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Age and growth of yellowfin and bigeye tuna in the western and central Pacific Ocean from otoliths

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WCPFC Projects 82 and 94

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Contents

1 Executive summary

This paper describes a regional study of yellowfin tuna age and growth in the western and central Pacific Ocean (WCPO) using otoliths, and an update of bigeye tuna growth estimation with the inclusion of newly collected daily-aged otoliths for small fish.

For yellowfin tuna, age data for 1567 fish were obtained for the study, consisting of 119 daily age estimates and 1448 annual age estimates. Otoliths were selected for analysis from the WCPFC Tuna Tissue Bank using a 1-cm length-stratified approach. Most otoliths were from fish between 30 and 160 cm fork length (FL); however, only 62 otoliths were available from fish ≥150 cm FL and only nine of those were from fish ≥160 cm FL. All otoliths were sectioned and read by Fish Ageing Services Pty Ltd (FAS). A new algorithm was developed to estimate decimal (fractional) age using the counts of opaque zones and otolith measurements. The algorithm does not rely on a single assumed birth date for all fish, otolith edge type, or increment formation period, and provides a more sensible conversion of zone count to age, particularly for species with protracted spawning, such as yellowfin tuna and bigeye tuna.

The longevity of yellowfin tuna was found to be at least 15 years, although 89% of fish were <6 years old. Limited direct age validation is available for yellowfin tuna in the WCPO; however, analysis of two chemically-marked otoliths (Farley et al. 2019), and edge type analysis, indicate that one opaque zone is deposited annually in yellowfin tuna otoliths.

The new decimal age algorithm produced age estimates that are consistent with the daily age data and exhibit much less variability in length at age, particularly at young ages (<3-4 years). Parameter estimates for standard von Bertalanffy and Richards growth models were obtained from the combined daily and annual age estimates, with the Richards model preferred based on statistical tests and residuals analysis. The resulting Richards model parameter estimates using only high readability age determinations were L_∞ = 152.0 cm FL, k = 0.40 yr^{-1}, b = 0.85 and t_0 = -0.55 yr.

No significant differences were found in growth between sexes, but there was some evidence of longitudinal differences, with yellowfin tuna sampled between 140-180°E growing to a larger size-at-age than those sampled to the east and west.

For bigeye tuna, daily age counts were obtained for an additional 34 small fish ranging from 14 to 40 cm FL. These samples were included to strengthen the growth analysis previously reported by Farley et al. (2018a) and to aid the estimation of the L1 parameter within the assessment model. The new age algorithm developed for yellowfin tuna was also applied to the bigeye tuna annual count data used in Farley et al. (2018a). Parameter estimates for standard von Bertalanffy and Richards growth models were obtained from the updated combined daily and annual age estimates, with the Richards model preferred based on statistical tests and residuals analysis. The resulting Richards model parameter estimates using only high readability age determinations were L_∞ = 161.1 cm FL, k = 0.24 yr^{-1}, b = 0.58 and t_0 = -2.26 yr.

2 Introduction

The 2017 stock assessment for yellowfin tuna in the western and central Pacific Ocean (WCPO) recommended that new estimates of age and growth be developed for yellowfin tuna (Tremblay-Boyer et al., 2017). This recommendation was made based on how influential new growth estimates for bigeye tuna (Farley et al., 2017) were on the assessment in 2017, noting the similarities in the fisheries for the two species. In addition, the current assessment model for yellowfin tuna predicts a decline in the selectivity of large fish for longline fisheries, a counter-intuitive result that can occur if the growth is incorrectly specified within the assessment model.

In December 2017, the Western and Central Pacific Fisheries Commission (WCPFC) endorsed the project "Yellowfin tuna age and growth" (Project 82). The aims of the project were to develop protocols to estimate the annual age of yellowfin tuna, and to prepare and read 1500 otoliths for annual age estimation.

Work on the project began in 2018 and exploratory results were presented at SPC's 2018 Pre-Assessment Workshop (PAW) and at SC14. A comparison of zone counts from otoliths and spines showed that spines are useful to verify the location of the first three increments in otoliths, but spines are not suitable for annual age estimation beyond three years of age, as early zones are lost due to resorption and vascularisation (Farley et al., 2018b). Conversely, the results indicated that otoliths are a suitable structure for estimating annual age of yellowfin tuna, and the analysis of two strontium chloride marked otoliths indicated that the deposition rate of opaque zones in those otoliths was annual (Farley et al., 2019).

As part of this project, we also attempted to document and better understand differences in ageing methodologies between laboratories in the Pacific. Fish Ageing Services Pty Ltd (FAS) and CSIRO estimate the age of tunas in the western Pacific using 'annual ageing' methods while IATTC estimate the age of tunas in the eastern Pacific using 'daily ageing' methods. FAS also estimate the daily age of small fish but consider daily ageing to be difficult and that counts of presumed daily growth increments may lead to an underestimation of age for fish > 1 year old. At the 2018 PAW, it was recommended that an inter-laboratory ageing workshop be undertaken to compare ageing techniques between the laboratories, standardise the approaches for daily increment counts, and analyse mark-recapture otoliths for age validation. The workshop was scheduled for early 2019 but was delayed until late June 2019 due to the US Federal Government shutdown (Farley et al., 2019). The workshop showed that the preparation of otoliths for daily ageing is similar between labs; however, the interpretation differs in "problematic" areas of the otoliths. It was also observed that the micro-structure of otoliths from the WPO is more difficult to interpret compared to the micro-structure in the eastern Pacific Ocean (EPO) otoliths. The results of preliminary age validation work in the western Pacific suggest that daily ageing methods underestimate age of yellowfin tuna >74 cm FL from the WCPO (Farley et al., 2019).

A second workshop on ageing yellowfin and bigeye tuna was undertaken in late 2019 in Panama City, Florida (Allman et al., in prep). The workshop was important to ensure consistency across laboratories in annual ageing methods, and included scientists from NOAA, ICCAT, University of Maine, Louisiana Department of Wildlife and Fisheries, NRIFSF as well as CSIRO and FAS. The workshop indicated that the ageing protocols were in general agreement among laboratories.

The need for, and benefit of, these inter-laboratory workshops was evident; however, they did result in flow-on delays to delivery timeframes of the yellowfin tuna ageing project. While preliminary results were presented at the 2020 PAW, this paper presents the final results of the yellowfin tuna project, and updates earlier results for bigeye tuna through the inclusion of daily age counts for an additional 34 small fish ranging from 14 to 40 cm FL.

3 Yellowfin tuna

3.1 Methods

3.1.1 Otolith selection

The aim of the study was to construct a WCPO-wide, sex-aggregated growth curve for yellowfin tuna in the WCPO assessment region. Otoliths from over 5,000 yellowfin tuna have been collected since 2009 and archived into the WCPFC tuna tissue bank. Most otoliths were from fish between 30 and 160 cm fork length (FL). We selected over 1500 otoliths for ageing using a 1-cm length-stratified approach. The number of otoliths selected from each assessment region was in proportion to the catch in the region, as far as practicable. For regions where the number of otoliths available was lower than required, additional otoliths were selected from other regions. Additional otoliths from fish smaller than currently available in the tuna tissue bank (<30 cm FL) were specifically collected for daily ageing. All otoliths were sent to FAS for sectioning and reading. Otoliths were registered into the sample monitoring system and weighed to the nearest 0.1 mg (if whole and undamaged).

Figure 1 and Figure 2 show the otolith sampling locations and size frequency, respectively, of fish with age estimates included in the final growth analysis. Note that very few large yellowfin tuna were available for ageing; only 62 of the fish aged were ≥150 cm FL, nine of which were ≥160 cm FL.

3.1.2 Age estimates

Otoliths were prepared for daily and annual age reading based on the method used by FAS for routine ageing of other tuna species. For daily ageing, the method involves preparing single longitudinal (frontal) sections from the primordium to the postrostral axis of the otolith, through the primordium (Williams et al., 2013) and counting assumed daily growth zones. Since we are confident in daily age estimates only for small/young fish (see Farley et al., 2019), we restricted the daily ageing work to fish <70 cm FL.

For annual ageing, the otolith preparation method involves embedding a row of five otoliths in resin and cutting up to four serial transverse sections from each otolith including or adjacent to the primordium (Anon 2002). The sections were read at 25x magnification illuminated with transmitted light. The opaque zones were counted from the primordium to the otolith edge, and an otolith readability score was assigned to each reading. Previous daily ageing work using the transverse section helped locate the first annual opaque zone (Farley et al., 2018b). An opaque zone on the margin was only counted if it was fully formed. A customised image analysis system was used to measure the distance between the primordium to the distal edge of each of the opaque zones, and to the edge of the otolith. Note that for bigeye tuna, the otolith measurements were made from the first inflection rather than the primordium (Farley et al 2017); either is fine to use if all measurements are made from the same location for the species. In addition, the otolith edge type classification was recorded as opaque, narrow translucent, or wide translucent, and was assigned an edge type confidence score. Edge type analysis was undertaken to examine monthly variation in zone formation (Campana 2001).

3.1.3 Decimal age

Farley et al. (2017) developed an age algorithm for bigeye tuna to estimate a decimal (fractional) age for each fish. The algorithm used counts of opaque zones, otolith edge type, capture date and a nominal birthdate (i.e., the same birthdate for all fish). However, as noted in Farley et al. (2018a), not all individuals in a population will hatch on the same day. Fish that hatch earlier than the nominal birth date will be older than calculated (and vice versa). However, the growth curve estimated from the combined length-at-age data should not be biased as it is assumed that similar numbers of the fish will have hatched prior to and after the nominal birth date.

The use of a nominal birthdate in the algorithm, however, is problematic if the age data are to be integrated into the assessment as conditional age-at-length data because the stock assessment model has a quarterly time step and the ages all fall into one quarter for any particular sampling quarter. To refine the age estimates, we investigated whether otolith weight could be used since it is correlated with fish age (Francis and Campana, 2004). The hypothesis is that fish with a larger-than-average otolith weight for their estimated age are actually older (i.e., have an earlier birthdate); conversely fish with a smaller-than-average otolith weight for their estimated age are actually younger. However, as approximately half of the age estimates do not have an associated otolith weight measurement (due to the otolith being broken), substantially fewer age estimates are available for the growth analysis. Since otolith size is also correlated with fish age, and measured distances between opaque zones within the otolith section were available for all fish, we examined whether these measurements would be a better morphometric measurement to use.

To do this, we developed a new age algorithm to estimate decimal age using just the counts of opaque zones and otolith measurements. Otolith measurement data were used to calculate:

1) <u>The relationship between otolith size and daily age in young fish.</u> In this case otolith size is the distance from the primordium to the otolith edge in the transverse section. Daily age estimates were obtained from the longitudinal section in the ‘sister’ otolith. The daily age-otolith size relationship was estimated using a power curve (see Figure 3). Note that we limited the analysis to fish ≤70 cm FL as we are confident in the daily age estimates for fish up to that size.
2) <u>The mean width of each annulus (annual increment; 1 year of otolith growth)</u>. This was calculated using the otolith measurements taken routinely for each otolith included in the annual ageing. The distance between the terminal edge of each opaque zone was calculated, and the mean size estimated for each age group (see Figure 4).

Decimal age was calculated for each fish using the following three steps:

Step 1: Use the daily age-otolith size relationship from #1 above to estimate the age of each fish when the first opaque zone was completed in the transverse section. This was done using the measurement from the primordium to the distal edge of the first opaque zone. For fish with no opaque zones (young-of-year, YOY), total age was estimated using the measurement from the primordium to the otolith edge.

Step 2: Calculate the number of complete annual increments in the otolith. 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.

Step 3: Estimate the time elapsed after the last counted opaque zone was deposited and when the fish was caught. This was calculated using the size of the marginal increment as a proportion of the mean size of the complete annulus for that age group (from #2 above).

Total age was estimated by adding together the age components estimated in each step. For YOY, age was calculated using Step 1 only. Figure 5 illustrates the steps involved using an otolith with four completed opaque zones as an example.

3.1.4 Growth analysis

A von Bertalanffy (VB) growth model was fit to the age and length data following the methods described in Farley et al. (2017). The VB model has the form:

$$L_t = L_\infty (1 - e^{-k(t - t_0)})$$

where L_t is the fork length at age t, L_∞ is the mean asymptotic length, k is a relative growth rate parameter (year^{-1}), and t_0 is the age at which fish have a theoretical length of zero. We used maximum likelihood estimation assuming a Gaussian error structure with mean 0 and variance σ^2.

For comparison, a Richards growth model, which allows for an S-shaped curve and is sometimes referred to as a generalized logistic, was also fit to the data. The Richards growth curve was parameterized as:

$$L_t = L_\infty (1 - 1/b * e^{-k(t - t_0)})^b$$

where all parameters are defined as for the VB model except t_0 now 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. We again used maximum likelihood estimation assuming a Gaussian error structure with mean 0 and variance σ^2. Akaike's information criterion (AIC) (Akaike 1974) was used to compare the fits.

To investigate whether growth differs by sex, we fit separate models to the data for each sex. East-west differences in growth were investigated by fitting separate models to the data from three longitudinal bands (<140°E, 140-180°E, >180°E).

3.2 Results and Discussion

3.2.1 Age estimates

Age data for 1567 yellowfin tuna were included in the final growth analysis; consisting of 119 daily age estimates and 1448 annual (decimal) age estimates. This excluded 17 age estimates that were identified as likely outliers; i.e., the fish size was unlikely to be correct given the otolith weight and/or age estimate obtained (see Figure 6). The longevity of yellowfin tuna was found to be at least 15 years, although 89% of fish were <6 years old. Otolith weight was obtained for 937 samples; the remaining samples were missing some part of the otolith. Figure 6 shows the relationship between otolith weight and fish size.

Appendix A shows examples of sectioned otoliths from yellowfin tuna of different sizes with the opaque zones indicated.

3.2.2 Age validation, verification and corroboration

Daily age

Limited direct age validation is available for yellowfin tuna in the WCPO. As noted in the Introduction, preliminary age validation, using mark-recapture methods, was reported by Farley et al. (2019). Although only two otoliths were available for analysis, and both were from the Coral Sea, the results provide evidence that counts of daily growth zones are not a reliable source of age information for yellowfin tuna >74 cm FL (the smallest of the two fish examined).

Three previous studies estimated the daily age of yellowfin tuna in the western and central Pacific using otoliths. Uchiyama and Struhsaker (1981) estimated the daily age of yellowfin tuna from the central Pacific (Line islands and Hawaii). Yamanaka (1990) validated a daily deposition rate using whole otoliths from 12 small (25-40 cm FL) yellowfin tuna held captive in Hawaii. The study went on to estimate the age of 139 yellowfin tuna (16-79 cm FL), using whole and sectioned otoliths, caught in the Philippines. Finally, Lehodey and Leroy (1999) estimated the daily age of yellowfin tuna from a broader area of the western equatorial Pacific between 120^{o}E and 170^{o}W. Figure 7 compares the daily age at length estimates from these studies, with estimates from the eastern Pacific (Wild 1986) and the current study. The estimates obtained in the current study are similar and intermediate to the two studies from the western Pacific, which all generally show faster growth rates compared to fish from the central and eastern Pacific.

Annual age

In addition to the information on daily ages, the two otoliths examined in the mark-recapture experiment (Farley et al. 2019) indicated that counts of annual growth zones may be a reliable source of age information for yellowfin tuna in the western Pacific (Farley et al., 2019). This was the first verification on the annual periodicity of opaque zones in otoliths for yellowfin tuna in the Pacific.

Based on edge type analyses for age classes 1 to 3, we suggest that opaque zones in transversely sectioned otoliths formed predominantly between May and October/November (Figure 8). The highest proportion of otoliths with opaque margins were sampled in June, declining gradually over the following months. This suggests that one opaque zone was deposited annually in these age classes during this period. Additional mark-recapture samples to confirm these finding would be desirable, particularly samples from equatorial regions.

Recent bomb radiocarbon work in the Atlantic has provided validation of annual ageing methods for bigeye and yellowfin tuna in the Gulf of Mexico (Andrews et al., 2020). The application of this method to existing otolith collections may provide an additional source of verification of age estimates, and is currently being explored (Farley et al., 2020). An international workshop on ageing yellowfin and bigeye tuna, which included otolith reads from the Andrews et al (2020) study, indicated that the ageing protocols were in general agreement among participating laboratories using 'annual ageing' methods (Allman et al., in prep).

3.2.3 Growth analysis

Parameter estimates from fitting VB and Richards models to the yellowfin tuna otolith data are given in Table 1. For both models, the results are almost identical using all otoliths compared to using only those with high readability (Table 1, Figure 9, Figure 11). Thus, residuals are shown only for the high readability models (Figure 10, Figure 12). Both models provide very similar fits, but based on AIC, the Richards model provides a slightly better fit (Table 1). The residuals for both models show a slight S-shaped pattern at young ages (< 3 years); as such, we tried fitting a two-phase VB log k growth model (see Eveson et al. 2015), but this did not remove the pattern and gave almost the same AIC value as the Richards model.

Figure 13 shows the Richards model fit to the high readability age data and the VB growth curve (with offsets estimated for age classes 2 to 8) estimated internally in the 2017 stock assessment based on the model's fit to the length and weight frequency data (diagnostic case, Tremblay-Boyer *et al*. 2017). Estimated growth for the two models is similar for smaller (<80 cm) fish; however, the 2017 assessment model estimated that yellowfin tuna grow to larger average size at older age (+8.5 cm for quarterly age class 28, which was the oldest age class included in the assessment) than the otolith-based growth curve.

Of the 1567 fish where decimal age was assigned, 458 were females, 766 were males and 343 were immature or had an unknown sex determination. Note that only 6.3% of females were aged ≥5 years, while 23.5% of males were aged ≥5 years. It is unknown whether this is due to females being less prevalent in the population than males at older ages, misidentification of gonads, or due to an unknown sampling bias. Previous studies have noted a bias in the sex ratio towards male in larger length classes (i.e. >130 cm FL) and it has been suggested that this may be due to differential natural mortality rather than sexual dimorphism in growth (Schaefer et al. 2001). However, this is the first evidence of a bias in sex ratio at age in yellowfin tuna, with a greater proportion of males in older age classes. A similar bias towards males in older age classes was not detected for bigeye tuna in the WCPO (Farley et al. 2017).

The parameter estimates and mean growth curves from fitting a Richards model to the data for males and females separately (including immature fish and fish of unknown sex with length <5 cm for both sexes) are similar (Figure 14, Table 2). Males have a slightly larger L_∞ estimate; however, taking standard errors into account, there is no significant difference between the L_∞ parameters for males and females (Table 2). Note that because the data for females above age 5 years is minimal, the standard error estimate for L_∞ for females is reasonably large.

Richards growth curves fit to the data from the three longitudinal bands suggest fish in the central region (between 140-180°E) grow to a larger size than those sampled to the east and west (Table 3, Figure 15). Also, the mean growth curve for the eastern region (>180°E) has an apparent inflection in growth (Figure 15), estimated to be at 0.75 years (Table 3); however, the sample size for this region is too small to be certain about this finding.

4 Bigeye tuna

4.1 Methods

4.1.1 Age estimates

Otoliths from 34 small bigeye tuna ranging from 14 to 40 cm FL were selected for daily ageing to aid the estimation of the L1 parameter within the assessment model. Longitudinal sections were prepared for each otolith and daily age estimated following Williams et al. (2013).

No additional annual ageing of bigeye tuna has been undertaken since Farley et al. (2018a). However, the new age algorithm developed for yellowfin tuna (see section 3.1.3) was applied to bigeye tuna using the counts of opaque zones and otolith measurements from Farley et al. (2018a). The relationship between otolith size and daily age in young fish was estimated using the distance from the first inflection point to the otolith edge in transverse sections and daily age estimates from reading the longitudinal sections of 20 'sister' otoliths. We limited the analysis to fish ≤70 cm FL (<1 year), which is the maximum size and (daily) age we are confident in based on mark-recapture age validation work (Farley et al., 2018b, 2019). The daily age-otolith size relationship was estimated using a power curve (Figure 16). The mean width of each annulus (annual increment) was calculated using the otolith measurement data taken routinely for each otolith (see Farley et al. 2018a) (Figure 17).

These revised annual age estimates and all available daily age estimates were combined. Figure 18 and Figure 19 show the otolith sampling locations and size frequency, respectively, of all bigeye tuna included in the growth analysis.

4.1.2 Growth analysis

Von Bertalanffy and Richards growth models were fit to the updated daily and annual age data for bigeye tuna, following the same methods described in section 3.1.4 for yellowfin tuna.

4.2 Results and Discussion

4.2.1 Age estimates

Age estimates for the 34 additional small bigeye tuna selected for daily ageing ranged from 41 to 144 days. Combined with the previous data from Farley et al. (2018), this resulted in a total of 1264 age estimates to be included in the growth analysis; consisting of 92 daily age estimates and 1172 annual (decimal) age estimates. This excluded 13 age estimates that were identified as likely outliers; i.e., the fish size was unlikely to be correct given the otolith weight and/or age estimate obtained.

4.2.2 Growth analysis

Parameter estimates from fitting VB and Richards models to the bigeye tuna otolith data are given in Table 4. For both models, the results are very similar using all otoliths compared to using only those with high readability (Table 4, Figure 20, Figure 22). Thus, we concentrate here on the high readability model results. Based on the residual plots (Figure 21,

Figure 23) and AIC values (Table 4), the Richards model provides a better fit. The residuals for the VB model show a slight S-shaped pattern (Figure 21), whereas the residuals for the Richards model are centred around zero and show no pattern (

Figure 23).

The new Richards growth curve for bigeye tuna is similar to the VB curve estimated previously and used in the 2018 assessment (see Farley et al., 2018a; Vincent et al., 2018) (Figure 24).

5 Summary

This is the first large-scale study of age and growth of yellowfin tuna in the western and central Pacific and has provided new otolith-based age estimates for inclusion in the regional stock assessment. The longevity of yellowfin tuna was found to be at least 15 years, although 89% of fish were <6 years old. Although direct validation of the periodicity of the (opaque) growth zones in otoliths is limited, edge type analyses indicated that the growth zones are deposited annually. Analysis of two mark-recapture otoliths also indicated an annual deposition rate of opaque zones in otoliths. Participation in inter-laboratory workshops has helped standardise the ageing approaches used to count daily increments and has helped ensure consistency in otolith preparation and reading protocols used to count annual growth zones.

The new decimal age algorithm developed for yellowfin and bigeye tuna produced age estimates that are consistent with the daily age data and exhibit much less variability in length at age, particularly for younger fish. The algorithm does not rely on a single assumed birth date for all fish, otolith edge type, or increment formation period, which can lack precision. The new algorithm also solves the problem of fish being aggregated into the same quarterly age class in the assessment.

The Richards growth curve estimated for yellowfin tuna is substantially different, particularly for older age classes, to that estimated internally from length and weight frequency data in the 2017 stock assessment model. The substantially smaller mean lengths at age for the older fish estimated from otolith data can be expected to have a significant impact on the upcoming assessment. Additionally, it will be instructive to include the new yellowfin tuna conditional age-at-length data in the new assessment to see how the MULTIFAN-CL model can (or cannot) reconcile these data with the size frequency data.

Significant differences in growth between sexes for yellowfin tuna were not found; however, the data for females is limited above age 5 and we suggest accumulation of more data is required for a robust comparison. It is unknown whether the low number of older females is due to differential mortality rates and/or an unknown sampling bias. Evidence of longitudinal differences in growth were found for yellowfin tuna, with fish sampled between 140-180°E growing to a larger size than those sampled from east and west of this region.

The new Richards growth curve estimated for bigeye tuna is similar to the VB curve estimated previously and used in the 2018 assessment.

Further direct age validation studies for yellowfin and bigeye tuna ageing methods, spanning the entire size range and expected range of longevity, are urgently needed in the Pacific.

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7 Tables and Figures

Table 1. Parameter estimates from fitting von Bertalanffy (VB) and Richards growth models to the yellowfin tuna length at age data, using all otolith readings and only high confidence readings (i.e. readability score ≥ 3). Standard errors for the parameter estimates are given in parentheses. The sample size (n) is also presented.

MODEL	Data	n	L_∞	k	b	t_0	σ	AIC
VB	All data	1567	150.5 (0.72)	0.440 (0.007)	--	-0.245 (0.014)	7.80 (0.14)	10891.9
VB	High confidence + daily ages	1471	150.3 (0.74)	0.442 (0.007)	--	-0.244 (0.014)	7.67 (0.14)	10175.5
Richards	All data	1567	152.2 (1.03)	0.397 (0.017)	0.847 (0.048)	-0.548 (0.124)	7.78 (0.14)	10887.3
Richards	High confidence + daily ages	1471	152.0 (1.06)	0.398 (0.018)	0.847 (0.048)	-0.547 (0.125)	7.65 (0.14)	10171.0

Table 2. Parameter estimates from fitting a Richards growth model to the yellowfin tuna otolith data by sex. Standard errors for the parameter estimates are given in parentheses. Note that immature fish and fish of unknown sex with length <55 cm are included in the models for both sexes.

MODEL	Sex	Readability	n	L_∞	k	b	t_0	σ
Richards	Females	All	631	149.7 (2.54)	0.388 (0.032)	0.801 (0.063)	-0.669 (0206)	7.467 (0.210)
Richards	Males	All	939	154.5 (1.18)	0.377 (0.019)	0.802 (0.046)	-0.675 (0.147)	7.340 (0.169)

Table 3. Parameter estimates from fitting a Richards growth model to the yellowfin tuna otolith data by longitudinal bands. Standard errors for the parameter estimates are given in parentheses.

MODEL	Longitude	Readability	n	L_∞	k	b	t_0	σ
Richards	<140°E	All	308	146.71 (1.54)	0.44 (0.05)	0.75 (0.12)	-0.64 (0.39)	6.64 (0.27)
Richards	140-180°E	All	1110	155.28 (1.46)	0.39 (0.02)	0.96 (0.09)	-0.42 (0.18)	7.83 (0.17)
Richards	>180°E	All	147	144.06 (2.41)	0.69 (0.03)	8368 (251)	0.76 (0.03)	7.35 (0.43)

Table 4. Parameter estimates from fitting von Bertalanffy (VB) and Richards growth models to the bigeye tuna length at age data, using all otolith readings and only high confidence readings (i.e. readability score ≥ 3). Standard errors for the parameter estimates are given in parentheses. The sample size (n) is also presented.

MODEL	Data	n	L_∞	k	b	t_0	σ	AIC
VB	All data	1264	151.8 (0.74)	0.383 (0.006)	--	-0.414 (0.019)	6.70 (0.13)	8403.9
VB	High confidence + daily ages	1010	151.1 (0.92)	0.386 (0.008)	--	-0.410 (0.020)	6.66 (0.15)	6705.8
Richards	All data	1264	158.8 (1.39)	0.267 (0.014)	0.617 (0.026)	-1.836 (0.219)	6.56 (0.13)	8351.7
Richards	High confidence + daily ages	1010	161.1 (1.68)	0.242 (0.013)	0.577 (0.020)	-2.258 (0.237)	6.45 (0.14)	6640.4

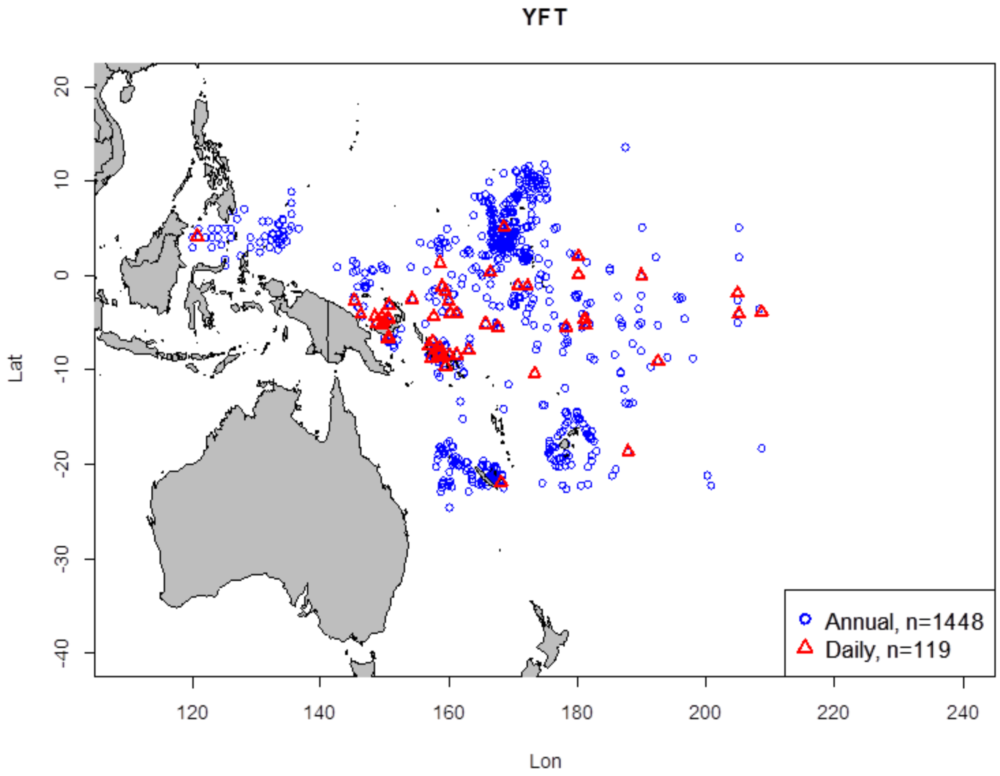


Figure 1. Map of the sampling locations for yellowfin tuna included in the growth analysis. Otoliths shown in blue were selected for annual ageing and those shown in red were selected for daily ageing. Longitude shown in degrees east.

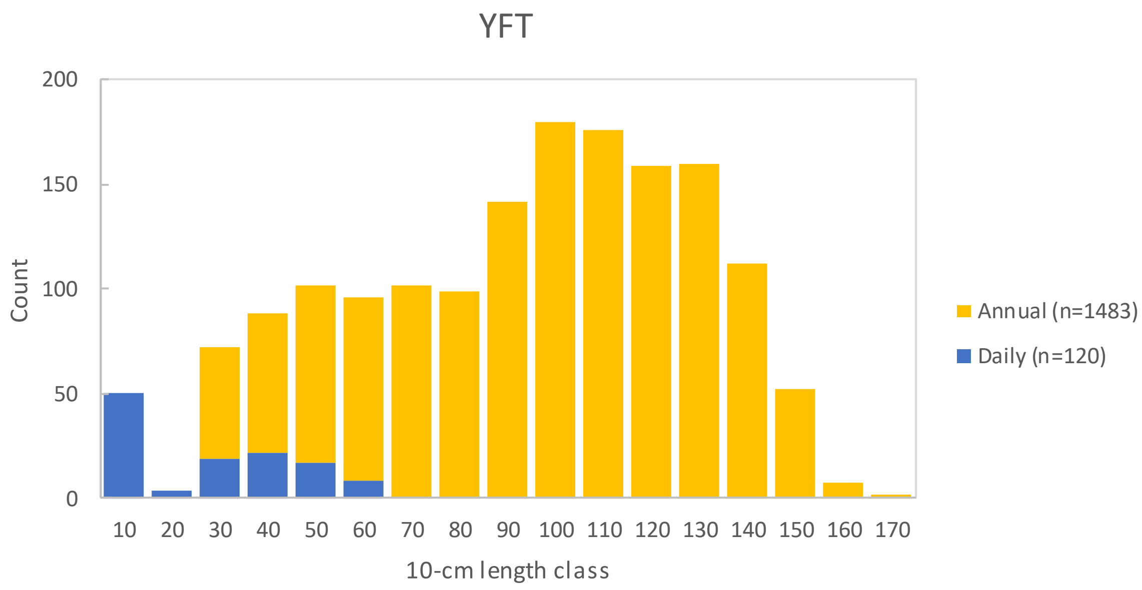


Figure 2. Length frequency of yellowfin tuna included in the growth analysis. The lower boundary length value of the bin is shown.

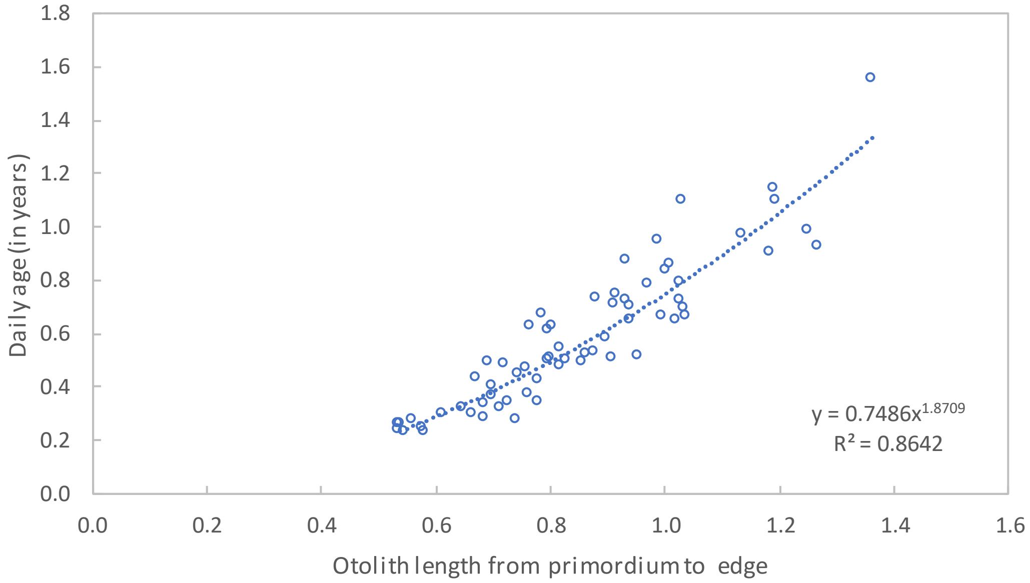


Figure 3. Daily age vs otolith size with fitted power curve for yellowfin tuna. Otolith size is the distance from the primordium to the edge in sectioned otoliths. n=67.

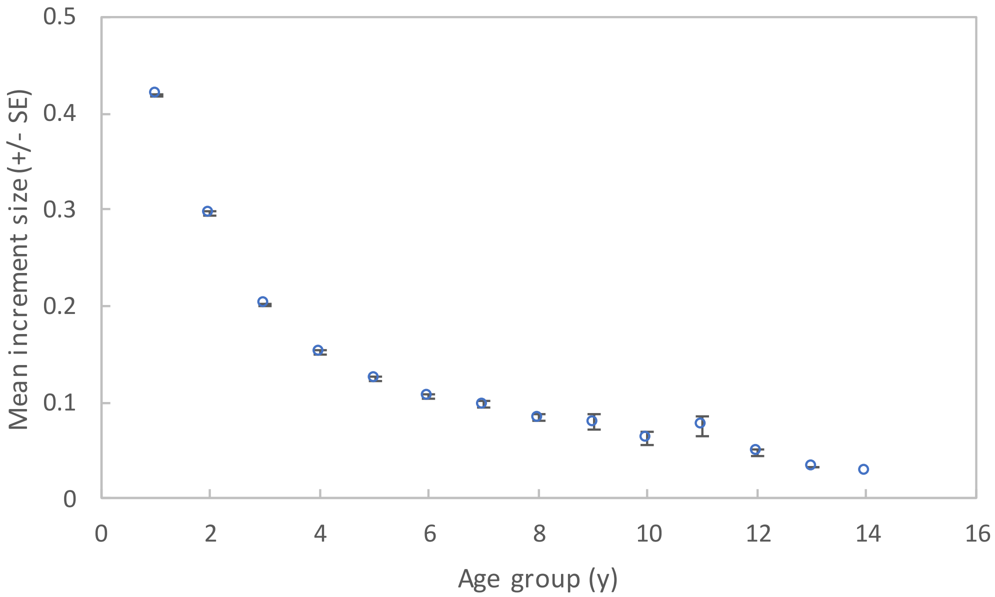


Figure 4. Mean (+/- SE) annual increment width in millimetres by age class for yellowfin tuna.

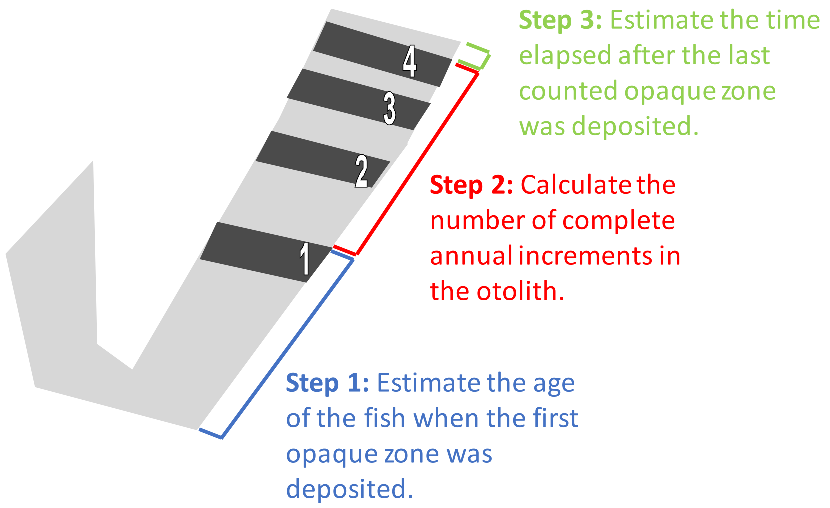


Figure 5. Illustrative example of the steps used to estimate the decimal age of yellowfin or bigeye tuna with four complete opaque zones. Step 1 is estimated using the daily age-otolith size relationship using the distance measured from the first inflection to end of the first opaque zone. Step 2 is the number of opaque zones counted minus 1. Step 3 is the marginal increment measurement as a proportion of the mean size of the complete annulus for the age group.

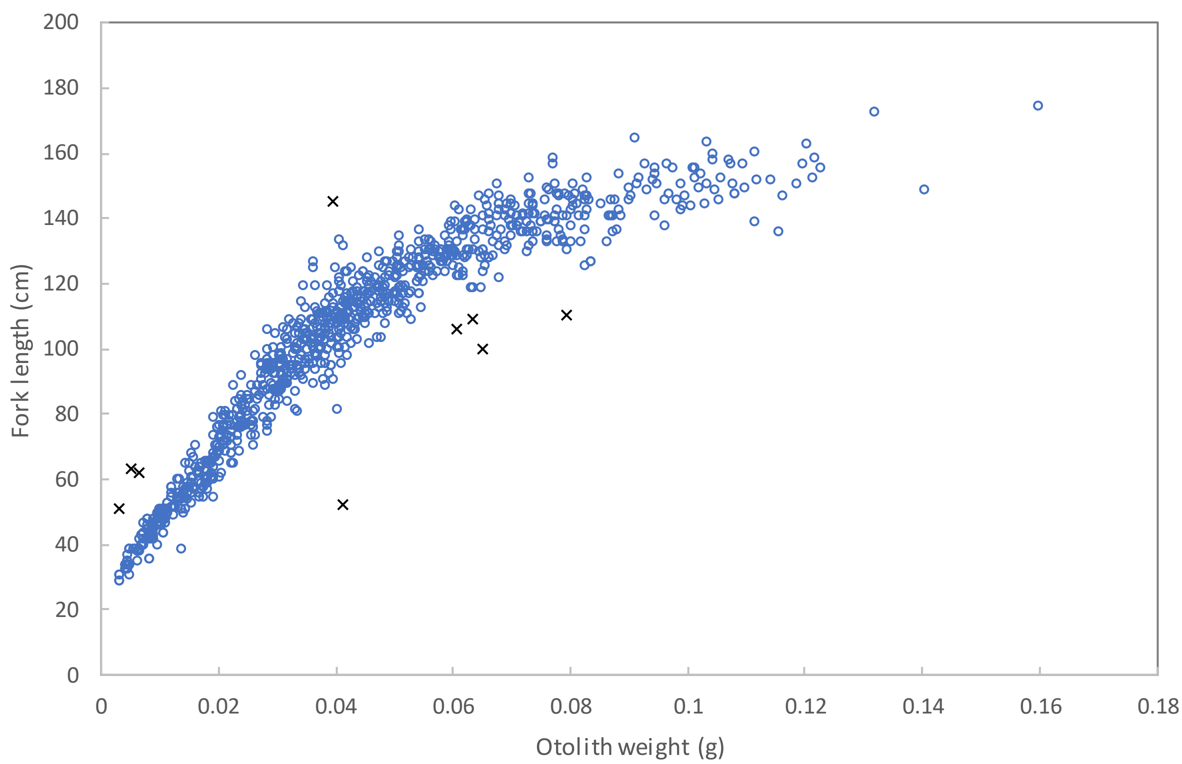


Figure 6. Relationship between otolith weight and fish length for yellowfin tuna. Outliers are indicated by X.

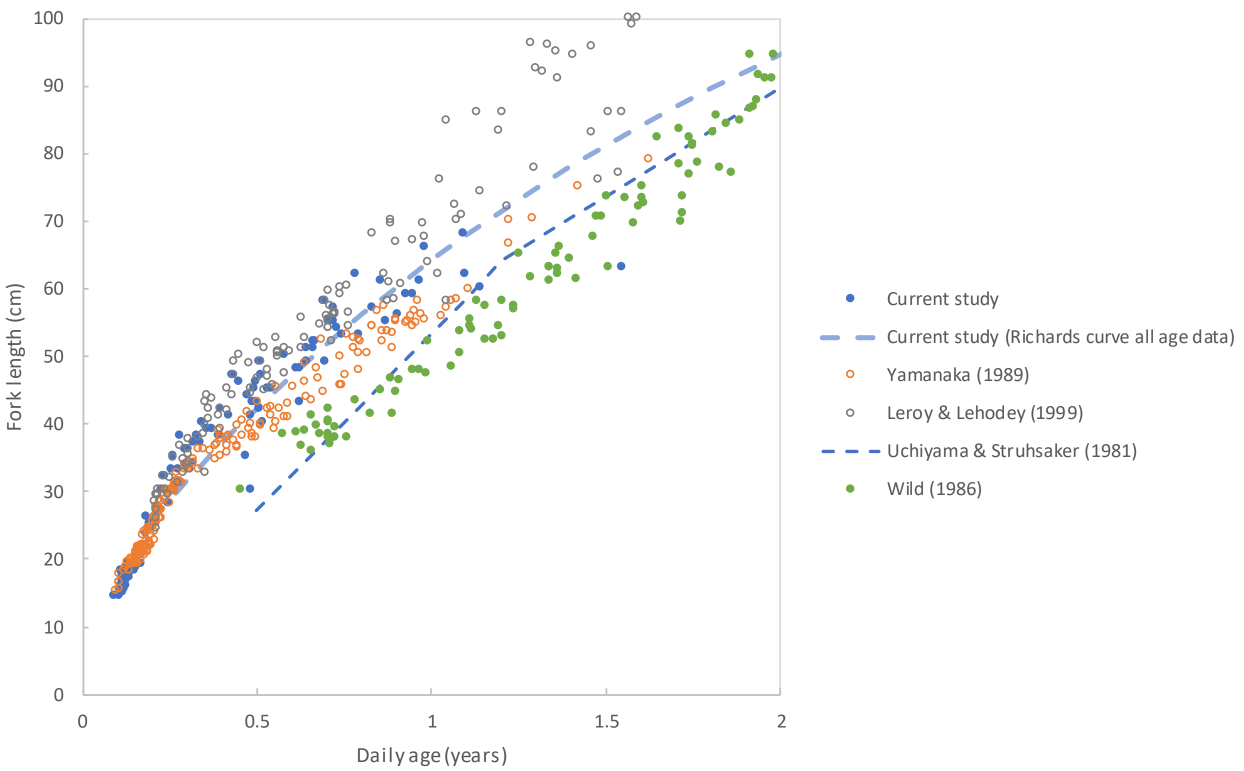


Figure 7. Comparison of daily age at length estimates for yellowfin tuna in the current study with those obtained previously in the western Pacific (Yamanaka, 1998; Leroy and Lehodey, 1999), the central Pacific (Uchiyama and Struhsaker, 1981; linear regression shown) and the eastern Pacific (Wild, 1986). The Richards growth curve estimated using all the length at age data in the current study is also shown. The data is limited to fish ≤100 cm FL.

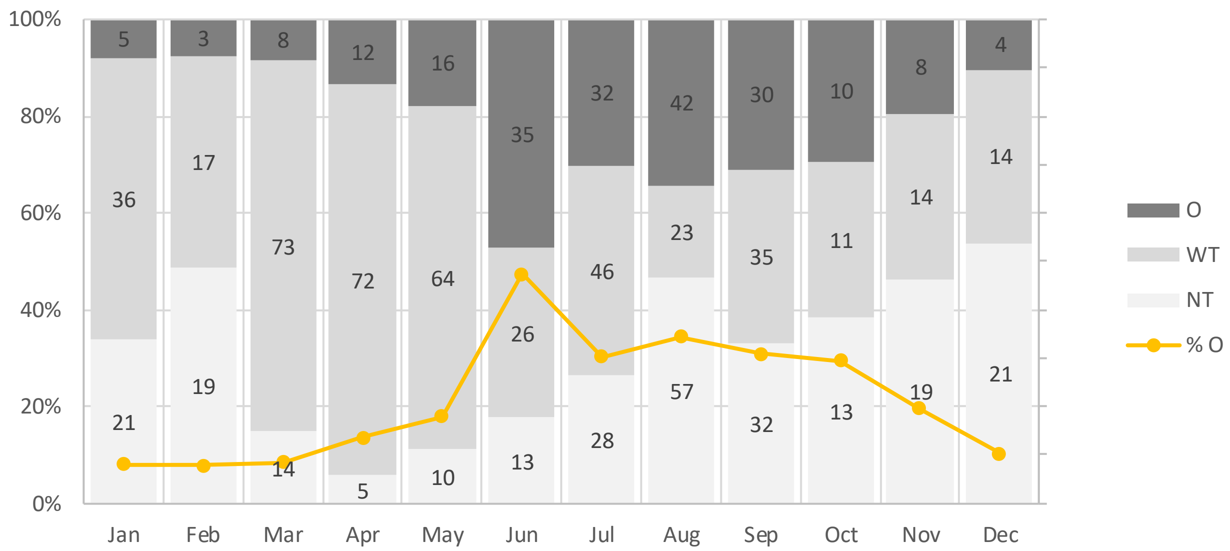


Figure 8. Proportion of otoliths with edge type classified as narrow translucent (NT), wide translucent (WT) or opaque (O) for yellowfin tuna sampled. The proportion of otoliths with opaque edge types is also shown. Sample size is shown for each edge classification and month. Edge type data were restricted to age classes 1 to 3 because partial increments are easier to identify and correctly classify at the otolith edge.

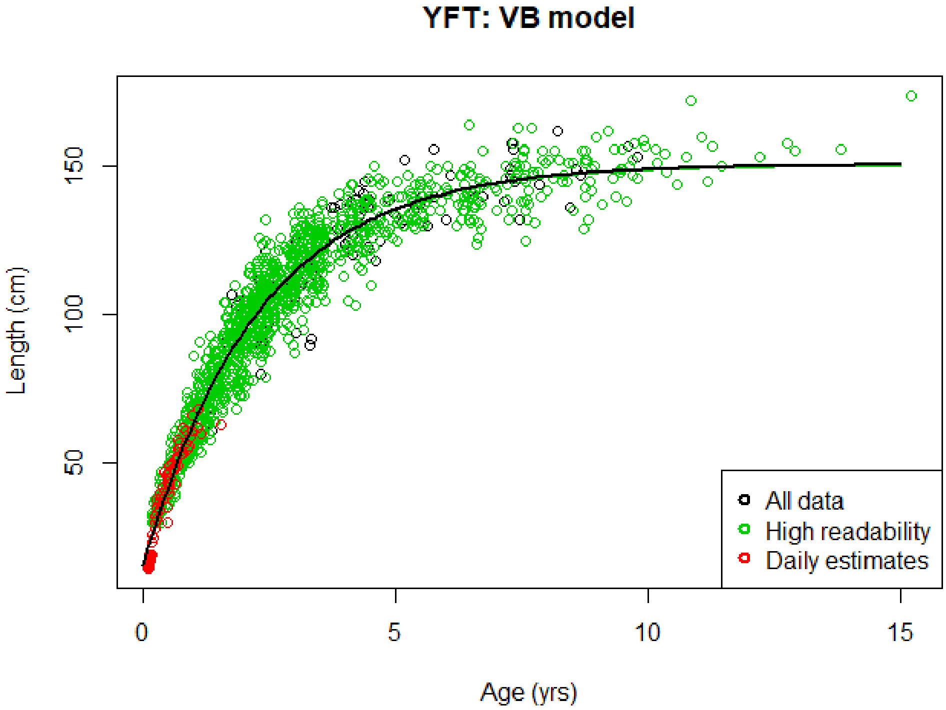


Figure 9. VB growth model fit to the yellowfin tuna length at age data, using (i) all otolith data (black line) and (ii) only high readability otolith data (green line). Note that the mean growth curves are indistinguishable. Daily age data are included in both models.

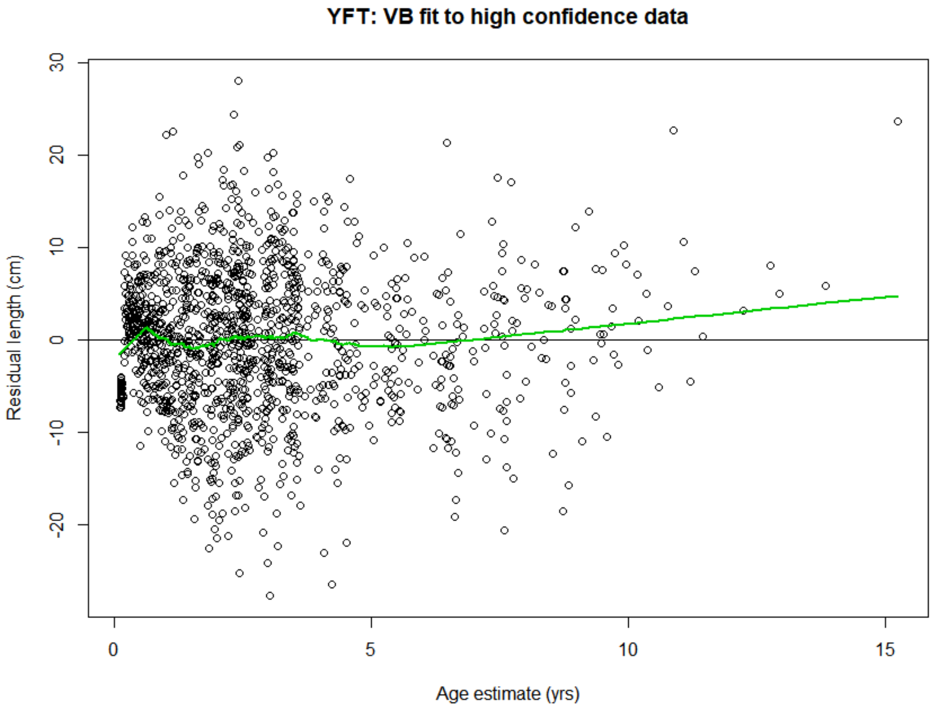


Figure 10. Diagnostic residual plot for the fit of the VB growth model to the yellowfin tuna length at age data, using only high readability otolith data.

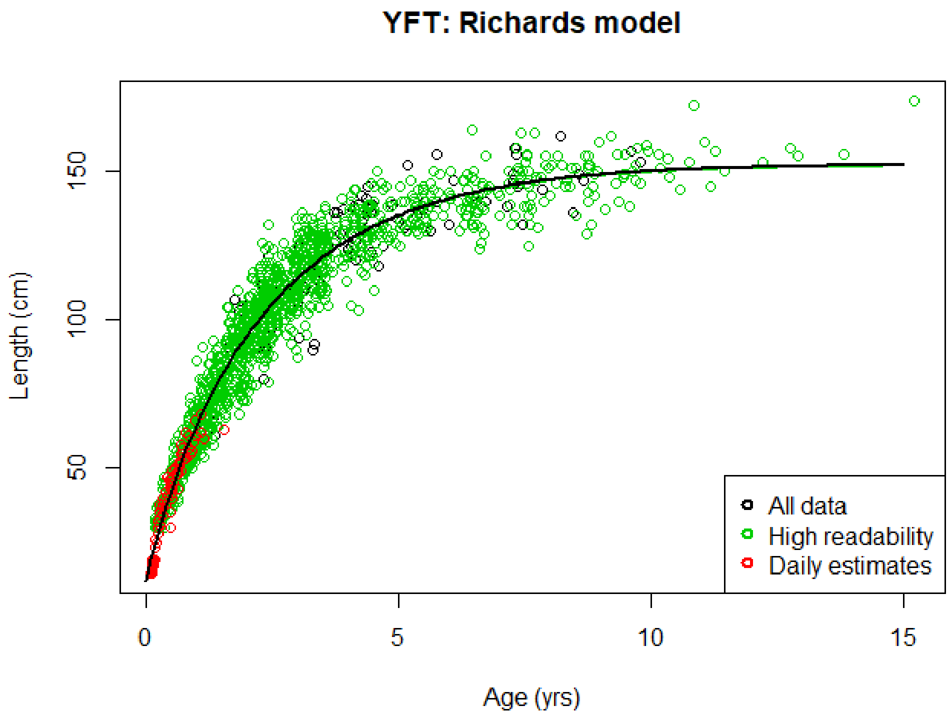


Figure 11. Richards growth model fit to the yellowfin tuna length at age data, using (i) all otolith data (black line) and (ii) only high readability otolith data (green line). Note that the mean growth curves are indistinguishable. Daily age data are included in both models.

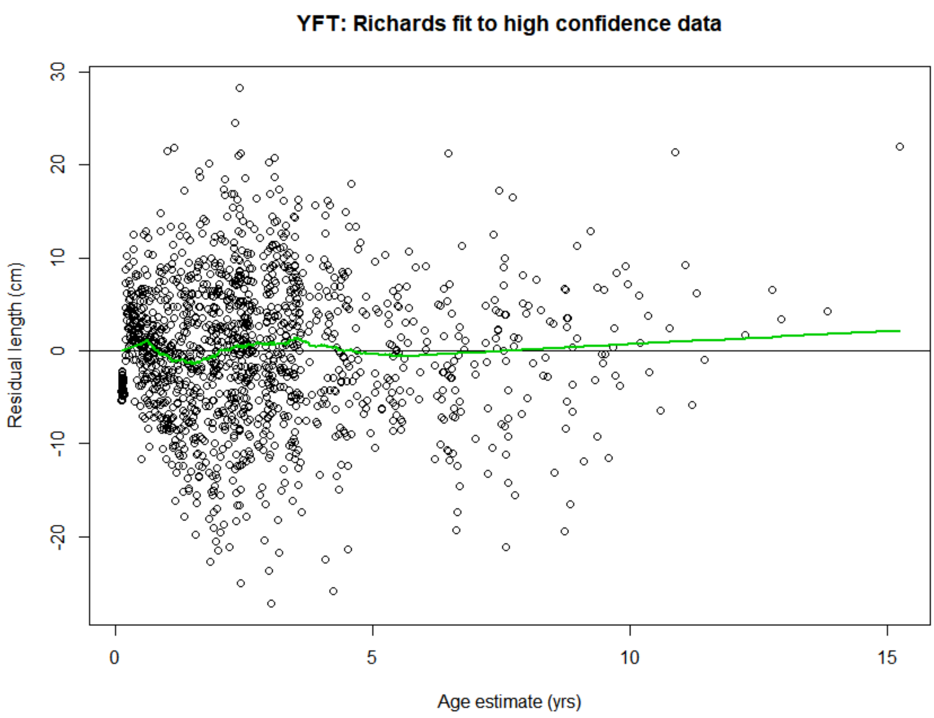


Figure 12. Diagnostic residual plot for the fit of the Richards growth model to the yellowfin tuna length at age data, using only high readability otolith data.

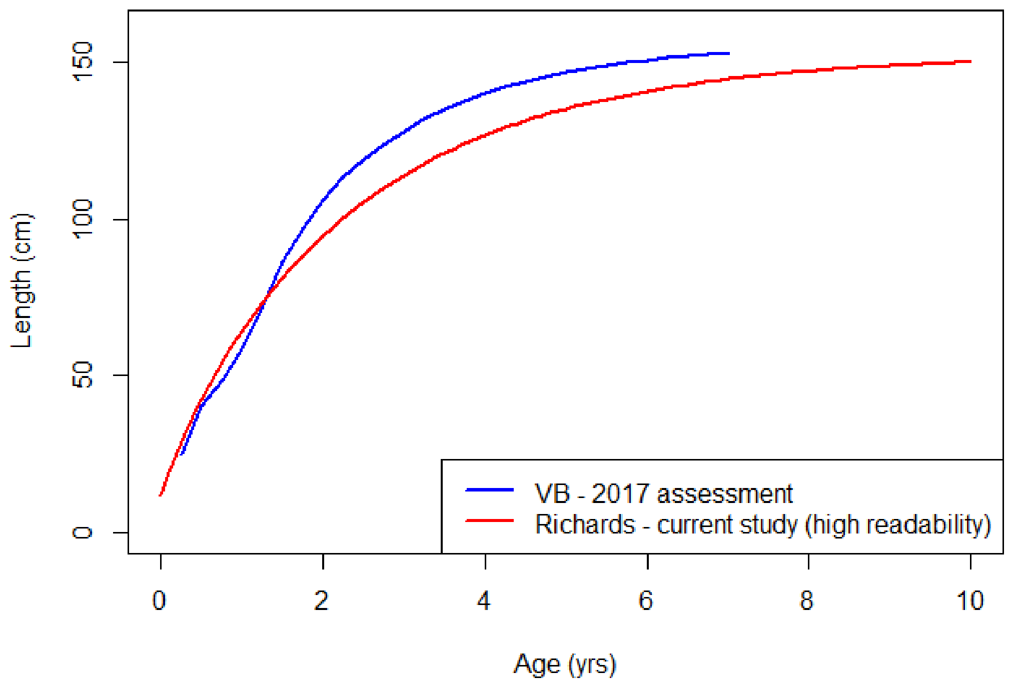


Figure 13. Comparison of yellowfin tuna mean lengths at age from the Richards model fit to high readability data and from the VB growth curve estimated internally by the 2017 yellowfin tuna stock assessment model (Tremblay-Boyer *et al.* 2017). The latter also estimated growth offsets for age classes (quarters) 2-8 to account for apparent non-VB growth of younger yellowfin tuna.

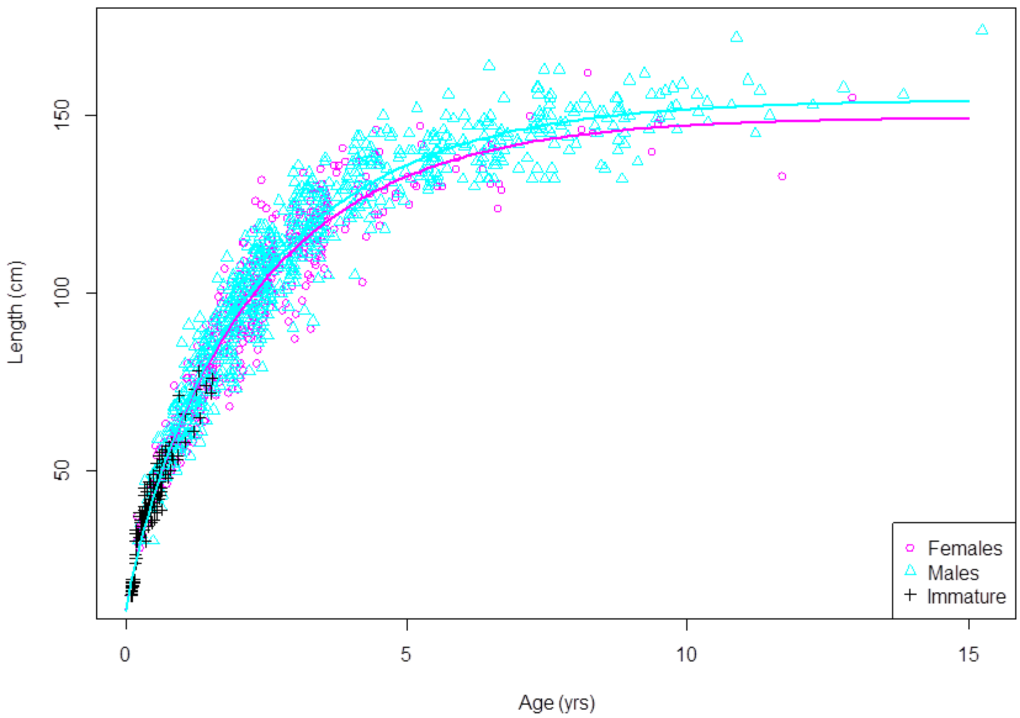


Figure 14. Richards growth model fit to yellowfin tuna male and female data separately.

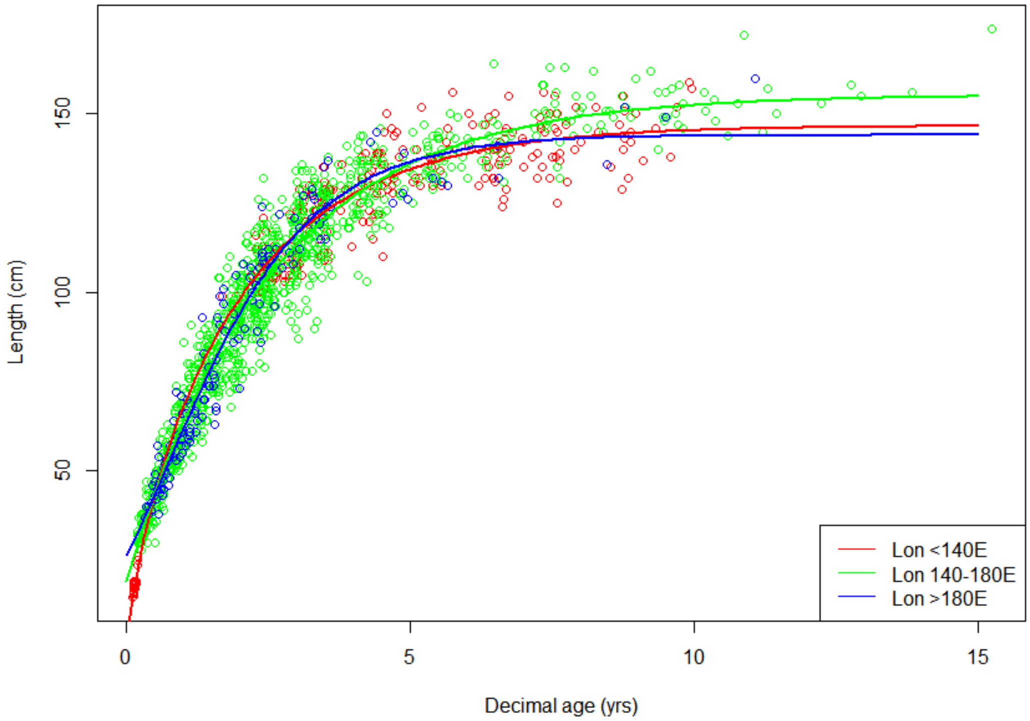


Figure 15. Richards growth model fit to the yellowfin tuna data from three longitudinal bands separately.

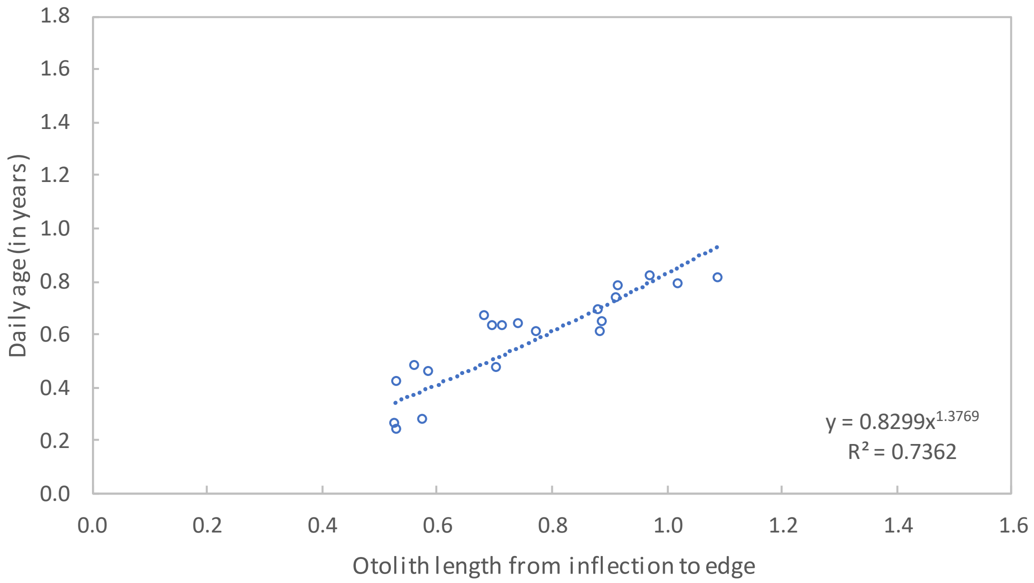


Figure 16. Daily age vs otolith size with fitted power curve for bigeye tuna. Otolith size is the distance from the first inflection point to the edge in sectioned otoliths.

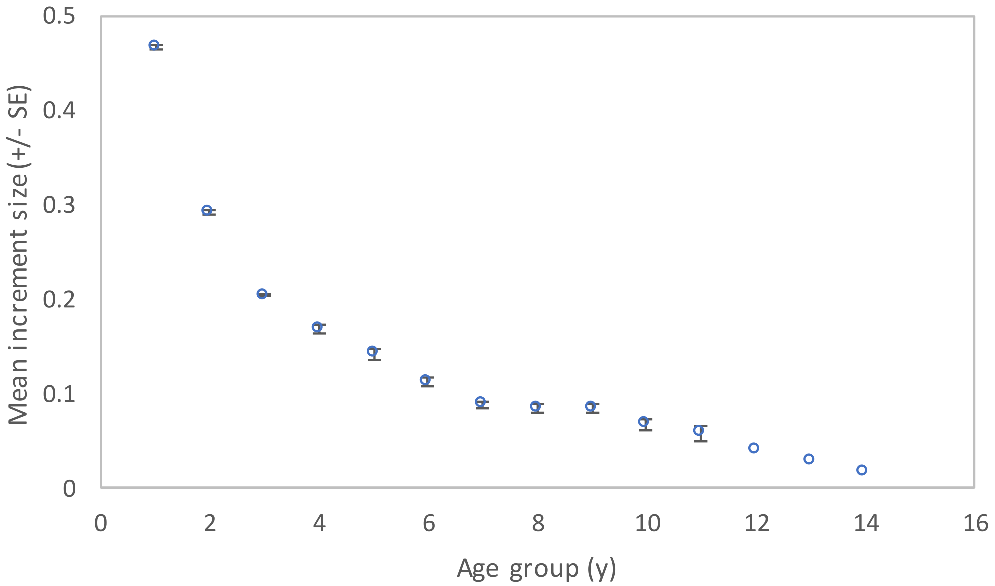


Figure 17. Mean (+/- SE) annual increment width in millimetres by age class for bigeye tuna.

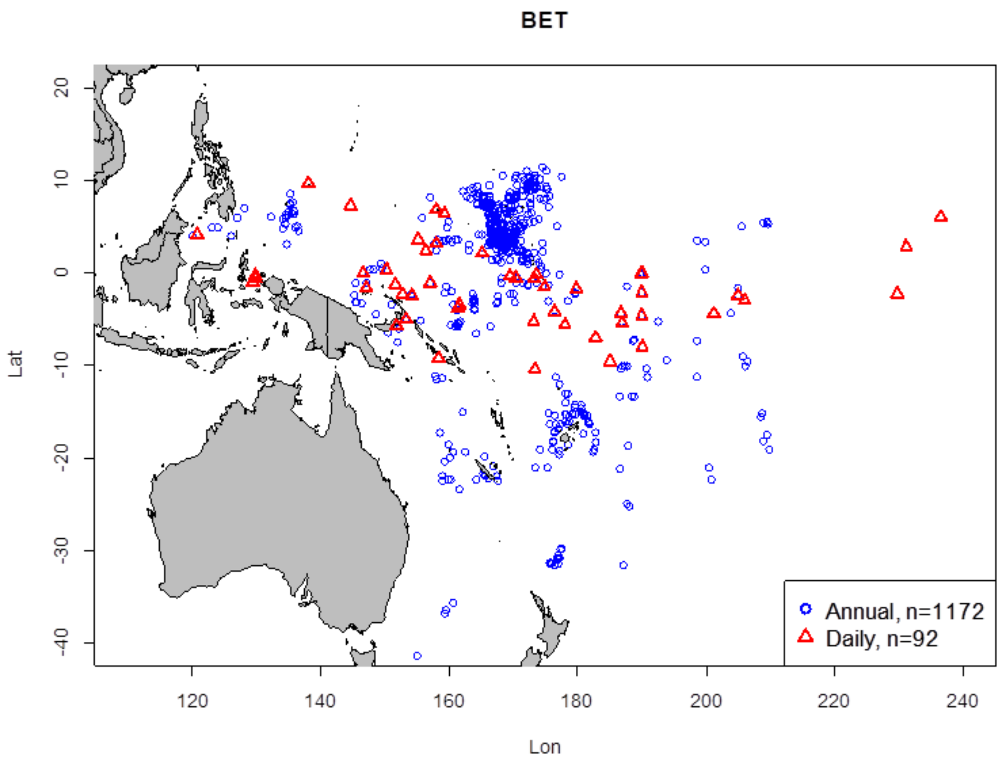


Figure 18. Map of the sampling locations for bigeye tuna otoliths aged. Otoliths shown in blue were selected for annual ageing and those shown in red were selected for daily ageing. Longitude shown in degrees east.

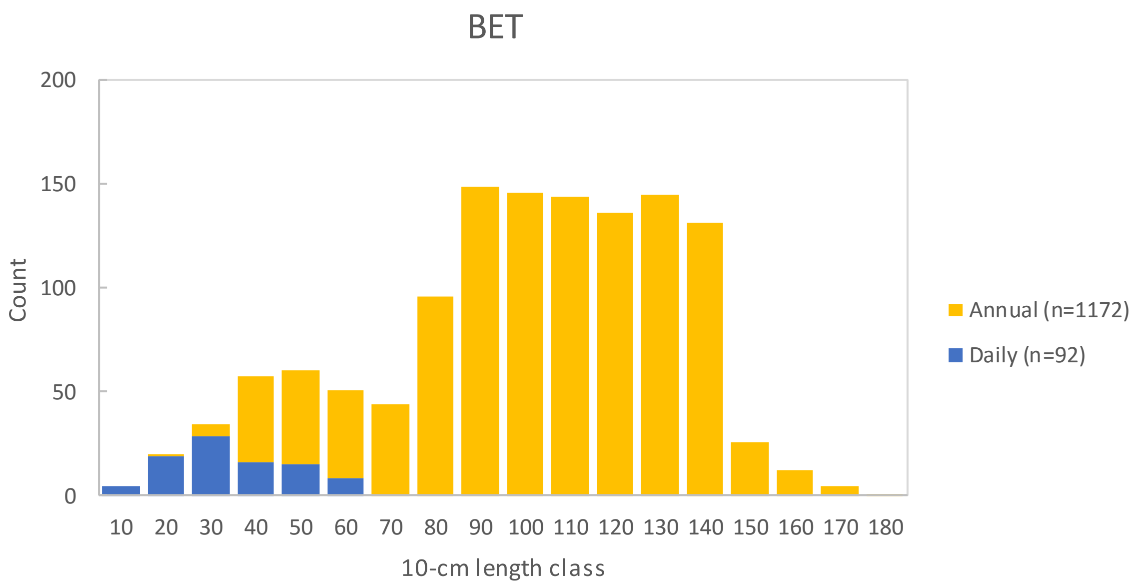


Figure 19. Length frequency of bigeye tuna included in the growth analysis. The lower boundary length value of the bin is shown.

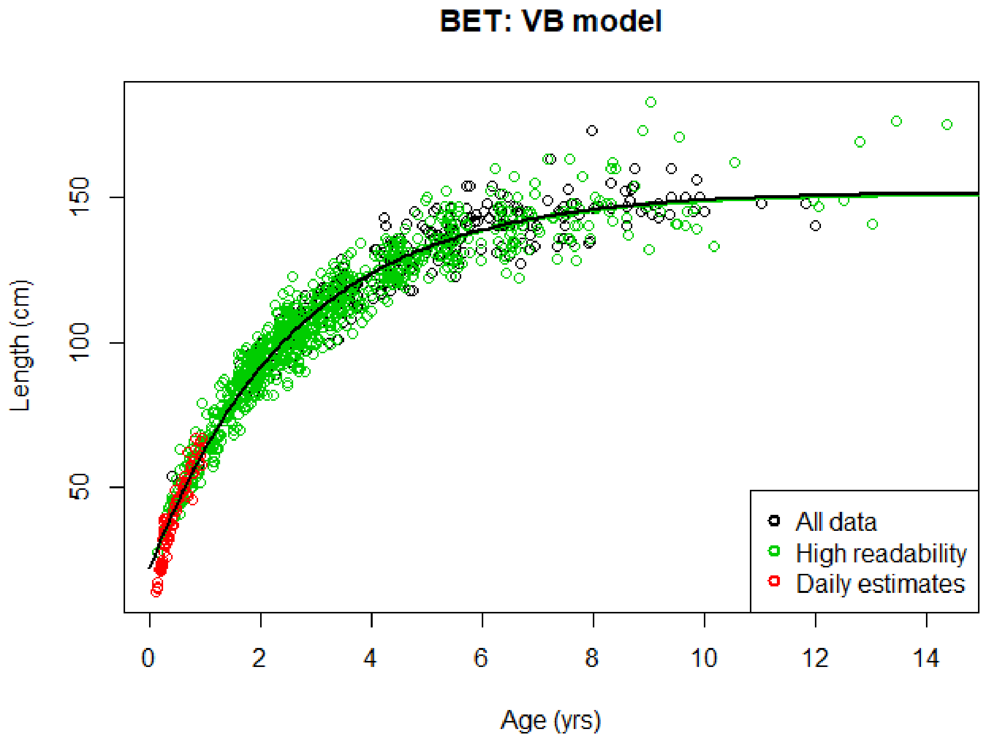


Figure 20. VB growth model fit to the bigeye tuna length at age data, using (i) all otolith data (black line) and (ii) only high readability otolith data (green line). Note that the mean growth curves are indistinguishable. Daily age data are included in both models.

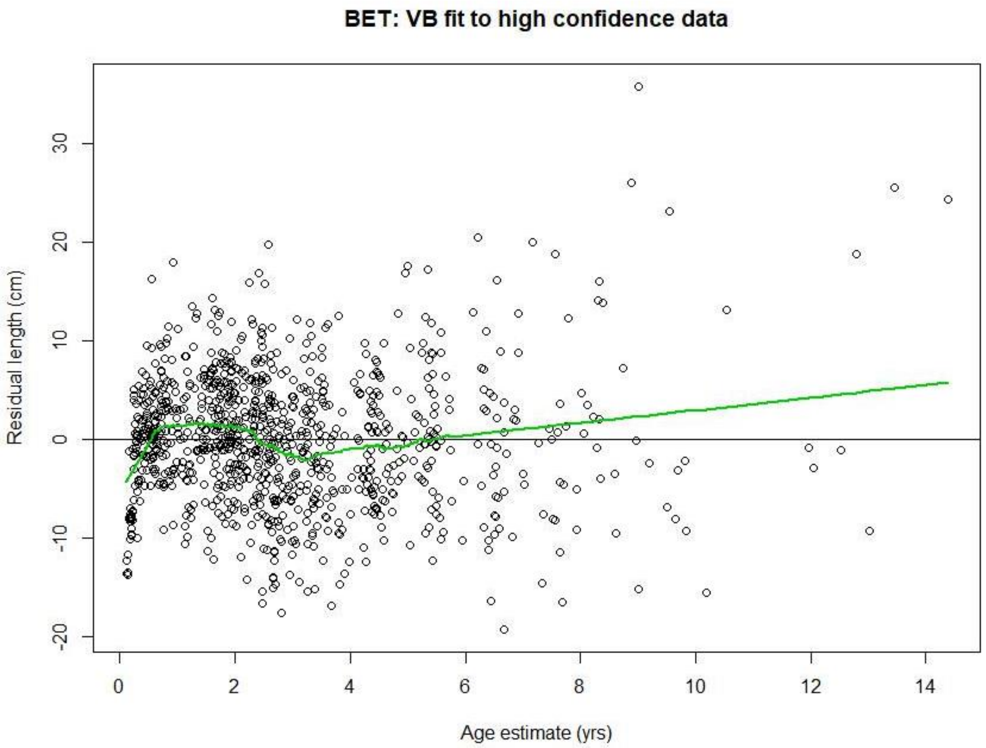


Figure 21. Diagnostic residual plot for the fit of the VB growth model to the bigeye tuna length at age data, using only high readability otolith data.

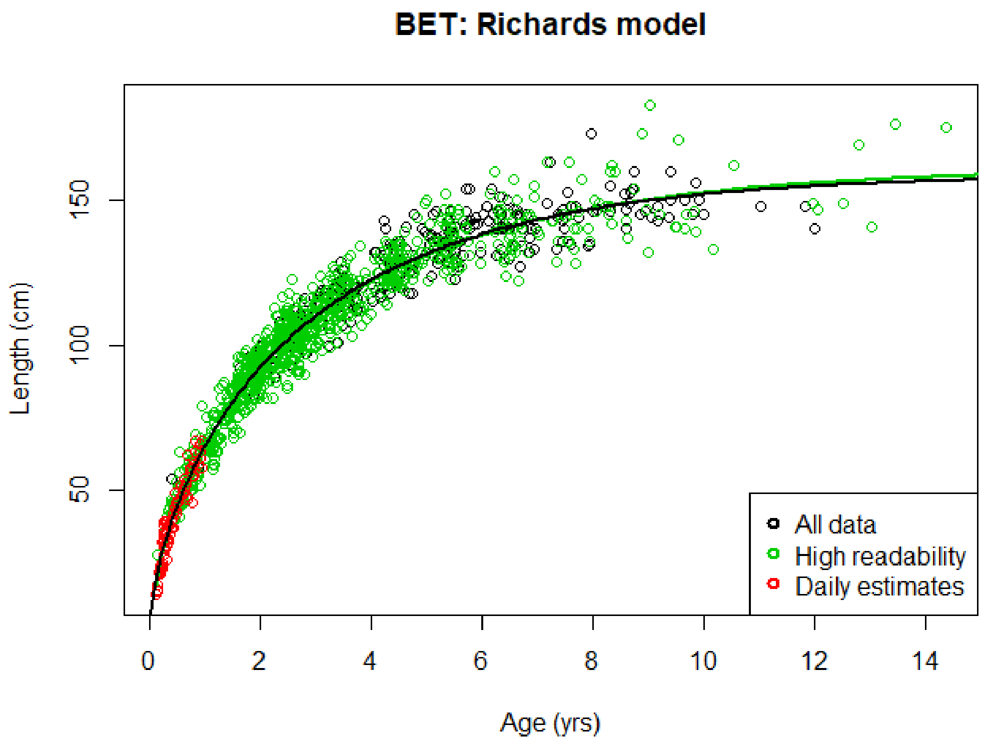


Figure 22. Richards growth model fit to the bigeye tuna length at age data, using (i) all otolith data (black line) and (ii) only high readability otolith data (green line). Note that the mean growth curves are almost indistinguishable. Daily age data are included in both models.

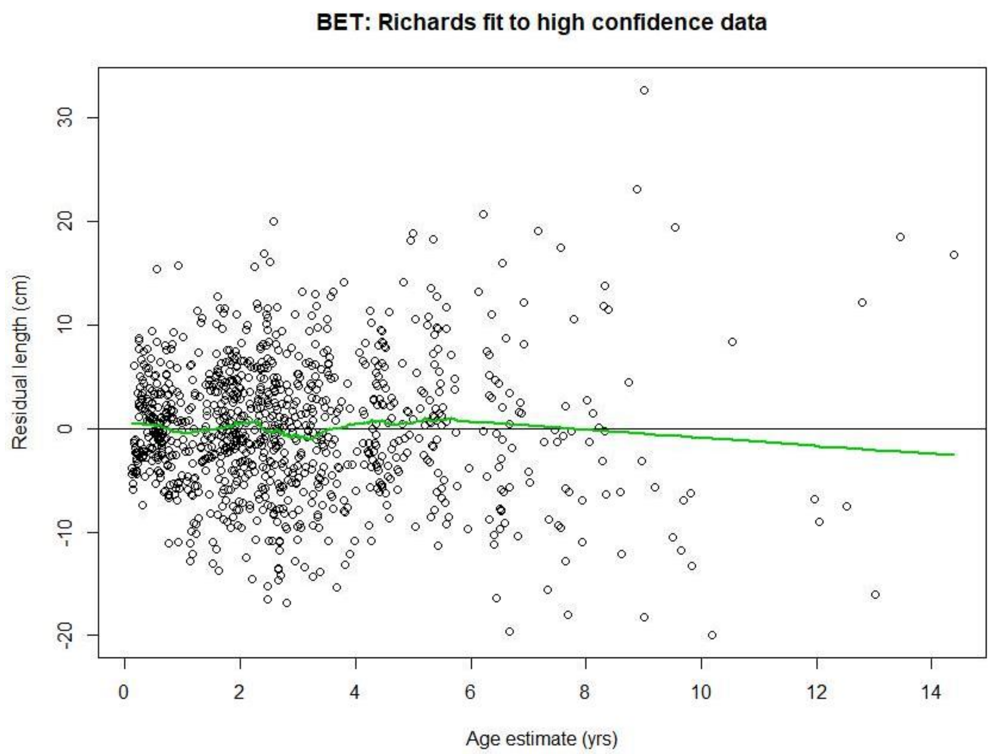


Figure 23. Diagnostic residual plot for the fit of the Richards growth model to the bigeye tuna length at age data, using only high readability otolith data.

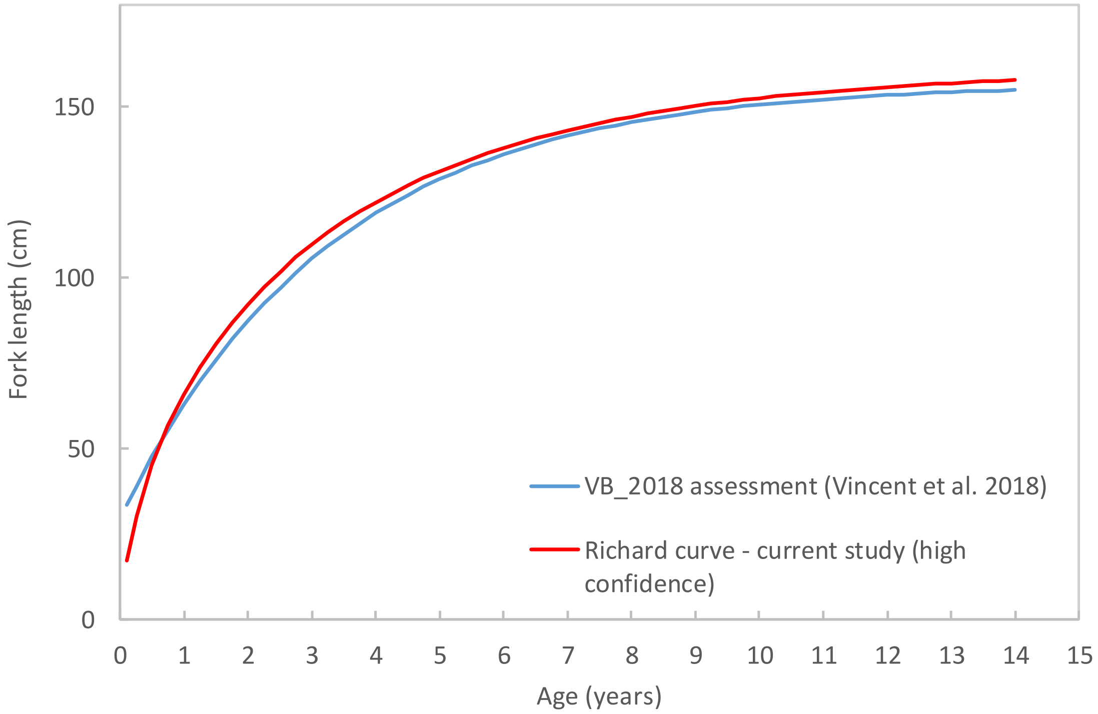
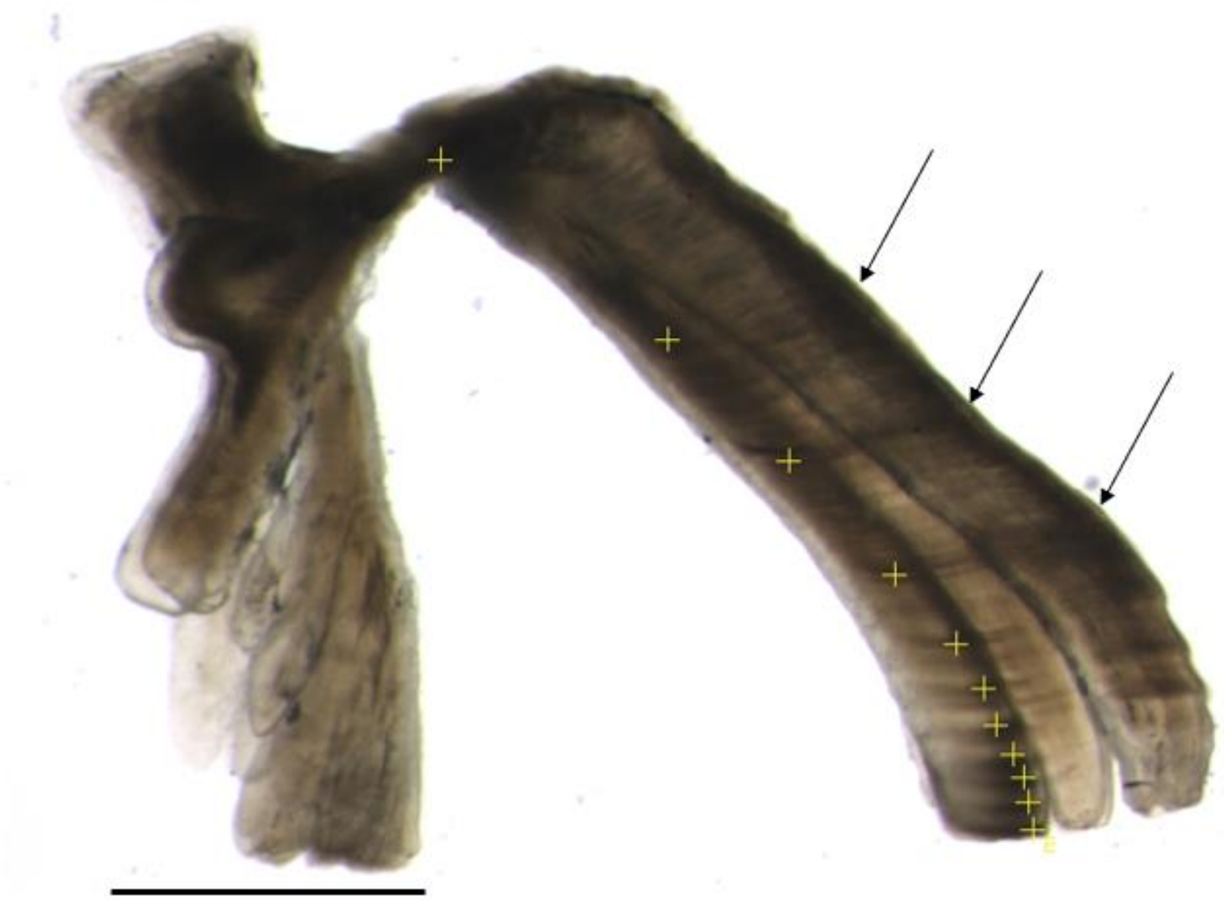


Figure 24. Bigeye tuna Richards growth model fit to the high confidence age data compared to the curve used in the 2018 bigeye tuna stock assessment (Vincent et al., 2018).

Appendix A



Append Figure 1. YFT Sample 138090 (section 305_015_008). Nine opaque zones and Opaque (O) edge. The first three opaque zones (black arrows) are exceptionally clear. The fish has a fork length of 150 cm. Scale bar 1mm.

Append Figure 2. YFT sample 117735 (section 305_015_318) Five opaques zone with a Wide Translucent edge. This fish has a fork length of 147 cm. Scale bar 1mm.

Append Figure 3. YFT Section 123011 (section 305_015_326). Fourteen opaque zones with a WT edge. The fish has a fork length of 174 cm. Scale bar 1mm.

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