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GROWTH OF BIGEYE TUNA (*THUNNUS OBESUS*) IN THE EASTERN ATLANTIC OCEAN FROM TAGGING-RECAPTURE DATA AND OTOLITH READINGS

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SUMMARY

*Growth of bigeye tuna (*Thunnus obesus*) in the eastern Atlantic Ocean is studied from (1) 625 bigeye tagged and recaptured with a fork length (FL) range 37-124 cm, (2) otoliths collected on 108 bigeye in Dakar from which 83 were use to validate the growth ring deposit by oxy-tetracyclin antibiotic injection, and (3) otoliths from 147 bigeye collected in Abidjan. For otoliths, the sizes of Dakar bigeye range from 37 cm to 112 cm FL (almost all juveniles), those from Abidjan from 29 cm to 190 cm (juveniles and adults). Growth curves obtained from the two different sets of data are similar so all data are combined to give a single growth curve for bigeye with K=0.180 yr^{-1} , L_∞ = 217.3 cm and t_0 = -0.709 year. The interest of this approach is the confirmation of the daily rate for ring deposit on otoliths and the use of both tagging and otoliths' reading to estimate growth parameters.*

RÉSUMÉ

*La croissance du patudo (*Thunnus obsesus*) dans l'Atlantique Est est étudiée à partir de (1) 625 patudos marqués et recapturés d'une longueur à la fourche (LF) de 37 à 124 cm, (2) des otolithes de 108 patudos collectés à Dakar dont le dépôt des anneaux de croissance a pu être validé pour 83 d'entre eux par l'injection d'antibiotique oxy-tetracycline et (3) les otolithes de 147 patudos collectés à Abidjan. Pour les otolithes, les tailles des patudos de Dakar s'étalent de 37 à 112 cm de LF (presque tous des juvéniles), celles d'Abidjan de 29 cm à 190 cm (juvéniles et adultes). Les courbes de croissance obtenues de ces deux jeux de données sont équivalentes aussi les données sont combinées et fournissent une courbe de croissance de K = 0.180 an^{-1} , L_∞ = 217.3 cm et t_0 = -0.709 an. L'intérêt de cette étude réside dans la confirmation du rythme journalier de dépôt des stries des otolithes et dans l'utilisation combinée des données de marquage et de lecture d'otolithes pour évaluer les paramètres de croissance.*

RESUMEN

Se estudia el crecimiento del patudo (Thunnus obesus) *en el Atlántico este a partir de (1) 625 patudos marcados y recapturados de una longitud a la horquilla entre 37-124 cm, (2) otolitos de 108 patudos recogidos en Dakar, de los cuales se ha podido validar el depósito de los anillos de crecimiento para 83 mediante inyección de antibiótico oxi-tetraciclina y (3) otolitos de 147 patudos recogidos en Abidján. Respecto a los otolitos, las tallas del patudo de Dakar oscilan entre 37 cm y 112 cm FL (casi todos juveniles), y las del patudo de Abidján entre 29 cm a 190 cm (juveniles y adultos). Las curvas de crecimiento obtenidas de los dos conjuntos diferentes de datos son similares, por lo que se combinan todos los datos para facilitar una única curva de crecimiento para el patudo con K=0,180 yr^{-1}, L∞=217,3 cm y t_0= -0,709 por año. El interés de este enfoque reside en la confirmación de la tasa diaria de depósito de anillos de otolitos y en la utilización combinada de los datos de marcado y de lectura de otolitos para evaluar los parámetros de crecimiento.*

KEYWORDS

Bigeye tuna, Thunnus obesus, Growth curves, Otoliths, Tagging-recapture data, Atlantic Ocean

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1 Introduction

From 1996 to 2000 a research program, called MAC for "Mattes de thons Associées aux Canneurs", was implemented on the school associated fishing technique developed in the 80's by Dakar baitboats (Fonteneau *et al.* 1996; Hallier and Delgado 2000; Hallier *et al.* 2001). Tagging was one of the research tools used by this program and 3102 bigeye were tagged and released. Growth studies were not an objective of the program but scientists took this opportunity to collect data necessary for this kind of study. At the same time, the Bigeye Tagging Year Programme (BETYP) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) started in 1999 for a four-year duration. Within the framework of this programme, bigeye growth study was implemented within MAC program by collecting and reading otoliths. This document is presenting bigeye tuna growth results based on those two sources of data.

2 Materials and methods

2.1 Otolith's collection

A total of 376 bigeye tuna caught by Dakar baitboats off west coast of Africa were injected with OTC during the tagging operations listed in § 2.5. All together 219 OTC injected bigeye tunas were recaptured which yielded 108 readeable otoliths but only 83 presented well-marked OTC marks that can be used for the validation process of the ring deposit rate. As bigeye caught by baitboats from Dakar are almost all juveniles (FL < 110 cm), adults bigeye were sampled in Abidjan together with juveniles. A total of 147 otoliths coming from French purse seiners fishing in the Gulf of Guinea were collected at canneries during thawing operations. The size distribution of the 255 bigeye whose otoliths were read is given in **Figure 1**. According to bigeye stock structure in the Atlantic Ocean, fish sampled belong to the same stock.

2.2 Otolith preparation

Sagittae were extracted from each fish and stored in a small numbered plastic jar. Later, at the laboratory, they were cleaned in sodium hypochlorite (household bleach), rinsed in distilled water and air-dried. Otoliths were prepared according to the methods described in Secor *et al*. (1992) and adapted for tunas by Stéquert et *al*. (1996).

The right otolith was embedded in a polyester resin (Sody 33) and a transverse section was made with a low-speed Buehler Isomet saw to obtain a slice containing the primordium or nucleus. The resulting section was affixed with thermoplastic glue (Crystalbond 405) to a glass side, ground with a 1200 grid wet sand paper and polished with 3 and 1 µm alumina paste until the primordium region was reached. The section was turned upside-down, re-glued, ground and polished again until reaching the primordium and obtaining a thin section of 100 µm maximum. The surface of this section was etched with 5% EDTA (ethylene di-amine tetra acetate, pH=7.1 buffered with KOH) to emphasize the increments used to estimate the age of fish. Duration and quality of etching were monitored under light microscope equipped with a 100x immersion objective.

2.3 Age reading

Micro-increments were counted under a light microscope (Olympus Model BX 40) with a 10x ocular and a MPL 100x dry objective, permitting a theoretical resolution of approximately 1 µm structures. Three independent counts (each one was made at different times without prior knowledge of the previous one) were realized by one reader from the nucleus to the edge of the ventral part of the transverse section, along the counting path (CP) (**Figure 2**). For control purpose, some otolith readings with a Scanning Electron Microscope (SEM) were performed and revealed that, for larger fish, the resolution power of the light microscope was not sufficient. Therefore, 44 otoliths from 47 cm to 190 cm FL tunas were read with SEM.

2.4 Validation

This process is set to confirm that only one increment is laid down each day. For that, the number of increments from the OTC mark to the ventral edge of the otolith is compared to the number of days at liberty.

Concentrations of OTC (oxy-tetracycline) used for injections were 50 mg per kg of fish weight. Sagittae were prepared as the others but observations of sections were done under ultraviolet light (UV) with an epifluorescence microscope (Leica Model DMRE). Filter used is the D (epireflective light) from Leica with an excitation wavelength from 355nm to 425 nm. On each otolith section, the exact position of the OTC mark was plotted with the software TNPC® on the picture obtained without UV light. Then, counts were done under Olympus light microscope as for normal otoliths and the picture was used to identify the increment corresponding to the OTC mark.

2.5 Tagging-recapture data

Mainly ordinary "spaghetti" tag were used during MAC program. But during BETYP, some sport designed tags, called Betyp tags were used together with traditional tags. Tagging procedures and data collection used during MAC were standard (Kearney 1982).

When tagging operations were conducted on board baitboats, fishing mainly in the north of Mauritania, and when tunas were recaptured, lengths were recorded to the nearest centimetre or half-centimetre as well as dates in order to calculate growth and time at liberty. Only fish with accurate size and known dates and positions at tagging and at recapture are used for growth study. Accuracy of dates and positions are often related. For instance an approximated date will always be associated to an approximated position; tags with this type of records were not retained.

To take into account a possible stress following tagging which could affect growth of the fish, only fish with more than 14 days at liberty are retained. This is a normal procedure in tag-recapture studies for growth.

Two types of measurement errors can affect fish growth either at tagging or at recapture. A size at recapture lower than the size at tagging is obviously a measurement error that will result in a negative growth. This result can come either from a measurement error on size at tagging (too high) or from a measurement error at recapture (too low). We can call this error a type I measurement error. But all types-I errors will not produce a negative growth, they can just result in a slower growth rate. Therefore, the removal of all fish with negative growth will eliminate only part of type-I errors and will bias the data. Another type of measurement error (type-II) will result in a growth rate too fast. A tagging size lower than reality or a recapture size higher than reality will result in a faster growth rate. If it is not too great, it is difficult to detect from fish having a faster growth rate than others. Only large type-II errors can be detected by an abnormal high growth rate. But this is not easy to set the edge between a fast growing fish and a measurement error type-II. In these conditions, removing some of the fastest growth rates except for those that are too obvious can easy bias data.

When data were recorded, codes on the quality of the measurements or the quality of the staff that measured the fish and recorded the recapture data were registered. When the tagger had some doubt on his measurement a code 1 was given to the size, otherwise the size code was 2 (accurate size). When the size at recapture was recorded the same procedure for the accuracy of the measurement was noted. The place where the recapture was discovered (on board, in port at unloading, in canneries) and the quality of the staff (member of the scientific team, or other staff – fisherman, stevedore, worker) were also coded. Therefore, to avoid most of the measurement errors, it was decided to consider only the fish with the highest quality codes. Consequently, only the fish with sizes at tagging and at recapture with the code 2 and whose recapture data were recorded by scientific staff were kept for this study. On the 1597 bigeye recaptured in MAC program, only 625 were retained according to the selection given above.

The distributions of the size frequencies of tagged and recaptured bigeye used in this study are given in **Figure 3**.

2.6 Growth methods

2.6.1 von Bertalanffy growth model

Both tagging data and otoliths data were adjusted to the von Bertalanffy equation.
The original von Bertalanffy equation is written as a differential equation and under the following hypothesis: growth in weight =anabolism-catabolism with anabolism proportional to body surface (in l^2) and catabolism proportional to body weight (in l^3). Then, we can written:

$$\frac{dw_t}{dt} = \frac{dl_t^3}{dt} = 3l_t^2 \frac{dl_t}{dt} = \alpha l_t^2 - \beta l_t^3$$
$$\Rightarrow \frac{dl_t}{dt} = \frac{a}{3} - \frac{b}{3} l_t = A - Bl_t \quad (1)$$

with A and B as constants.

1) To estimate K, L_∞ and t_0 from *n* couples of data {age, length} coming from otoliths reading, the equation (1) is integrated between t=0 and t and $l_{(t=0)}$ and $l_{(t)}$

$$\int_0^l \frac{dl_t}{A - Bl_t} = \frac{-1}{B}\int_0^l \frac{d(A - Bl_t)}{A - Bl_t} = \int_{t_0}^t dt$$

$$\ln\left(\frac{A - Bl_t}{A}\right) = -B(t - t_0)$$

$$\begin{cases} l_t = L_\infty\left(1 - e^{-K(t - t_0)}\right) \\ L_\infty = \dfrac{A}{B} \quad and \quad K = B \end{cases}$$

Based on the hypothesis that measurement errors on l are normally distributed (and no error on the age reading), the parameter estimation is reached by minimizing the negative of the log-likelihood as follows:

$$L_1 = n\ln\left(\sigma_1\sqrt{2\pi}\right) + \sum_{i=1}^{n}\frac{\left(\hat{l}(a_i) - l(a_i)\right)^2}{2\sigma_1^2}$$

2) To estimate K and L_∞ from *m* triplets of data {size at t_1, size at t_2, t_2-t_1}, the equation (1) is integrated between $t=t_1$ and $t=t_2$ and $l_{(t1)}$ and $l_{(t2)}$:

$$\int_{l_1}^{l_2} \frac{dl_t}{A - Bl_t} = \int_{t_1}^{t_2} dt$$

$$\ln\left(\frac{A - Bl_2}{A - Bl_1}\right) = -B(t_2 - t_1)$$

$$\begin{cases} l_2 = \dfrac{1}{B}\left[A - (A - Bl_1)e^{-B(t_2 - t_1)}\right] = L_\infty - (L_\infty - l_1)e^{-K(t_2 - t_1)} \\ l_1 = \dfrac{1}{B}\left[A - (A - Bl_2)e^{B(t_2 - t_1)}\right] = L_\infty - (L_\infty - l_2)e^{K(t_2 - t_1)} \end{cases}$$

When considering that l_1 is measured with accuracy and with the hypothesis of a normal distribution of l_2 measurement errors (or, to the contrary, by admitting that l_2 is measured with accuracy and with the hypothesis of a normal distribution of l_1 measurement errors), the estimation of the parameters is obtained by minimizing the negative of the log-likelihood as follows:

$$L_2 = m\ln\left(\sigma_2\sqrt{2\pi}\right) + \sum_{i=1}^{m}\frac{\left(\hat{l}_2(i) - l_2(i)\right)^2}{2\sigma_2^2}$$

3) To combine the two set of data (otoliths and tag-recapture), we calculate $l_{(a)}$ and $l_{(recapture)}$ with the help of the two following equations and with the same set of parameters K, L_∞ and t_0 :

$$\begin{cases} l_a = L_\infty\left(1 - e^{-K(a - t_0)}\right) \\ l_2 = L_\infty - (L_\infty - l_1)e^{-K(t_2 - t_1)} \end{cases}$$

Then, we minimize the following negative log-likelihood by setting the ratio $\dfrac{\sigma_1}{\sigma_2}$:

$$L_3 = L_1 + L_2 = n\ln\left(\sigma_1\sqrt{2\pi}\right) + m\ln\left(\sigma_2\sqrt{2\pi}\right) + \sum_{i=1}^{n}\frac{\left(\hat{l}(a_i) - l(a_i)\right)^2}{2\sigma_1^2} + \sum_{i=1}^{m}\frac{\left(\hat{l}_2(i) - l_2(i)\right)^2}{2\sigma_2^2}$$

Kirkwood (1983) designed another approach to combined age-at-length and tagging data to obtain the von Bertalanffy parameters. But this other approach is not tested in this document.

4) We also use the FAO Vonbit software (Stamatopoulos and Caddy 1999) to estimate von Bertalanffy growth parameters. This linear regression approach is based on the following assumption.

Given data on size and age: (t_1, L_1), t_2, L_2),….(t_n, L_n), it can be shown that for a given value of K, size can be expressed linearly in the general form

$$L_t = a_0 + a_1 X_t \qquad (1)$$

where a_0 and a_1 are parameters of a simple linear regression and the independent variable X_t is a function of t. Expression (1) on length at age does not depend on a knowledge of the secondary parameters L_∞ and t_0. The constant a_0 represents size at any age t_a and the coefficient a_1 refers to size increase over the period t_a and any other age t_b. The general expression (1) can take two convenient forms:

$$a_0 = L_\infty \qquad a_1 = -L_\infty e^{Kt0} \qquad X_t = e^{-Kt} \qquad (1a)$$

$$a_0 = L_0 \qquad a_1 = L_0 - L_\infty \qquad X_t = e^{-Kt} - 1 \qquad (1b)$$

Expression (1a) is the familiar von Bertalanffy growth function as rearranged by Beverton (1954) and Beverton and Holt (1957) where t_0 represent age at which length is zero, and L_∞ an asymptotic maximum length reached when age increase in definitively.

Expression (1b) is the original von Bertalanffy equation (1938) using the same principle of an asymptotic L_∞ and a constant L_0 to express a theoretical length at age zero.

In this approach the driving parameter is K, trials values of which each generate a regression line (1) with an associated coefficient of determination R^2. The optimum K is the value for which R^2 is closest to 1. Once this optimum has been established the secondary parameters L_∞, t_0 and L_0 can be computed directly, using expressions (1a) and (1b), the value of optimum K and any two estimated sizes L_i and L_j.

2.6.2 Other growth models

With the length at age data from otolith readings, two other growth models were also tested:

- Gompertz growth model expressed by $FL_t = L_\infty\ e(-ae^{-Kt})$
- Richards growth model expressed by $FL_t = L_\infty/(1+e^{(-Kt+b)})^m$

where
FL_t = Fork Length at age t;
L_∞ = asymptotic Fork Length
K = growth coefficient
t_0 = theoretical age for FL = 0;
a, b and m = parameters

3 Results

3.1 Growth equation from otolith reading

3.1.1 Validation of bigeye tuna age

The reading of the 83 OTC otoliths in relation with the time at liberty is given in **Figure 4**. The distribution of the data in two sets: one between 10 and 119 days at liberty and another between 243 and 412 days is due to the seasonality of the fishery. The bigeye tagged between the 14/08/1999 and the 29/11/1999 were recaptured between the 01/09/1999 and the 11/03/2000 and then between the 27/06/2000 and the 14/11/2000. Between these two periods, the fish moved outside the fishery area and the fishery became less active.

As the slope of the line is very close to 1 (0.97), this confirms the laying of one micro-increment per day for bigeye between 44 and 95 cm FL.

3.1.2 Otolith reading

At first all otoliths were read under the light microscope (LM) but the comparison of growth curves obtained from tagging-recapture data and otolith readings showed a significant difference for larger fish underlying a possible underestimation of their ages. In order to test this assumption, the width of increments from the nucleus to the edge of the otolith was measured on a transverse section (**Figure 5a**). Above 2.2 mm from the nucleus, the width of the increment corresponds approximately to the LM resolution. **Figure 5b** shows that this threshold corresponds to a fork length of about 110 cm. Lehodey and al (1999) found this same limit for otolith readings of bigeye from the Western Pacific Ocean. This means that, for fish more or less around this size, the width of some of the increments might be to small to be counted under the light microscope. Then, it was decided to read 44 otoliths under SEM. Most fish chosen (34 out of 44 fish) were those with FL above 100 cm and up to 190 cm. But to be certain that small increments not unreadable under the LM were not present in fish with FL under 100 cm, 10 bigeye between 47 and 99 cm were also read with SEM. The plot of the differences in increment counts between SEM and LM is on **Figure 6**. Data were adjusted with a linear regression and the best fit was obtained with the linear regression equation given on the figure. Accordingly, there is no difference in increment counts between SEM and LM for fish with FL lower than 73.6 cm. Therefore, all counts of LM for fish greater than this length and not read with SEM were adjusted accordingly. The result is a file with for each fish its length (in cm) and the corresponding increments or age in days that can be then adjusted by a growth curve.

3.1.3 von Bertalanffy growth equation with otolith reading data

Data from the previous file are fitted to a von Bertalanffy function by using the minimum likelihood of the sum of square between the predicted length and the observed length. This is solved in an Excel file. Growth curve parameters obtained are L_∞ = 207.43 cm, K = 0.202 (year^{-1}) and t_0 = -0.613 year (**Figure 7**).

The same set of data was used with FAO Vonbit software which is based on a linear regression method for fitting the von Bertalanffy growth function. The growth parameters obtained are L_∞ = 206.976 cm, K = 0.203 (year^{-1}) and t_0 = -0.616 year and are very close to the previous ones.

3.1.4 Other growth equations with otolith reading data

Gompertz and Richards growth equations were also fitted to this set of data and results are given in **Table 1** together with those from otolith and tagging data.

3.2 Growth equation from tagging recapture

After the data selection described in the materials and methods section (§ 2.5), the 625 tagging-recapture data that remained were fit to a von Betalanffy model with L_∞. = 195.54 cm and K = 0.206 (year^{-1}). There is no estimation of t_0. To construct the curve the t_0 obtained from the otolith growth curve can be used and the corresponding curve is on **Figure 8**. The tagging-recapture data are well distributed around the growth curve; this is illustrated on **Figure 9**.

3.3 Growth equation from the combined tagging and otolith data

The combined data are fitted to a von Bertalanffy equation with L_∞. = 217.28 cm, K=0.180 and t_0 = -0.709.

4 Discussion

4.1 Size sample and age reading

The size of bigeye used in this otoliths study, is spreading over a wide range (from 29 cm to 190 cm) and even if fish larger than 90 cm FL represent only 13.3 % of the sample, every 10 cm class between 91 to 190 cm contains between 1 to 7 fish.

The study proved that the reading of otoliths increments for fish larger than 74 cm has to be made with a scanning electron microscope (SEM), otherwise age will be underestimated for a given size and consequently L_∞ will be much larger.

4.2 Validation

The reading of otolith marked with OTC showed that OTC marks are associated with a more or less thick mark that could not be readable even with SEM. It is presumed that this phenomenon is associated to the stress bear by the fish when it is caught, tagged and injected with OTC; this stress being more or less pronounced according to fish (i.e. the mark being more or less thick according to fish). This is why fish with time at liberty less than 10 days were rejected.

Because 1) OTC injected bigeye are all juveniles, 2) they were almost exclusively recaptured when still juveniles (overall only 3.5 % of bigeye recaptured were greater than 100 cm FL) the validation of the rate of increment deposit per day was only confirmed for juvenile bigeye (the greater bigeye was 95 cm FL at recapture). The rate of deposit of one increment per day is therefore validated only for bigeye with FL lower than 96 cm. However, when the assumption of this one day rate is made for all size bigeye, the von Bertalanffy parameters obtained are very similar to those obtained from tagging recapture data (**Figure 10**). We can therefore admit that the one day rate is valid during the all life of bigeye tuna (cf references CSIRO and IATTC on bigeye and yellowfin tuna).

4.3 Tagging-recapture

The study of tuna behaviour in the associated school fishing technique, where tagging was performed, supports the idea that tuna experienced some stress when tagged that can affect their behaviour (Bardon, 2002). The duration between tagging and the return of tagged fish to a normal behaviour was estimated between 2 and 7 days by Bardon (2002) according to species and sizes. The return to a normal behaviour was appreciated as the time when the number of recapture after tagging was at its maximum. This perturbed behaviour was also noticed for tunas tagged with archival tags. This perturbed behaviour might have some effect on the growth. Therefore, we chose to exclude fish with time at liberty less than 15 days in order to minimise this possible effect of tagging stress on the growth of the fish. However, one can argue that to minimise this effect, it might be necessary to keep only the fish with larger times at liberty. To test the effect of these fish with short time at liberty, we delete all bigeye with time at liberty less than 61 days (about 2 months) from the file. The values obtained (L_∞ = 213.78 cm and K = 0.176 year^{-1}) are close to the otolith values and even closer to the combined values.

4.4 Comparison to other growth curves

The Gompertz and Richards models give L values too low (lower than 180 cm) while bigeye with larger FL are not rare in catches especially in longline fisheries.

Bigeye growth has been studied by various methods in all major oceans : length frequency (Shomura and Keala, 1963; Kume and Joseph 1966; Suda and Kume 1967; Champagnat and Pianet 1974; Marcille *et al.* 1978; Weber 1980; Pereira 1984), tagging data (Cayre and Diouf 1984; Miyabe 1984; Hampton *et al.* 1998) and sclerochronology with scales (Yukinawa and Yabuta 1963), vertebraes (Alves *et al.* 2002), rays (Gaikov *et al.* 1980; Draganik and Pelczarski 1984; Delgado de Molina and Santana 1986; Sun *et al.* 2001) and otoliths (this present study, Lehodey *et al.* 1999) in Atlantic, Pacific and Indian oceans. Some of these results are compared in **Table 2** by giving the size for each year from 1 to 14 and are illustrated in **Figure 11**. Clear *et al.* (2000) used bigeye otoliths for age determination but they were able to identify annual increments instead of daily increments.

We will not discussed here the differences between all those curves, it is just necessary to mention that the growth curve from this study is situated in the middle of most curves and it presents the advantage of being the combination of two different approaches. Each of the different data set is giving very similar results especially if only tagged fish with time at liberty more than 2 months are considered. The advantage of this work is to validate the daily rate of otolith increments for bigeye tagged and injected with OTC and recaptured over one and an half year. The daily rate has been then applied to bigeye over a wide range of sizes (29-190 cm FL). The growth parameters obtained have been compared to those from tagging-recapture data giving even more strength to their values because of their similarity. It will be interesting to recapture OTC tagged bigeye with a much longer time at liberty. This is still possible as bigeye is a long living species and all tagged fish were juveniles. As well, tagging adult bigeye can bring some more information on the growth rate of large bigeye from tagging-recapture data. Furthermore, there might be some differences in growth rates according to areas or oceans or between surface and deep swimming bigeye. However, on the different studies, some were based on surface caught bigeye and others on longline caught fish and they were from different areas and oceans. Parameters values do not seem to be related to these factors but more to the method used (length frequency, tagging data, hard part age reading).

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Table 1. Estimated parameters of the growth models for bigeye tuna, *Thunnus obesus*, (all sexes, n=255 for otolith data and n=625 for tagging data) in the eastern Atlantic Ocean (FL in cm, t_0 in years).

Growth models	L_∞	*K*	t_0	*A*	*b*	*m*
von Bertalanffy otoliths	207.43	0.202	-0.613			
von Bertalanffy tagging	195.54	0.206				
Gompertz	179.13	0.4088		1.7268		
Richards	178.63	0.424			-7.185	2280.4

Table 2. Bigeye lengths at each age according to different growth studies.

Year	*Present study 2004*	*Hampton et al, 1998*	*Delgado and Santana 1986*	*Cayre and Diouf 1984*	*Draganik and Pelczarski 1984*	*Kume and Joseph 1966*	*Suda and Kume 1966*	*Gaikov et al. 1980*	*Sun et al. 2001*	*Alves et al. 2002*	*Clea et al 2000*
	Otoliths and tagging	Tagging data	Ray of dorsal fin	Tagging data	Ray of dorsal fin	Length frequency	Length frequency	Ray of dorsal fin	Ray of dorsal fin	Caudal vertebrae	Otolith annual increments
1	54.8	28.4	55.9	44.5	45.8	30.6	40.9	45.8	68.8	48.2	74.2
2	81.5	72.7	80.9	70.2	81.3	80.0	73.4	78.8	94.3	72.6	97.8
3	103.9	101.7	101.8	93.2	109.6	113.9	99.8	106.6	115.1	94.2	115.4
4	122.6	120.5	119.1	113.8	132.0	137.0	121.3	130.0	132.2	113.4	128.6
5	138.2	132.9	133.6	132.1	149.8	152.8	138.8	149.7	146.1	130.5	138.5
6	151.2	140.9	145.7	148.5	164.0	163.6	153.0	166.2	157.5	145.6	145.9
7	162.1	146.2	155.7	163.1	175.3	171.0	164.6	180.1	166.8	159.0	151.4
8	171.2	149.6	164.1	176.2	184.2	176.1	174.0	191.8	174.4	170.8	155.6
9	178.8	151.8	171.1	187.8	191.3	179.5	181.6	201.7	180.7	181.4	158.7
10	185.1	153.3	176.9	198.3	197.0	181.9	187.8	210.0	185.8	190.7	161.0
11	190.4	154.2	181.8	207.6	201.5	183.5	192.9	216.9	190.0	199.0	162.7
12	194.9	154.8	185.8	215.9	205.0	184.6	197.0	222.8	193.4	206.4	164.0
13	198.6	155.2	189.2	223.3	207.8	185.4	200.3	227.7	196.2	212.9	165.0
14	201.6	155.5	192.0	230.0	210.1	185.9	203.0	231.9	198.4	218.7	165.7

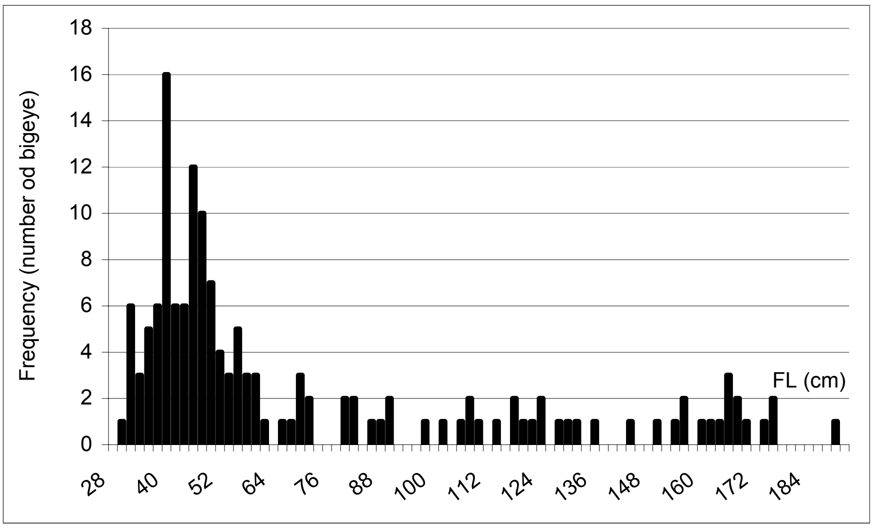

Figure 1. Size distribution of bigeye collected in Abidjan and Dakar and used for otolith growth study.

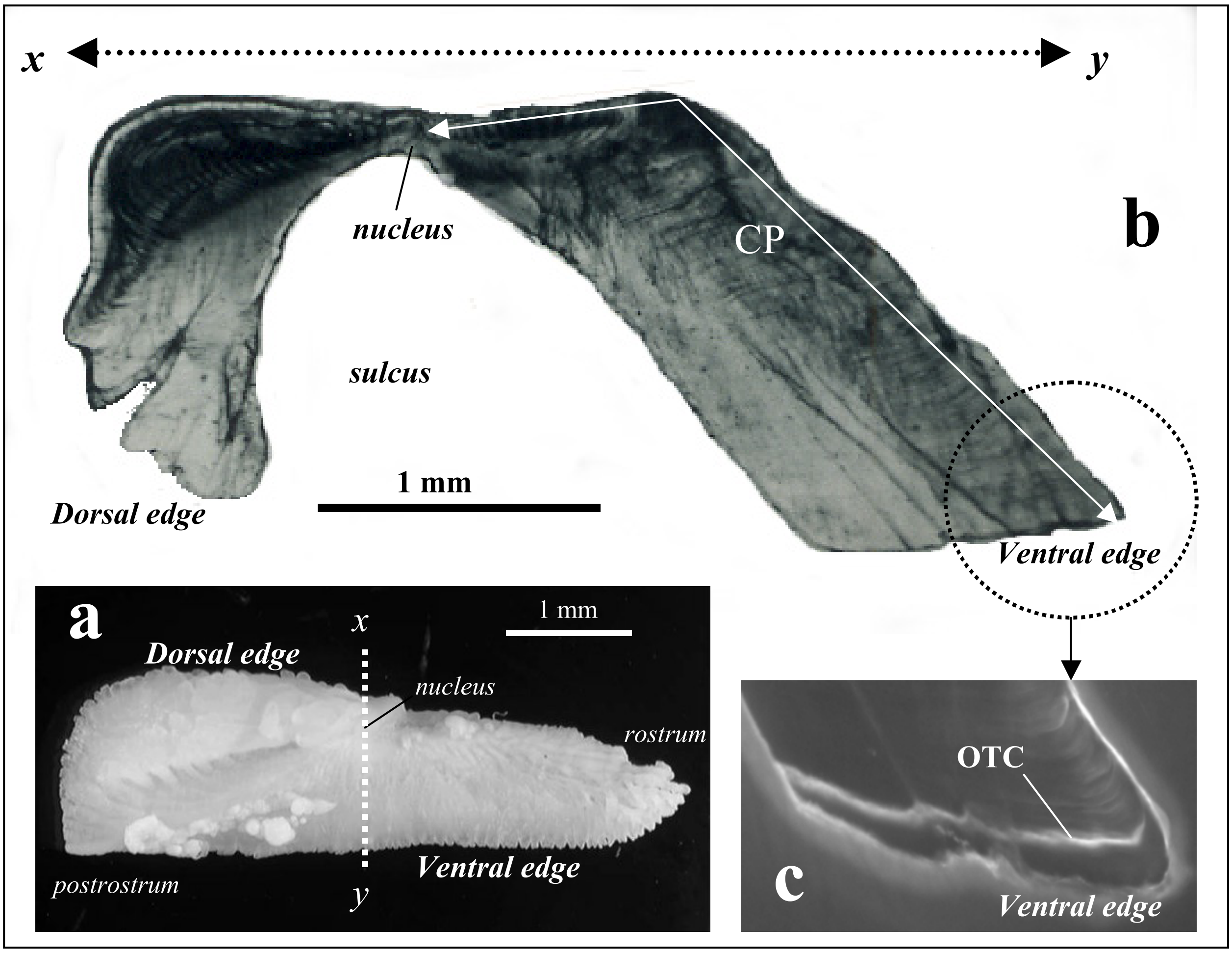

Figure 2. Illustration of (a) the right otolith from a 75 cm FL bigeye; (b) Transverse section of an otolith from an oxy-tetracycline injected of a 116 cm FL bigeye with the type of measurement taken on the otolith and the counting path (CP) of the micro-increments; and c) Detail of the oxy-tetracycline (OTC) mark.

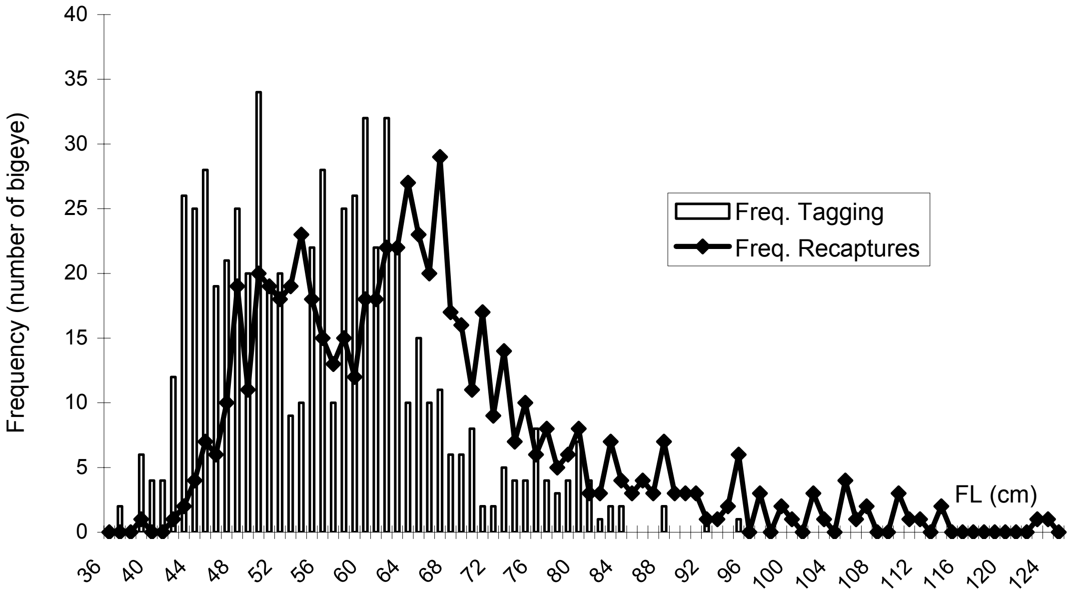

Figure 3. Size distribution of bigeye at tagging and at recapture used for growth study.

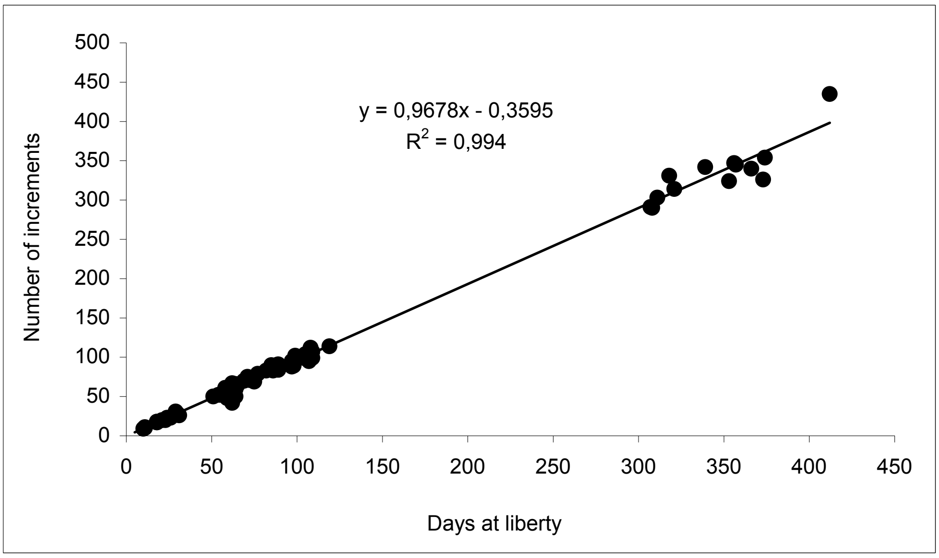

Figure 4. Relation between the number of micro-increments and the time at liberty.

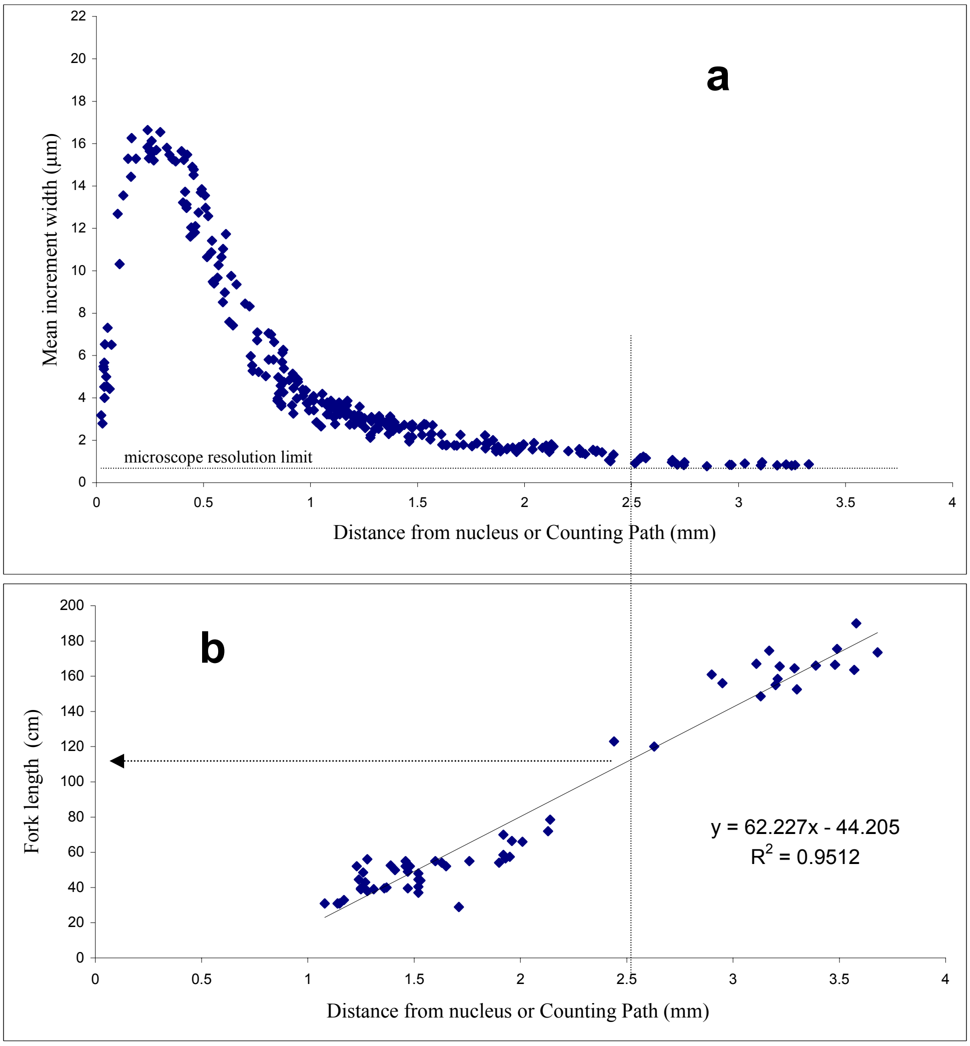

Figure 5. Increment width versus distance from nucleus (a) idem versus bigeye FL (b).

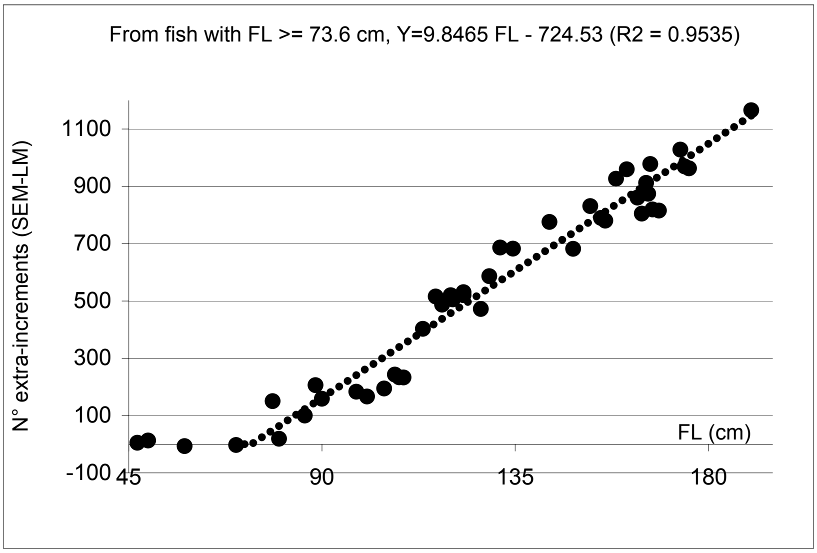

Figure 6. Number of extra-increment counted with the SEM versus the bigeye length.

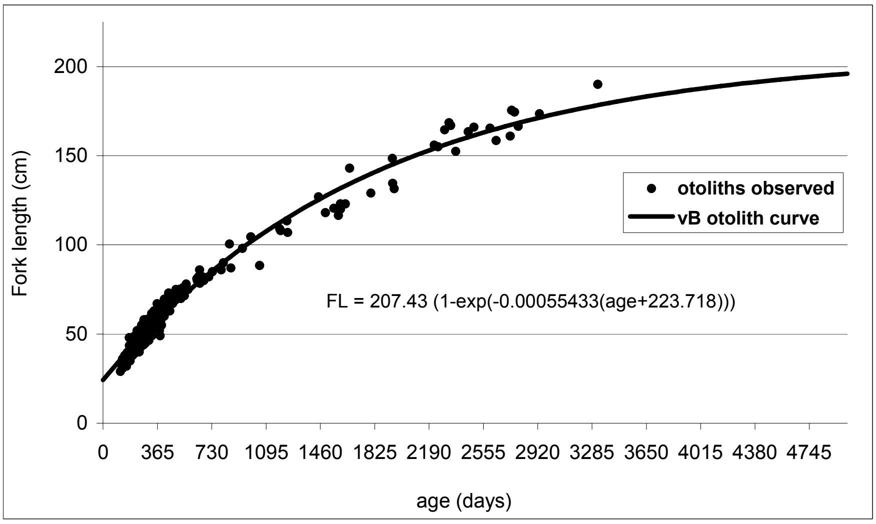

Figure 7. Age of the bigeye (from otolith reading) versus length and the von Bertalanffy growth curve fitted to these data with the corresponding equation.

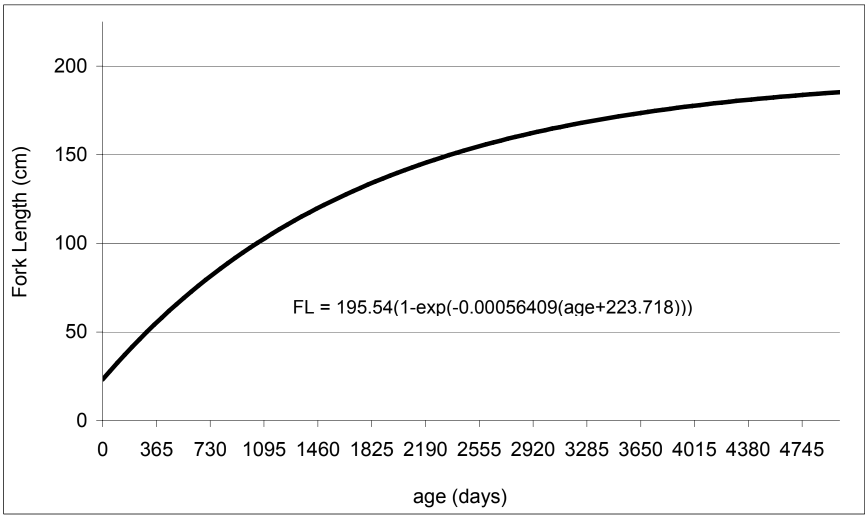

Figure 8. The von Bertalanffy growth curve fitted to tagging-recapture data and with t_0 from the otolith growth equation with the corresponding equation.

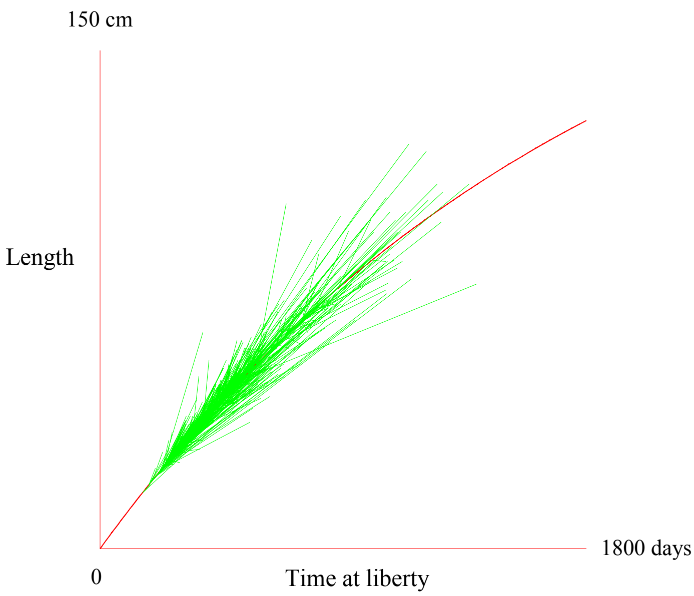

Figure 9. Distribution of tagging-recapture data around the previous von Bertalanffy growth curve.

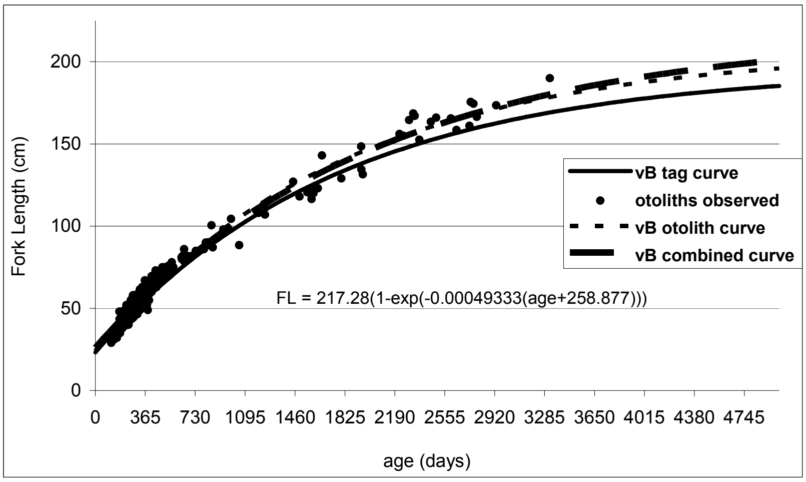

Figure 10. Ages read with otoliths and von Bertalanffy growth curves obtained from otoliths, from tagging-recapture data and from the combined data with the corresponding equation.

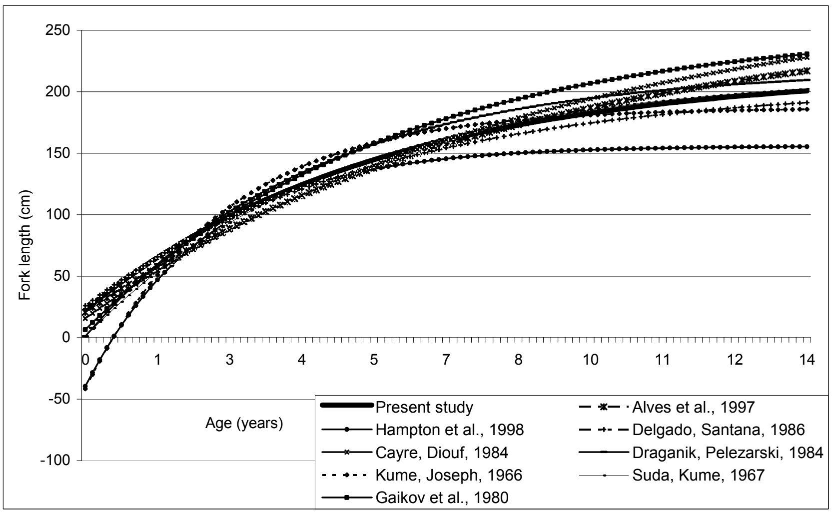

Figure 11. Comparison between the present study growth curve and others obtained by different authors in the Atlantic, Indian, and Pacific Oceans.