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PRELIMINARY RESULTS ON AGE AND GROWTH OF BIGEYE TUNA (*THUNNUS OBESUS*) FROM THE WESTERN AND CENTRAL PACIFIC OCEAN AS INDICATED BY DAILY GROWTH INCREMENTS AND TAGGING DATA

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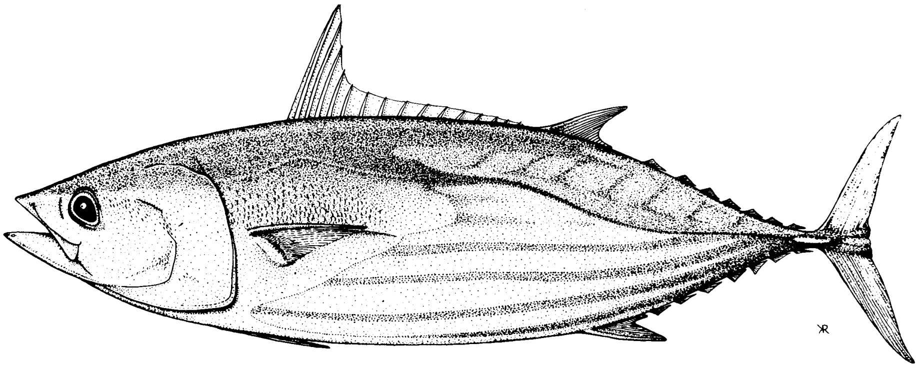

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Introduction

Bigeye tuna (*Thunnus obesus*) have similar overall distribution limits as yellowfin tuna. However, the adults (>100 cm FL) have the lowest dissolved oxygen tolerance and lowest water temperature preference (11–15°C) of the tropical tuna species (Brill 1994). They therefore tend to be found deeper in the water column during the day, although there appears to be regular movement towards the surface at night (Holland et al. 1990). Bigeye tuna mature at a size of 100 - 130 cm probably during their third year of life (Calkins 1980). They spawn in the warm (>26°C) surface waters, i.e. approximately between 30°N and 20°S in the western Pacific and between the equator and 20°N in the eastern Pacific (Nishikawa et al. 1985). Examination of sex ratio data shows a general predominance of male fish, becoming more prominent as size increases (Kikawa 1966; Kume and Joseph 1966). Stock assessments carried out to date have generally assumed a Pacific-wide stock structure. However the hypothesis of two separate east and west stocks with some degree of exchanges can not be totally excluded. Bigeye tuna are an important component of tuna fisheries throughout the Pacific Ocean. They are the principal target species of the large ‘distant-water’ longliners from Japan and Korea and of the smaller ‘fresh sashimi’ longliners based in several Pacific Island countries. The longline fishery takes medium to large (100-170 cm) fish while the surface fishery catches small fish (40-80 cm).

The age and growth of bigeye tuna have been studied by several authors using different methods such as modal analysis of length frequencies in the catches, the deposition of rings in scales (Yukinawa and Yabuta 1963) or vertebrae, and the analysis of tagging data. There is no study using otoliths, either with annual or daily increments. A lot of uncertainties remain about the growth parameters estimates produced in these analyses because of the restricted size range of the samples (in particular the lack of small fish), the lack of validation in the hypothesis of annual or semi annual marks on the hard parts, the problems inherent to the length frequency method, and the conflicting results regarding sexual differences in the growth of large fish or the existence or not of a phase of decreasing growth rate for fish around 60 cm.

As for yellowfin tuna (cf. WP YFT–2), we use in this study both otolith counts of daily micro-increments and data from a large tagging experiment to investigate the growth of bigeye tuna in the WCPO. Results suggest a period of slow growth in the second year of life. Additional samples in the size range where the growth variation occurs are needed to confirm this pattern.

Material and method

The methods used in this study are identical to those presented in WP YFT–2 for the yellowfin growth study.

Tagging data

The Regional Tuna Tagging Project (RTTP) allowed to release 6,748 tagged bigeye tuna throughout the western Pacific from Indonesia to the dateline between latitudes 10 °N and 20°S (Figure 1). A large number of tagging occurred in the Coral Sea east of Cairns because tagging opportunities are good in this region, where bigeye and yellowfin tuna form large aggregations accessible by handline fishery. 638 bigeye tuna (9.5 %) have been recaptured. As for yellowfin tuna, recaptures reflect the spatial distribution of the fisheries across the western central equatorial Pacific. After screening of the data (with the same criteria than for yellowfin), 264 returns with reliable dates and lengths at release and recapture were selected (Table 1). They provide a good data set covering a wide range of release lengths (30 - 126 cm), recapture lengths (46 - 185 cm) and times at liberty (70 - 2,549 days).

Otolith data

The otolith-increment counts consist of 149 samples in the length range 25 - 157 cm in fork length. These samples were taken from a total collection of 161 fish (34 collected during the RTTP, 127 provided by the programme ECOTAPP at the ORSTOM Centre in Tahiti). These samples are spatially distributed throughout the western and central Pacific (Figure 1), however, as for the yellowfin tuna samples and for similar reasons, the otoliths sampled in French Polynesia come from larger individuals. Only specimens considered to be either ‘excellent’ or ‘good’ in terms of readability were analysed.

Results

Tagging data

In the estimation of the monthly growth rate from tagging data, the bias that can produce samples with much longer time at liberty than one month is more acute for the bigeye tag returns than for yellowfin tuna. Indeed, while 92 % of the selected tag returns for yellowfin had a time of liberty at sea of less than 1.5 year, the proportion is only 34 % for bigeye (Table 1) and 40 % remained at sea more than 3 years. Therefore, to approach the actual monthly growth rate, a compromise must be sought to keep enough data while removing samples with longer time of liberty at sea. A good compromise seems to keep samples with a time at sea < 1,000 days, allowing to retain 141 samples (Figure 2). The evolution of this estimated monthly growth rate indicates a significant decrease with a minimum rate (1.6 cm/month) for fish with a size distributed around 60 cm. Then, the mean growth rate increases until 2.5 cm /month for fish size of 80-90 cm, before decreasing again regularly with the increasing size.

Otolith readings

In comparison to the yellowfin otoliths, the bigeye otoliths present more contrasted increments and are consequently easier to read. On the other hand, bigeye appear to be significantly longer lived than yellowfin and after approximately one thousand (i.e., ~3 yr) growth increments the otolith reading becomes more and more difficult as the increment width reaches the limit of the optical microscope resolution (Figure 3). Therefore, we have estimated the parameters of the von Bertalanffy growth model for both the whole data set and the data restricted to fish not older than 3 years. Both parameter estimates fit apparently well the data (Figure 4). The restriction to samples not older than 3 years leads to a lower L_∞ and a higher K (Table 2), which is not surprising if we consider that the counts for the few samples older than 3 years are underestimated. However, although the residuals are fairly scatter about zero, there is a slightly marked trend in the interval 0 to 1.5 years.

The variation of increment density along the transverse section (Figure 3) was observed on a sub-sample of 20 otoliths, following the same method used for yellowfin (see WP YFT–2). As for this latter species, we observe a phase of low increase in density, that despite a large individual variability, occurs approximately between ages one and two years (Figure 5), i.e., shifted by 0.5 year compared to the pattern observed for yellowfin tuna.

Composite model

Hampton et al. (1998) used both tagging and otolith data sets to fit a von Bertalanffy growth curve according to the method described by Kirkwood (1983). A first fit suggested that the ages counted from otolith samples with an age > 3 years were likely underestimated. A refit of the composite model excluding otolith samples from fish > 110 cm yielded slightly different parameter estimates (Table 2). In order to display the tagging data on the same figure as the otolith data, the ages at release of tagged fish were estimated from the inverse growth function (composite model), and the time at liberty added. This represents an estimate of age at recapture, which is plotted against length at recapture in Figure 6. The composite growth model provides a reasonable fit both to the tagging and otolith data. However, if the distribution of the residuals is fairly even about zero, there are apparent trends in tagging and otolith residuals. In particular, fish recaptured before two years appears to have systematically a smaller size than expected. Despite this, the composite growth model improves considerably the estimate of the von Bertalanffy growth parameters as demonstrated by the comparison on Figure 6. Particularly because the tagging data extend indirectly the range of age/size observation and therefore constrain the value of L_∞ in a realistic range.

Modified von Bertalanffy model

The variations observed in the monthly growth rate from tag returns and in the density of growth increments, with the trends observed in the residuals from the von Bertalanffy growth curve estimates, suggest that as for the yellowfin tuna, there is a period of slow growth in the second year of life of bigeye tuna. However, as it occurs latter, at a larger size and a lower growth rate, this period of slower increase has less impact on the general growth curve, although the effect is clearly visible in the evolution of the monthly growth rate. A preliminary fit of the MVB model with the otolith data is given on Figure 7. We calculated the expected results for the instantaneous growth rate, 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 (Figure 8). Both growth curves are very similar. However, the slight variation of the growth rate in the MVB model results in a clear variation of the expected monthly growth rate. Comparison of this latter with the monthly growth rate observed from tag returns (Figure 2) shows similar evolutions, although the expected maximum decrease occurs at mid-size 70 cm and the observed seems to be around 50-60 cm. The variation of the theoretical increment density occurs between ages 400 and 650 days, which is the range observed in the sample studied (Figure 5). In summary, these preliminary results indicate that the VBM growth model reproduces the growth pattern of bigeye in the WCPO, however, because the model is flexible and sensitive and the growth variation has a relatively low amplitude, additional data are needed in the size range where the growth variation occurs (60-100 cm) to provide a definitive estimate of the growth parameters.

Growth by sex

Several problems occur to clearly examine the sexual dimorphism in the growth of bigeye. The sexual identification is difficult in the juvenile phase, e.g. there are only 2 males and 3 females identified on the 53 individuals younger than 1.5 years that were sampled for the otoliths. Beside, a reliable age for individuals older than 3 years appears difficult to obtain with the method based on the reading of otolith daily growth increments. Regarding the tagging data for which the returns are based on the commercial fisheries, the chance to obtain with a good reliability the sex of the fish recaptured is really low. Therefore, the range of age available for investigating sexual difference in growth is very limited. The figure 9 shows that the ages estimated in this range for both sexes are similarly distributed according to the length and no apparent difference can be detected at this stage.

Discussion

There is no absolute validation of the daily periodicity of growth increment for bigeye tuna in the western and central Pacific Ocean. However the numerous similitudes with yellowfin tuna in their morphological and physiological adaptations, their close phylogenic position, as well as the general coherence in the results of the growth studies for yellowfin and bigeye suggest that the daily periodicity assumption is highly plausible, at least in the range 0-3 years. In addition, tagging data provide indirect validation of the growth curve defined from the supposed daily growth increments.

Several tagged bigeye have been recaptured in excess of six years at liberty (the longest period at liberty is currently 7.02 yr). These fish were aged between two and three years at release, which suggests that significant numbers of fish survive at least until eight years of age, that is likely two or three years (30-50%) more than yellowfin tuna. By using both otolith and tagging data, it was possible to obtain a growth curve covering the whole range of age for the population, excepted the first two months of the life. Estimates of the parameters of the von Bertalanffy growth equation calculated by various investigators are listed in table 3 and the corresponding growth curves are shown in Figure 10. The difference is particularly marked between the Pacific and Atlantic studies, since all the analyses from Atlantic Ocean excepted one give a value of $K < 0.2$ yr^{-1} (Table 3). It is worth to note that one analysis from tagging data in the Atlantic failed in estimating the von Bertalanffy growth parameters because mark-recapture data exhibited “slower growth rates in size range of 50-60 cm” (Miyabe 1984). This observation would confirm that the variation in growth observed in this study is specifically linked to the development of the species as already suggested for yellowfin and not due to environmental regional variations.

In agreement with its longer life cycle comparatively to the yellowfin, the maturation of bigeye also occurs latter. The minimum size at first maturity of Pacific bigeye tuna is reported as 91-100 cm (Kikawa 1953 in Miyabe 1994) corresponding to an age of 2 years, but most of the fish mature at a size between 100 and 130 cm (Calkins 1980), i.e., after 2.5 yr (1.6 yr for yellowfin). Similarly, the period of slower growth detected for bigeye appears to be shifted by ~0.5 year comparatively to yellowfin. Therefore, for both species, the period of slower growth occurs during the year that precedes the first maturation.

An other similitude with the yellowfin is that the development of the gas bladder reduces dramatically the minimum swimming speed for maintaining hydrostatic equilibrium as shown by Magnuson (1973) and reproduced on figure 11. As the development of the gas bladder reduces the energy requirement of the general metabolism, a positive impact could be expected in term of somatic growth. This effect would appear to be approximately around 80 cm ± 10 cm (~1.6 yr ± 0.4 yr) for bigeye and around 75 cm ± 15 cm (~1.1 yr ± 0.3 yr) for yellowfin (Figure 11). But paradoxically, it would take place approximately during the same period than the observed slower growth phase. Moreover, the age at which most of the fish reach maturation, and which is supposed to produce a negative impact on the somatic growth, occurs in both species a few months after this period of slower growth. Indeed, we show on figure 12 that it is possible to combine these positive and negative effects to obtain a phase of slower growth as observed and modelled in this study. An additional information given by this growth model is that a positive effect alone (i.e., the effect of the gas bladder) on the somatic growth is not sufficient to reproduce the observed variation in growth. This latter is reproduced in two cases: negative effect alone or a combination of positive and negative effects. If both effects are considered, it is necessary to assume that (i), the energy required for the first maturation process is higher than the gain of energy resulting from the development of the gas bladder and (ii), that the energy requirement for maturation is maximum a few months before the age of effective maturation (FL_{50}). Such assumptions are far to be unrealistic, particularly because the period of maturation processes preceding the spawning likely requires high level of energy, especially if the fish stock endogenous energy under the form of lipid or protein reserves (e.g., in the liver) to prepare the spawning period.

Several additional investigations will be necessary to precise and detail the results presented in these both studies. Much more numerous and diverse should be the studies to explain the growth variations: observation at sea, experiments in captivity, comparison with other tuna (especially skipjack that has no gas bladder), classical and archival tagging, simulations with individual based models, etc… Nevertheless, from a tuna stock management point of view, the growth models proposed for yellowfin and bigeye tuna in the WCPO bring a significant improvement in the description of the growth of their populations and should be considered in the future stock assessment analyses.

Acknowledgments: We are particularly grateful to our colleagues of the programme ECOTAPP (EVAAM/IFREMER/ORSTOM) in Tahiti for their helpful support in the collection of otolith samples. This work was supported by the European Union-funded South Pacific Regional Tuna Resource Assessment and Monitoring Project of the Oceanic Fisheries Programme of the Secretariat of the Pacific Community.

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Tables

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

Time at liberty (yr)	Total	Selected
0 to 0.5	235	14
0.5 to 1.0	112	58
1.0 to 1.5	46	18
1.5 to 2.0	39	27
2.0 to 2.5	13	6
2.5 to 3.0	56	35
3.0 to 3.5	4	2
3.5 to 4.0	48	44
4.0 to 4.5	11	5
4.5 to 5.0	20	15
5.0 to 5.5	11	8
5.5 to 6.0	13	12
6.0 to 6.5	19	15
> 6.5	7	5
Unknown	4	
Total	638	264

Table 2. WCPO bigeye tuna 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 Composite model*	
Selected otolith samples	(All samples)		(age < 3 yr)		(age < 3yr)	
L_{∞}	228.59	(18.42)	203.59	(22.78)	166.3	(0.015)
t_0	-0.425	(0.058)	-0.394	(0.066)	-0.389	(0.017)
K	0.226	(0.030)	0.266	(0.049)	0.349	(0.027)
R^2	0.974		0.973			

* Hampton (1998)

Table 3. Review of growth parameters for bigeye tuna in the Pacific (shaded) and Atlantic (clear) Ocean

Sampling range	N	Von Bertalanffy growth parameters			Location	Method	Reference	Comments
FL (cm)		L∞	K	to				
	192	156.82	0.427	0.53	Pacific (west)	Tagging data	Hampton et al. (1998)	
82-150	64752	187.0	0.380	0.53	Pacific (east)	Length frequency	Kume and Joseph (1966)	K and t_o adjusted to annual intervals
80-155*		179.3	0.367	-0.27	Pacific	Length frequency	Shomura and Keala (1963), Female (1)	transformation of weight to length
80-155*		190.7	0.324	-0.33	Pacific	Length frequency	Shomura and Keala (1963), Male (1)	Transformation of weight to length
		214.8	0.207	-0.02	Pacific (west & central)	Length frequency	Suda and Kume (1967) (1)	
60-150*	463	215.0	0.208	-0.01	Pacific	scales	Yukinawa and Yabuta (1963) (1)	Two rings per year. K and t_o adjusted to annual intervals.
44-179	236	264.0	0.120	-0.68	Atlantic (east)	Caudal vertebrae	Alves et al. (1997)	Annual rings. No evidence of sexual dimorphism in size
40-150	130	285.4	0.113	-0.50	Atlantic (east)	Tagging data	Cayré and Diouf (1984)	
61-139	2858	338.5	0.104	-0.54	Atlantic (east)	Length frequency	Champagnat and Pianet (1974)	
58-187		206.1	0.182	-0.74	Atlantic	Ray of dorsal fin	Delgado de Molina and Santana (1986) (2)	
56-190	77	218.8	0.230	-0.02	Atlantic (central)	Ray of dorsal fin	Draganik and Pelczarski (1984)	Annual rings
50-200	1480	253.8	0.173	-0.15	Atlantic (east)	Ray of dorsal fin	Gaikov et al. (1980)	Suggest two opaque and hyaline deposits by year
45-150		259.6	0.149	-0.40	Atlantic (east)	Length frequency	Marcille et al. (1978) (2)	
39-126	127	-	-	-	Atlantic	Tagging data	Miyabe (1984)	No fit, due to the tendency of mark-recapture data to exhibit slower growth rates in size range of 50-60 cm. (Fig 2.2 shows clearly the decrase in the period 100-300 days after the release of the 50-60 cm FL bigeye tuna)
35-190		381.5	0.085	-0.4	Atlantic	Length frequency	Pereira (1984) (2)	
40-190		491.6	0.054	-0.952	Atlantic	Length frequency	Weber (1980)	

* estimated from the curve
(1) in Miyabe and Bayliff (1998)
(2) in Pallares et al. (1998)

Figures

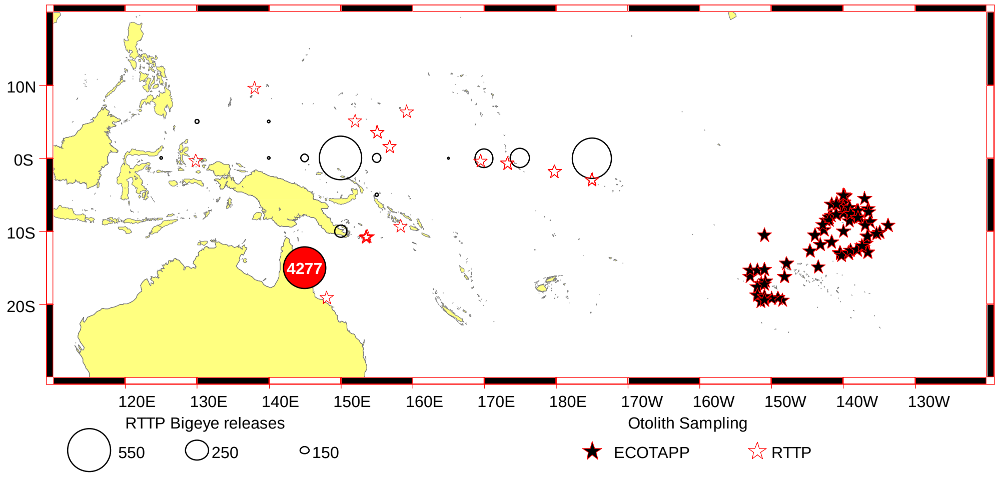

Figure 1. Location of RTTP bigeye tuna releases and geographical distribution of otolith samples

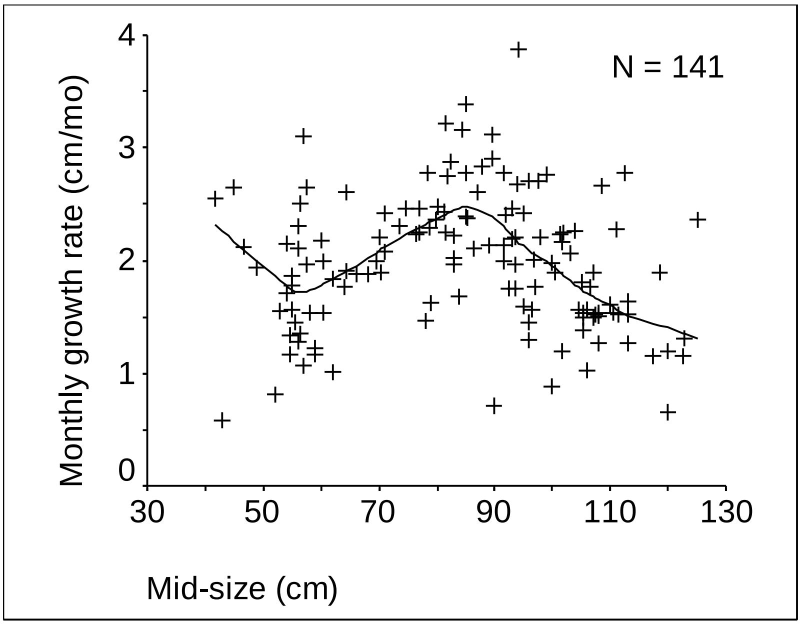

Figure 2. Growth rates of bigeye tuna of the western and central Pacific based on tag returns from the RTTP. Mid-size is the average length between release and recapture. A lowess function (30%) is used to show the trend of the growth rate as the size increases.

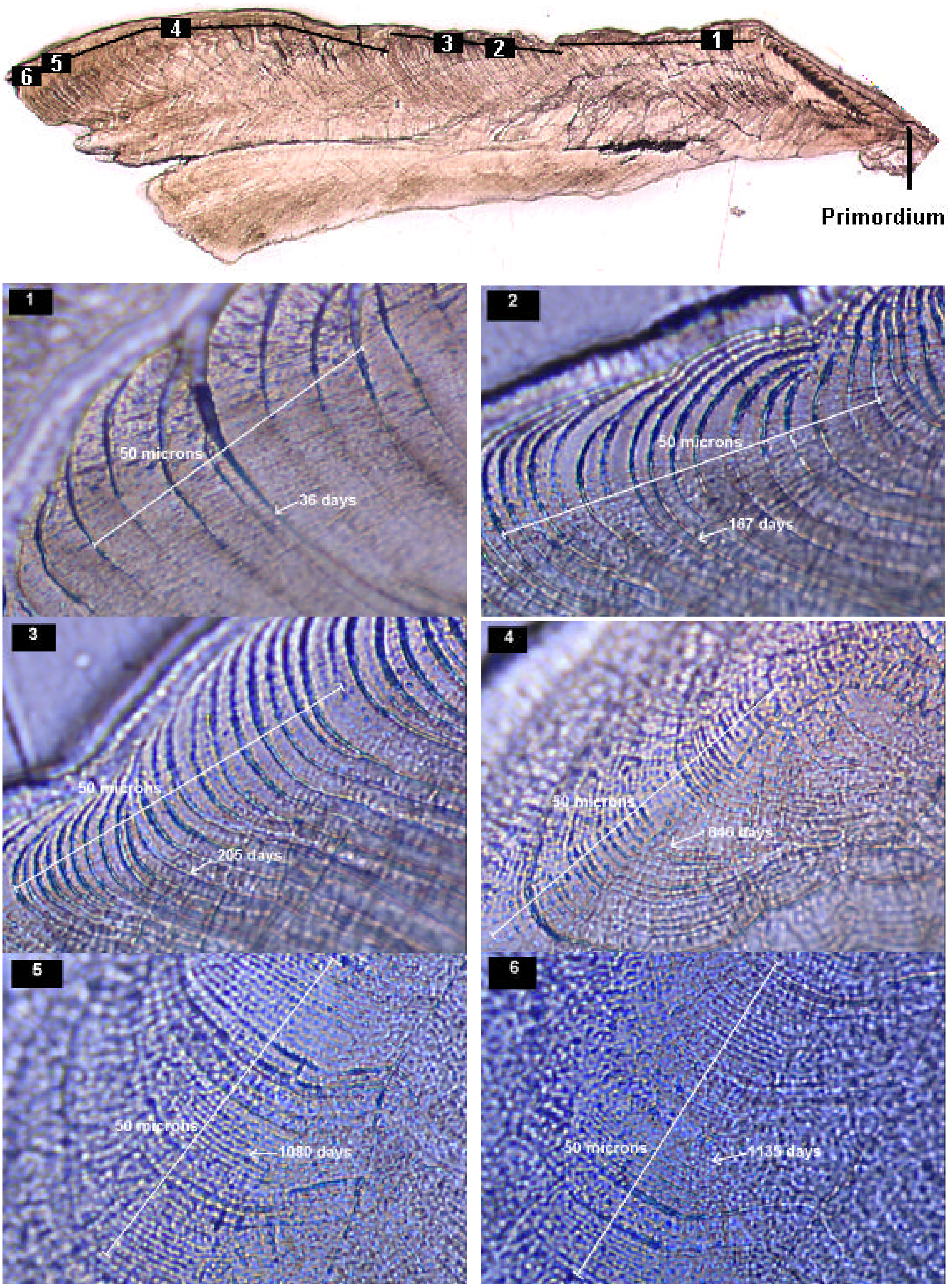

Figure 3. Thin transverse-sections of sagittal otolith of bigeye tuna (male, 128 cm FL) showing the variation of increment width along the reading transect (magnification is x50 for the general view, and x1000 for box 1 to 6)

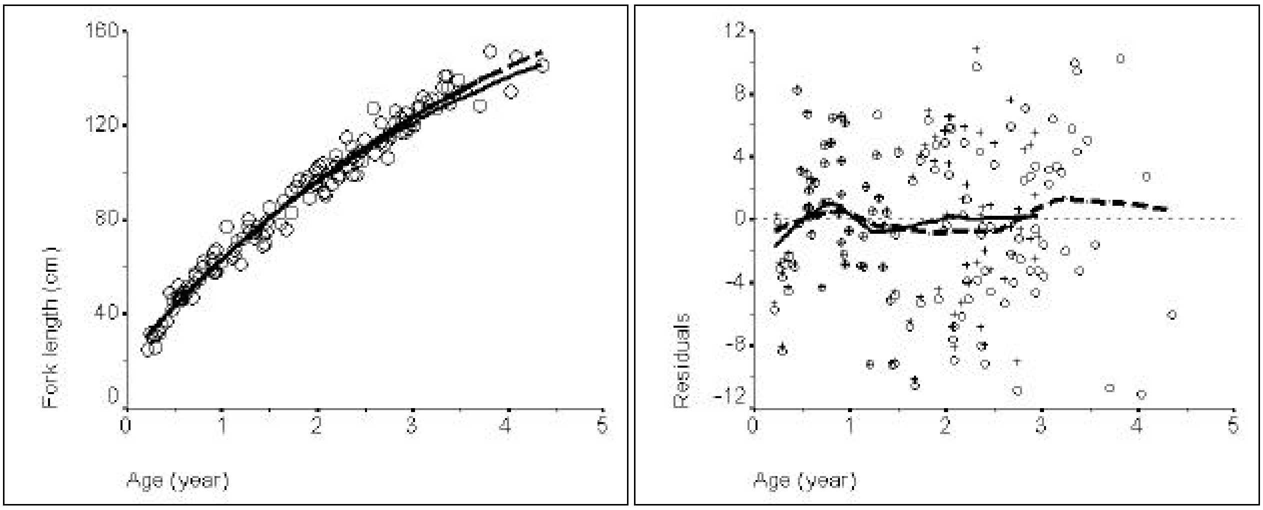

Figure 4. Plots of von Bertalanffy growth curves and residuals according to the otolith readings for all samples (dotted line) and samples of age < 3 years (continuous line). A lowess function (50%) is used to show the trend in the residuals.

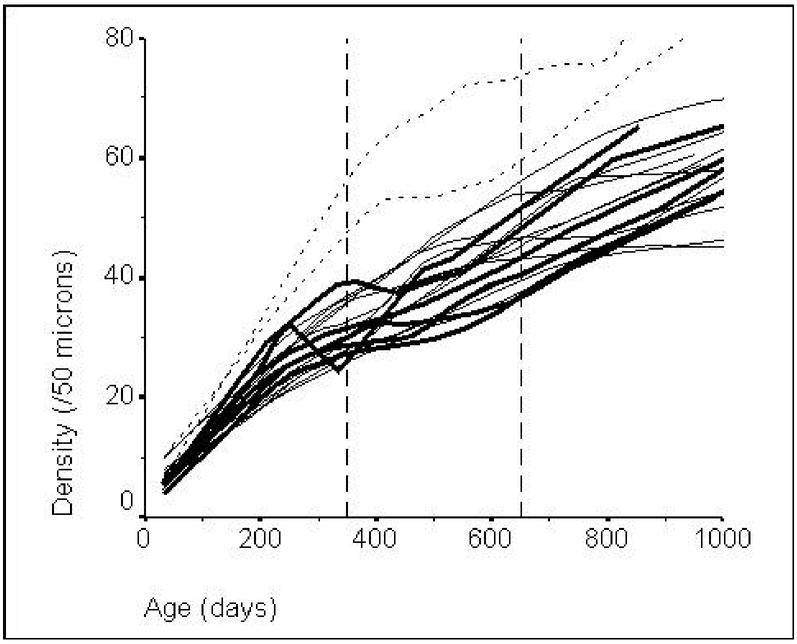

Figure 5. Variation of increment density along the otolith transverse section of bigeye tuna according to the age in days related to the reading zone. Lowess function (50%) are used to figure the trend in the data series.

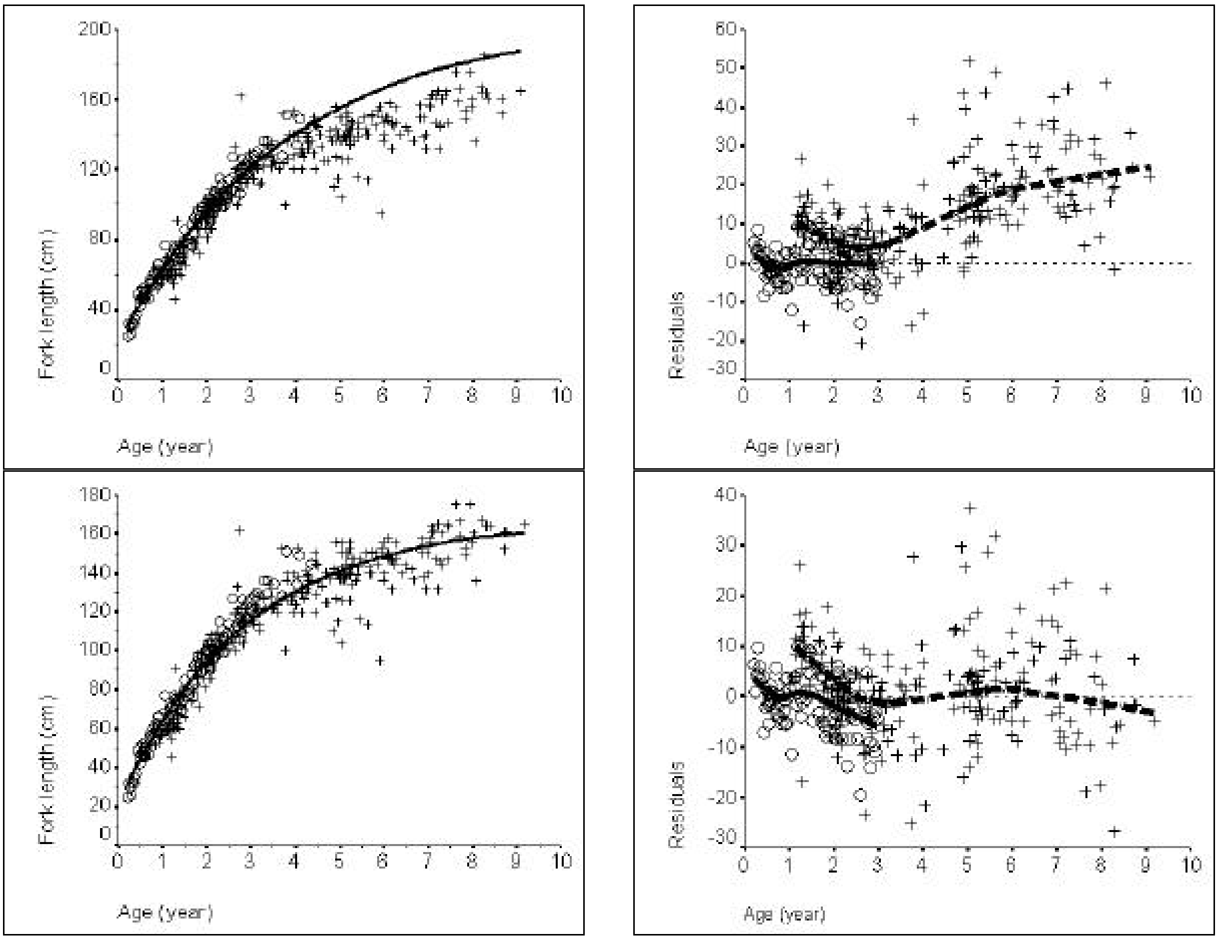

Figure 6. Von Bertalanffy growth curves and residuals from estimates using otolith data (top) and both otolith and tagging data sets (bottom). The open circles are otolith data, the crosses are for tagging data. The age at recapture is calculated in adding the time of liberty at sea to the estimated age at release. On the residual plots, open circles represent the otolith residuals and dotted line their trend; similarly, crosses and continuous line are for tagging residuals.

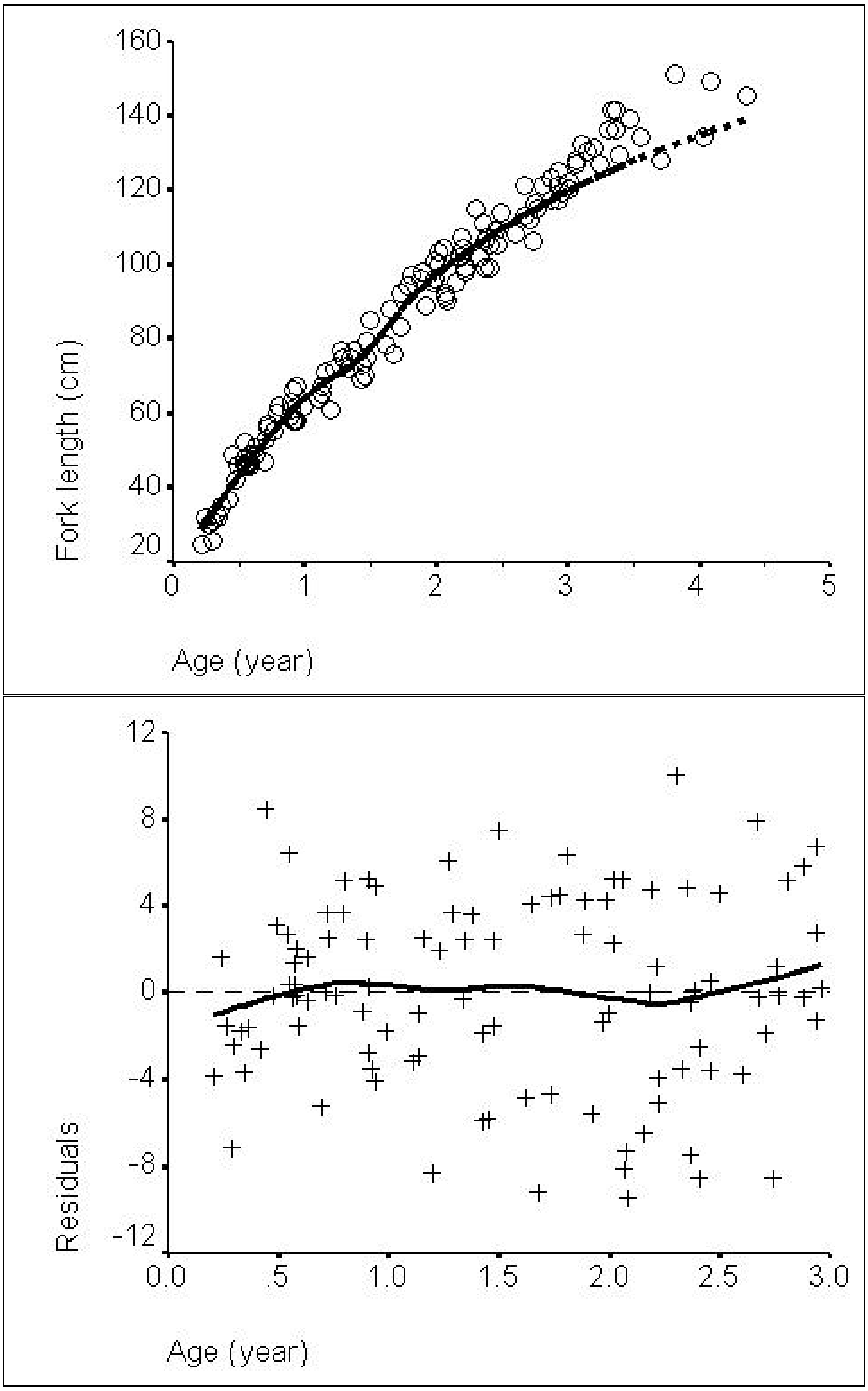

Figure 7. Preliminary estimate of the von Bertalanffy modified growth curve and residuals according to the readings of bigeye tuna otoliths. A lowess function (50%) is used to show the trend in the residuals. Samples older than 3 years are not considered for the estimation.

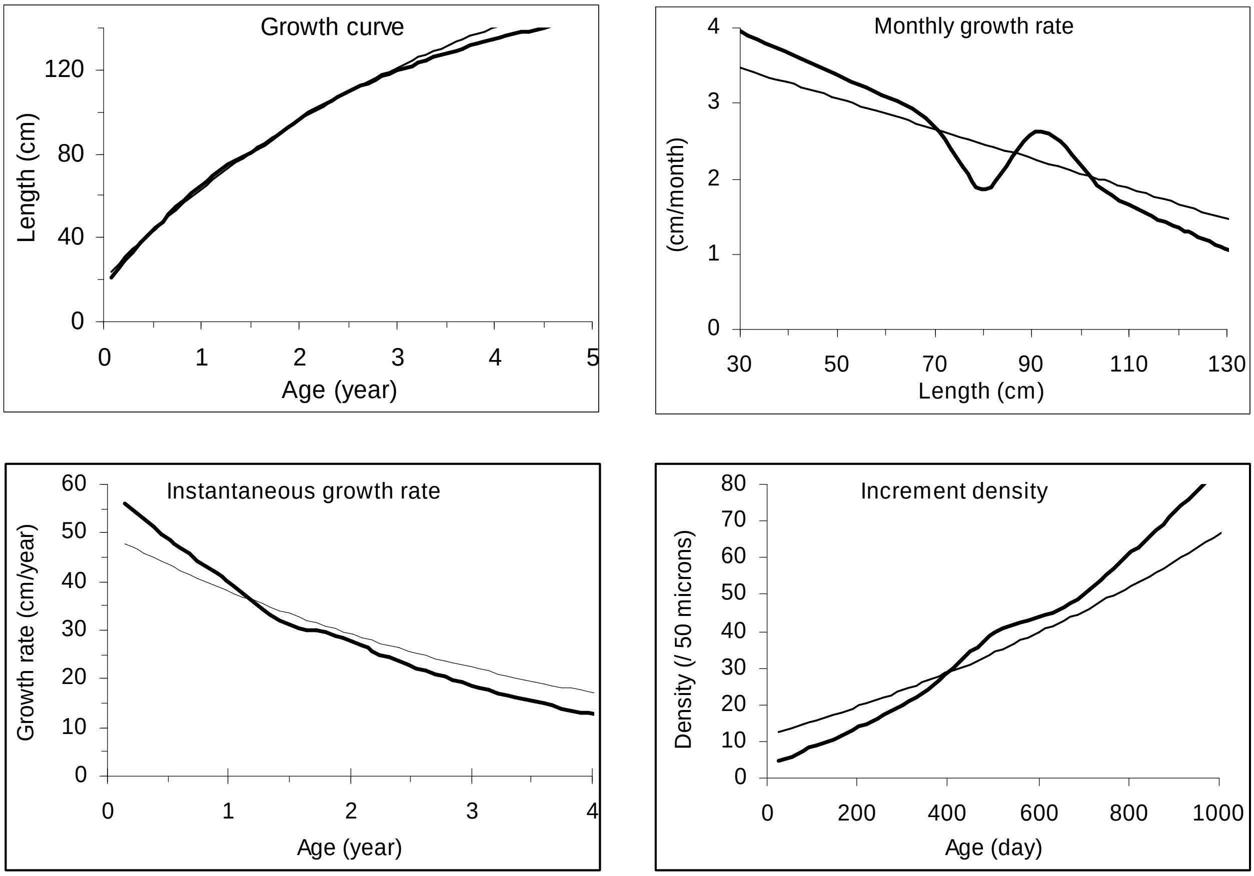

Figure 8. Changes induced on the Von Bertalanffy growth model and its consequences by introducing a variation of K according to a normal distribution N(t). The thick black line represents the modified model and the thin black line the von Bertalanffy model. (Linf = 166.7; K =0.385; to = -0.28;tm = 1.427;s = 0.25; a = 0.02)

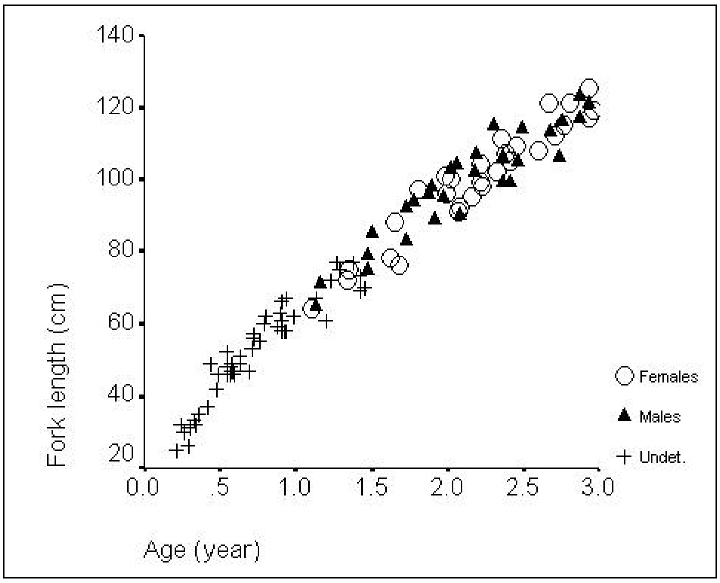

Figure 9. Distribution of bigeye otolith samples by sex

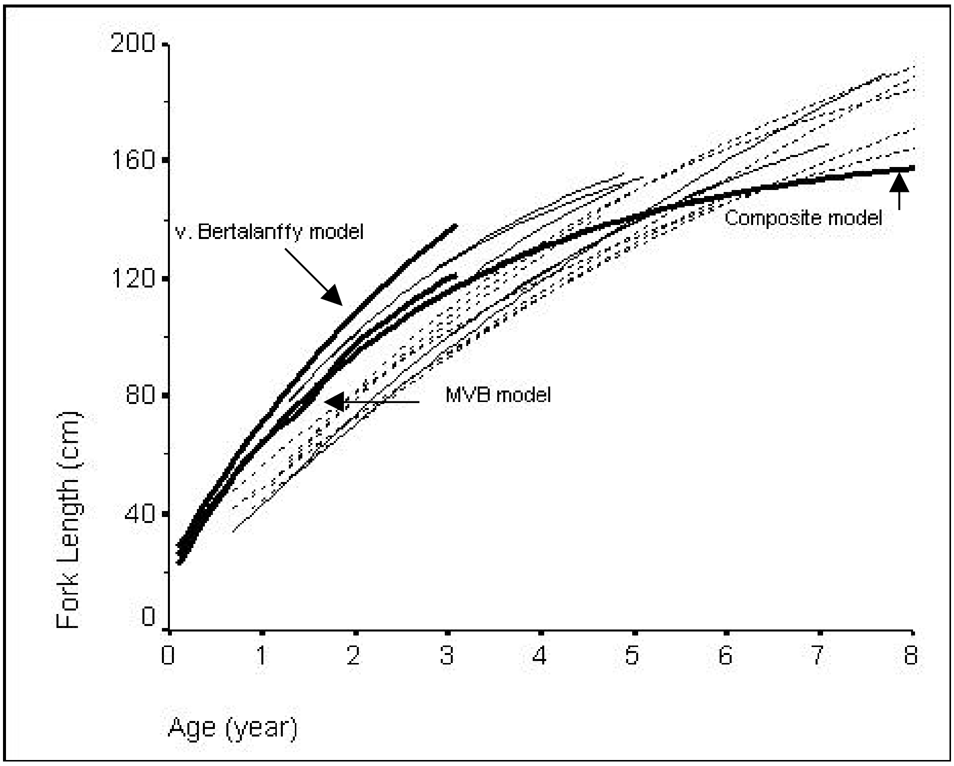

Figure 10. Comparison of the WCPO bigeye growth curve estimated in the present study to estimated growth curves from different regions (see references in Table 3). Dotted lines = studies in Atlantic; thin continuous line = studies in Pacific; thick continuous line = this study

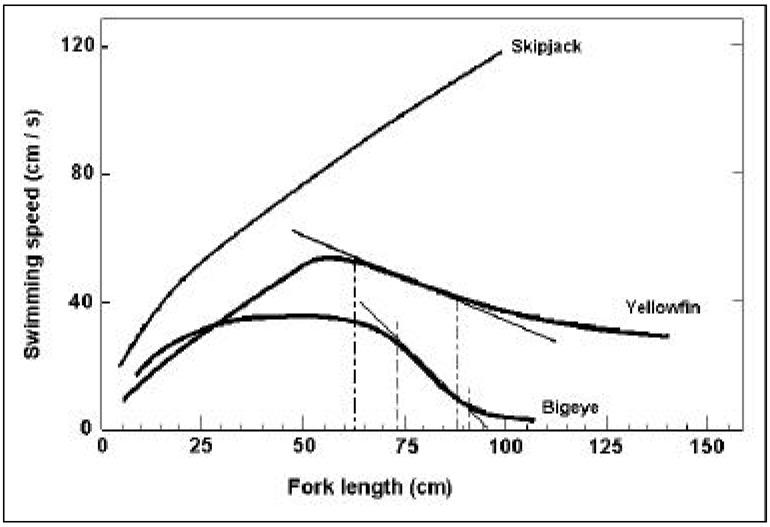

Figure 11. Estimated minimum swimming speeds of three tropical tuna species for maintaining hydrostatic equilibrium in (a) cm/s and (b) body length /s (Redrawn from Magnuson 1973). At the difference of skipjack tuna, bigeye and yellowfin tuna develop a gas bladder allowing to reduce their minimal swimming speed. The sizes at which the maximum decreasing gradient occur are presented for bigeye and yellowfin curves.

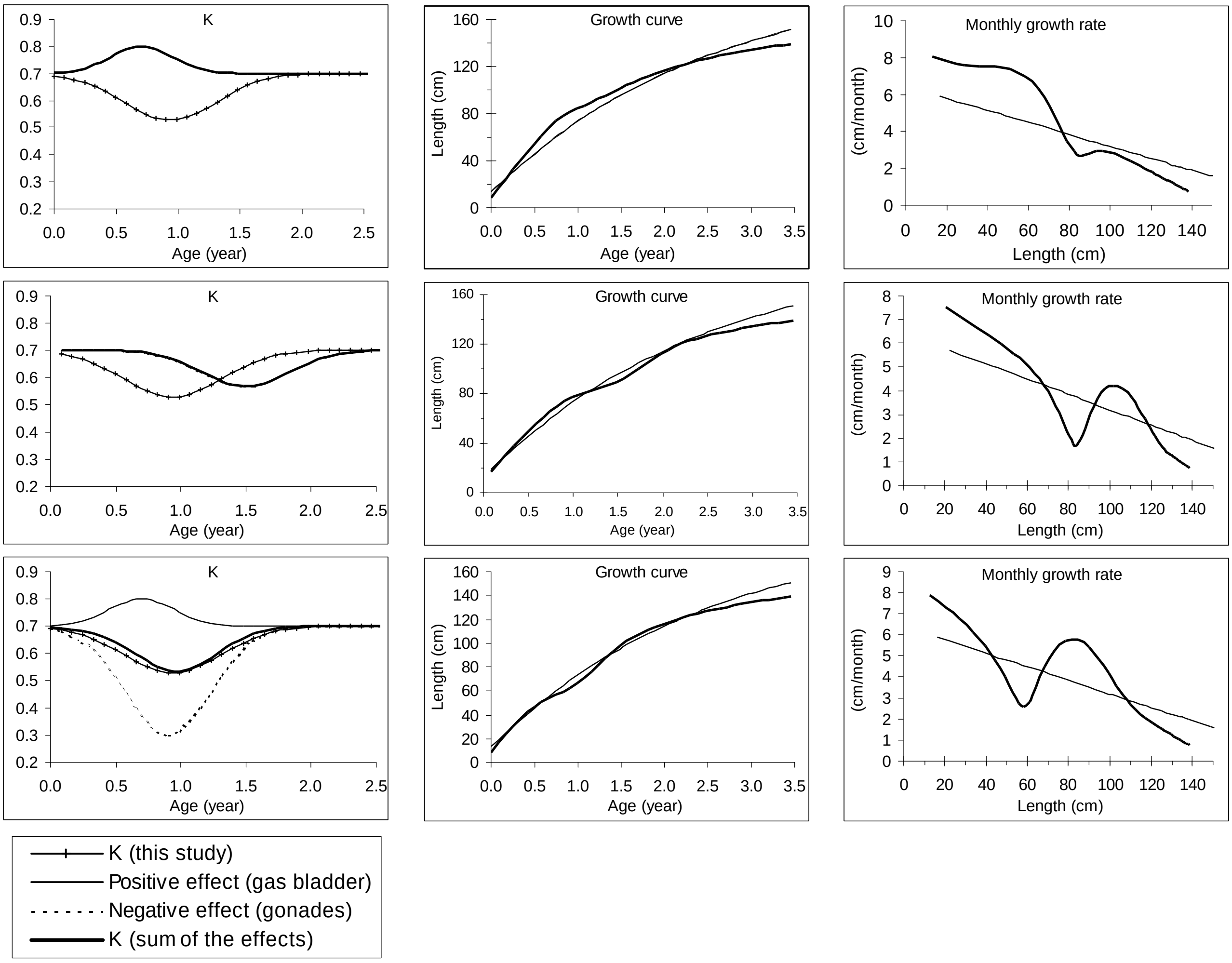

Figure 12. Theoretical changes induced in the growth by positive and negative effects, alone or combined, described by normal functions affecting the value of K. From top to bottom: positive effect alone, negative effect alone, combined effects. On growth curve and monthly growth rate plots, the thick black line represents the modified model and the thin black line the von Bertalanffy model.