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AN OVERVIEW OF YELLOWFIN TUNA GROWTH IN THE ATLANTIC OCEAN: VON BERTALANFFY OR MULTISTANZA GROWTH?

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SUMMARY

*This paper reviews and discusses the growth curves of yellowfin tuna (*Thunnus albacares*) estimated by ICCAT scientists during the last 40 years. Comparing results obtained by the analysis of modal progressions, by recoveries of tagged fishes and by age readings of hard parts, it can be concluded that yellowfin tuna follow in the Atlantic, and in other oceans, a complex multistanza growth curve, similar to human growth, and not a simple von Bertalanffy growth model. It is also realistic to assume, based on the catch at size by sex in the Atlantic and on other information, that male yellowfin show higher asymptotic sizes than females. This hypothesis would need to be confirmed in the Atlantic by tagging and sexed recoveries of adult yellowfin. The paper also recommends evaluating the potential changes in yellowfin growth that could have occurred during the last 20 years. The realisation of the large-scale tagging programme recommended in 2010 by the SCRS would be the only way to estimate well the present growth of yellowfin tuna and their geographical variability.*

RÉSUMÉ

*Ce document examine et discute des courbes de croissance de l'albacore (*Thunnus albacares*) estimées par les scientifiques de l'ICCAT au cours de ces 40 dernières années. Si l'on compare les résultats obtenus de l'analyse des progressions modales, des récupérations des poissons marqués et des lectures des pièces dures aux fins de la détermination de l'âge, on peut conclure que l'albacore suit dans l'océan Atlantique et dans d'autres océans une courbe de croissance complexe multistance, similaire à la croissance humaine, et non un simple modèle de croissance von Bertalanffy. Il est également réaliste de postuler, sur la base de la prise par taille par sexe dans l'Atlantique et d'autres informations, que l'albacore mâle connaît des tailles asymptotiques supérieures à celles des femelles. Cette hypothèse aurait besoin d'être confirmée dans l'Atlantique au moyen du marquage et de la récupération d'albacores adultes par sexe. Le document recommande en outre d'évaluer les changements potentiels dans la croissance de l'albacore susceptibles d'avoir eu lieu au cours de ces 20 dernières années. La réalisation du programme de marquage à grande échelle recommandé en 2010 par le SCRS serait le seul moyen de bien estimer la croissance actuelle de l'albacore et sa variabilité géographique.*

RESUMEN

*En este documento se examinan y debaten las curvas de crecimiento de rabil (*Thunnus albacares*) estimadas por los científicos de ICCAT durante los últimos 40 años. De la comparación de los resultados obtenidos a partir de los análisis de progresiones modales, de las recuperaciones de peces marcados y de las lecturas de edad de partes duras, puede concluirse que el rabil sigue, en el Atlántico y en otros océanos, una curva de crecimiento compleja multiestanza, similar al crecimiento humano, y no un modelo de crecimiento simple von Bertalanffy. También sería realista asumir, basándose en la captura por edad y por sexo en el Atlántico y en otra información, que el rabil macho muestra tallas asintóticas más grandes que las hembras. Esta hipótesis tiene que confirmarse en el Atlántico mediante el marcado y la recuperación por sexos de rabiles adultos. En este documento también se recomienda que se evalúen los cambios potenciales en el crecimiento del rabil que podían haberse producido en los 20 últimos años. La realización del programa de marcado a gran escala recomendado por el SCRS en 2010 sería el único modo de estimar adecuadamente el crecimiento actual del rabil y su variabilidad geográfica.*

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KEYWORDS

Yellowfin, growth, tagging, age determination

1. Introduction

Since the beginning of the ICCAT work and the first stock assessment done by SCRS scientists, the growth of yellowfin tuna used in the Atlantic has been described using various models and parameters, and obtaining a great diversity of growth curves. The first models followed a Von Bertalanffy (VB; Von Bertalanffy 1938) growth based on modal progressions (Le Guen and Sakagawa 1973), and this growth was already used in the first ICCAT yield per recruit and VPA models used (Fonteneau and Lenarz 1974, Lenarz *et al.* 1974). However, this simple VB model has been seriously questioned and de facto abandoned for Atlantic yellowfin since the late 1970s, based on the analysis of Fonteneau (1979) showing that juvenile yellowfin between 42 and 70 cm exhibited slow growth rates, instead of the very fast growth assumed for these small sizes by the VB model derived by Le Guen and Sakagawa (1973). This result was obtained by modal progressions and by the recoveries of small yellowfin tagged, both analyses showing similar and consistent results (Fonteneau 1979). This multistanza growth was first described by Fonteneau as a suite of 2 VB models, the first one between birth and early juvenile period, and the second one for pre-adults and adults. This complex growth was later modelled by Gascuel *et al.* (1992) as a fully parameterized multistanza model (the model starting at recruitment, not at birth) and this model has been since permanently used by ICCAT scientists in all SCRS stock assessments. However this 2 stanza growth has been recently questioned by SCRS, following the Shuford *et al.* (2007) paper and its VB model, and this new uncertainty has been kept in the discussion of the recent SCRS reports. The goal of this paper is to discuss the growth pattern of Atlantic yellowfin based on these various analyses and on the potential biases in the various methods used to estimate this growth, and also comparing the yellowfin growth estimated in the Atlantic to the growth patterns recently estimated in other oceans. Its goal is to open a wide historical and prospective discussion on the growth of yellowfin and on the prospects for future improvements in its knowledge and modelling.

2. Yellowfin growth estimated by various methods in the Atlantic

2.1 Age readings

Direct age reading of hard parts has been used for some time to estimate yellowfin tuna growth based on the counting of yearly and/or daily rings in the otoliths, dorsal spines or vertebrae (Le Guen and Sakagawa 1973, Wild and Foreman 1980, Uchiyama and Struhsaker 1981, Wild *et al.* 1995, Lessa and Duarte-Neto 2004). Age reading has been useful in many cases, allowing estimating the absolute age at size, and the average growth and the variability of age observed at given sizes. Relatively few studies based on sclerochronology have been conducted for yellowfin in the Atlantic, the most recent one being based on the age reading of 132 otoliths collected in the eastern and western Atlantic, and covering the full size range of yellowfin, i.e. 5-179 cm (Shuford *et al.* 2007). This study concluded that yellowfin growth followed a VB growth with parameters t_0=-0.0420 y, k=0.281 y^{-1}, and L_∞=245.5 cm. This result appeared in total contradiction with previous studies based on other methods, for instance because of its very high L_∞ and of the fast growth of its juveniles.

2.2 Modal progressions

Modal progressions (Petersen method) have been used for Atlantic yellowfin by various authors (Le Guen and Sakagawa 1973, Fonteneau 1979, Capisano and Fonteneau 1991). This method is considered to be interesting for this stock because yellowfin are characterized by an active spawning season between December and March in the Eastern Atlantic (Albaret 1974, Capisano and Fonteneau 1991). As a consequence, clear modes are most often well visible in the size distribution of small and medium yellowfin (e.g. < 100 cm) and the apparent growth of these monthly modes are most often easy to follow over time from one month to the next (**Figure 1**).

However, these modes tend to be widely overlapping at large sizes, and they are much more difficult to identify and to follow. Modal progression analyses conducted for yellowfin show a slow modal progression of juvenile yellowfin at an average rate of less than 2 cm per month between 42 and 70 cm, and a time period of about 16 months between those 2 sizes. Furthermore, it should be noted that the first analysis by modal progression done by Le Guen and Sakagawa (1973) did not identify these slow modal progressions. This problem was mainly due to the fact that small yellowfin (<60 cm) were seldom caught by historical fisheries (**Figure 2**). Their choice of the VB model was probably also due to the classical use by many fishery scientists of the historical VB model and its simple but strong biological basis. The slow modal progression observed for yellowfin at very small sizes in the range 42-70 cm (i.e. <2 years), appears in contradiction with the fast average growth rates predicted by the VB models in this size range (**Figure 3**).

2.3 Recoveries of tagged tunas

The apparent growth observed between tagging and recovery of tagged tunas has been for some time one of the best and more convincing data sources allowing to estimate tuna growth. Several tagging operations of yellowfin tuna have been done aboard ORSTOM research vessels off Pointe Noire (Congo) throughout the 1970s. These small scale tagging operations allowed recovering several hundred of tagged tunas[3], mainly yellowfin and skipjack, which were used to estimate the growth of yellowfin (Fonteneau 1979). The apparent growth of the recovered juvenile yellowfin was nearly identical to the results of modal progressions, showing a very slow growth during the juvenile phase. This result has been since widely confirmed by the various ICCAT tagging programs and all associated recoveries of small yellowfin, as well as by subsequent analyses through modal progression (Capisano and Fonteneau 1991).

The yellowfin recoveries currently available allow to estimate an average growth rate of 1.5 cm/month between 40 and 75 cm (**Figure 4**), i.e. a slow growth rate in contrast with the average very fast growth rates estimated in this ranges of sizes by all VB models: 3.3 cm/month by Le Guen and Sakagawa (1973) and 3.2 cm/month by Shuford *et al.* (2007). As a consequence, the time period required to grow from 40 to 75 cm can be estimated from recoveries at about 1.4 years (reaching 16.6 months at 75 cm), when only 7.6 months (i.e. 0.6 year) are required according the to the VB models of Le Guen and Sakagawa (1973) and Shuford *et al.* (2007).

Recovery data of tagged yellowfin in the Atlantic also show that the 25 transatlantic yellowfin recovered after a long duration at sea (an average of 2.5 years), showed sizes at recovery that were close to the maximum size of the species (about 140 cm). These recoveries clearly show a growth pattern typical of large yellowfin, but that significantly differs from the growth expected for these tunas by the Shuford *et al.* (2007) VB model (**Figure 5**). The VB growth model overestimates the growth of these 25 large yellowfin by an average of more than 20 cm. Mark-recapture experiments allow to obtain robust estimates of relative growth between observed sizes at tagging and recovery for each individual. However, the quality of the results is highly dependent on the quality of the size measurements at tagging and recovery. It appears that errors in sizes at recovery are often important, especially in the Atlantic due to the great heterogeneity of the data files and to their often poor validation. This contrasts for instance with the good homogeneity and quality of the data from the Indian Ocean Tuna Commission that have benefited from a team fully dedicated to the processing and management of recoveries . The validity of these results also depends on potential gear selectivity bias (e.g. slow growing tunas or smaller fishes being more vulnerable to a given gear) and to potential effects of tags on the growth rates (probably a very minor bias). Although these potential biases should be kept in mind and better estimated, they are probably minor ones as compared to age reading errors for instance.

3. Yellowfin growth estimated in other oceans

When the VB growth model has been used in the early works of all tuna Commissions to model yellowfin growth, it appears that this model has been now abandoned by all tuna RFMOs: IATTC, WCPC, IOTC and ICCAT. Many of the stock assessments done nowadays are estimating yellowfin growth internally in their stock assessment models (MFCL by WCPFC or SS3 by IATTC), or externally (IOTC). Growth pattern estimated for yellowfin in these 3 areas are difficult to compare as they cannot be described by simple equations, but they always tend to show slower growth rates for juvenile yellowfin, and never the very fast growth rates estimated in the VB models.

4. Discussion

4.1 Which uncertainties associated with age readings of hard parts?

Age reading of hard parts has been successfully used for centuries to estimate ages of fishes, but age readings contain errors, and these errors have to be estimated. The results obtained by this technique are in fact widely dependent on various additive factors such as:

[3] These historical tagging and recovery data have been submitted to the ICCAT secretariat in February 2012.

- A good sample of hard parts covering all the sizes and fishing strata, preferably by sex.
- The good preparation of the samples,
- The type of equipment used to read the increments: for instance the use of an electron microscope to read the daily rings may be necessary
- The readers of hard parts: its expertise, independent readers reading the same otoliths, etc.
- The good correspondence between the number of increments and the time periods of interest, i.e. day or year. The deposit of daily increments has been shown for yellowfin in the Pacific (Wild and Foreman 1980, Uchiyama and Strushaker 1981, Wild *et al.* 1995) and Indian (Morize *et al.* 2008, Dortel *et al.* 2011) oceans. Tagging results done with tetracycline are necessary to validate the rate at which increments are deposited but they do not exist today in the Atlantic Ocean. Such tetracycline tagging and the subsequent age reading of the recovered tunas should be planned in the future large scale ICCAT tagging programme recommended by the SCRS.

As the uncertainties faced by each set of age readings are most often quite cryptic and difficult or expensive to evaluate (e.g. conducting multiple readings by independent readers or using an electron microscope), their results remain most often uncertain and their results also often questionable. In particular, age estimates from otolith reading are generally computed as the average of the different readings available, excluding increment counts that do not seem consistent with other readings. An illustrative example of this type of uncertainty was recently provided for bigeye tuna in the Indian Ocean by Stéquert and Conand (2000, 2004), and by the results of the large scale Indian Ocean tagging program (IOTTP). In 2000, these authors proposed to the IOTC a first study of age readings done with an optical microscope at 1000x magnification (10x ocular and 100x dry lens). This study concluded that bigeye was following a Von Bertalanffy growth curve with the following parameters: L_∞ =303.9 cm and k= 0.145 y^{-1}. However, the L_∞ estimated by this 2000 study was considered as being too high and unrealistic by IOTC scientists, and the authors were questioned upon the validity of their age readings. In 2004, Stéquert and Conand proposed a new growth curve based on the reading of the same set of otoliths, but using an electron microscope at 2,500 magnification. This new study concluded that bigeye was following a Von Bertalanffy growth curve with the following basic parameters: a more realistic L_∞=169 cm and k= 0.361 y^{-1}. The use of a scanning electron microscope (SEM) allowed the authors to explain why the number of increments was increasingly underestimated for large fish when using the optical microscope. For large bigeye tunas the width of the micro-increments is usually less than one micron when the theoretical resolving power of optical microscope is 0.2 micron, but under one micron observation and counting of micro-increments become very questionable. As a consequence, the authors concluded that the use of SEM is definitively required for counting micro-increments of bigeye tunas over 100 cm fork length. In 2010, the multiple recoveries of tagged bigeye from the IOTTP provide a good way to validate or not the new age readings obtained by Stéquert and Conand (2004). The analysis of the growth increments observed from the recovered bigeye are showing a complex multistanza growth curve, very similar to that of yellowfin growth curve. Between 40 and 65 cm: VB average growth rates can be estimated at 3.10 cm/month, when the observed growth rates on recoveries are at only 1.76 cm/month (and with a low variance). As a result, it appears that the growth rates of small bigeye under 70 cm are well under the fast growth rates estimated in this size range by the VB model. The 2,158 small bigeye tagged and recovered after less than 1 year at liberty are nearly all under the VB curve estimated by age readings (Figure 6). The reasons of this major discrepancy remain unclear, but the unanimous conclusion of the IOTC scientists was to favour the multistanza curve estimated from recoveries.

For the Atlantic yellowfin, the same doubts should be raised concerning the growth curve proposed by Shuford *et al.* (2007). These serious doubts are visible on **Figure 7**, showing the incoherence between modal progressions of juvenile yellowfin and this VB growth pattern. They are also visible on the PLOTREC figure showing the Shuford growth curve and the changes of sizes of recovered tagged yellowfin as a function of their time-at–sea (**Figure 8**). This figure shows that a great majority of recovered yellowfin, small and large individuals, are showing sizes well under the expectation of the model: small fishes showing much lower growth rates, and large fishes showing sizes well under the excessively large L_∞.

4.2 Which best methods for estimating growth?

There is no doubt that when growth can be estimated by various methods (age readings, Petersen and tagging), all these methods should preferably be used simultaneously, and their results should preferably/necessarily be consistent. When there are major discrepancies between the results obtained by the various methods, for instance in the case of the Shuford *et al.* (2007) growth curve, a choice has to be made between them. In this case, we would strongly favour the recommendation frequently developed by John Gulland during the early SCRS meetings when he was saying that: *"the best and more convincing growth curve of tunas should be based on recoveries of well measured tunas, as these recoveries are always the best way to really provide strong visual* *observed evidence of the real tuna growth"*. As an example of this rule, the transatlantic recovery of a yellowfin recently observed, a fish tagged at 70 cm and recovered 9.1 years (or 3,323 days) later at 161 cm is a very convincing fact upon the real growth of this tuna. On the opposite, a potential age reading of 2000, 3,000 or 3,300 daily rings on the otolith of the same fish would be more questionable by its nature. In the case of Atlantic yellowfin and following this basic Gulland's advice, as modal progression and tagging results are in good agreement to indicate a multistanza growth curve and a slow juvenile growth between 40 and 70 cm, this growth pattern should be kept as the best hypothesis in all the today ICCAT stock assessments. The potential causes of bias in age readings should be explored to understand the causes of their dubious results. Integrated methods are now available to estimate growth by including different sources of information, i.e. mark-recapture experiments, length-frequency and direct ageing data (Eveson *et al.* 2004). In addition, statistical tests for model comparison and selection should be used to select between VB and other more parameterized models (Burnham and Anderson, 2002).

4.3 Age at recruitment?

In the past and current fisheries it appears that the main yellowfin recruitment takes place predominantly each year during the 3rd quarter and at a modal size of 45 cm, i.e. about 1.45 kg (**Figure 8**). Very little is known today in the Atlantic on the pre–recruits of yellowfin, i.e. between birth and recruitment, as their large biomass has never been identified nor caught by fisheries, but at least the real age of the young recruits at 40 cm should be well identified. The main spawning season of yellowfin is observed in the Gulf of Guinea at the end of the year and during the first quarter (**Figure 9**). The base hypothesis adopted since the late 1970s by SCRS scientists was that these 45 cm recruits were born during the same year, and then showing during this 6 month "cryptic" period a fast growth at an average growth rate of 7.5 cm/month. This fast growth rate is similar but higher than the 5.2 cm average growth rate estimated by the Shuford *et al.* (2007) VB model during this early period. On the opposite, the Gascuel *et al.* (1992) model does not intend to cover this early period and only targets the recruited fishes. Some tagging of very small yellowfin, aquaculture experiments, and age readings of these small yellowfin would fully confirm the validity of the historical ICCAT hypothesis: yellowfin growth is very fast between the larvae and the recruitment stage at 45 cm.

4.4 Differential growth of male and female yellowfin?

Such differential growth has been observed for many animals in the living world. It is very rare that adult males and females show the same maximum sizes. However, a potential difference in L_∞ has been seldom envisaged or analyzed for tunas stocks, even when there a large body of evidence supports this hypothesis. Such hypothesis that female yellowfin had a lower L_∞ than male yellowfin was put forward by Albaret (1973) based on the sex ratio at size that has been routinely observed for Atlantic yellowfin since the early 1970s. Results show that yellowfin females become significantly dominant between 130 and 145 cm while males become significantly dominant at sizes larger than 150 cm (**Figure 10**).

Such pattern in sex ratio at size can be explained by a differential L_∞ of the 2 sexes, female yellowfin being 10 to 15 cm smaller than males. Such differential growth has been observed for other tuna species and in other oceans (e.g. Williams *et al.* 2012) and by the results of the recent recoveries by sex of large yellowfin recently collected in the Indian Ocean that will soon firmly confirm this hypothesis, yellowfin females clearly showing a lower L_∞ than male (unpublished data). This differential growth of male and female yellowfin introduces a new complexity in the stock assessment work and in the estimation of catch-at-age. In particular, the slicing method currently used by ICCAT to convert the catch-at-size matrix into a catch-at-age matrix is no more valid, as the CAS and growth of the 2 sexes are quite different (**Figure 11**). In the current slicing method, most old females (probably at age 5 or older) are classified in the 130 to 140 cm size range, and then in the age 4 group. Such bias may affect the estimation of spawning stock size, as the age structure of female catches now tend to be unrealistic. It should be a priority to better estimate the growth by sex and to incorporate this result in the future ICCAT stock assessment work.

4.5 Human and yellowfin growth?

Human growth has been widely studied and modelled by many scientists and doctors. As very large samples of individuals of humans are easily followed from birth to death, the average human growth and its variability are of course very well known. Its main characteristics can be summarized as following:

1) It has been perfectly demonstrated that human growth follows a complex multistanza pattern **Figure 12**) Such growth can be modelled only using complex growth models based on 5-6 parameters or by ad hoc multi-stanza growth models (Karlberg 1987).

2) Human growth is clearly different for males and females, male always showing larger asymptotic sizes (for instance 7.4 % larger for Caucasian males in 1960: average maximum size of 162 cm, and 174 cm for females and males, respectively). The corresponding size distribution of this sample of human males and females is shown **Figure 13**.

3) In such case, any growth study of the combined sexes would tend to estimate a non realistic asymptotic size intermediate between males and females.

4) Human growth has been permanently changing over centuries and regions, as a function of changes in environmental factors and human feeding.

Surprisingly, these 3 characteristics of the human growth appear to be consistent with yellowfin tuna growth:

(i) the review of past and current data suggests that yellowfin growth follows a complex multistanza model and not a VB model. Such complex growth can be modelled from birth to death only using complex models, for instance more complex than the Gascuel *et al*. (1992) or the Laslett *et al.* (2002) growth models

(ii) Yellowfin growth is probably different for males and females, males showing larger asymptotic sizes (about 10-15 cm larger), and current estimates of L_∞ may not be realistic, being wrongly estimated half way between the asymptotic sizes of males and females.

(iii) The potential changes in yellowfin growth should be studied, as the environmental changes and the changes in fisheries (exploitation rates and FAD-associated schools fishing) may have produced changes in the yellowfin growth.

More cooperation between fishery scientists and experts in human growth and its modelling should possibly be useful.

4.6 Maximum age of yellowfin significantly caught?

Longevity is an important parameter in any analytical stock assessment, as it may be unrealistic to run age structure models on 6 year classes if there are significant numbers of surviving fishes caught at ages over 10 or 15 years. All analytical stock assessments works are of course using a + group, but this category should preferably correspond to a relatively minor proportion of the total biomass. In the Atlantic, as in other oceans, most yellowfin stock assessment works have been done using 5 year classes and a 6^{th} + group. This practice may be questionable, based on the apparent longevity of yellowfin tuna (for instance the yellowfin tagged at 2 years and recently recovered after 9 years at liberty, then at an estimated age of 11 years) or taking into account the consistent numbers of tagged yellowfin that are still recovered in the Indian Ocean at ages over 6 years. Longevity of yellowfin tuna as well and the influence of the plus group should therefore be better estimated and taken into account in future SCRS yellowfin stock assessments.

4.7 Yellowfin growth in 2012 and the Gascuel et al. (1992) parameters?

The Gascuel *et al.* (1992) model, based on modal progressions, is consistent with recoveries available at the end of the1980s (**Figure 14**). However, the possibility that yellowfin growth may have been modified since the 1990s should now be envisaged. Such changes in growth has been observed for southern bluefin tuna (Polacheck *et al.* 2004) and could be due to changes in exploitation rates, to the large numbers of FADs seeded since the mid-1990s (the ecological trap hypothesis: FADs may alter growth of juvenile yellowfin; Marsac *et al*. 2000, Hallier and Gaertner 2008) or because of changes in environmental factors. This potential change in the yellowfin growth curve has not been analyzed by scientists, but it should now be envisaged. As a first look to this question, the following **Figure 15** shows a PLOTREC figure with the Gascuel *et al.* (1992) curve and the ICCAT yellowfin recoveries recovered since 1990 (i.e. only 143 individual with > 60 days-at-sea, 52% tagged in the Western Atlantic, many of them tagged by recreational fishermen and with potentially large uncertainty in the sizes at tagging). This figure would tend to show that many of these recently recovered yellowfin did not follow the Gascuel *et al.* (1992) curve, a majority of the long duration recoveries showing slower than expected growth rates. This preliminary comparison does not have a quantitative value, as these anomalies in growth could be due to geographical effects, to errors in size, etc., but it would reinforce the need to examine the validity of the Gascuel curve parameters today (based on recoveries and on modal progressions).

4.8 Why such multistanza growth of yellowfin?

This fundamental biological question remains today without comprehensive and universal answer. When the various growth stanzas observed between growth and death are now well described by scientists and appear to be very similar worldwide, the full eco-biological explanation of this complex growth pattern remains poorly studied and understood by scientists. Mechanisms such as acquisition of sexual maturation, development of the swim bladder, as well as changes in habitat and prey with size/age could explain the growth phases that have also been observed for southern bluefin (*Thunnus macoyii*) and bigeye tunas (Eveson *et al.* 2004). There are good expectations that comprehensive energy budget of yellowfin (Kooijman 2010) during the various stages of its life would probably explain these various growth stanzas (Jusup *et al*. 2011). This work should preferably be done at a comparative worldwide scale.

5. Conclusion

The present historical overview of the yellowfin growth allows to reach 8 firm conclusions in relation with past and future work by SCRS on the growth of this species:

(1) They are very strong converging evidence that yellowfin follows a complex multistanza growth similar to the Gascuel model, as observed in the Indian and Pacific Oceans, and not a VB-type growth model. This conclusion is now strongly and repeatedly obtained, based on modal progressions and on tagging results (and also on the most recent age readings of recovered tunas in the Indian Ocean). This complex growth curve can probably be explained by the various eco-physiological growth phases of yellowfin: larvae, juvenile, maturing fishes, and adult yellowfin. Further investigations are needed to model from birth to death such complex growth, preferably starting from larvae;

(2) The Von Bertalanffy growth model should be now considered as being unrealistic for yellowfin as it does not describe the slow growth pattern that has been observed in the Atlantic ocean and worldwide, for juvenile yellowfin between 40 and 70 cm;

(3) Stock assessment modelling of tuna stocks should never envisage to use a growth curve with an asymptotic size well above the maximum sizes observed at sea: a biologically realistic L_∞ should necessarily be lower than the maximum sizes in the catch-at-size. A realistic range of plausible L_∞ for Atlantic yellowfin should for instance necessarily be in a range between 158 cm (or less) and 170 cm (taking note that 90% and 99% of historical yellowfin catches by longliners were observed above these 2 sizes), and never at 245 cm (as in the Shuford *et al.* (2007) model).

(4) Yellowfin longevity can be estimated at about 8 to 10 years or possibly more (the 11 years old recent yellowfin); the sizes of these oldest yellowfin are always close to the larger sizes observed and to realistic estimates of L_∞. This potential longevity should be well handled in stock assessment and projections of stock status. It should for instance be consistent with natural mortality and estimated fishing mortality (Hoenig 1983).

(5) Age reading of yellowfin tunas done using optical microscope should be compared and validated with an electron microscope to eliminate the potential risk that the insufficient discriminant power of optical microscope could produce increasingly biased estimates of the age for old individuals. Multiple independent age readings should also be done so as to estimate the precision in age estimates and ensure the validity of these age readings.

(6) Potential changes in the yellowfin growth curve since the 1992 study by Gascuel et al. should be investigated, as this change is suggested by the post 1990 yellowfin recoveries and by apparent changes in sex ratio at size.

(7) Potential growth heterogeneity between the growth of males and females yellowfin, and a potentially significantly higher L_∞ of males, should be explored, by careful age reading of large sexed yellowfin and large scale tagging, as this hypothesis could explain the sex ratio of yellowfin observed in the Atlantic since the early 1970s. In the short term, scientists should already explore the feasibility to estimate more realistic CAS by sex, their use in alternate stock assessments, and their potential impact on the stock status as investigated for albacore (Hoyle 2008, Schirripa 2009).

(8) Large scale and well controlled tagging programs (such as the recent IOTC tagging program) are the best and probably the only way to fully estimate realistic growth of tunas, and by sex: the large scale tagging program recommended by SCRS is urgently needed to obtain for yellowfin a realistic growth curve by sex in the various areas of the Atlantic, in the current context of the 2010th fisheries and ecosystems (as the historical growth pattern estimated in the late 80s may not be valid today).

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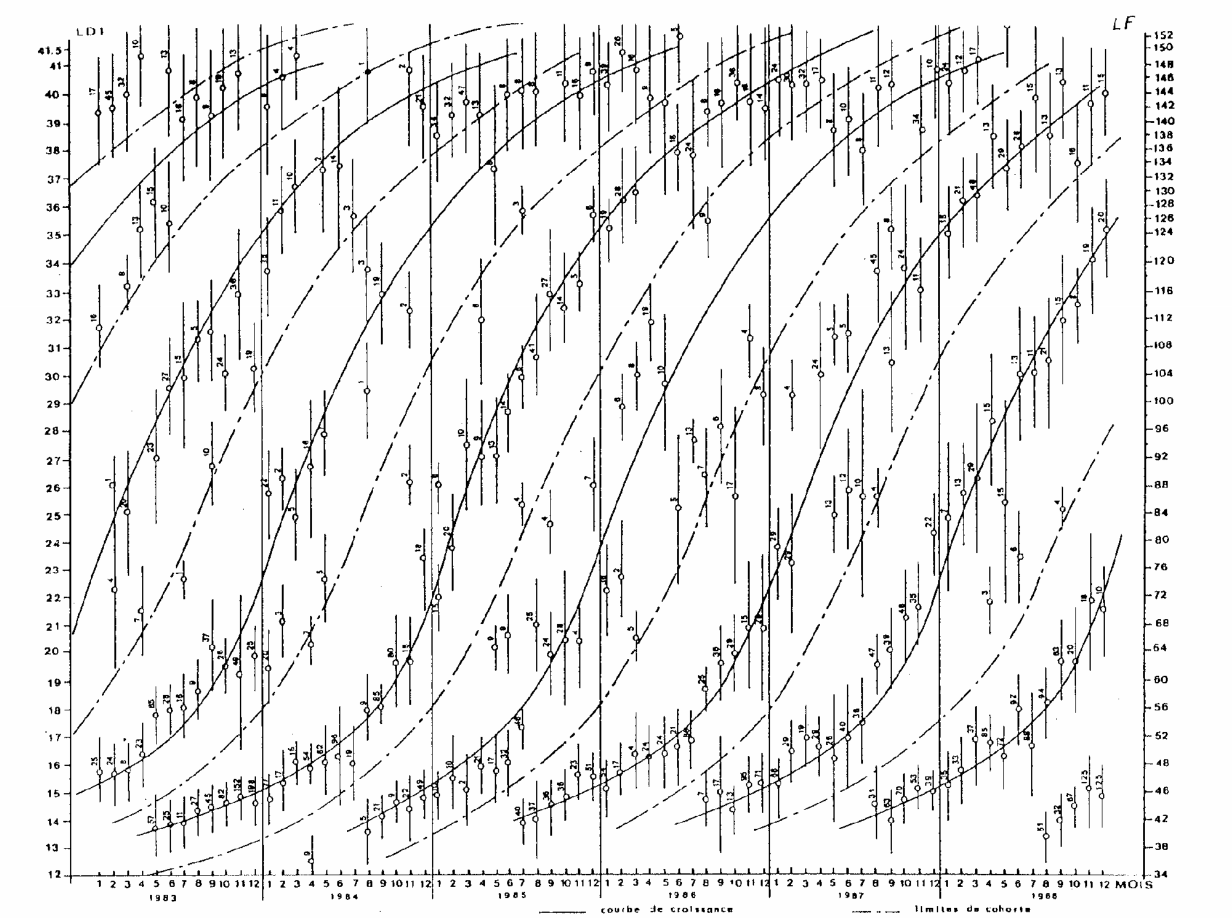

Figure 1. Monthly position and sizes identified by Capisano & Fonteneau 1991 in the size distributions of yellowfin caught by PS. The solid line link the modes following the Gascuel *et al.* 1992 model.

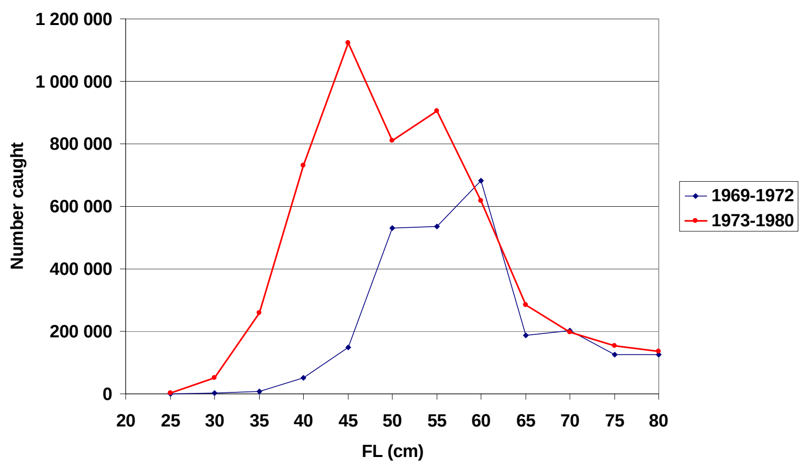

Figure 2. Yellowfin catch at size observed in the Atlantic before the Le Guen and Sakagawa study (1969-1972) and after this study (period 1973-1980)

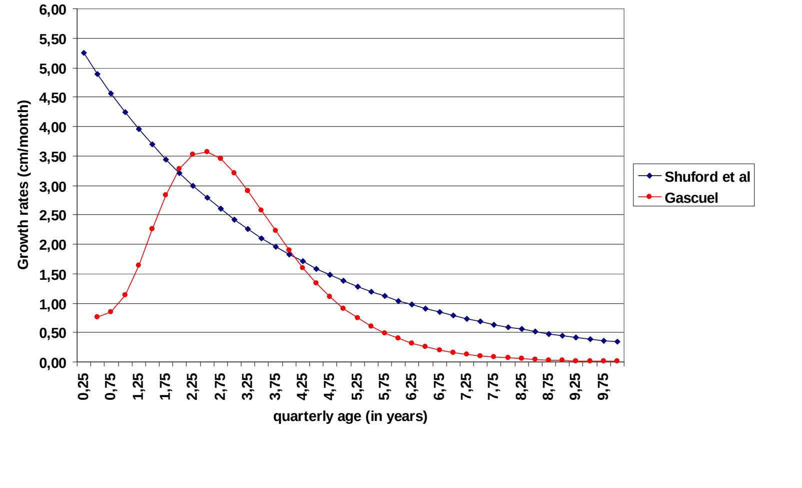

Figure 3. Monthly quarterly growth rates of yellowfin estimated by the Gascuel *et al.* (1992) and Shuford *et al.* (2007) models

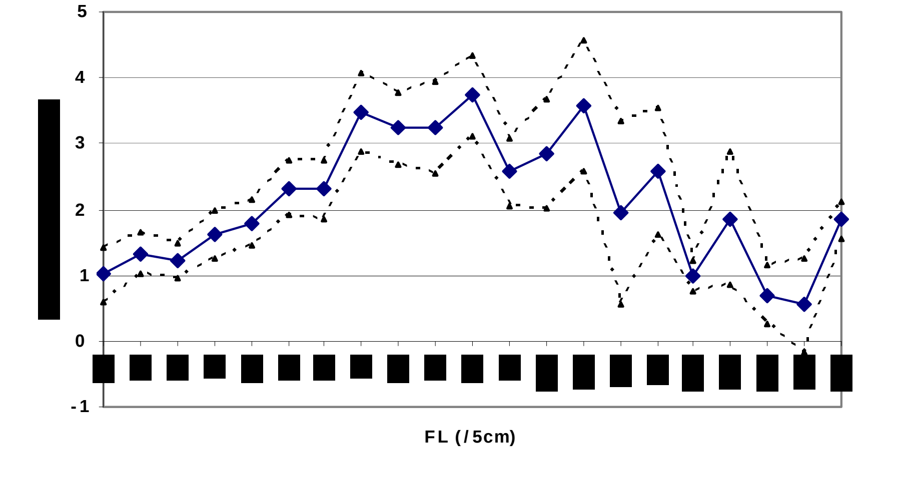

Figure 4. Average growth rates by 5 cm class of fork length estimated by the Gascuel and Fonteneau (2008) method for Atlantic yellowfin, based on the 2012 ICCAT recoveries (> 60 days at sea). Dashed lines indicate estimated 95% intervals of confidence around growth rates.

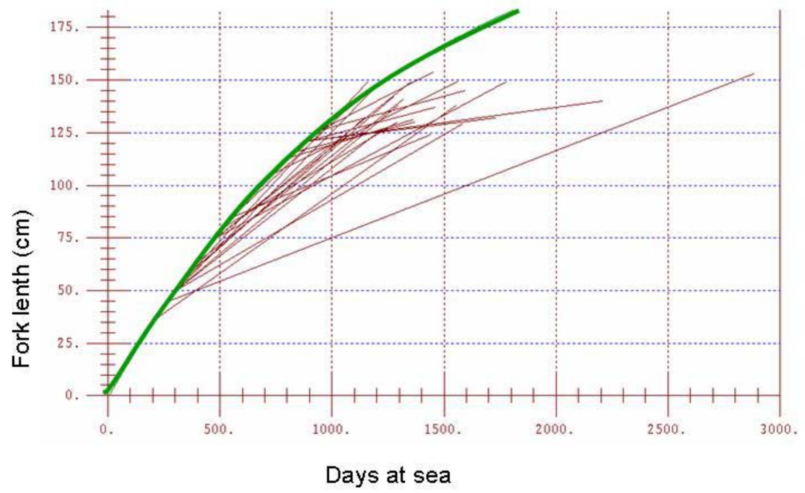

Figure 5. PLOTREC graph showing the Von Bertalanffy growth curve of yellowfin estimated by the Shuford *et al.* 2007 model and growth of recovered transatlantic yellowfin (Fonteneau and Nordstrom 2000).

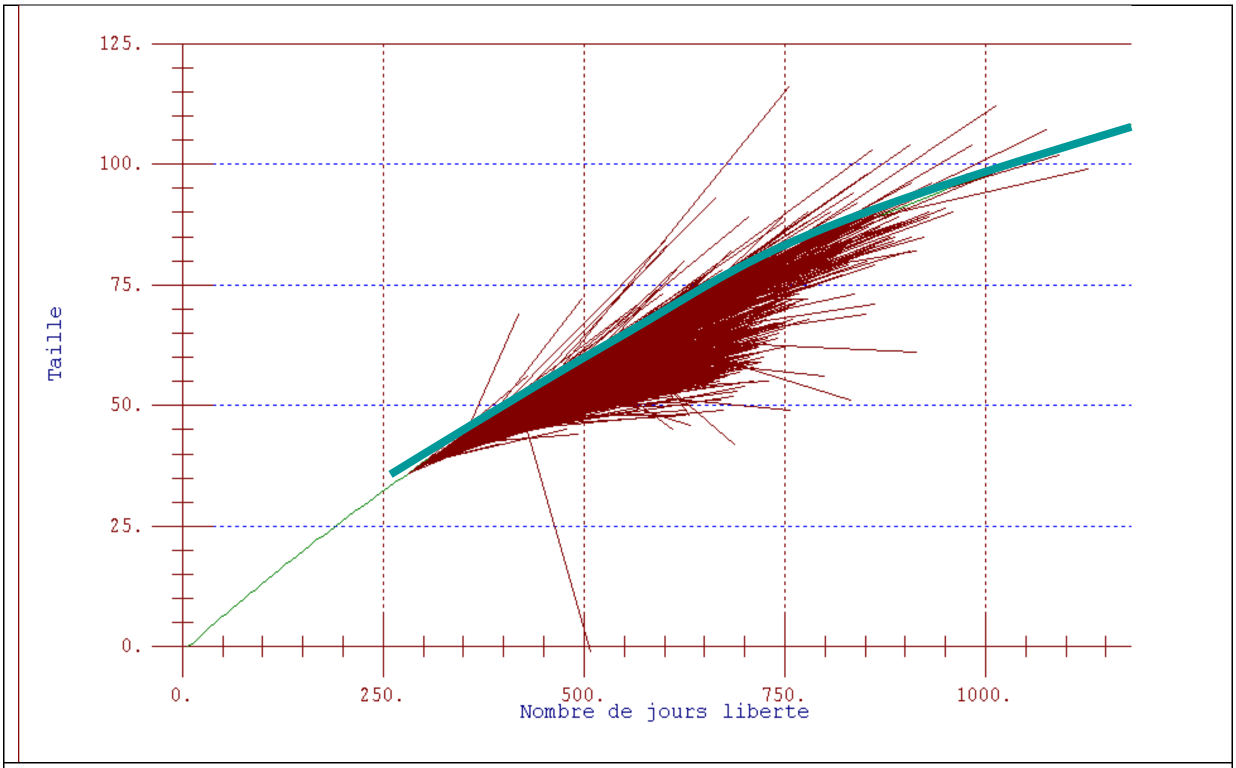

Figure 6. PLOTREC graph showing the Von Bertalanffy growth curve of bigeye estimated by Stéquert and Conand (2004) in the Indian Ocean and recoveries of tagged bigeye showing a duration at sea between 60 and 365 days (Fonteneau and Nordstrom 2000).

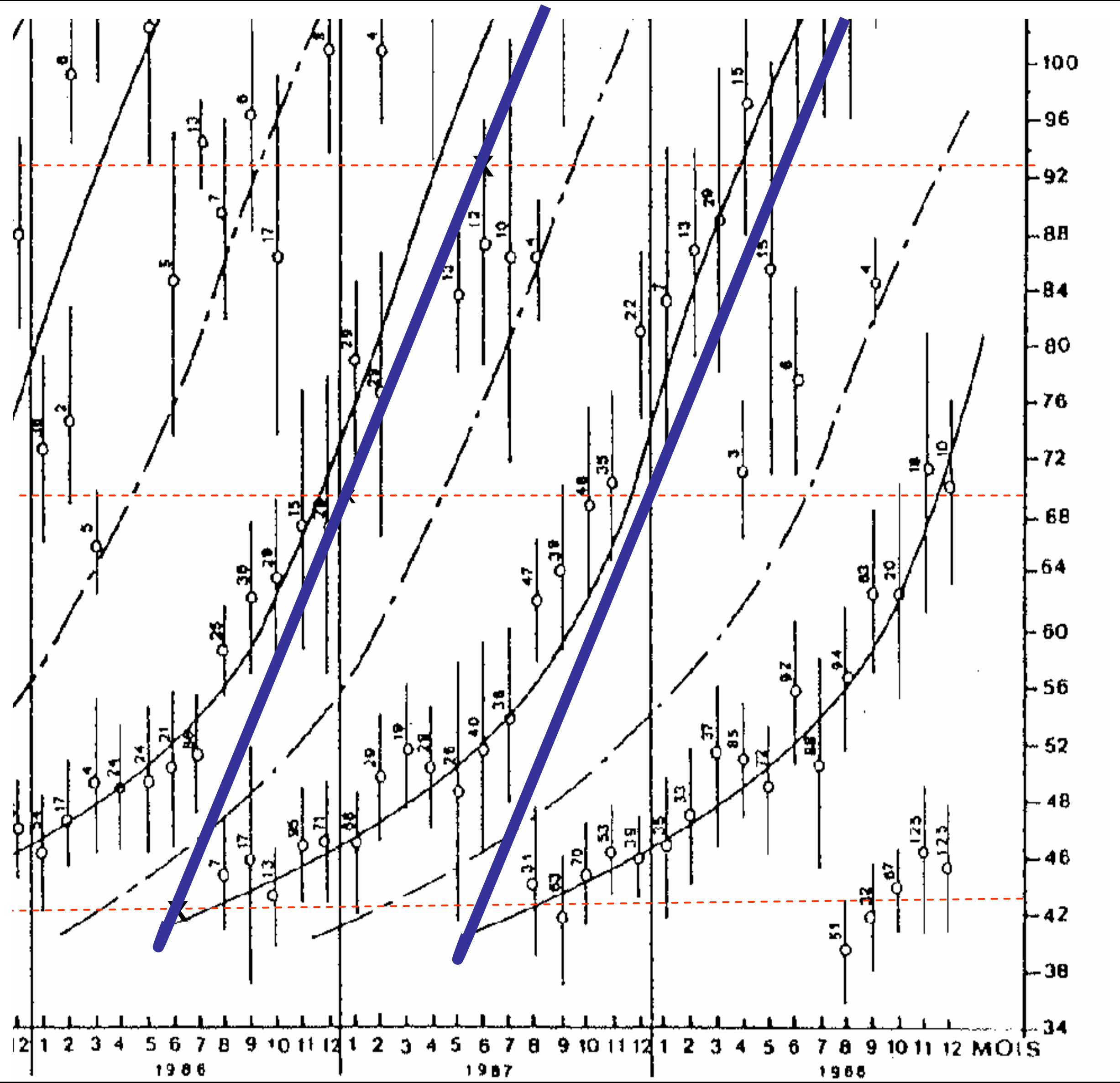

Figure 7. Typical modal progressions of small yellowfin identified in the Eastern Atlantic (taken form Capisano and Fonteneau 1991), and Von Bertalanffy growth curve estimated by Shuford *et al.* 2007 (blue curve).

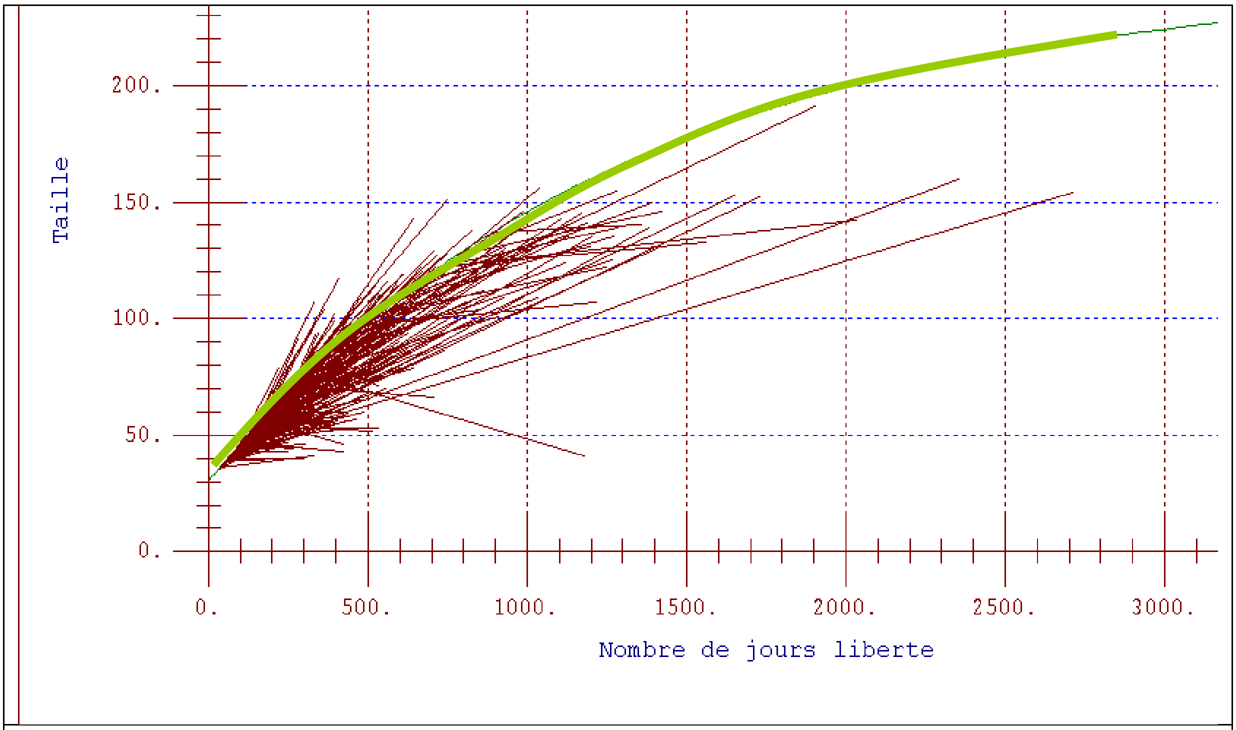

Figure 8. Plotrec graph showing the Shuford *et al.* (2007) growth curve and changes of sizes of recovered tagged yellowfin, as a function of their time at sea.

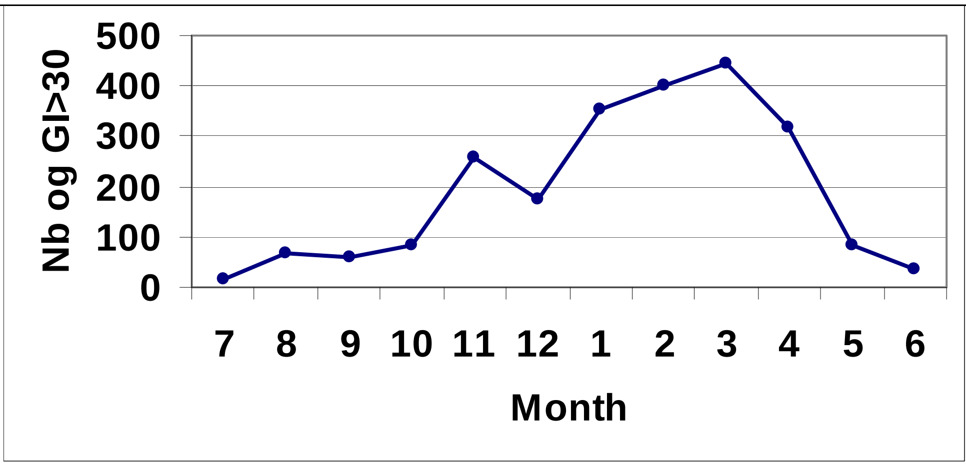

Figure 9. Average monthly percentages of high Gonad Index (>30) of yellowfin in the Gulf of Guinea (1990 data set, taken from Capisano and Fonteneau 1991).

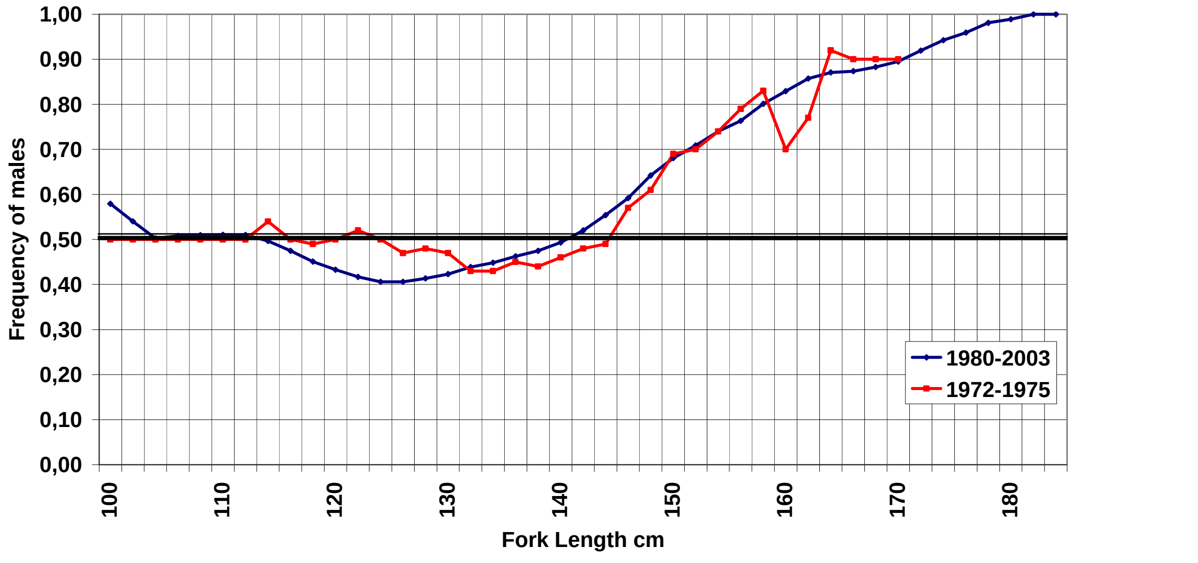

Figure 10. Sex ratio at size of yellowfin, proportion of males, in the Eastern Atlantic observed in 1975 and in 2003. The excess of female at intermediate large sizes is highly significant (Chi2 test) because of the large numbers of fish samples at these sizes.

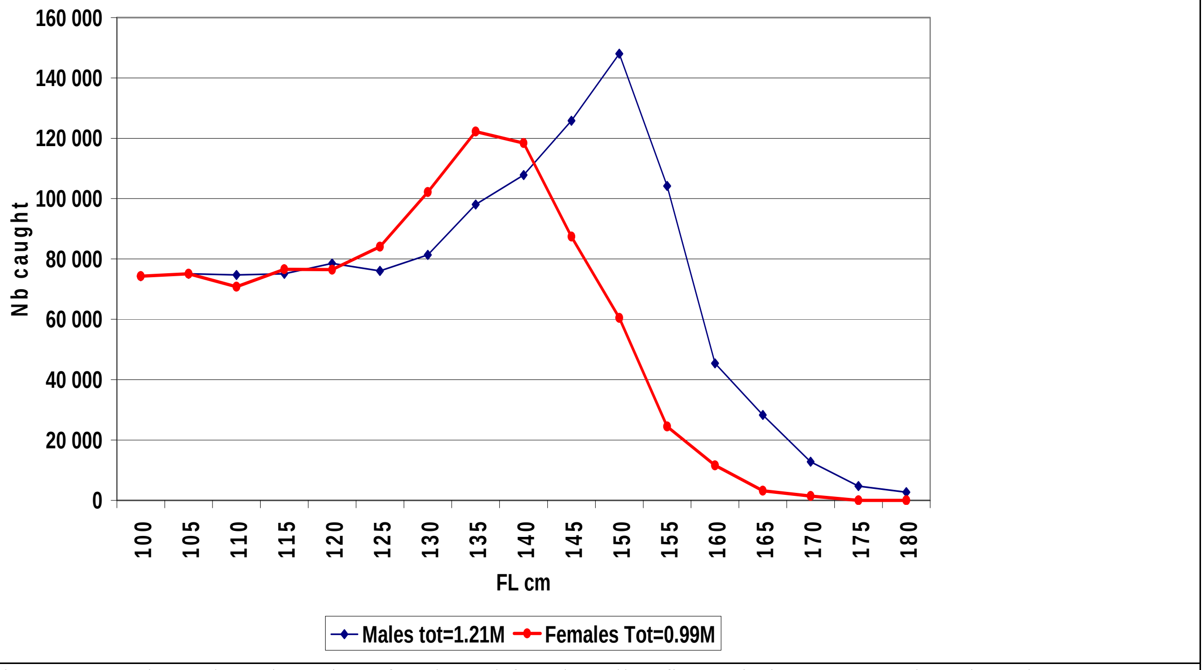

Figure 11. Estimated catch at size of male and female yellowfin, period 1987-2006, based on the average sex ratio at size observed.

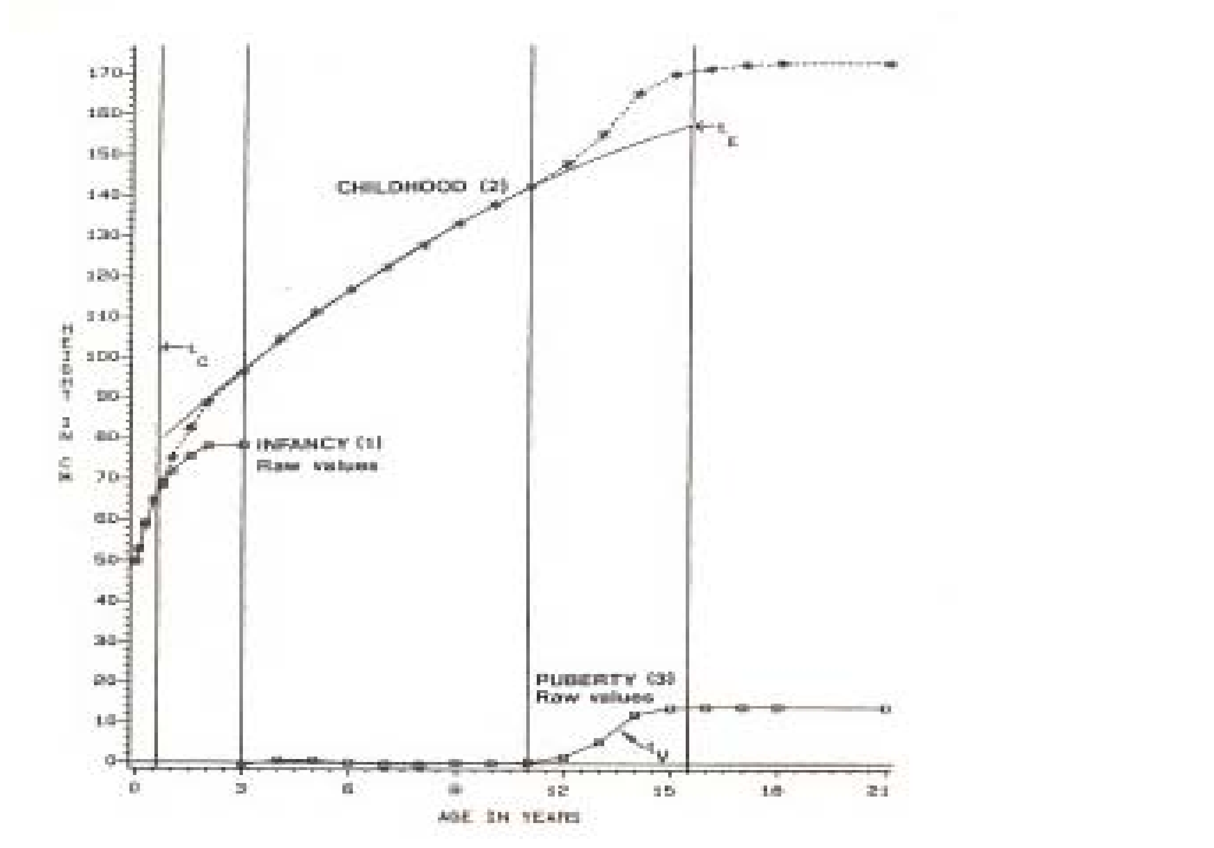

Figure 12. Overview of human growth pattern (taken from Karlberg 1987).

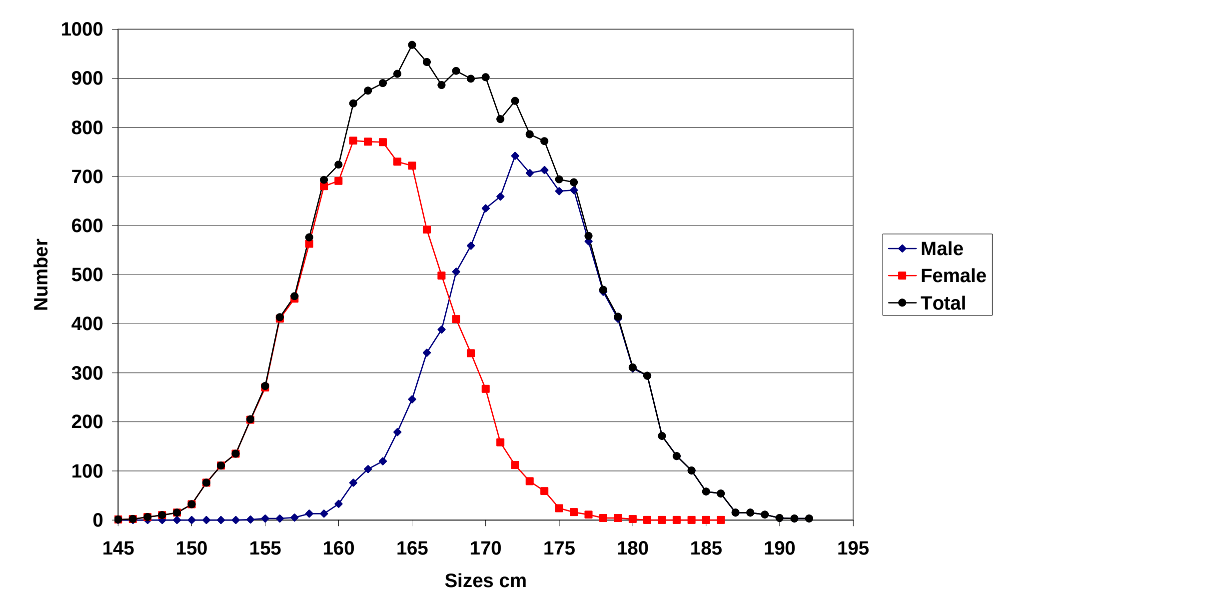

Figure 13. Frequency of adult human males and females in a sample of 10,000 Caucasians in 1960. The combined frequency of the 2 sexes is also shown.

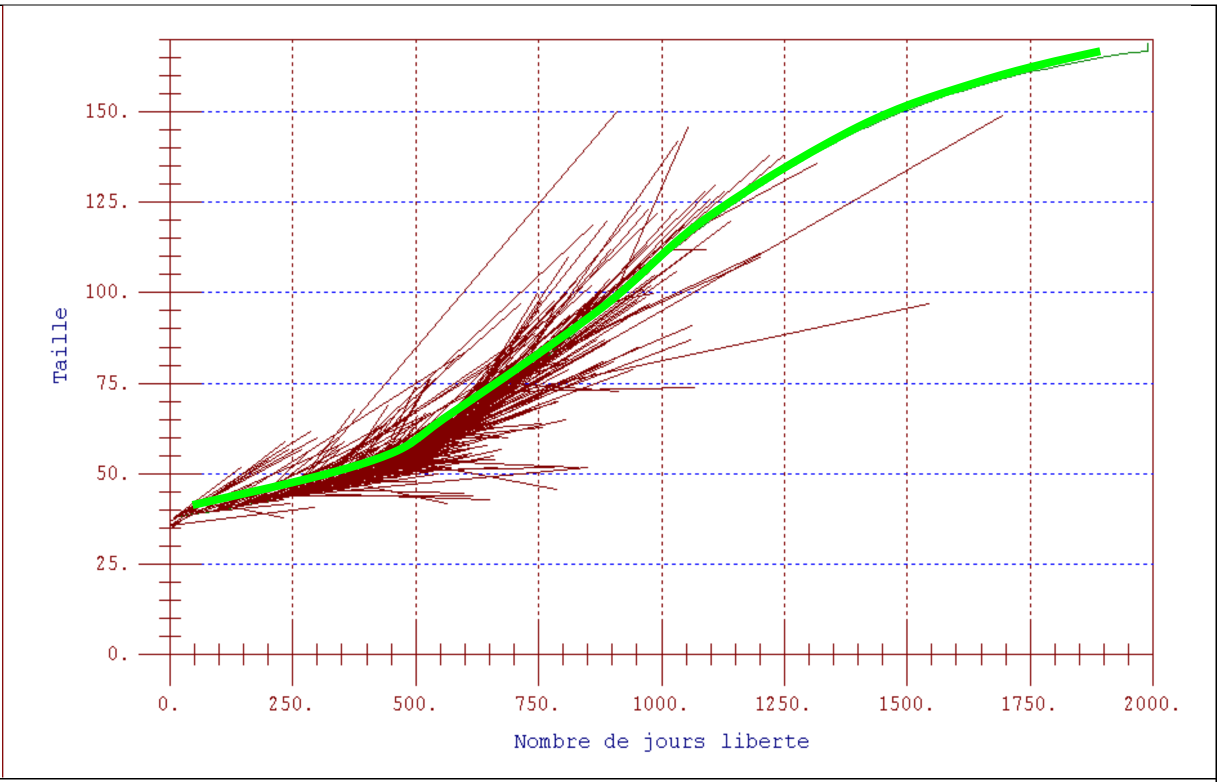

Figure 14. Plotrec graph showing the Gascuel *et al.* (1992) yellowfin growth curve and recoveries available at the time of the study.

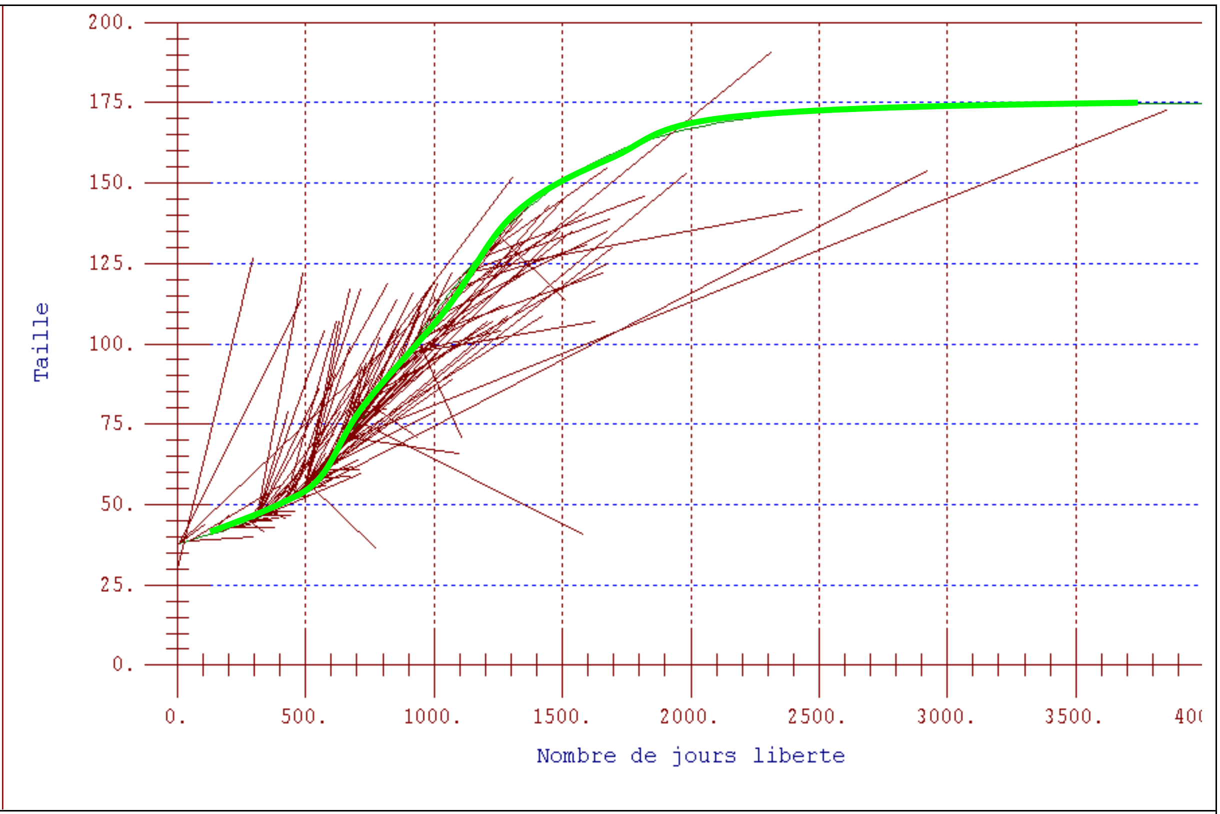

Figure 15. Plotrec graph showing the Gascuel *et al.* (1992) growth curve and recoveries obtained since 1990 (after this study).