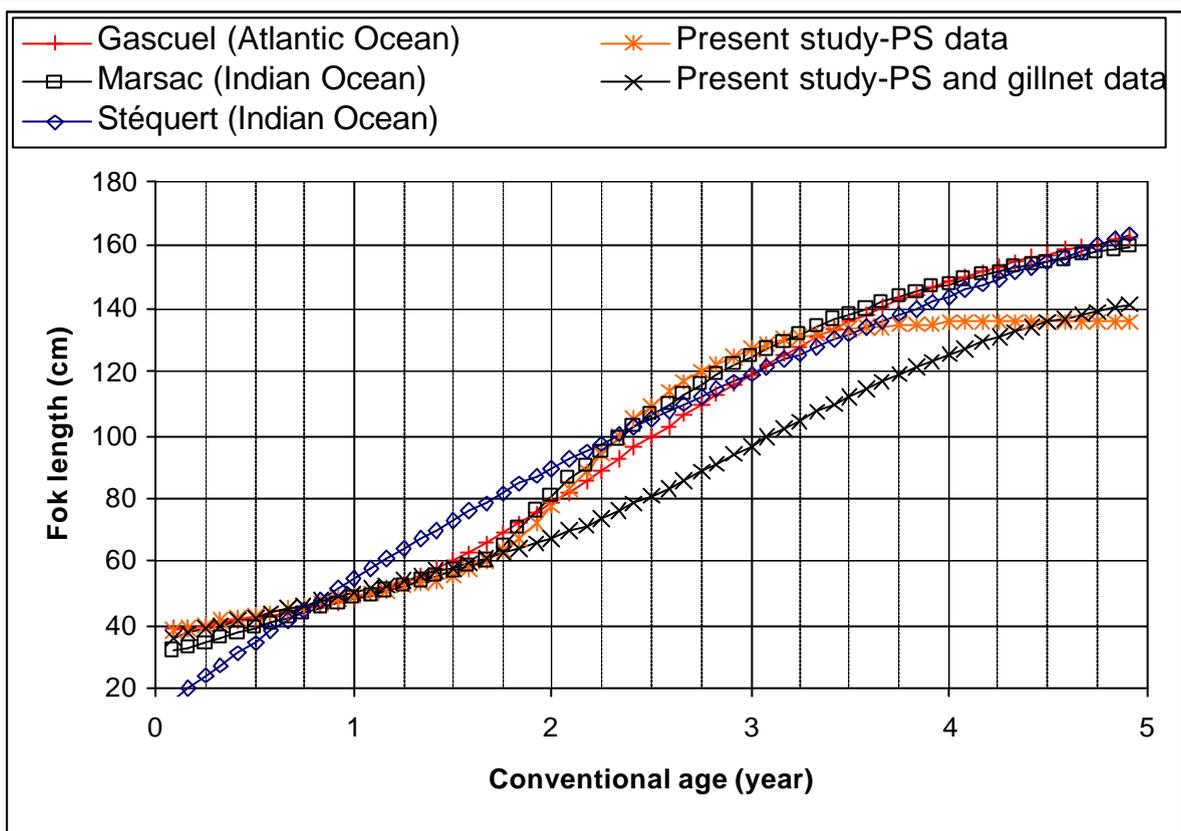


Figure 6: Comparison of yellowfin tuna growth curves established by several investigators

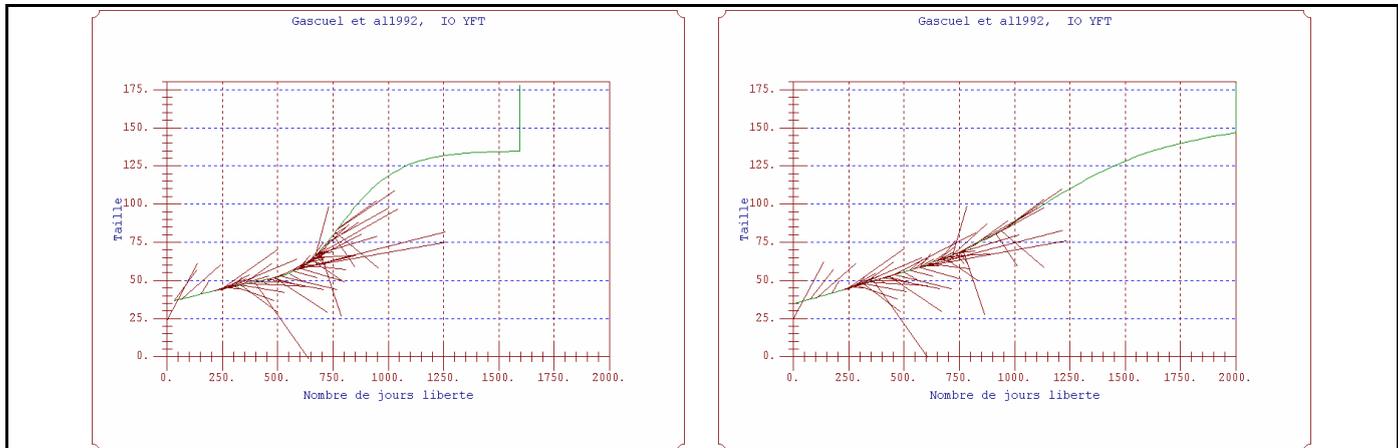


Figure 7: Fitting of tagging results of the Maldives on the two selected models. On the left, Model with PS data, on the right Model with addition of omanese and iranese data

Table 1: Equations of the selected growth models for Yellowfin tuna in the western Indian Ocean.

Model	Equation
Von Bertalanffy	$FL_t = FL_{\infty} \cdot [1 - \exp(-K \cdot (t - t_0))]$
Von Bertalanffy generalized	$FL_t = FL_{\infty} \cdot [1 - \exp(-K \cdot D \cdot (t - t_0))]^{1/D}$
Gompertz	$FL_t = FL_0 \cdot \exp[G \cdot (1 - \exp(-g \cdot t))]$
Richards	$FL_t = FL_{\infty} / [1 + \exp(-K \cdot t + a)]^m$
Gascuel	$FL_t = FL_0 + b \cdot t + [FL_{\infty} - (FL_0 + b \cdot t)] \cdot [1 - \exp(-K \cdot t)]^m$

when FL_t = fork length at age t
 FL_{∞} = asymptotic fork length
 K = coefficient of growth

t_0 = theoretical age for $FL = 0$
 G = instant growth rate at age 0
 g = growth rate of G parameter

a, b, m and D = parameters

Table 2,a: Estimated parameters of the growth models for Yellowfin tuna in the western Indian Ocean according to the PS data.

Parameters		Von Bertalanffy	Von Bertalanffy generalized	Gompertz	Richards	Gascuel
Fork length at age 0	FL ₀			22.98		36.99
Asymptotic fork length	FL _∞	154.77	180		134.62	136.34
Theoretical age at fork length 0	t ₀	1.16	-4.11			
Growth speed at age 0	b					12
Coefficient of growth	K	0.88	17.06		6.17	2.25
Instant growth rate at age 0	G			2.82		
Growth rate of G parameter	g			0.30		
Origin parameter	a				18.28	
Power parameters	m/D		0.04		0.09	137.46
Correlation coefficient	R ²	0.970	0.960	0.968	0.980	0.988

(all sexes are taking into account, n=229) (FL in cm, t₀ in years).

Table 2,b: Estimated parameters of the growth models for Yellowfin tuna in the western Indian Ocean according to all the data.

Parameters		Von Bertalanffy	Von Bertalanffy generalized	Gompertz	Richards	Gascuel
Fork length at age 0	FL ₀			31.58		34.77
Asymptotic fork length	FL _∞	150.79	180		136.47	152.07
Theoretical age at fork length 0	t ₀	1.70	-5.75			
Growth speed at age 0	b					15.35
Coefficient of growth	K	0.80			4.40	0.84
Instant growth rate at age 0	G		7.75	2.68		
Growth rate of G parameter	g			0.18		
Origin parameter	a				18.07	
Power parameters	m/D		0.05		0.07	17.76
Correlation coefficient	R ²	0.938	0.981	0.989	0.992	0.992

(all sexes are taking into account, n=296) (FL in cm, t₀ in years).

Table 3,a: Estimated monthly growth rate of Yellowfin tuna in the western Indian Ocean considering PS data.

Fork length interval (cm)	Average growth rate (cm.month ⁻¹)	
30-50	1,00	1,19
50-60	1,38	
60-70	3,65	3,85
70-80	5,30	
80-90	5,75	
90-100	5,52	
100-110	4,78	
110-120	3,58	
120-130	1,96	
130-140	0,25	

Table 3,b: Estimated monthly growth rate of Yellowfin tuna in the western Indian Ocean according to all the data.

Fork length interval (cm)	Average growth rate (cm.month ⁻¹)	
30-50	1,28	1,31
50-60	1,34	
60-70	1,72	
70-80	2,23	2,20
80-90	2,61	
90-100	2,72	
100-110	2,62	
110-120	2,39	
120-130	1,94	
130-140	1,38	

Table 4: Growth rates of yellowfin tuna estimated in and outside the Indian Ocean

Area	Method	Growth rates (cm.month ⁻¹)	Length range (cm)	Source
Central Pacific Ocean	Otoliths	4.2	17 to 64	Uchiyama and Strushaker, 1981
		2.7	64 to 93	
East Pacific Ocean	Otoliths	3.0	50 to 115	Wild, 1986
	Otoliths	7.5	15 to 35	Yamanaka, 1990
		2.9	35 to 79	
Atlantic Ocean	Tagging	1.5	tagged < 60 cm liberty <90 days	Fonteneau Unpubl.
		2.9	tagged >65 cm all duration	
Pacific Ocean		2.0	tagged < 60 cm liberty <90 days	
		2.7	tagged >65 cm all duration	
Indian Ocean	Scales	3.39	52 to 92	Huang et al., 1973
	Vertebrae	1.1 to 2.9	55 to 178	Romanov and Korotkova, 1988
	Bhattacharya	2.5 to 3.2	41 to 95	Yesaki, 1991
Maldives	Tagging	2.74		Yesaki and Waheed, 1992
Madagascar	Modal Progr.	2.8 to 3.2	45 to 70	Marcille and Stéquert, 1976
Central Indian Ocean	Modal Progr.	2.9 (1.5?)	30 to 70	Anderson, 1988
Western Indian Ocean	Otoliths	6	> 30	Stéquert and al., 1995
		4	60 to 80	
		3	> 110	
	Tagging	2.3		Cayré and Ramcharrun, 1990
	Bhattacharya	1.3	34 to 39	Marsac and Lablache, 1985
		1.6	39 to 57	
	Bhattacharya	1.5	44 to 62	Marsac, 1991
4.0		66 to 81		
Gulf of Oman	Bhattacharya	1.3	Males 61 -70	Firoozi and Carrara, 1992
		3.9	Males 85 -107	
		1.2	Fem. 62-70	
		2.5	Fem. 83-103	
Western Indian Ocean	Bhattacharya	1.0	38 to 56	Present study
		4.8	56 to 120	
Western Indian Ocean and Gulf of Oman	Bhattacharya (migration hypothesis)	1.3	36 to 66	
		2.5	66 to 120	