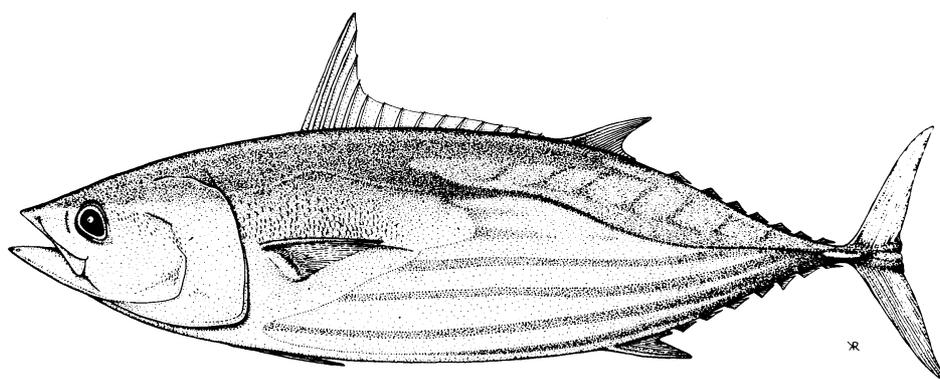


WORKING PAPER YFT-2

**AGE AND GROWTH OF YELLOWFIN TUNA (*THUNNUS ALBACARES*)
FROM THE WESTERN AND CENTRAL PACIFIC OCEAN AS INDICATED BY
DAILY GROWTH INCREMENTS AND TAGGING DATA**

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Foreword: This Working Paper is an update of WP 12 presented at the 11th SCTB. It includes additional results on otolith readings, some error and editorial corrections, and investigate the theoretical effects of the Von Bertalanffy Modified (VBM) growth model on the growth rate and the density of increments of the otoliths. These new results, with the promising preliminary study using length frequencies confirm the previous analysis.

Introduction

Yellowfin tuna (*Thunnus albacares*) inhabit the surface layer of all the warm seas of the world except the Mediterranean sea. Two stocks more or less independent are proposed in the Pacific Ocean: the stock of the Eastern Pacific Ocean (EPO) and the stock of the Western-Central Pacific Ocean (WCPO). The latter is probably the world largest stock for this species. Yellowfin catches in the WCPO have almost doubled since 1980, peaking at approximately 400,000 t in 1993. Yellowfin are caught at a variety of sizes by the various gear types. Longliners land mainly fish >100 cm FL, while purse seiners (and pole-and-line boats) target both small (40–60 cm FL) and large fish.

Yellowfin spawning appears to be Pacific-wide and bounded in its northern and southern extremes by the 26°C surface isotherm. While the occurrence of larvae is continuous across the equatorial Pacific within a zone approximately ten degrees north and south of the equator, three areas of higher larval density have been tentatively recognized: 130–170°E, 180°–160°W and east of 110°W. Spawning occurs year round, possibly with a peak in the November–April period. Some data also suggest different spawning seasons for areas east (March–September) and west (November–April) of 180°. In the eastern Pacific (Suzuki 1994) the smallest female found with mature ovaries was 84 cm, and the estimated length at 50-percent maturity was 95 cm. In the central equatorial Pacific a few yellowfin tuna reach maturity at about 70–80 cm, but recent data collected by the University of Hawaii indicate that the majority do not mature until they reach 100–110 cm. However, the time necessary to attain spawning condition could be linked to food supply (Itano, pers. comm.).

Mark recapture experiments involving tetracycline injection at sea demonstrated that eastern Pacific yellowfin north of the equator deposit growth increments daily on their otoliths in the thawed fork-length range from 40 to 110 cm (Wild and Foreman 1980). Sexual dimorphism has been detected in eastern Pacific yellowfin in terms of growth in length and weight (Wild 1986). Wild (1986), using daily ring methods for yellowfin tuna in the eastern Pacific shows that young females are initially larger than males of the same age, the growth curves cross one another at around age 2 (about 95 cm FL) and thereafter males are larger than females. On the other hand, age and growth studies through the length frequency analysis of yellowfin tuna in the Philippine waters shows that the growth rate of males is higher than that of females (Yesaki 1983, Wild 1994). A consistent feature of all analyses of sex ratio is the rapid decline in the percentage of females at around 140 cm.

From the three oceans, different growth analyses lead to contradictory conclusions about the appropriate growth model for yellowfin tuna. It is not clear if the yellowfin tuna growth follows a classical Von Bertalanffy model or if there are two different growth periods with a slow down period for young fish (FL < 60 cm). Studies from modal analysis for small yellowfin tuna in the Eastern Atlantic (Fonteneau 1980; Bard 1984), in the south-western Pacific (Brouard et al. 1984) and the western Indian Ocean (Marsac and Lablanche 1985) indicate a period of slow growth rate during the juvenile phase. On the other hand, in the eastern Pacific, the growth rate of tagged yellowfin in the length range from 25 to 100 cm does not show an apparent period of decrease (Wild and Foreman 1980).

In this study, we use both otolith counts of daily micro-increments and data from a large tagging experiment to investigate the growth of yellowfin tuna in the western and central Pacific Ocean

(WCPO). Results confirmed the occurrence of a period of slow growth in the juvenile phase of yellowfin in the WCPO. A growth model is proposed by using the classical Von Bertalanffy model with the growth parameter K varying according to a normal distribution. The biological significance of this model is discussed and results are compared to previous studies devoted to yellowfin tuna growth.

Materials and methods

Tagging data

During the Regional Tuna Tagging Project (RTTP) from 1989 to 1992, special efforts were made to tag and release substantial quantities of yellowfin; 30,960 yellowfin were tagged, from which 3,483 (11.2 %) have been recaptured and the tags returned to the Oceanic Fisheries Programme of the Secretariat of the Pacific Community (SPC). The tagging method was similar to that described by (Hampton 1997). Releases were distributed widely throughout the western tropical Pacific from Philippines and eastern Indonesia in the west, to Kiribati in the east (Figure 1). Reported recaptures also spanned this area, reflecting the essentially continuous spatial distribution of the fisheries across the western central equatorial Pacific.

The screening of the tagging data involved selecting returns of yellowfin tuna with reliable dates and measures of fork length (FL) at release and recapture. We rejected also the fish with a time at liberty <30 days to minimize the potential bias in length increment due to the tagging operation. Table 1 gives the aggregated returns by time at liberty. It shows that yellowfin tags have been returned up to 4+ years (maximum 1857 days) after release. The selection criteria were satisfied for 1187 (34.1 %) tag returns for a size range in fork length (FL) between 35 and 160 cm.

Otolith data

During the RTTP, 704 yellowfin tuna otolith samples were collected and a small number of individuals injected with oxytetracycline (OTC) before releasing. Eleven of these fish that were tagged in the Solomon Islands in September-October 1991 were recaptured, and the otolith recovered. Unfortunately, 8 of the 11 returns did not have recapture dates precise enough to allow a reliable assessment. Those samples were sent to Dr A. Wild of the IATTC and Dr Stequert of ORSTOM for reading. Dr Wild used a light microscope and the cellulose acetate replica method (Wild 1986) and Dr Stequert used a scanning electron microscope (SEM) to read a transversal cross-section (Stequert et al. 1995). An additional 68 yellowfin tuna otolith samples were kindly provided by the Centre ORSTOM in Tahiti. These samples were collected during several scientific cruises carried out by the program ECOTAPP in the French Polynesia Exclusive Economical Zone in the central Pacific (Figure 1). The distribution of length frequencies in figure 2 shows that the ECOTAPP sampling provides otolith samples of larger individuals. The main reason explaining this situation is the difference in the type of fishing gear used. The ECOTAPP scientific cruises were longline exploratory fishing cruises whereas the tagging programme used the pole and line for the release phase.

Finally a sub-sample of 180 yellowfin otoliths covering the largest possible size range (20-145 cm in FL) and with the minimum number of individuals of undetermined sex was used (Figure 2). However, the sex of yellowfin tuna <35-40 cm can rarely be distinguished, and as already observed by several authors there was no female for size >140 cm in FL. The samples were prepared according to the methods described in Secor et al. 1992 and Stéquert *et al.* (1995). The transverse cross-sections of otoliths were read under a light microscope (LEICA DMLB 100) at a x400 or x1000 magnification. A few samples were observed with a SEM (Figure 3) at the CSIRO in Hobart to compare and verify the interpretation of the daily rings.

The reading of microincrements was made on the external part of the transverse section. However in some cases the internal zone is also used since the increments in this area are regularly spaced without overlapping. Unfortunately they are very sensitive to the etching and polishing phases and consequently

are not always visible. The reading is directed along the axis of maximum concavity of increments. A sub-sample of 22 otoliths was read by two different readers. The other otoliths were read several times by the same reader. A scale of reliability in the reading was used with three categories: “high” (all the daily rings are visible, very low variability between different counts), “medium” (some missing series but easily extrapolated) and “low” (large missing series of clear daily rings). Only “high” and “medium” categories were then used in the analysis.

Results

Tag returns

Tagging data were used to estimate the monthly growth rate. Ideally, only fish with time at liberty of one month should be retained. But this is obviously not possible since we need a large enough data set. Despite the potential bias that can produce the samples with much longer time at liberty than one month, the tagging data indicate a significant decrease of the growth rate for fish with a size distributed around 50-60 cm in fork length (Figure 4). The mean growth rate is above 3 cm/month before 40 cm, decreases until 2 cm/month at approximately 55 cm and increases until 3cm/month for fish of 80 cm, before decreasing regularly as the length increases.

Otolith readings

The results of counts carried out by Drs Wild and Stequert on the OTC marked otoliths are presented in Table 2, and an example of a SEM view for one of the three samples is shown on Figure 5. Both counts are very consistent with a daily deposit of increments on the otolith. This result, with those of Wild et al. 1995) in the Eastern Pacific, and Uchiyama and Struhsaker (1980) and Yamanaka (1990) in the Central Pacific, would indicate that yellowfin tuna deposit one increment each day in their sagittal otoliths throughout the Pacific, at least in the size ranges investigated (25-110 cm). However, Dr Wild concluded that yellowfin otoliths from the western Pacific were much more difficult to interpret and showed greater variability in increment spacing than those from the eastern Pacific.

For 17 of the 22 otoliths of the sub-sample read by two different readers, the difference does not exceed $\pm 6\%$ and no systematic bias occurs between readers since the difference is centered on zero. The reliability in counts for fish < 60 cm is high, but the reading becomes more and more difficult as the size of fish increases (Figure 6). Systematically, for fish of same size, counts of low credibility have less daily rings than counts of medium or high credibilities.

The fits of the Von Bertalanffy (1) growth models to the age estimated with daily rings counts were tested by using a nonlinear least-square regression program (SPSS 1998).

$$L_t = L_\infty [1 - \exp(-K(t - t_o))] \quad (1)$$

L_t is the fork length (cm) at age t (year), L_∞ is the asymptotic fork length (cm), K is the growth coefficient, t_o is the t-axis intercept. The figure 7, showing the growth curve and the residuals, suggests that the von Bertalanffy model is not really satisfactory to describe the growth of yellowfin tuna over the whole size range. The growth appears to slow down during the first phase of the life with a maximum decrease between ages of 0.5 to 1 year, for a fork length corresponding approximately to 45 and 70 cm respectively. It is clear that a growth model that would follow the variation in growth observed from these otolith should present three inflexion points, making useless the other growth models usually proposed in the literature (such as Gompertz, logistic, Richards or generalized von Bertalanffy models).

On a sub-sample of 20 otoliths, the variation of the increment density has been investigated along the transverse section. From part to part, several counts of increments inside areas of 50 microns were related to the age in days of the fish in the center of these areas. The change in density increments are

presented on figure 8, using a lowess function to facilitate the interpretation of the superimposed data series. Despite an evident individual variability, there is a clear pattern with two phases of increasing density separated by a period of low or stable increase of increment density. The plateau starts after age 250 (± 50) days (0.7 yr) and finishes after age 450 (± 50) days (1.2 yr). The overall pattern indicates a period of low increase in increment density related to the period of somatic growth increase immediately following the maximum observed decrease (Figure 7).

Modified von Bertalanffy (MVB) growth model

Our results from otoliths and tagging data together with similar observations and the two stanza growth pattern already proposed by several authors give consistent information that necessitate to reconsider the growth model of the yellowfin in the western Pacific. For reasons detailed in the discussion, we can hypothesize that during the pre-adult phase, some physiological or behavioral changes, possibly linked to the environment, result in a deficit of somatic growth. Due to the individual variability over the yellowfin tuna population, the age at which this change occurs in the WCPO would be distributed around a mean age and distributed according to a normal distribution. Therefore, we can describe such a change in the growth rate by introducing in the growth model a variation of K according to a normal distribution. This is made by replacing K by $K-N(t)$ in equations (1) with $N(t)$ the normal distribution (2) :

$$N(t) = \frac{a}{s\sqrt{2p}} \exp\left[-(t - t_m)^2 / (2s^2)\right] \quad (2)$$

where t_m is the mean age (year) in the yellowfin population when the deficit in growth occurs, s is the standard deviation and a is a parameter proportional to the maximum decrease of K reached for $t = t_m$.

The fit of the MVB growth model (Table 3 and Figure 9) shows a significant improvement in the modelling of the growth as estimated by the otolith readings. In particular the MVB growth model results in a good distribution of the residuals centered around zero and without trend. The mean age at which K reaches its maximum decrease is estimated at 0.94 year (FL = 65 cm). Compared to the Von Bertalanffy model, the modified model gives a lower estimation for L_{∞} (151.7 cm) that is attained much faster, since its value of K is much higher (Table 3).

Validation of the modified von Bertalanffy (MVB) model

It is useful to investigate the consequences of the modification introduced into the von Bertalanffy model. Using the parameter estimates of Table 3, we calculated the expected results with both the normal and the modified von Bertalanffy models for the instantaneous growth rate (G , the derivative of the growth model). To compare with our observations from tagging data and counts of increment density, we also calculated the mean monthly growth rate and the variation of increment density under the assumption of a linear relationship between the somatic growth rate and the width of otolith increments (Campana and Neilson 1985). The MVB growth curve, that may appear only lightly different of the von Bertalanffy growth curve (Fig.10a) results nevertheless in considerable changes regarding the evolution of the instantaneous and monthly somatic growth rates (Fig 10b and 10c). While the theoretical monthly growth rate is calculated for periods of exactly one month, the monthly growth rate calculated from tagging data (Fig. 4) is calculated from fish with a period of liberty at sea sometimes much more longer than one month. Despite this difference that could explain the generally lower observed growth rate, the striking feature is the very similar evolution between the observed and expected monthly growth rates. In particular, in both cases there is a maximum decrease at mid-size 55 cm and a maximum increase of 2 cm/month around 80 cm. For the variation of the theoretical increment density (Fig. 10d), we simply supposed the increment width proportional to G . Therefore, an increasing G will result in an increasing width of increment, leading consequently to a decreasing density. In these conditions, we obtained an identical pattern to the one observed in Fig. 8, i.e., a phase of lower increase of density between ages 250 and 450 days (~ 8 and 15 months) .

Tagging data can also be used to test the validity of a growth curve by calculating the age at release according to this growth curve (using the inverse function or an iterative algorithm) and the lengths at release. The age at recapture is calculated by adding the time of liberty at sea to the estimated age at release. The age and length at recapture are then plotted and compared to the growth curves. If the growth equation represents adequately the growth of the yellowfin tuna during the period of liberty in the area studied, then the distribution of the tagging data should be evenly scattered along the growth curve. As shown on Figure 11, the modified Von Bertalanffy growth model reproduces much better the growth of the tagged yellowfin than does the normal Von Bertalanffy model, although tagged fish are slower growing than predicted by otolith model. Nevertheless, the modified Von Bertalanffy growth model allows to describe the growth of the old individuals which were not available in the size range of the otolith sample. Therefore, this model proposed from otolith counts for which the oldest individual sampled was 3.4 years old could be extended to the size/age range of the tagging data set, that is probably quite representative of the whole population (oldest individual = 6.5 years).

Growth by sex

The estimation of growth parameters in relation to the sex does not allow to conclude to a sexual dimorphism in growth. The Figure 12 shows that both male and female curves are perfectly superimposed until the age of 2 year (120 cm in FL). Thereafter, the curves diverge but the uncertainty in the estimation of L_{∞} (table 4) for the female growth curve is too high to consider such a difference as significant. The estimation of L_{∞} for females is made difficult for samples of large female yellowfin tuna (>140 cm FL) are scarce. If the growth pattern is similar for both sexes, therefore this absence of large female yellowfin could be due to different mortality rates by sex.

Discussion

While some experimental data confirm the assumption that increment width is proportional to the growth rate (Paperno et al. 1997), some other suggest that the increment width-growth relation can not be verified in some species (Secor et al 1989, Francis et al. 1993). Results of the present study would indicate that yellowfin tuna is a species for which the assumption can be accepted, at least in the investigated range of ages 0-800 days. Despite the obvious individual variability, all the studied samples show a period of slower increase of increment density, in agreement with the growth model that proposes a period of lower somatic growth rate between 8 and 15 months (mean=11.4). Given the diversity in the life histories of the fish sampled (in particular, they have different sexes and birth dates), this constant pattern would indicate that the variation in growth depends on physiological stage (s) rather than environmental conditions. However, such a variation in growth visible in the pre-adult phase in the WCPO was not observed in the EPO by Wild and Foreman (1980). Could the environment in these two different oceanic regions be responsible of this observation ?

Results of this study indicate as it has been already observed by different authors that the growth of the yellowfin in certain region of the oceans does not follow the classical Von Bertalanffy growth curve. In the WCPO, the apparent decrease of the growth rate for pre-adult yellowfin is observed both from a large set of tagging data and from counts of otolith microincrements, and similarly for males and females. Therefore, instead to consider that fish grow independently with random fluctuations about the same von Bertalanffy curve, we suppose that during their young phase, there is a systematic decrease of growth during a certain period of time. It is proposed to model this phase of the growth by including in the Von Bertalanffy model the possibility for K to vary according to a normal distribution. Such a modification is not simply a fitting procedure, but allows to describe mathematically the effect on the population growth model of temporary decreases of individual growth rates during a specific period of the life cycle.

The growth curve proposed in the present study for the yellowfin tuna in the WCPO differs quite significantly of those estimated in different part of the three ocean especially in the age period of 1 to 3 years (Figure 13). However, age and growth of yellowfin tuna have been more often estimated by length

or weight frequency analyses (Moore 1951, Davidoff 1963, Hennemuth 1961, Le Guen and Sakagawa 1973, Wankowski 1981, Gascuel et al. 1992) than by counts of microincrements on otoliths (Uchiyama and Struhsaker 1981, Wild 1986, Stequert et al. 1995). The growth curves resulting from length (weight) frequency analyses are affected by a sum of uncertainties such recruitment, mortality, sampling and biases in sizes due to the gear selectivity. More importantly, there is a strong uncertainty for estimating a birth date, given the duration of the extended spawning periods (probably continuous within 10N-10S) and by “the need to anchor the growth curves to the time axis by a suitable choice of age for a particular size” (Wild, 1994).

From a bio-energetic point of view, the growth can only occur if there is an excess in the energy provided by the food ingested after excretion has taken place and metabolism has been satisfied (Pitcher and Hart 1994). In other words, the ingested food provides a quantity of energy used by the fish to maintain its metabolism and to grow, either in the form of somatic or gonadal growth. This can be described in the following energy budget (e.g., Kitchell et al. 1978):

$$C = R + U + F + G + \Delta B \quad (4)$$

where C is the rate of ingested food, R the rate of metabolism, U the rate of excretion, F the rate of egestion, G the rate of gamete production and ΔB the rate of growth. Therefore, a variation in growth should result from a variation of one or several terms of the equation (4). The estimation of the parameters of the normal distribution from the MVB model indicates that the decrease of the growth parameter is maximum (- 0.172) at the mean age of 0.9 year (FL = 65 cm). Regarding the reproduction, we could consider that the first development of the gonads and the maturation process require a quantity of energy producing a deficit in the somatic growth. However, though minimum fork length of first maturation have been effectively observed at 70-80 cm (~1 yr) for yellowfin in the equatorial Pacific, the length at which 50 % of the population is mature (FL₅₀) was estimated to 105 cm (1.6 yr) for the equatorial western Pacific (Itano, *pers. comm.*), i.e., several months after the maximum deficit of growth.

Indeed, different ecological and physiological factors can influence each of the terms of equation (4). The metabolic rates change according to the temperature, the size of the fish and the ration size of food. It is observed that bigger 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 necessary to sustain the swimming. Yellowfin tuna has a gas bladder which grows allometrically, becoming progressively larger as the fish increases. Until he attains 2 kg (~ < 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 absolute units (cm /s)” (Magnuson 1973).

Moreover, the development of the gas bladder associated with the increase in size also corresponds to a change in the behavior (the fish moving deeper) and consequently in an extension of the habitat with potentially different conditions of temperature, oxygen concentration, food, etc.... The age at which this change in behavior occurs can vary, e.g., because yellowfin remain in school association with surface skipjack tuna, or because the food is more accessible in surface than in sub-surface, or reversely. Indeed, from equation (4) the availability of food appears critical for the growth. Besides, the effect of food ration on otolith increment width has been demonstrated in experimental studies (Paperno et al. 1997). In addition to the ration level, the type and the size of prey items are also important. There are some examples of fish species that begin to grow faster when they are several years old and become large enough to switch to small fish as prey (e.g., in Pitcher and Hart 1994). Theoretically, the additional energy required for the gonad maturation can be compensated by an increase in the ration size. However, environmental conditions must be favorable, i.e., provide unlimited food and adequate temperature. Such considerations could be helpful to explain that no deficit of growth of the pre-adult

phase occurs in the eastern Pacific. The region of study in the WCPO is mainly constituted by the warm and oligotrophic “warmpool” while in the eastern Pacific the upwelling provides relatively cold and rich waters. In fact, the situation is probably more complex. The importance of interannual events such as El Niño-La Niña on the displacement of surface tuna stocks in the WCPO has been demonstrated (Lehodey et al. 1997) leading to the hypothesis that the westward advection of rich water masses of the central upwelling could enhance the secondary and tertiary productivity in the warmpool, particularly in a convergence zone on the eastern edge of the warmpool (Lehodey et al. 1998). Large concentrations of oceanic anchovy (*Enchrasicholina punctifer*), a major food source for yellowfin, are regularly observed in this convergence zone from which is coming a large part of the catch. Therefore, the access to this new source of forage could correspond to a sudden increase of the growth rate. More generally, at the individual level, high variability of the growth rate is susceptible to occur in relation to the availability and the constitution of tuna forage, although movements deduced from tagging data have shown that skipjack tuna (and probably yellowfin) can follow the ENSO related displacements of the favorable zone of convergence (Lehodey et al., 1997).

The results presented in this study can change significantly the stock estimations produced with dynamic population models as the growth pattern proposed is significantly different from those estimated elsewhere. Thus it is important to confirm this first analysis and to consider simultaneously the other biological functions occurring in the life of yellowfin. In particular, the reproduction, the feeding behavior with the availability in food and the behavior linked to the development of the gas bladder are susceptible to affect the growth pattern.

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Tables

Table 1. Total and selected returns of tagged yellowfin tuna by time at liberty.

Time at liberty (yr)	Total	Selected
0 to 0.5	2157	441
0.5 to 1.0	732	441
1.0 to 1.5	366	208
1.5 to 2.0	120	55
2.0 to 2.5	43	16
2.5 to 3.0	25	12
3.0 to 3.5	13	7
3.5 to 4.0	7	5
> 4.0	3	2
Unknown	15	
Total	3483	1187

Table 2. Comparison between numbers of micro-increments and numbers of days at liberty for saggital otoliths of OTC marked yellowfin tuna in the western Pacific (only samples with reliable recapture date are provided)

No Sample	FL (cm) release	FL (cm) recapture	Days at liberty	Count (1) (mean numb.)	Count (2)
T00105	42	43	49	44.4	50
T00138	35	39	21	21.3	21
T00159	62	90.5	175	157	175

(1) Wild (light microscope, acetate replica of the otolith surface)

(2) Stequert (SEM, transverse section)

Table 3. WCPO yellowfin growth parameters estimates (standard errors between brackets) according to the Von Bertalanffy growth model with K fixed and K varying in relation to a normal distribution

	Von Bertalanffy K fixed		Von Bertalanffy K = K - N(t)	
L_{∞}	199.6	(15.6)	151.7	(10.7)
t_0	-0.177	(0.035)	-0.085	(0.037)
K	0.390	(0.052)	0.728	(0.153)
t_m	-		0.936	(0.052)
s	-		0.380	(0.116)
a	-		0.164	(0.125)
R^2	0.95		0.96	

Table 4. WCPO yellowfin growth parameters estimates (standard errors between brackets) by sex according to the modified Von Bertalanffy growth model.

	Male (N = 55)		Female (N = 63)	
L_{∞}	146.7	(8.4)	177.1	(31.1)
t_0	-0.049	(0.065)	-0.167	(0.090)
K	0.805	(0.149)	0.511	(0.183)
t_m	0.923	(0.061)	0.891	(0.084)
σ	0.326	(0.111)	0.278	(0.137)
a	0.178	(0.119)	0.065	(0.070)
R^2	0.969		0.951	

Figures

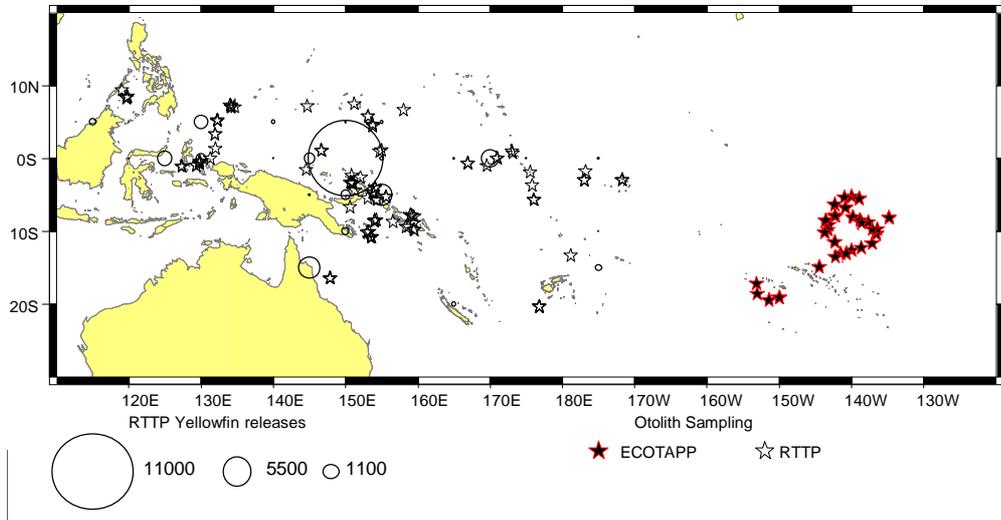


Figure 1. Location of RTTP yellowfin releases and recaptures and geographical distribution of otolith samples

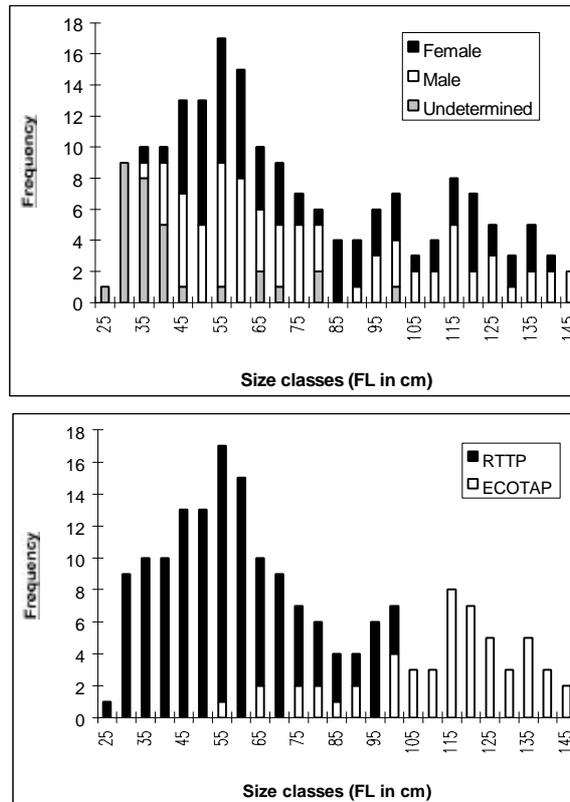


Figure 2. Length frequencies histograms by sex (left) and by type of cruise (right) of yellowfin tuna sampled for the otolith study

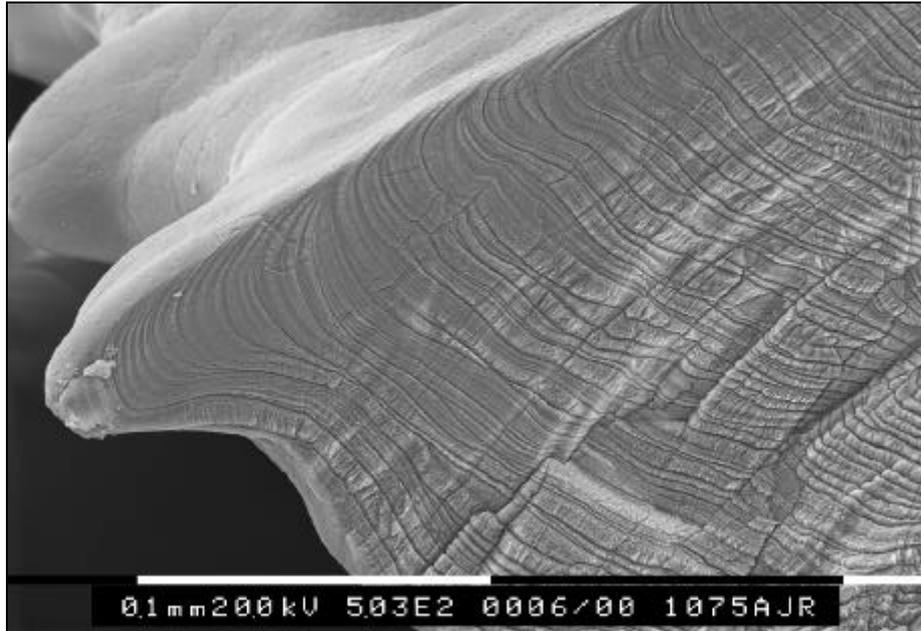


Figure 3. SEM view of a yellowfin tuna saggital otolith showing microincrements (image made at the CSIRO, Hobart, Australia)

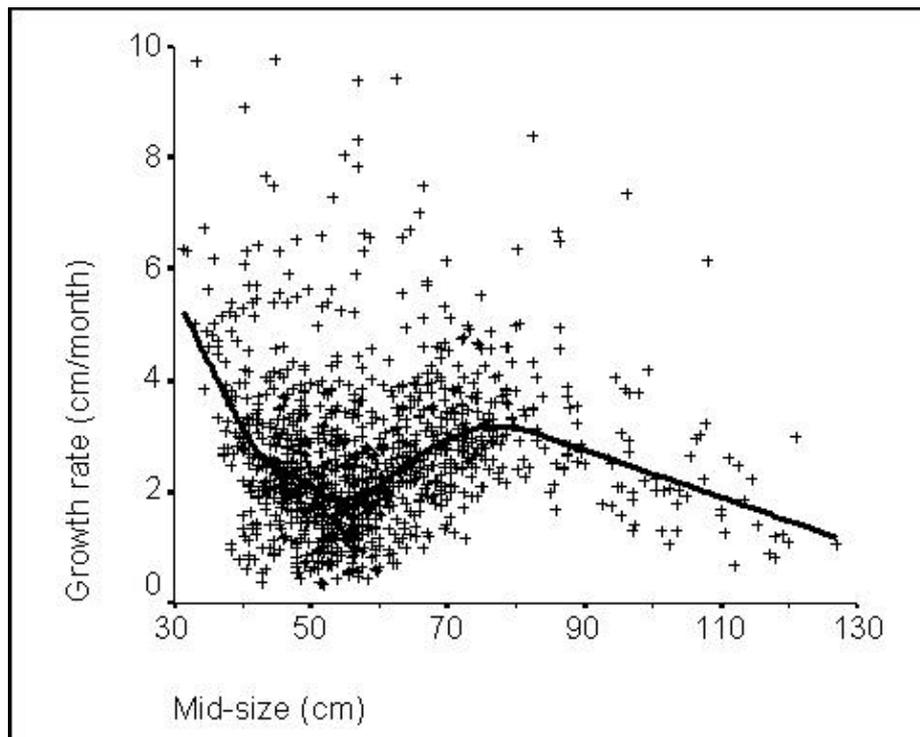


Figure 4. Growth rates of yellowfin tuna of the western and central Pacific based on tag returns from the RTTP. Mid-size is the average length between release and recapture. (a lowest function is used to show the trend of the growth rate as the size increases)

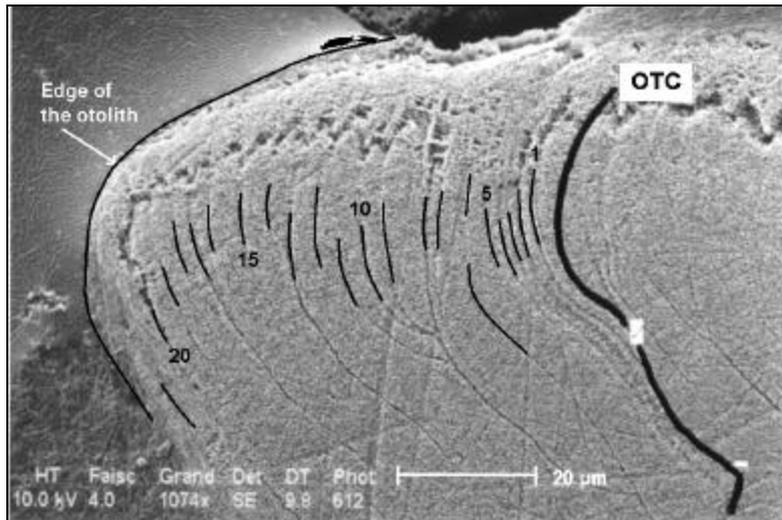


Figure 5. SEM view of the transverse cross-section of an OTC marked otolith of yellowfin tuna. The fish was recaptured after 21 days at sea and 21 increments were counted since the OTC mark (from Stequert, LASAA, Brest, France)

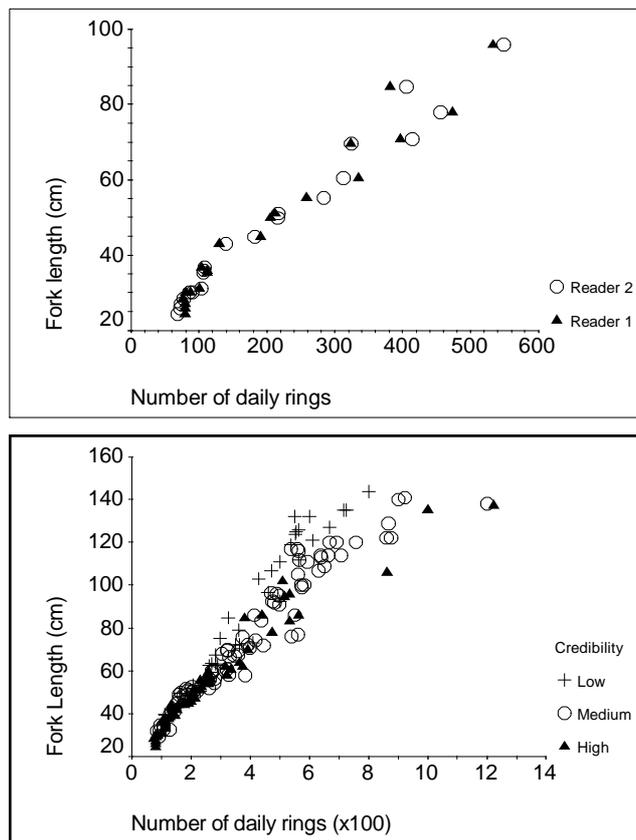


Figure 6. Otolith reading. Comparison between counts of daily increments for yellowfin tuna otolith by two different readers and counts of daily rings according to the length of fish by category of credibility in the reading

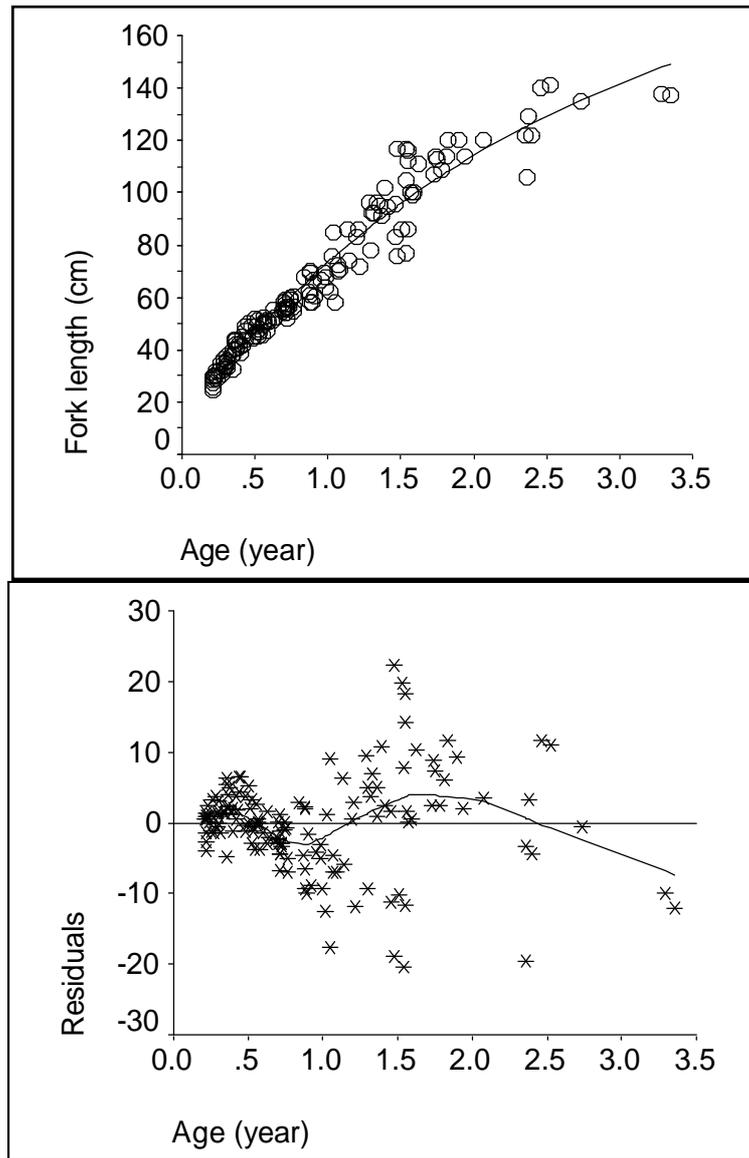


Figure 7. Plots of Von Bertalanffy growth curve and residuals according to the otolith readings. (A lowess function is used to show the trends in the residuals)

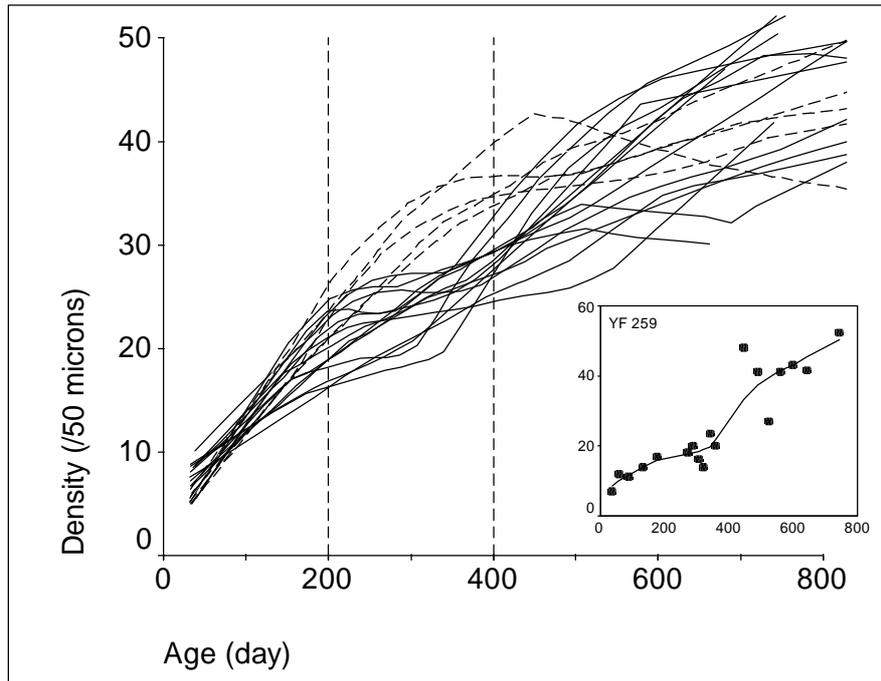


Figure 8. Variation of increment density along the otolith transverse section according to the age in days related to the reading zone. The box shows how the lowess function is used to figure the trend in the data series.

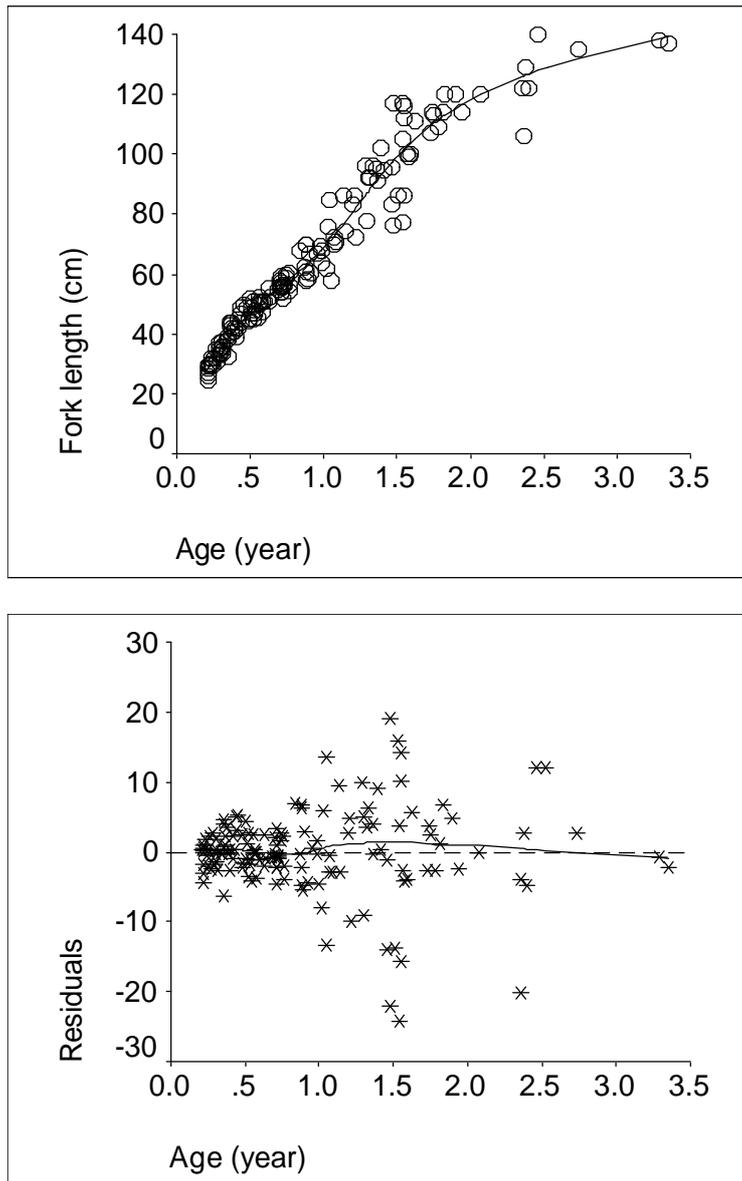


Figure 9. Plots of Von Bertalanffy growth curve including a variation of K according to a normal distribution $N(t)$ and their respective residuals (A lowess function is used to show the trends in the residuals)

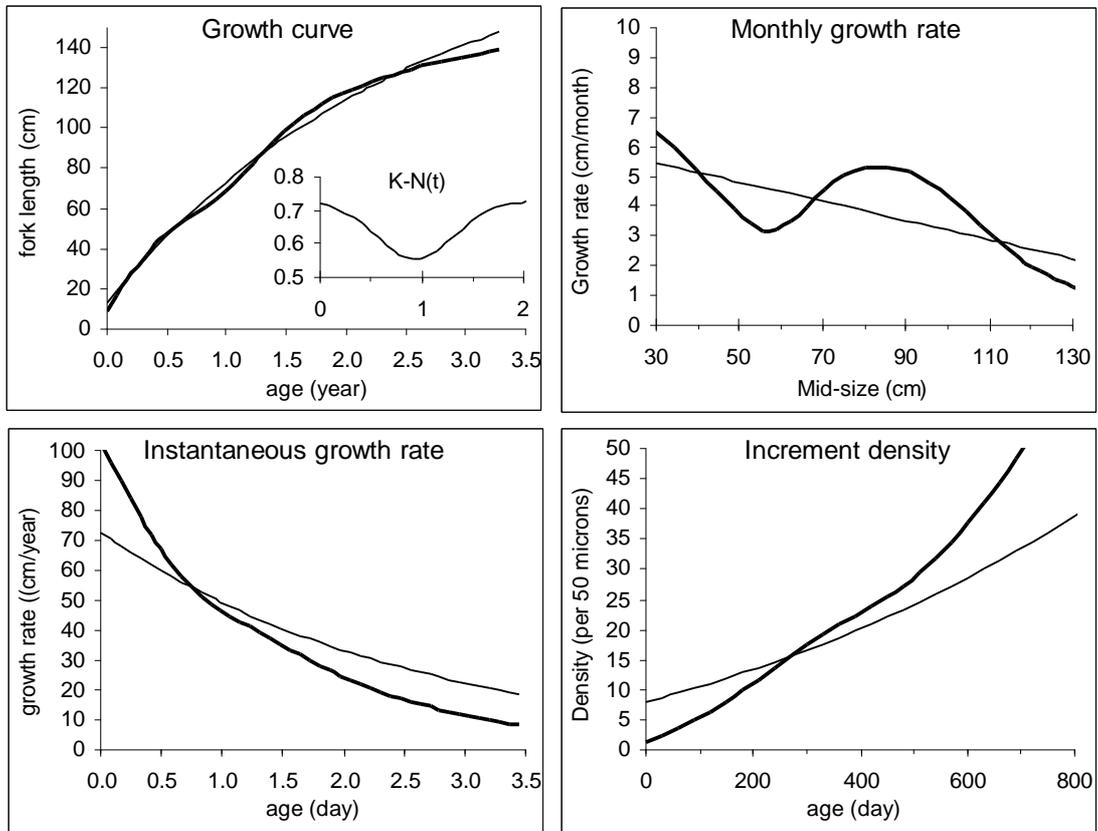


Figure 10. Changes induced on the Von Bertalanffy growth models and its consequences by introducing a variation of K according to a normal distribution $N(t)$.

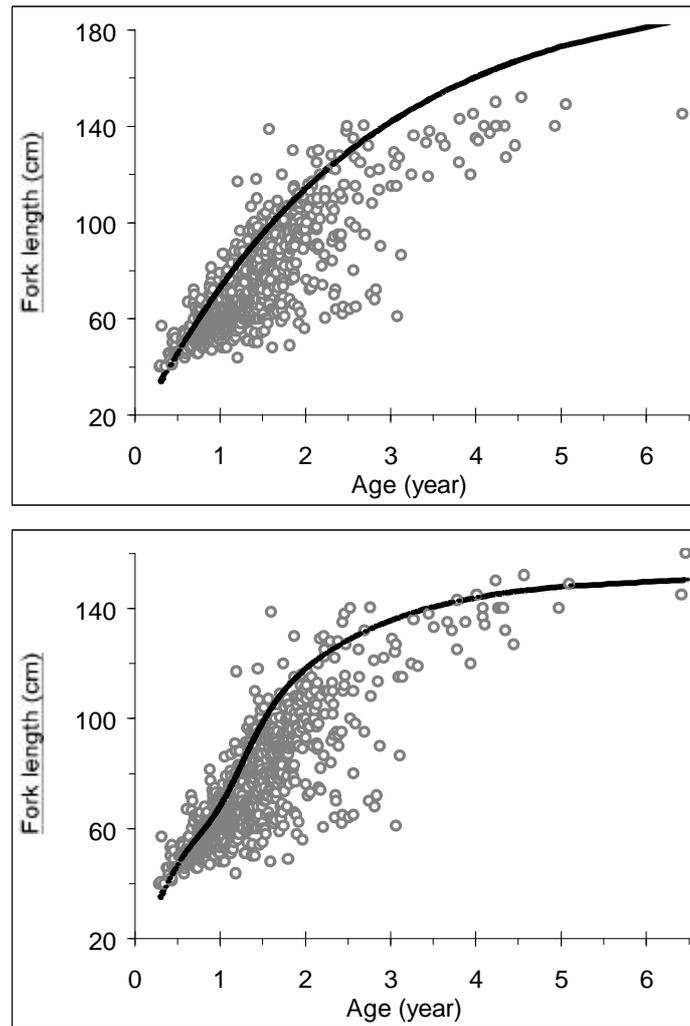


Figure 11. Validation of the growth models estimated from otolith counts by using tagging data; von Bertalanffy (left) and modified von Bertalanffy (right) models. Age at release is estimated using the length at release and the growth curve. The data plotted are recapture data. The age at recapture is calculated in adding the time of liberty at sea to the estimated age at release.

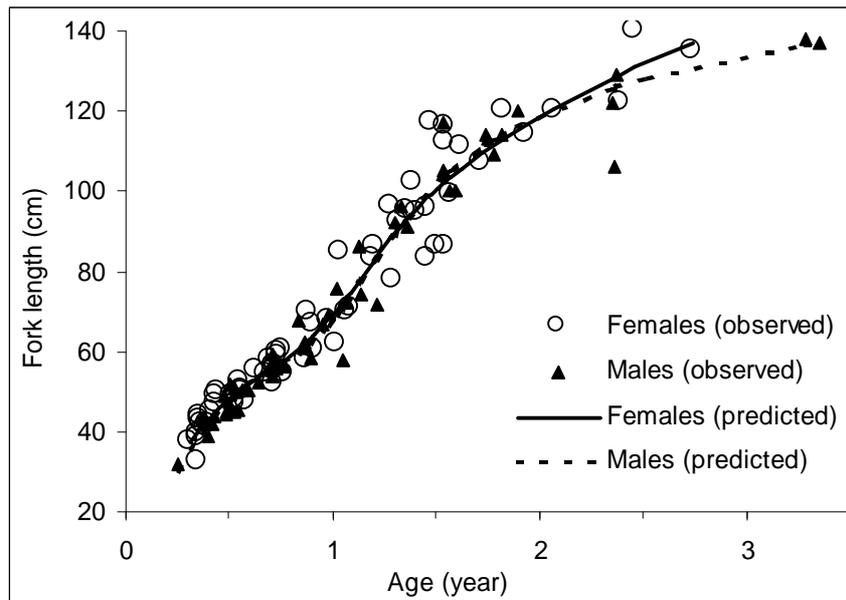
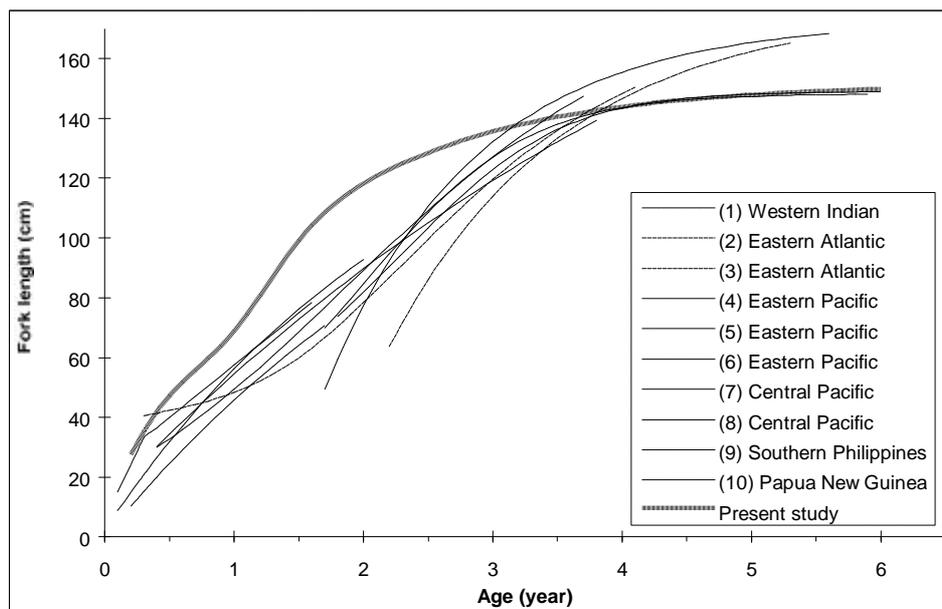


Figure 12. Plots of modified Von Bertalanffy growth curves by sex.



(1) Stequert *et al.*, 1995 (otolith daily rings); (2) Gascuel *et al.*, 1992 (length frequencies); (3) Le Guen & Sakagawa, 1973 (weight frequencies); (4) Wild, 1986 (otolith daily rings); (5) Hennemuth, 1961 (length frequencies); (6) Davidoff, 1963 (length frequencies); (7) Uchiyama & Struhsaker, 1981 (otolith daily rings); (8) Moore, 1951 (length frequencies); (9) Yamanaka, 1990 (otolith daily rings), Wankowski 1981 (length frequencies).

Figure 13. Comparison of the WCPO yellowfin growth curve estimated in the present study to estimated growth curves from different regions.