Updating the estimation of age and growth of yellowfin tuna (*Thunnus albacares*) in the Indian Ocean using otoliths

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Executive summary

This paper provides an update on yellowfin tuna (*Thunnus albacares*) otolith ageing activities in the western Indian Ocean that have occurred since Farley et al. (2021). Age estimates were obtained for 136 yellowfin tuna, using both daily (n=46) and annual (n=90) ageing methods. The youngest was aged 44 days and the oldest was 11.4 years.

The new age data were combined with age data obtained in the 'GERUNDIO' project[1] (Farley et al. 2021), providing a total of 386 age estimates for analysis. Four growth models were fit to the age and length data (von Bertalanffy (VB), Richards, VB log k, and 2-stage VB), with the 2-stage VB model providing the best fit, particularly for small fish (< ~55 cm fork length, FL). The length-at-otolith weight data (which is independent of the age estimation method) showed a change in otolith growth at ~55 cm FL, which is consistent with the length-at-age data and lends support to the 2-stage VB model. Overall, our analysis shows that fish grow rapidly after birth, reaching ~60 cm FL by age 1 and ~95 cm FL by age 2. Mean asymptotic length was estimated to be ~167 cm FL, slightly higher than estimated in Farley et al. (2021). The updated data analysis indicates that males reach larger sizes, on average, than females.

[1] Collection and analysis of biological samples of tropical tunas, swordfish, and blue shark to improve age, growth and reproduction data for the Indian Ocean Tuna Commission (IOTC), FAO Contract No. 2020/SEY/FIDTD/IOTC - CPA 345335.

We continue to recommend that additional otoliths are collected from the northern and eastern regions of the Indian Ocean, and that these otoliths are aged to provide further information on growth and longevity of yellowfin tuna at the oceanic scale. These data will be useful for assessing whether there are regional differences in growth, and may also provide information regarding inter-annual variation in growth.

1. Introduction

Yellowfin tuna (*Thunnus albacares*) is a highly migratory species that inhabits the epipelagic zone of tropical and subtropical waters of the three major oceans, from latitudes of approximately 45°N to 45°S (Collette et al. 2001). Their spawning areas are restricted to environments with warm sea surface temperatures (>20°C) and mesoscale oceanographic activity (Reglero et al. 2014; Schaefer 2001). Yellowfin tuna represents an important source of nourishment and livelihood for numerous nations around the world (FAO 2020; Guillotreau et al. 2017). It is also a significant component of the global fisheries market, being among the top 10 most fished marine species, and constitutes the second largest tuna fishery worldwide (FAO 2020; McKinney et al. 2020). As such, this species experiences significant fishing pressure, with global catches reaching about 1.45 million tonnes in 2018 (FAO 2020).

Yellowfin tuna is managed as a single stock within the Indian Ocean. Genetic studies indicate that the population structure within the Indian Ocean is complex (Kunal et al. 2013; Barth et al. 2017), and a recent study suggests at least two genetic groups in the western Indian Ocean, with different contributions from north and south of the equator (Grewe et al. 2020). The 2021 stock assessment for yellowfin tuna in the Indian Ocean (with data up to 2020), which considers both stock abundance and fishing mortality, indicated that the stock is overfished and subject to overfishing (Fu et al. 2021; IOTC 2021). An integral part of developing stock assessment models is to have a sound understanding of growth (Maunder and Piner 2015; Methot and Wetzel 2013). Growth models are used in stock assessments to convert length measurements of the catch to age measurements, and to model biomass and fishing processes over time (Murua et al. 2017).

The age and growth of yellowfin tuna has been investigated widely in the Atlantic, Pacific and Indian Oceans (see review by Murua et al. 2017). Several approaches have been used to estimate the growth of yellowfin tuna in the Indian Ocean, including: (1) modal analyses of length frequencies, (2) the examination of daily and annual increments in calcified structures (e.g., otoliths and vertebrae) and (3) growth information obtained from tag and recapture data. Recent studies have generally supported a two-stanza growth curve for Indian Ocean yellowfin tuna, with a slow initial growth phase up to ~60 cm FL followed by much faster growth.

The 2021 yellowfin tuna stock assessment conducted using Stock Synthesis (SS3) used two growth options: the 'ad hoc' two-stanza growth curve from Fonteneau (2008) and the two-stanza growth curve from Dortel et al. (2015). Fonteneau (2008) estimated growth using tag-recapture data from the Indian Ocean Tuna Tagging Programme (IOTTP; Murua et al.

2015), whereas Dortel et al. (2015) used the IOTTP tag-recapture data along with otolith-based daily age estimates from Sardenne et al. (2015) and modal progressions in length frequency data from the purse seine fishery collected in 2000-2010.

In 2020, the European Union and the IOTC supported the "GERUNDIO" project for the "collection and analysis of biological samples of tropical tunas, swordfish, and blue sharks to improve age, growth and reproduction data for the IOTC". As part of that project, biological samples were collected from the western part of the IOTC assessment region and analysed along with existing samples from previous research initiatives to provide preliminary otolith-based age and growth estimates for yellowfin tuna (Farley et al. 2021). In addition, age validation work for yellowfin tuna in the Indian Ocean was undertaken as part of the project by (i) analysing otoliths from fish that had been tagged and recaptured in the IOTTP and (ii) applying bomb radiocarbon (^{14}C) age verification methods to verify the annual ageing protocols used (see Ishihara et al. 2017; Andrews et al. 2020). Both methods provided evidence that the otolith ageing method being used is accurate (Farley et al. 2021; Fraile et al. (submitted)). The preliminary growth curve presented at the 23rd session of the WPTT (Farley et al. 2021) was used in sensitivity runs with SS3 for the 2021 assessment.

This paper provides an update on yellowfin tuna ageing activities that have occurred in the Indian Ocean since the completion of the 'GERUNDIO' project and presents growth models fit to the updated age and length dataset.

2. Methods

2.1. Otolith selection, preparation and reading

Otoliths from 136 yellowfin tuna collected in the western Indian Ocean in 2021 and 2022 were selected for age estimation based on fish length and sampling location. Otoliths from 46 small fish (20-50 cm FL) were selected for daily ageing and otoliths from 90 fish (60-184 cm FL) for annual ageing. The otoliths were cleaned, dried, and weighed to the nearest 0.001 g if complete. The otoliths were prepared and read following the methods described in Farley et al. (2021) and outlined below.

Daily ageing

Otoliths for daily age reading were prepared as either (i) single longitudinal (frontal) sections from the primordium to the postrostral axis of the otolith, through the primordium, or (ii) single transverse sections through the primordium following Williams et al. (2013). The number of visible microincrements (assumed daily growth zones) were counted from the primordium to the terminal edge of the section under high magnification on a compound microscope. All otoliths were prepared and read by Fish Ageing Services Pty Ltd (FAS) in Australia. Each sample was read twice by the same reader and if the difference in counts was >10%, then a third reading was completed. The average of the two closest readings was used as the final count. The distance from the primordium to the terminal edge of the otolith was measured for all transverse-sectioned otoliths.

Initially, we compared counts from longitudinal and transverse sections of paired otoliths from 9 fish (25-70 cm FL) and found age estimates from the longitudinal section were higher than from the transverse section for fish >42 cm FL. Given this, for the remaining 35 otoliths selected for daily ageing, longitudinal sections were prepared for otoliths from fish >42 cm FL (n=11) as they were considered more reliable. However, transverse sections were prepared for otoliths from fish ≤42 cm FL (n=23) as they were required to refine the daily age-otolith size relationship for the decimal age calculation (see section 2.3 below).

Annual ageing

Otoliths for annual age reading were prepared as multiple transverse sections following Anon (2002). All otoliths were prepared and read by the same experienced reader at FAS that read all samples in Farley et al. (2021). An image analysis system was used to read the sectioned otoliths via a dissecting microscope and transmitted light. The system counts and measures the distance of each manually marked opaque zone (marked on the outer edge of each opaque zone) from the primordium and collects an annotated image from each sample read. The opaque zones at the terminal edge of the otolith were only marked if they were complete and some translucent material was evident after the opaque zone. The otolith edge was classified as new opaque, narrow translucent or wide translucent based on the criteria developed for Pacific yellowfin tuna otoliths (Farley et al. 2017) and each reading was assigned a confidence score of 0-5 (poor-good). All samples were read by the same reader a second time to determine intra-reader ageing error. Average percent error (Beamish and Fournier 1981) and age difference tables were used to assess the precision of readings.

2.2. Decimal (annual) age calculation

Decimal age was calculated for each fish with an annual count based on the method developed for yellowfin and bigeye tuna (*Thunnus obesus*) in the western Pacific Ocean (Farley et al. 2020). The decimal ages for yellowfin tuna in Farley et al. (2021) were also re-calculated because the datasets used in the calculation were updated with additional data from the current study, plus the methods were revised slightly. Decimal age was calculated using three steps:

First, the age of each fish when the first opaque zone was completed in the transverse section was calculated. This was done using the updated data set of daily age and otolith size measurements from transverse sectioned otoliths. The updated daily age-otolith size relationship was estimated using a power curve (Append Figure 1) as it provided the best fit to the data.

Second, the number of complete annual increments in the otolith was calculated. A complete annual increment is one opaque zone + one translucent zone, which represents one year of growth, and is calculated as the total count of opaque zones minus 1.

Third, the time elapsed after the last counted opaque zone was deposited and when the fish was caught was estimated using the width of the marginal increment in the otolith as a proportion of the expected width of the complete annulus for that age class. Expected increment width was obtained by fitting an exponential decline relationship between age class and the annual increment width measurements for all fish examined for annual ageing[2] (see Append Figure 2).

The total age of each fish was estimated by adding together the age components estimated in each step. Note that for otoliths with zero or one opaque zones (within the range of the power curve in Append Figure 1), age was estimated using only the otolith measurement (i.e., only step 1).

2.3. Growth analysis

Four different growth models were fit to the age and length data for yellowfin tuna: (1) von Bertalanffy (1938) (VB); (2) Richards (1959); (3) VB with a logistic growth rate parameter (Laslett et al. 2002) (VB log k); and (4) 2-stage VB (similar to Hearn & Polacheck (2003) except the transition is parameterised in terms of age instead of length). Age estimates from both daily counts and from annual counts after applying the decimal age algorithm were included in the models.

The VB growth model has the form:

$$L_a = L_\infty(1 - e^{-k(a-a_0)})$$

where L_a is the fork length at age a, L_∞ is the mean asymptotic length, k is a relative growth rate parameter (year^{-1}), and a_0 is the age at which fish have a theoretical length of zero. We fit the model using maximum likelihood estimation assuming a Gaussian error structure with mean 0 and variance σ^2.

The Richards model can be expressed in different ways, but here we used the following parameterisation:

$$L_a = L_\infty(1 - {}^{1}\!/_{b}\, e^{-k(a-a^*)})^b$$

where L_∞ and k are defined as for the VB model, a^* determines the point of inflection and b governs the shape of the curve. Note that when b = 1, the Richards equation is equivalent to the VB equation.

The VB log k model has the form:

$$L_a = L_\infty \left\{ 1 - e^{-k_2(a-a_0)} \left(\frac{1 + e^{-\beta(a-a_0-\alpha)}}{1 + e^{\alpha\beta}} \right)^{-\frac{(k_2-k_1)}{\beta}} \right\}$$

where this function allows for a change in growth from a VB curve with growth rate parameter k_1 to a VB curve with growth rate parameter k_2. There is a smooth transition between the two

[2] In Farley et al. (2021), the expected increment width for a given age class was calculated as the empirical mean increment width from the otolith measurements taken routinely from the otoliths included in annual ageing. Here, we have revised to use the expected value from a fitted relationship between age class and increment width, which should be more robust for age classes without much data.

stages governed by a logistic function, where α governs the age at which the midpoint of the transition occurs and β governs the rate of the transition (being sharper for larger values).

The 2-stage VB curve has the form:

$$L_a = \begin{cases} \gamma L_\infty(1 - exp(-k_1(a - a_0))) & \text{for } a \leq \alpha \\ L_\infty(1 - exp(-k_2(a - a_0 - \tau))) & \text{for } a > \alpha \end{cases}$$

where $\tau = \alpha + \frac{1}{k_2}\log\left(1-\gamma(1-\exp(-k_1\alpha))\right)$.

This equation represents a VB curve with growth rate parameter k_1 and asymptotic length γL_∞ up to age α , then a VB curve with growth rate parameter k_2 and asymptotic length L_∞ after age α . The term τ is necessary to ensure the two curves match up at the change-point α . Note that the 2-stage VB model differs from the VB log k model in that it allows for a different L_∞ in the first growth phase. A possible disadvantage is that it has an abrupt switch between the two VB curves at age α , whereas the VB log k allows for a slower transition (through the β parameter).

To fit these models, we used maximum likelihood estimation assuming a Gaussian error structure with mean 0 and variance σ^2. Akaike's information criterion (AIC) (Akaike 1974) and plots of residuals were used to compare the fits.

3. Results

3.1. Daily and annual ageing

Age estimates were obtained from all 46 otoliths selected for daily ageing. Age ranged from 44 to 418 days. The age data were combined with the daily age data from Farley et al. (2021) providing a combined total of 120 daily age estimates for analysis (Figure 1).

Counts of opaque zones were obtained for all 90 otoliths read for annual ageing. The counts ranged from 0 to 11 years. Figure 2 is an example of an otolith prepared for annual ageing with the (assumed) annual opaque zones marked. The intra-reader average percent error between readings was 3.34% with a maximum difference of 2 years (Table 1) and age bias plots showed no bias.

Decimal age estimates (combined daily and annual) ranged from 0.12 to 11.7 years. The relationship between otolith weight and age was curvilinear with a high goodness of fit (Figure 3), suggesting that otolith weight may be a good indicator of age, particularly for small/young fish.

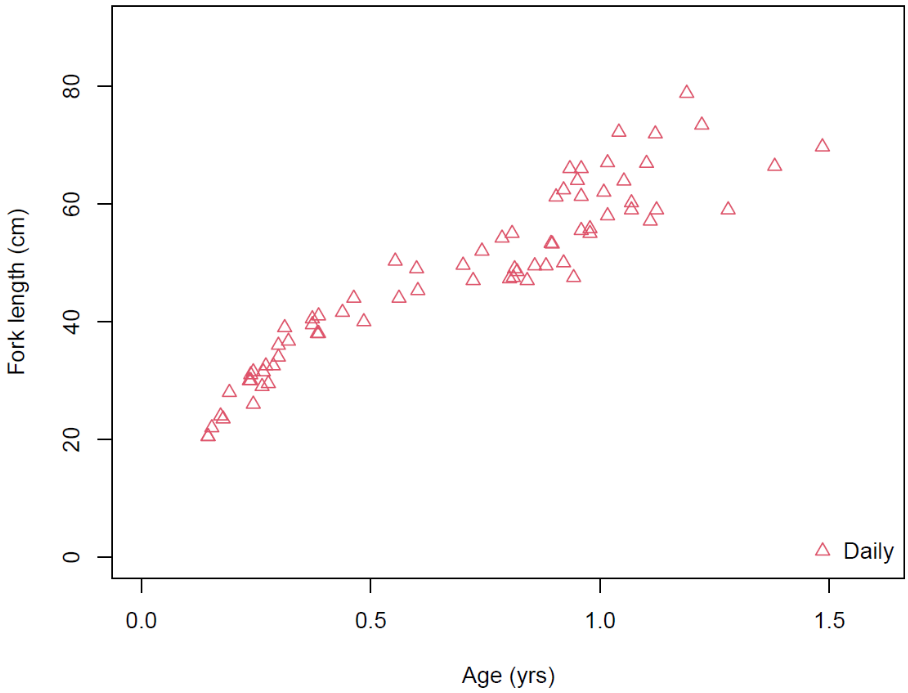


Figure 1. Relationship between daily age and fork length for yellowfin tuna.

Figure 2. Transverse preparation of a yellowfin tuna otolith prepared for annual reading showing presumed annual opaque zones (n=11) indicated by yellow crosses. Fish length 178 cm FL. Note that the two additional crosses (the first and last) mark the primordium and otolith edge respectively.

Table 1. Difference in age estimates between otolith readings by Fish Ageing Services (FAS) for yellowfin tuna in the current study.

Difference	Frequency	% Frequency
-2	1	1.1
-1	8	9.0
0	**70**	**77.8**
1	10	11.1
2	1	1.1
	90	100

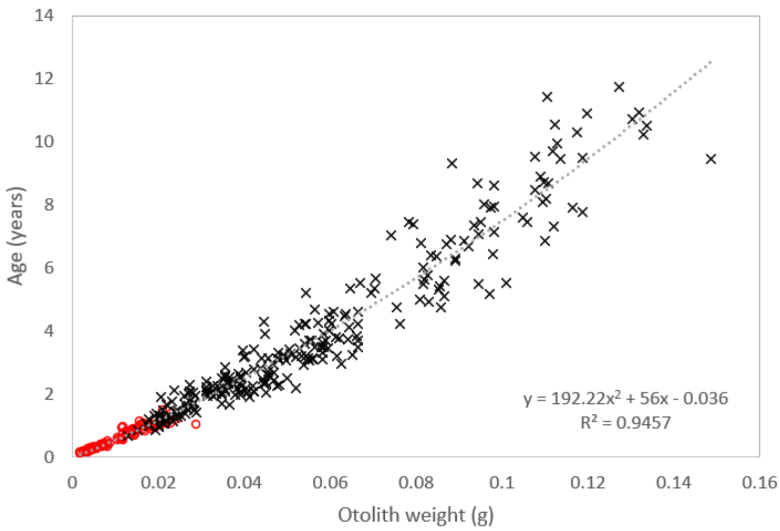


Figure 3. Relationship between otolith weight and estimated age for all yellowfin tuna (n=386). Black x's are decimal age estimates derived from annual counts and red circles are daily age estimates. The equation of the relationship and R^2 are indicated.

3.2. Growth analysis

A total of 386 age-length data points were included in the growth model (266 decimal annual age estimates and 120 daily age estimates). Figure 4 shows the sample locations of the yellowfin tuna with age and length data used in the growth models. Figure 5 shows the size frequency of fish included in the analysis. The 2-stage VB model provided the best fit to the data, in terms of AIC (Table 2) and fit to small fish (< ~55 cm FL) (Figure 6). The 2-stage VB model indicates there is a transition between two VB growth phases at age 0.82 years (53 cm FL), with a very high growth rate parameter in the first phase (k_1=3.1) followed by a lower growth rate parameter in the second phase (k_2=0.39) (Table 2). The other three models (VB, Richards and VB log k) provided almost indistinguishable fits (Figure 6, Table 2).

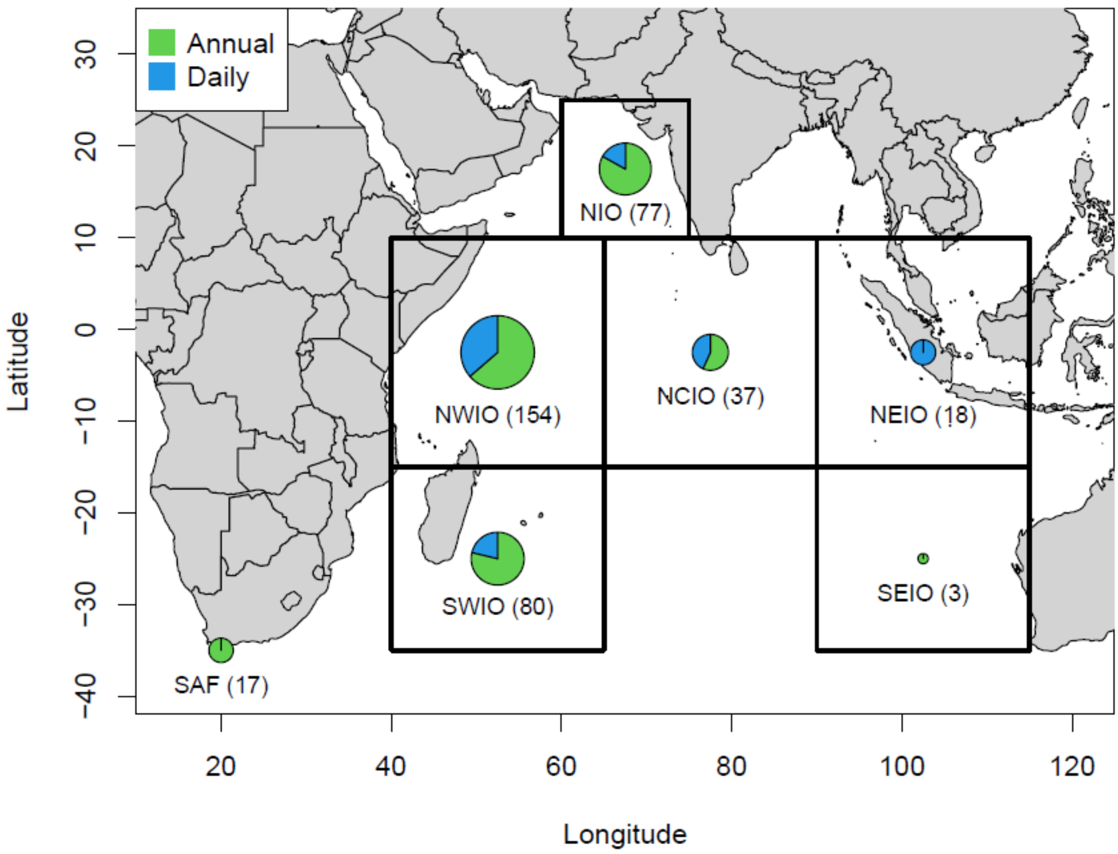


Figure 4. Map showing sample locations of yellowfin tuna included in the growth analysis. Circle size is proportional to total sample size (given in parentheses), with segments indicating annual (green) and daily (blue) age estimates. NIO = north Indian Ocean, NWIO = northwest Indian Ocean, SWIO = southwest Indian Ocean, NCIO = north central Indian Ocean, NEIO = northeast Indian Ocean, SEIO = southeast Indian Ocean, SAF = South Africa.

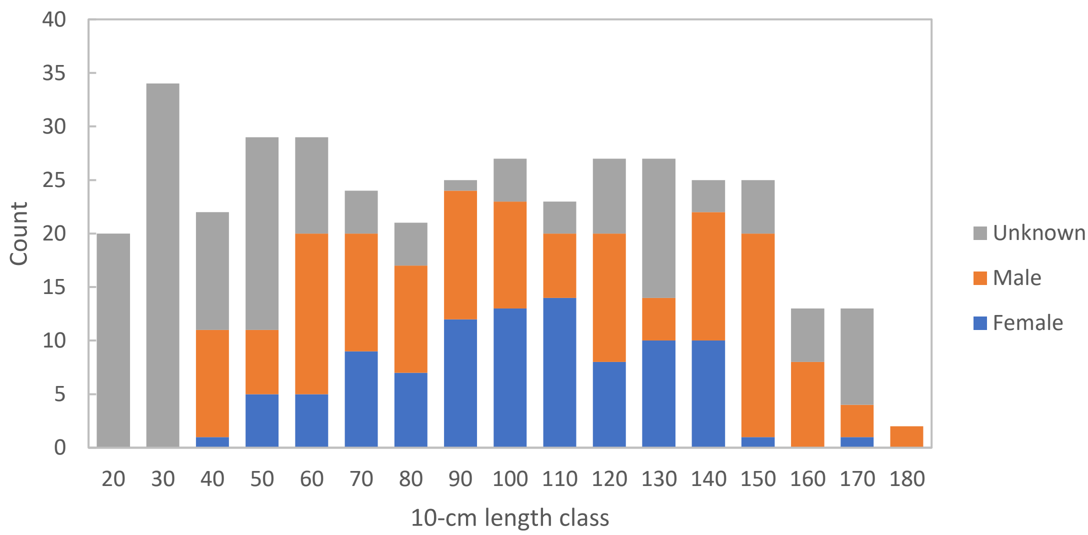
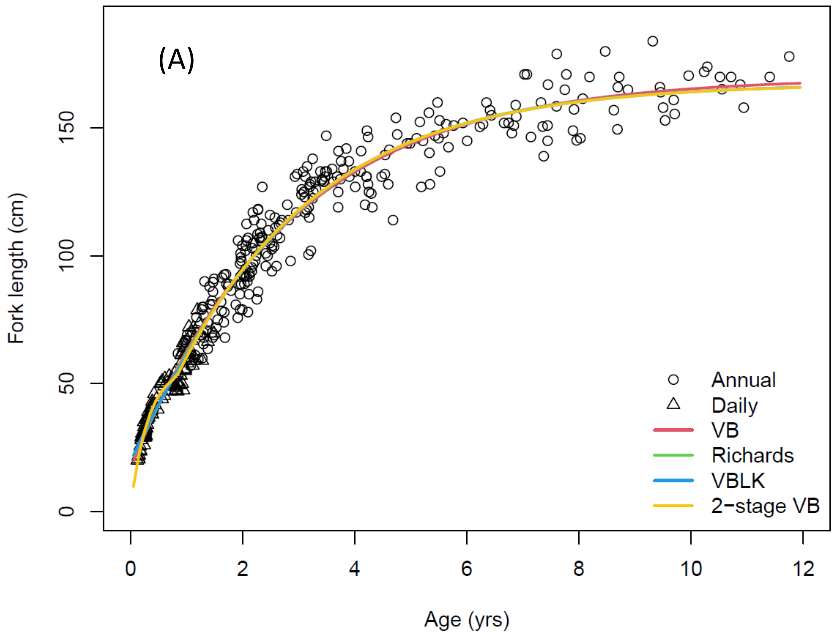


Figure 5. Length frequency (fork length) of yellowfin tuna included in the growth analysis (n=386). The lower bound of the length bin is shown.



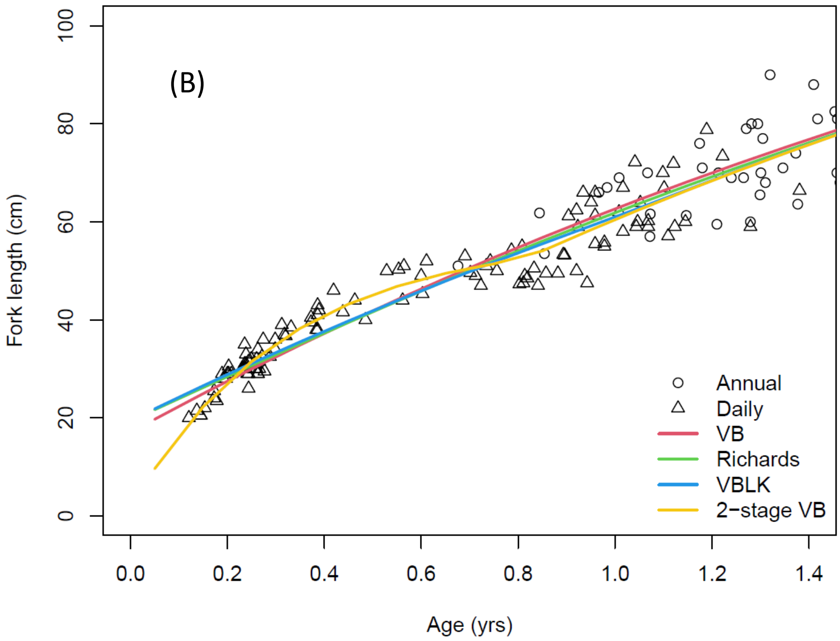


Figure 6. (A) Length-at-age data (daily and annual) for yellowfin tuna with von Bertalanffy (VB), Richards, VB log k (VBLK) and 2-stage VB growth models fit to the data. (B) A close-up of the length-at-age data and growth curves shown in (A) for small/young yellowfin tuna.

Table 2. Parameter estimates from fitting von Bertalanffy (VB), Richards, VB log k and 2-stage VB growth models to the yellowfin tuna length at age data (n=386). Standard errors for the parameter estimates are given in parentheses.

Model	L_∞	k/k_1	k_2	α	$b/\beta/\tau$	a_0/a^*	σ	AIC
VB	169.8 (1.6)	0.35 (0.01)	--	--	--	-0.30 (0.03)	7.83 (0.28)	2692.4
Richards	167.3 (2.0)	0.40 (0.03)	--	--	1.23 (0.19)	0.05 (0.21)	7.81 (0.28)	2691.9
VB log k	167.5 (1.8)	0.33 (0.03)	0.38 (0.02)	1.43 (0.40)	17.5 (68.0)	-0.38 (0.06)	7.78 (0.28)	2692.8
2-stage VB	167.5 (1.6)	3.1 (1.0)	0.39 (0.01)	0.82 (0.06)	0.34 (0.02)	-0.01 (0.05)	7.70 (0.28)	2684.9

Since otolith weight may be an indicator of age, we examined the otolith weight to fish length relationship of a larger number of samples (n=451) than were aged (n=386), to ascertain if the otolith growth was consistent with the observed fish growth. The results show a similar pattern in growth, with a transition at ~55 cm FL from a fast-growing phase to a slower-growing phase (Figure 7).

Preliminary data analysis indicated that males may grow slightly faster and reach slightly larger sizes, on average, than females (Figure 8, Table 3). This was also supported by the length-at-otolith weight data (Figure 9).

The length-at-age data were insufficient to model region-specific growth within the Indian Ocean; however, the current dataset does not indicate clear regional differences (Figure 10).

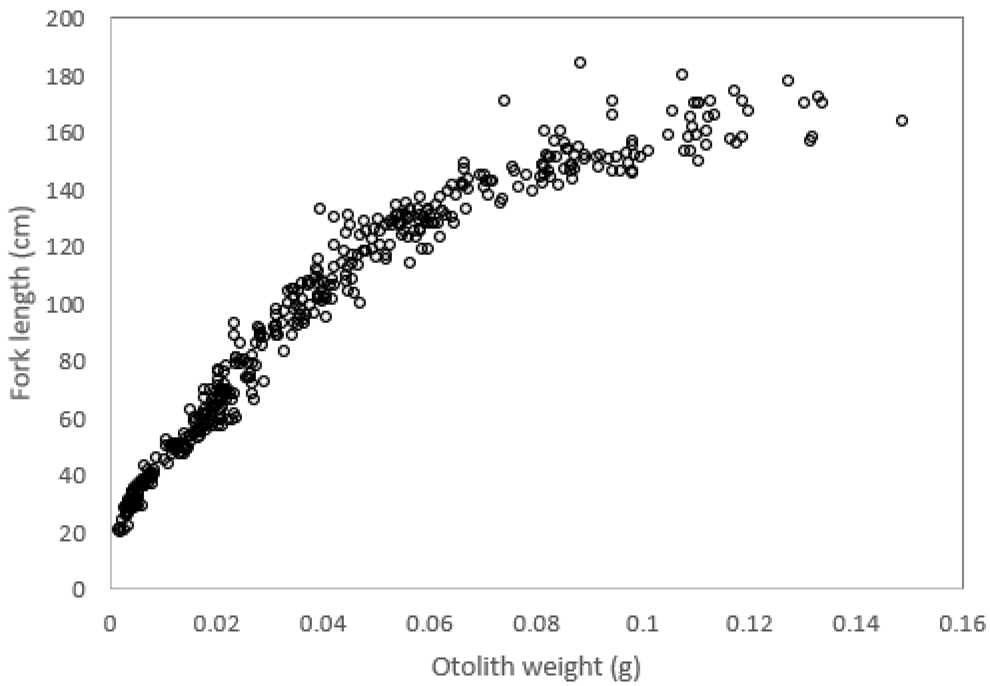


Figure 7. Relationship between otolith weight and fork length for yellowfin tuna in the Indian Ocean from the current study (n=451).

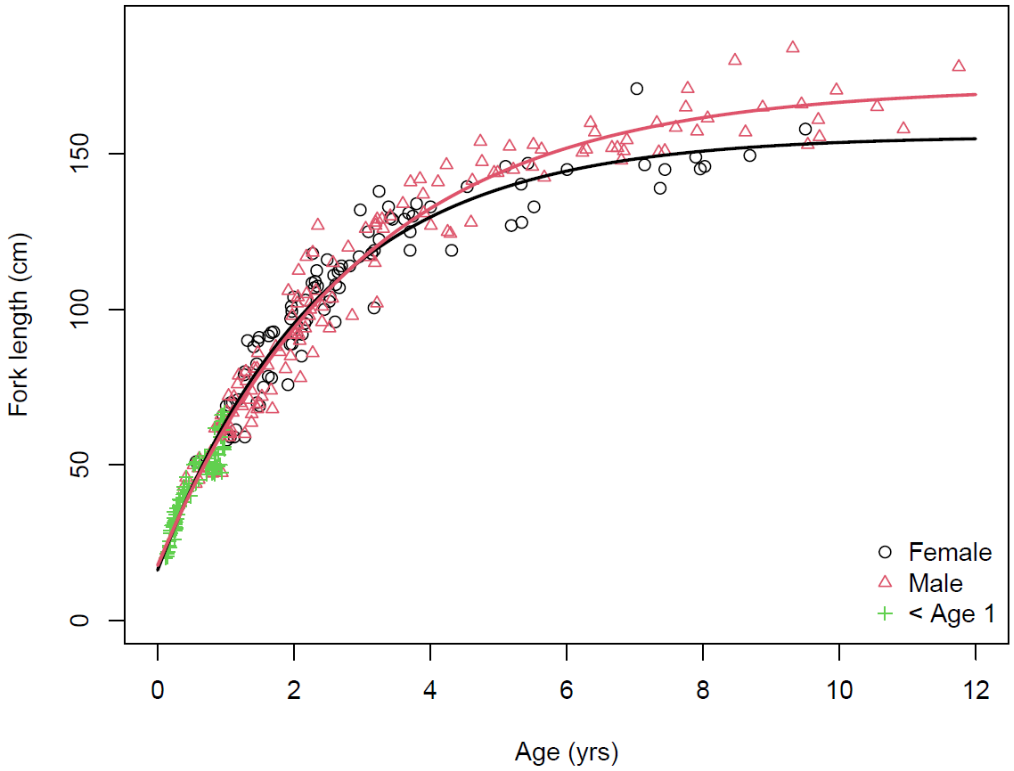


Figure 8. Length-at-age data for yellowfin tuna in the Indian Ocean by sex with the von Bertalanffy (VB) growth model fit to the data. Note that YOY fish (age < 1 year) with unknown sex are included in the models for both sexes. The data indicates that males may grow slightly faster and reach slightly larger sizes, on average, than females.

Table 3. Parameter estimates from fitting a von Bertalanffy (VB) growth model to sex-specific yellowfin tuna length at age data. Note that YOY fish (age < 1 year) with unknown sex (n=83) are included in the models for both sexes. Standard errors for the parameter estimates are given in parentheses.

Model	Sex	*n*	L_∞	*k*	a_0	σ
VB	**F**	179	155.8 (2.3)	0.42 (0.02)	-0.26 (0.02)	6.38 (0.34)
VB	**M**	223	171.6 (1.9)	0.34 (0.01)	-0.31 (0.03)	6.78 (0.32)

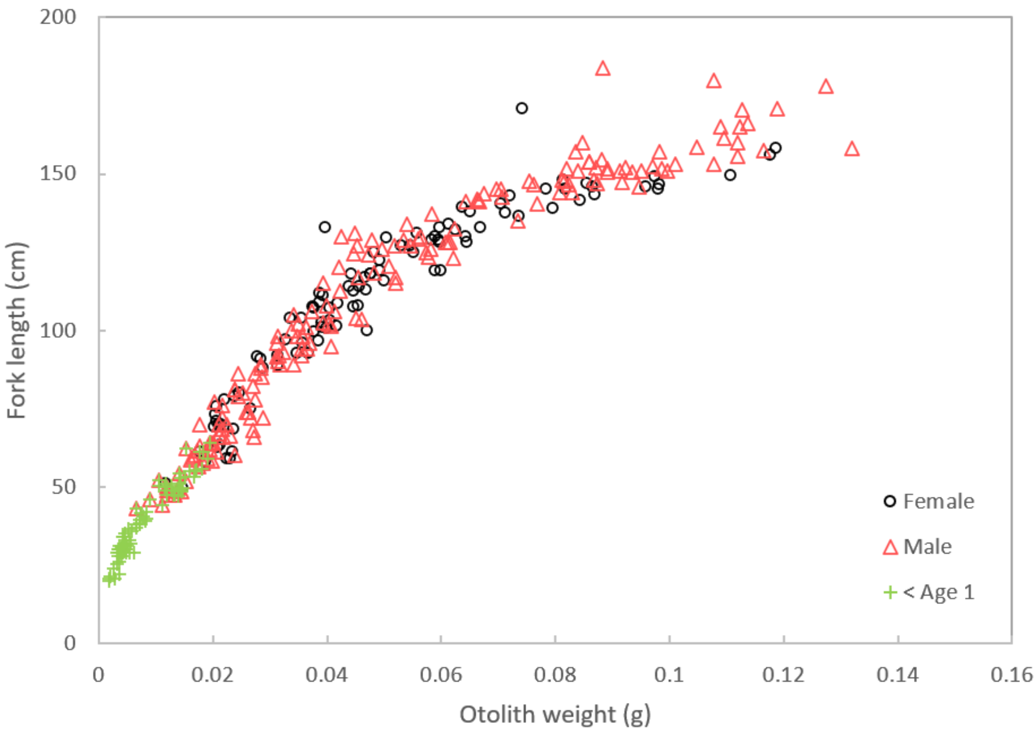


Figure 9. Relationship between otolith weight and fork length for yellowfin tuna in the Indian Ocean by sex (n=236). Note that YOY fish (age < 1 year) with unknown sex are also shown.

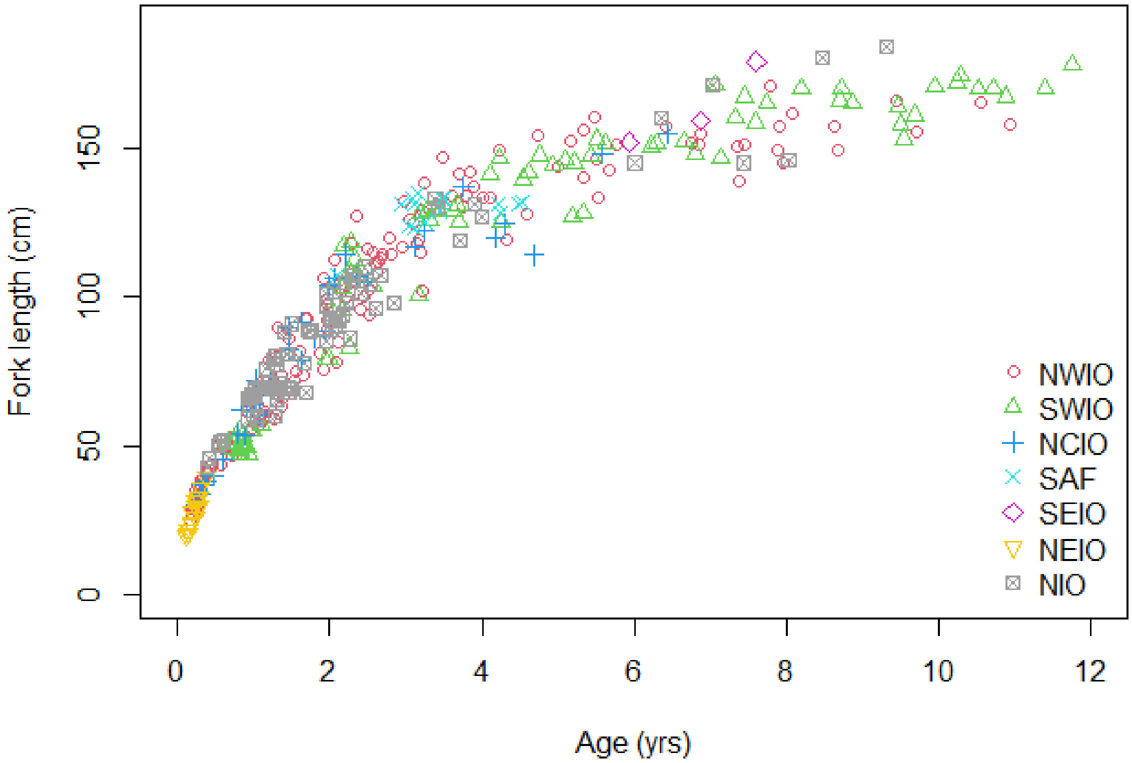


Figure 10. Length-at-age data for yellowfin tuna caught by region in the Indian Ocean. See Figure 4 for regions.

4. Discussion

This study updates Farley et al. (2021) that applied recently developed methods to estimate a decimal age for yellowfin in the Indian Ocean from counts of annual growth zones in sectioned otoliths. The decimal age estimates derived from both annual and daily counts obtained in this study were combined with those from Farley et al. (2021) for a total of 336 age estimates from yellowfin tuna ranging from 20 to 184 cm FL. The annual and daily age estimates aligned well (see Figure 6), supporting our method to calculate the decimal age of yellowfin tuna. Preliminary age validation/verification work using otoliths and data from the IOTTP provided evidence that the otolith ageing method used in this study is accurate (Farley et al. 2021).

The 2-stage VB growth model provided the best fit to the length at age data, particularly for fish < ~55 cm FL. The length-at-otolith weight data (which is independent of the age estimation method) also showed changes in growth consistent with the length-at-age data, which lends support for the 2-stage VB growth model. Overall, our analysis shows that growth is rapid in the first few years with fish reaching ~60 cm FL at age 1 and ~95 cm FL at age 2. Mean asymptotic length (L_∞) was estimated to be ~167 cm FL and maximum age is at least 11.7 years.

Growth for males and females was similar up to three to four years of age, after which the length-at-age for males was, on average, greater than that for females. Mean asymptotic length was estimated to be 171 cm for males and 155 cm for females. Growth curves for male and female yellowfin tuna in the Gulf of Mexico/Western Atlantic Ocean were also similar up to age three to four years, with males then reaching larger L_∞ than females (Picicco et al. 2021). Sex-specific growth was not observed for yellowfin tuna in the Western and Central Pacific Ocean (Farley et al. 2020).

The current dataset does not indicate clear regional differences in growth, but the region-specific sample sizes remain too small to be conclusive. We continue to recommend that additional otoliths are collected from the northern and eastern regions of the Indian Ocean where sample sizes are low, and that these otoliths are aged to provide further information on growth and longevity. These data will also be useful for assessing the potential for inter-annual variation in length at age affecting estimation of the growth curve.

Acknowledgements

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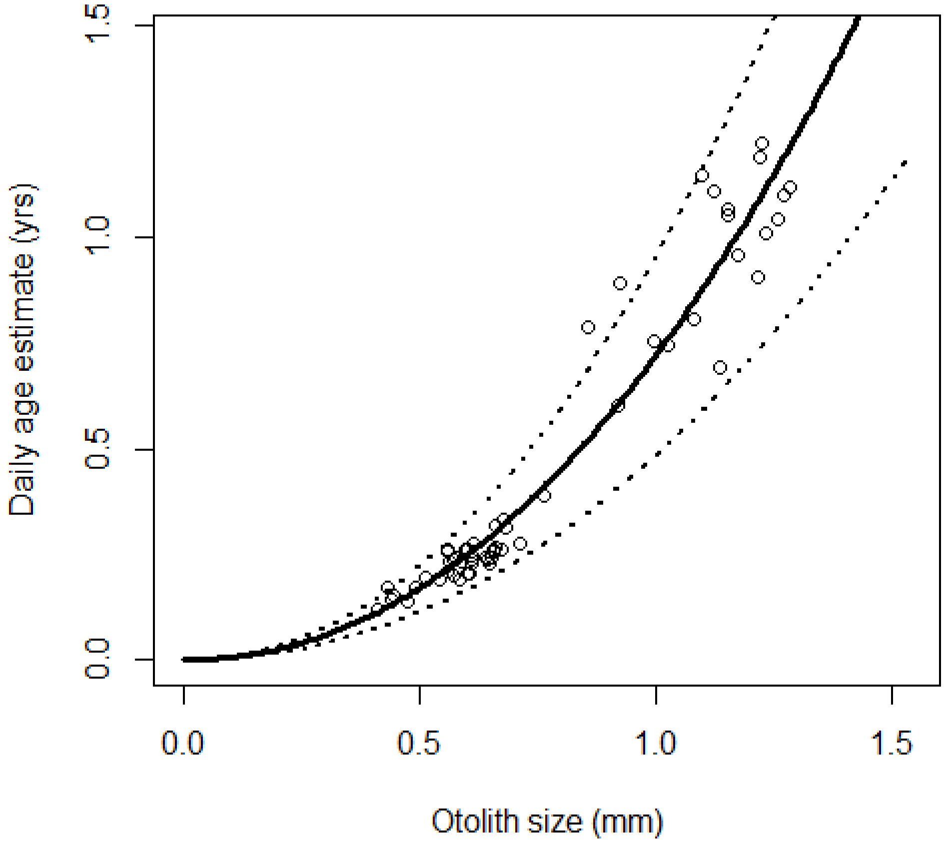
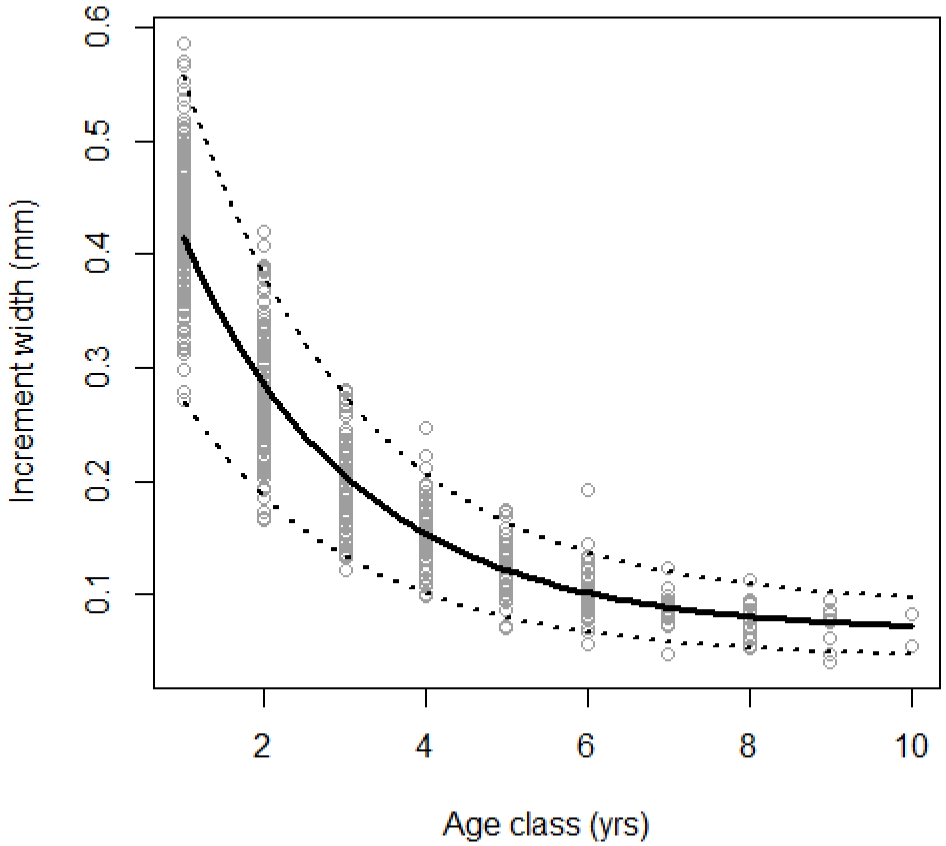
Appendix



Append Figure 1. Relationship between otolith size and daily age with fitted power curve for yellowfin tuna (dashed lines show approximate 95% confidence bounds). Otolith size is the distance from the primordium to the edge in transverse sectioned otoliths.



Append Figure 2. Relationship between age class and increment width for yellowfin tuna, with fitted exponential decline curve (dashed lines show approximate 95% confidence bounds).