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GROWTH OF ATLANTIC BLUEFIN TUNA DETERMINED FROM THE ICCAT TAGGING DATABASE: A RECONSIDERATION OF METHODS

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SUMMARY

Five issues complicate use of the ICCAT tagging database to estimate growth of Atlantic bluefin tuna: (1) lengths are in different units; (2) when time at liberty is short, observed length increment may reflect measurement error rather than growth; (3) many lengths were estimated rather than measured; (4) the magnitude of measurement error is unknown; and (5) growth rate may have a seasonal component that is not incorporated into the growth model. We deal with each issue to estimate the von Bertalanffy growth parameters. Estimates of K and L_∞ are 0.078 yr^{-1} (SE = 0.005) and 364.9 cm FL (SE = 19.0), respectively. These could be used in conjunction with an estimate of t_0 of -1.04 yr obtained from modal progression analysis. The L_∞ is lower than Turner and Restrepo (1994) but higher than other growth curves. Overall growth from tagging data may be useful, particularly for 2-10 year old fish which constitute the main ages tagged and recaptured and may be underrepresented in modal progression or hard parts or for which aging error or aging bias could be high.

RÉSUMÉ

Cinq problèmes compliquent l'utilisation de la base de données de marquage de l'ICCAT pour estimer la croissance du thon rouge de l'Atlantique: (1) les unités de longueur sont différentes, (2) lorsque le temps en liberté est court, l'incrément de longueur observé peut indiquer une erreur de prise de mesure plutôt que de croissance, (3) de nombreuses longueurs ont été estimées et n'ont pas été mesurées, (4) l'ampleur de la marge d'erreur n'est pas connue et (5) le taux de croissance peut avoir une composante saisonnière qui n'est pas incorporée au modèle de croissance. Nous tenons compte de chacun de ces problèmes pour estimer les paramètres de croissance de von Bertalanffy. Les estimations de K et L8 sont 0,078 yr-1 (SE = 0,005) et 364,9 cm FL (SE = 19,0), respectivement. Elles peuvent être utilisées avec une estimation de t0 of -1,04 yr obtenue à partir de l'analyse de progression modale. La L8 est inférieure à celle de Turner et Restrepo (1994), mais supérieure à celle d'autres courbes de croissance. La croissance globale obtenue sur la base des données de marquage peut être utile, notamment pour les poissons de 2 à 10 ans, correspondant à la tranche d'âge principale des poissons marqués et recapturés qui pourraient être sous-représentés dans la progression modale ou les pièces dures ou pour lesquels l'erreur de détermination de l'âge ou le biais de l'erreur de détermination de l'âge pourraient être élevés.

RESUMEN

Cuatro problemas complican la utilización de la base de datos de marcado de ICCAT para estimar el crecimiento del atún rojo del Atlántico: (1) las tallas se expresan en unidades diferentes; (2) cuando el tiempo en libertad es breve, el incremento de longitud observado puede ser el reflejo de errores de medición y no del crecimiento; (3) muchas tallas se estiman, no se miden, (4) se desconoce la magnitud del error de medición y (5) la tasa de crecimiento podría tener un componente estacional que no está incorporado en el modelo de crecimiento. Abordamos cada problema para estimar los parámetros de crecimiento de von Bertalanffy. Las estimaciones de K y L_∞ son 0,078 yr^{-1} (SE = 0,005) y 364,9 cm FL (SE = 19,0), respectivamente. Éstas podrían utilizarse junto con una estimación de t_0 de -1,04 yr obtenida a partir de un análisis de progresión modal. La L_∞ es inferior a la de Turner y Restrepo (1994)

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pero mayor que la de otras curvas de crecimiento. El crecimiento general obtenido a partir de los datos de marcado podría ser útil, sobre todo para los ejemplares con edades 2 a 10, que constituyen las principales edades marcadas y recuperadas y que pueden estar poco representadas en la progresión modal o en las partes duras o para las cuales el error de determinación de la edad o el sesgo de determinación de la edad puede ser elevado.

KEYWORDS

Bluefin tuna, body size, von Bertalanffy growth curves, tagging, least squares method

1. Introduction

The ICCAT tagging database has over five thousand recaptures of tagged bluefin tuna (*Thunnus thynnus*) from the period 1963 to 2012. Compared with other species present in the database, records for bluefin tuna are by far the most plentiful and informative; fish up to 260 cm FL have been tagged and recaptured, and the database contains a number of records of fish that spent 10 to 15 years at liberty before being recaptured. Overall, fish were tagged mostly in the months of June and July, and recaptures were likewise mostly from the summer months (**Figure 1**). Most of the fish were small at the time of tagging and two age classes dominate (**Figure 2**).

In theory, such data can be used to estimate the parameters of a growth curve (e.g., Turner and Restrepo 1994; Restrepo *et al*. 2010) but there are several practical considerations that complicate this. We identified five issues bearing on the validity of the analysis of bluefin tuna tagging data as follows:

1) lengths of tagged tuna have been expressed in various ways
2) when time at liberty is short, the observed length increment may reflect measurement error rather than growth
3) many of the lengths were estimated rather than measured
4) the magnitude of the measurement error is unknown
5) growth rate may have a seasonal component or other biphasic growth pattern that is not effectively modeled by the von Bertalanffy growth equation

We address these issues as part of the process of fitting a von Bertalanffy growth curve to the bluefin tuna tagging data, and assess the usefulness of estimating growth from tag return data in comparison to alternative methods.

2. Analytical issues

2.1 Initial data processing

2,274 complete tag, release and return paired records are present in the ICCAT database for Atlantic bluefin tuna (**Table 1**). These records are primarily of fish tagged and recaptured in the Western Atlantic. Most releases were done by U.S. purse seiners, with a few releases from rod and reel fisheries. Recapture data are less well documented compared to release information; 75% of records are of purse seines from unknown fleets (though geospatial coordinates indicate these are likely of U.S. origin), and the remaining quarter is a mixture of U.S., Canada, Japan and Spain, with purse seine and rod and reel as the primary gear types.

2.2 Methods for measuring fish

Several types of length measurements appear in the database, primarily fork length (FL, which is equivalent to lower jaw fork length, LJF) and total length (TL). Fork length occurs in approximately 70% of the records and most of the remaining measurements are of TL, with one record measured as curved fork length (CFL) and two with length expressed as eye to fork length (EYF). Curved fork and eye to fork length were converted to FL using the ICCAT and Hattour (2000) conversion factors, respectively. While a conversion factor is available for converting TL to FL (Hattour 2000), various investigators have expressed doubt about the meaning and validity of the measurements of TL in the database.

Consequently, we tested whether TLs were truly TLs or if they were instead FLs miscoded as TLs. We graphed the frequency of TL records as a function of time (**Figure 3**) and noticed that 85% of TL records clustered in the years 1966 and 1967. A closer look into these records indicated they were all released by the U.S. purse seine fishery, which meant that if we could determine whether or not the measurements were accurate, we could then determine whether to keep them or exclude them from the analysis. Focusing on the 1966 1967 time period, we looked into short-term recaptures (<3 months) to test the reasonableness of the data conversion. From these recaptures, we compared the growth of fish measured in FL at both release and recapture to growth of fish measured in TL at release and FL at recapture under two scenarios: 1. treating TL records as true TL measurements and 2. treating TL records as miscoded FL measurements and thus converting the records into FL (**Figure 4**). For these fish that were at liberty for a short amount of time, the mean observed growth of each group should essentially be equal and zero if TL measurements are accurate, yet growth increments at short times at liberty appeared to be positive and larger in the sample where TL was treated as TL (**Figure 4**). Converting these TL records to FL made the lengths at the time of tagging smaller, making the average short-term growth increment appear to be positive. We concluded that these TL release records are actually miscoded FLs. We added these records to the set of usable data and left out all other TL records for which we could not confidently determine the measurement type, which allowed us to boost the sample size without introducing bias.

2.3 Short times at liberty

When the times at liberty are short, the observed growth increments largely represent measurement error rather than somatic growth. Thus, many of the observed growth increments are unreasonable. We examined the distribution of unreasonable growth increments as a function of time at liberty **(Figure 5**) to determine a threshold time at liberty at which measurement errors are minimal while retaining as great a sample size as possible. Most of the negative and unreasonable increments occur for animals at liberty for less than 105 days (= 15 wk). Observed growth rates (cm/wk, **Figure 5**) were not extreme for those animals at liberty for more than 105 days. Consequently, we concluded that animals at liberty for more than 105 days exhibit real growth rather than just measurement error and these animals were used to fit growth curves.

2.4 Evaluating estimated lengths

We compared the performance of measured lengths and estimated lengths by looking at short-term recaptures (**Figure 6**). For suitably short times at liberty, growth should be minimal; hence, a comparison of the frequency distributions of apparent growth increments should constitute a comparison of measurement errors. For this comparison, we defined a short term recapture to be when time at liberty is less than or equal to 5 weeks for small and medium size fish (≤ 130 cm FL) and less than 10 weeks for large fish (> 130 cm FL). (The longer time at liberty is allowed for large fish because they grow more slowly and hence growth is not likely to be confused with measurement error.) The mean, short-term, growth increment for fish measured at time of tagging and recapture was -0.51 cm; for fish with estimated lengths, the mean was 0.52 cm, and for fish with one estimated length and one measured length the mean was 1.12 cm. The error values are all close to zero, suggesting that recorded growth increments for fish at liberty for short periods of time on average reflect measurement or length estimation error and not growth.

Fish that were measured at the time of tagging and at the time of recapture had apparent growth increments with a standard deviation of 7.52 cm (**Figure 6**). Fish whose length was estimated at the time of tagging and time of recapture had increments with a standard deviation of 7. 07 cm. Also, fish with one measured length and one estimated length had increments with a standard deviation of 16.34 cm, based on 18 records. The difference in variances for measured-measured and estimated-estimated fish was not statistically significant ($p = 0.76$, Bartlett's test) and the magnitude of the difference was so small that we conclude both types of measurement can be used. The variance of the increments for fish with one length estimated and one length measured was statistically significantly different from the variance for measured-measured and estimated-estimated fish ($p < 10^{-8}$); a reason for this is not apparent. However, the standard deviation of the increments for fish with one measured and one estimated length was still reasonably small (16.34 cm).

There are 166 records of short-term recaptures for fish measured at the time of tagging and recapture; 580 records for fish with estimated lengths at tagging and recapture, and only 18 records for fish with an estimated and a measured length. Because the means and standard deviations were very similar for measured-measured and estimated-estimated fish, we used records with both types of measurements in our analysis. We acknowledge that the records with one length measurement and one length estimate may have problems as evidenced by the higher estimated standard deviation of the short-term growth increments. However, we kept these records in the analysis to maintain the sample sizes for very small and very large fish. We tested the importance of this decision by running a second analysis that excluded these records. The ensuing von Bertalanffy parameter estimates were very close to those obtained by keeping the records of fish estimated at either release or recapture, but much less stable (K= 0.075 ± 0.009 (SE) , L_∞ = 375 cm ± 113 (SE)).

2.5 Magnitude of measurement error

Define an increment, *I*, to be the length at the time of recapture, L_r, minus the length at the time of tagging, L_t. Over a suitably short time at liberty, the expected value of an increment is zero. We assume growth is zero, the two recorded lengths are determined independently, the measurement error is the same at the time of tagging and recapture, and it does not vary with the length of the fish. Then the variance of the increments is

$$Var(I) = Var(L_r - L_t) = Var(L_r) + Var(L_t) = 2\sigma^2 \quad (1)$$

Where Var(L_r) and Var(L_t) refer to the variance of repeated measurements of the same fish and σ^2 is the measurement error. Hence, the measurement error standard deviation can be estimated by dividing the increment standard deviation by the square root of 2.

Applying equation (1) to the results in **Figure 6** produces estimates of measurement standard deviation (σ) of 5.32 cm for measured lengths and 5.00 cm for estimated lengths.

2.6 Effects of seasonality

A concern is that growth rates may vary seasonally so that animals at large for part of a year might show growth that, when expressed per unit of time, is not representative of a full year's growth. The effects of seasonality can be minimized by restricting consideration to animals at liberty for one or more full years. This is operationalized by restricting analysis to animals at liberty for *k* years plus or minus some number of weeks δ, where *k* is a whole number and $0 < \delta < 26$ wk. A smaller value of δ eliminates more bias but also reduces the sample size relative to a larger value of δ. The effects of seasonality are also minimized when times at liberty are large, e.g., the difference in growth rate (cm/mo) between von Bertalanffy growth and seasonally varying von Bertalanffy growth are smaller for an animal at liberty for 10 years and 4 weeks than they are for an animal at liberty for one year and 4 weeks (all other things being equal). Von Bertalanffy growth curves were fitted under various scenarios of δ for small (≤ 70 cm FL), medium (70 < length ≤ 130 cm FL) and large (>130 cm FL) fish (**Figure 7**).

The critical factor appears to be the window of time, δ, used for the large fish. There is a decreasing trend in the estimate of L_∞, and a corresponding increasing trend in K, as the window δ gets larger for large fish. Essentially, with a narrow window δ the sample size of large fish becomes small and the rate of curvature of the von Bertalanffy curve is difficult to determine with the result that estimates of L_∞ can grow very large (**Figure 7**). Furthermore, just like with large times at liberty, the effects of seasonality are minimized in larger, slow-growing fish. We therefore decided to keep all records of large fish in our analysis to decrease the uncertainty around L_∞.

For small and medium sized fish, increasing δ above 7 weeks adds comparatively few additional records and does not change the estimated values of K and L_∞ greatly (**Figure 7**). Thus, we adopt a value a $\delta = 7$ weeks for these size groups to minimize bias without inflating variance greatly. In the future, as data accrue, it should be possible to decrease the window δ further to minimize possible bias.

2.7 Possible biphasic growth pattern

A number of authors have suggested that some tunas, including southern bluefin tuna, may exhibit a two-stage or biphasic growth pattern whereby early growth is rapid but slows down temporarily at some point before accelerating and approaching a new asymptote (see, e.g., Hearn and Polacheck 2003). We examine the residuals of the fit of the ordinary von Bertalanffy growth to the tagging data to look for evidence of a biphasic growth pattern in section 3.1 below.

3. Fitted growth curves

We used the method of Fabens (1965) to fit von Bertalanffy growth curves. Wang (1998) maintains that this method produces biased estimates. We removed outliers by excluding records showing the fastest and slowest 1% absolute growth. We then bootstrapped the data in order to obtain estimates of the bias and standard errors (**Figures 8 and 9**).

Nonlinear least squares estimates of the von Bertalanffy growth parameters were K=0.078 and L_∞=364.9. Bootstrapped mean values were K=0.078 (SE = 0.005) and L_∞ = 364.9 (SE = 19.0) (**Figure 8)**, with estimated biases of less than one percent. It is not possible to estimate the value of t_0 using the method of Fabens (1965); estimates of this parameter must be obtained from information external to the analysis. Restrepo *et al*. (2010) used information on size at age derived from modal analysis of length frequency data to estimate t_0. The t_0 parameter merely shifts the von Bertalanffy curve along the time axis and a value can be selected so that the curve intersects a known size at age. Consequently, the size at age data obtained from the Restrepo *et al*. (2010) analysis of length frequencies can be used to determine a value of t_0 for the growth curved derived from the tagging data. To do so, we extracted the mean size at age 1 (L_1 = 54cm) derived from the modal analysis and obtained an estimate of t_0 from the inverted von Bertalanffy growth equation,

$$t_0 = 1 + \log(1 - L_1/L_\infty)/K \qquad (2)$$

The estimate of t_0 was -1.04 yr.

In general, our results were in agreement with the current growth model used in the assessment of bluefin tuna, particularly for younger age classes (<10 years), although our analysis indicated a greater mean size at age of older individuals (>10 years) (**Figure 10**). The value of the database for estimating growth would be greatly enhanced if additional large fish could be tagged and accurate tag information returned. Nonetheless, the current data are generally supportive of the current growth model used in the stock assessment and the tagging data provide valuable information for the ages over which fish were tagged. Restrepo *et al*. (2010) noted that the residuals for old fish seem to be negative and acknowledged that there was a possible sampling bias for old fish. An integrated analysis of all data (direct aging, modal analysis and tagging data) would be appropriate and reduce the overall bias if all data types are valid.

Separate growth curves are used for the assessment of eastern and western bluefin tuna even though the two curves are very similar. The tagging data are comprised mostly of fish caught in the western Atlantic; there are only 95 records of fish released or recaptured in the Mediterranean or eastern Atlantic. We fitted a curve to just the western Atlantic data and obtained results very close to those from the full data (L_∞ for data excluding the eastern Atlantic and Mediterranean was 371.4 cm instead of 364.9 cm for the full data; K changed in the fourth decimal).

3.1 Model fit

One way to judge the goodness of fit of the estimated growth curve is to draw a vector plot of the growth increments. To do this, the relative age of each fish at the time of tagging, A_t, is estimated from the length at tagging, L_t, by inverting the von Bertalanffy growth equation,

$$A_t = -\log(1 - L_t/L_\infty)/K \qquad (3)$$

The age at recapture is then taken to be the age at tagging plus the time at liberty. The resulting vectors of growth can then be compared to the fitted curve. The length and estimated age for each fish at the time of tagging falls on the fitted von Bertalanffy curve; one can judge the goodness of fit by how close the recapture ends of the vectors lie to the fitted curve (**Figure 11**).

Another way to judge goodness of fit is to plot the residuals (observed growth increment minus predicted growth increment (given size at tagging and time at liberty)) versus the computed relative age at the time of tagging. A mass of negative residuals at some intermediate relative age might be indicative of a biphasic growth pattern. However, no apparent pattern to the residuals is evident in **Figure 12**.

4. Conclusions

This work demonstrates that the ICCAT tagging database contains useful information on the growth of bluefin tuna. Extracting the information from the database requires care because there are a number of potential problems, but these problems are not insurmountable. Records of large fish at liberty for a large number of years are not only incredibly informative to growth studies, but also likely to be reliable since the issue of measurement error is minimized for larger fish and longer times at liberty. Furthermore, these records may prove useful in corroborating or disputing growth rates estimated through alternative methods.

Each piece of data used in growth estimation has its own biases and limitations. The precision and accuracy of direct age reading are contingent on having access to high quality samples, advanced equipment and verification methods (Fonteneau and Chassot 2012; Stéquert and Conand 2000, 2004). While growth bands are well defined in fish ages 0-10, scientists have noted the difficulty in interpreting growth bands in larger tunas (10+ yrs) due to crowding on the outer edges of the otolith. This may in part explain the inconsistencies observed between growth estimates derived from direct aging and estimated derived from tagging data (Stequert and Conand 2004; Shuford *et al.* 2007; Fonteneau and Chassot 2012). Furthermore, paired bands may form annually in larger tunas, leading to the potential overestimation of age in older tunas (Berry *et al.* 1977).

Francis (1988) argues that growth estimated from length data is not directly comparable to that estimated from age-data, pointing out that L_∞ estimated from tagging data pertains to the maximum length in the population whereas L_∞ estimated from aging data pertains to the mean asymptotic length. This, along with the lack of larger individuals in the sample may explain in part why L_∞ estimated from our sample is slightly higher than that estimated by Restrepo *et al.* (2010). Nonetheless, if the growth curve based on tagging data does in fact paint a more accurate picture of reality, then the growth potential of the stock described by the von Bertlanffy parameters currently used in stock assessment may not be accurate. Since this can make a difference in determining the recovery status of the stock, we recommend that further research be undertaken to shed light on this basic biological question.

Francis proposes a modification to the von Bertalanffy equation to make the comparison between direct aging data and tagging data possible. Because Francis' model is expressed in terms of a likelihood function, it facilitates incorporating the tagging data in an integrated analysis. We therefore recommend an integrated model, based on Francis' (1988) maximum likelihood estimator, be fitted to all available data (mark-recapture, direct aging and modal progression analysis) to produce growth parameter estimates that make full use of the available information.

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Table 1. Exclusion criteria used to filter out incomplete, erroneous and unreliable records from the analysis.

Initial number of paired (release-recapture) records in the database (ICCAT conventional tagging database for bluefin tuna, last updated 2013.04.23)	***5,680***
Justification for removal	**# paired records remaining**
I - Initial data processing	
Release or recapture date is unknown	5,523
Release or recapture length is unknown	2,819
Release or recapture measurement type (*i.e.*: EYF, FL, CFL, TL, LJF) is unknown	2,563
Time at liberty is negative	**2,274**
II – Further exclusion criteria	
Removed suspicious TL records (*i.e.*: all TL records other than 1966 & 1967 releases from US purse seines)	2,171
Removed all records with time at liberty ≤105 days	1,227
Removed all records of fish ≤130 cm FL at recapture that had been at liberty for more than *x* numbers of years +/- 7 weeks	1,018
Removed outliers (*i.e.*: 1% extreme growth)	**998**

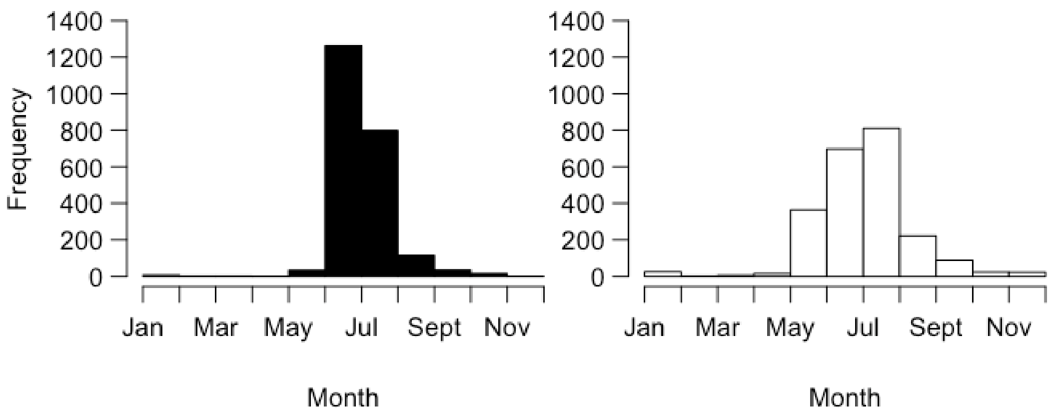

Figure 1. Number of records of fish tagged in each month (black) and recaptured in each month (white).

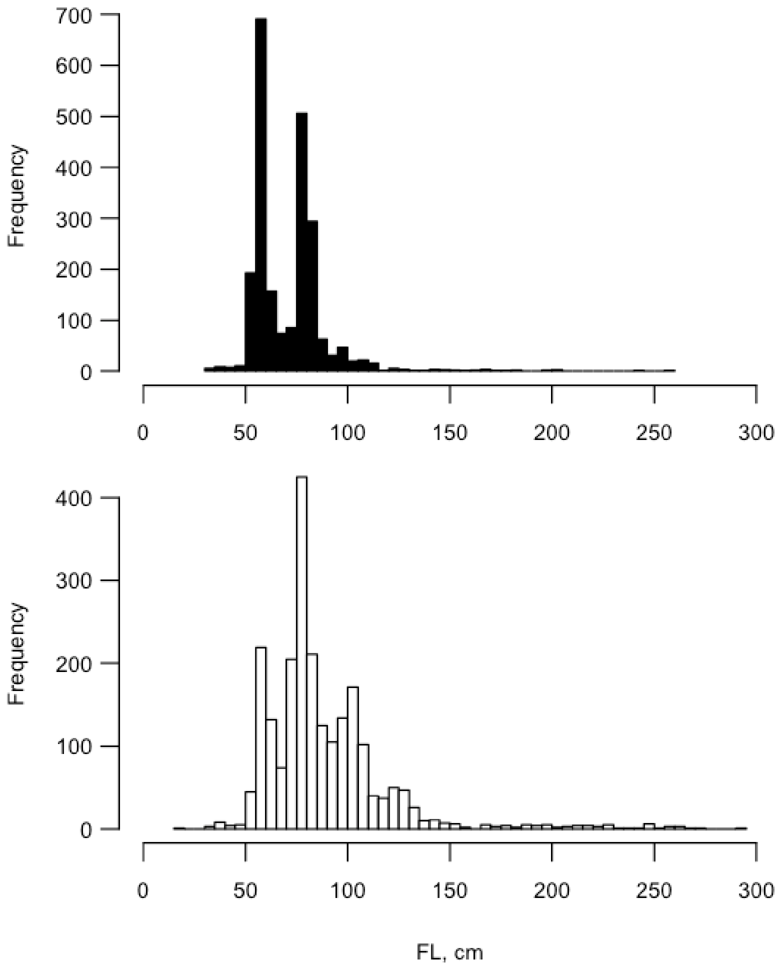

Figure 2. Sizes of recaptured fish at the time they were tagged (black) and recaptured (white).

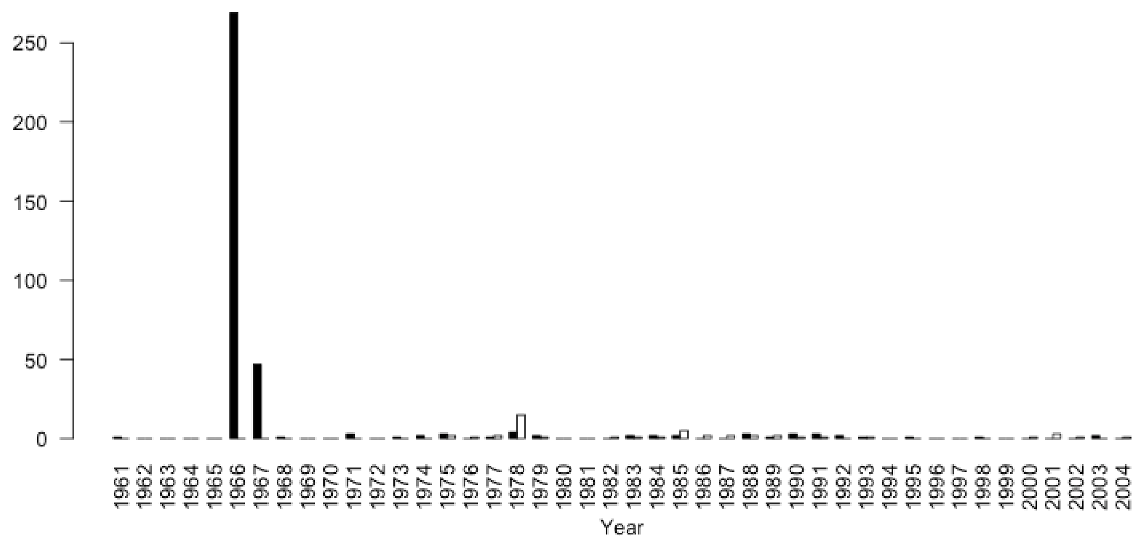

Figure 3. Sizes of fish measured in total length at the time of tagging (black) and recapture (white).

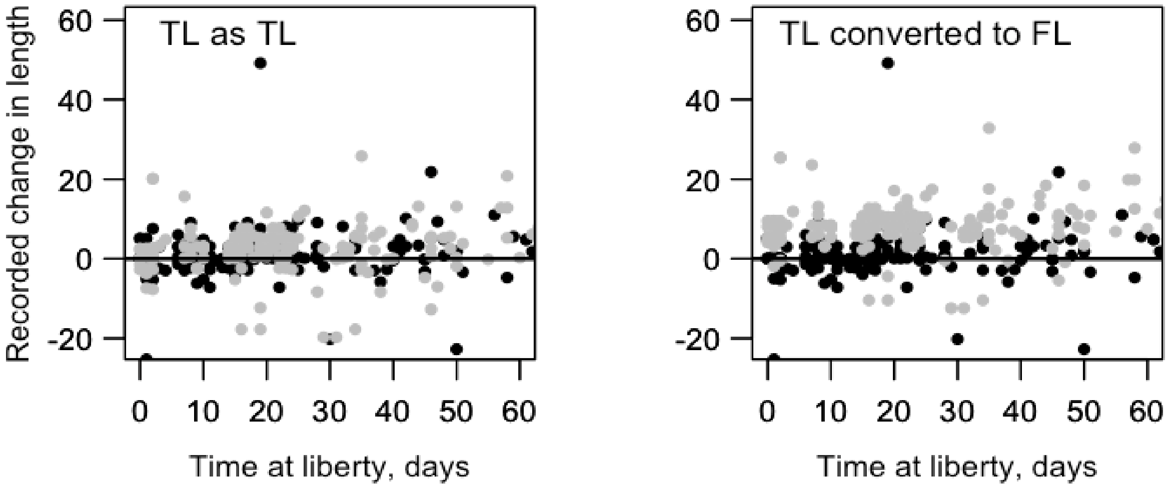

Figure 4. Recorded growth vs. time at liberty of short-term recaptures from 1966-1667 US purse seine fisheries. Times at liberty are less than 3 months. Fish with lengths recorded as FL at both release and recapture are shown in black and fish with lengths recorded as TL at release but FL at recapture are shown in gray. In the left panel, TL lengths were left unconverted, while in the right panel, all TL records were converted into FL using Hattour (2000) conversion factor TL = 1,1349*FL^{0,9931}.

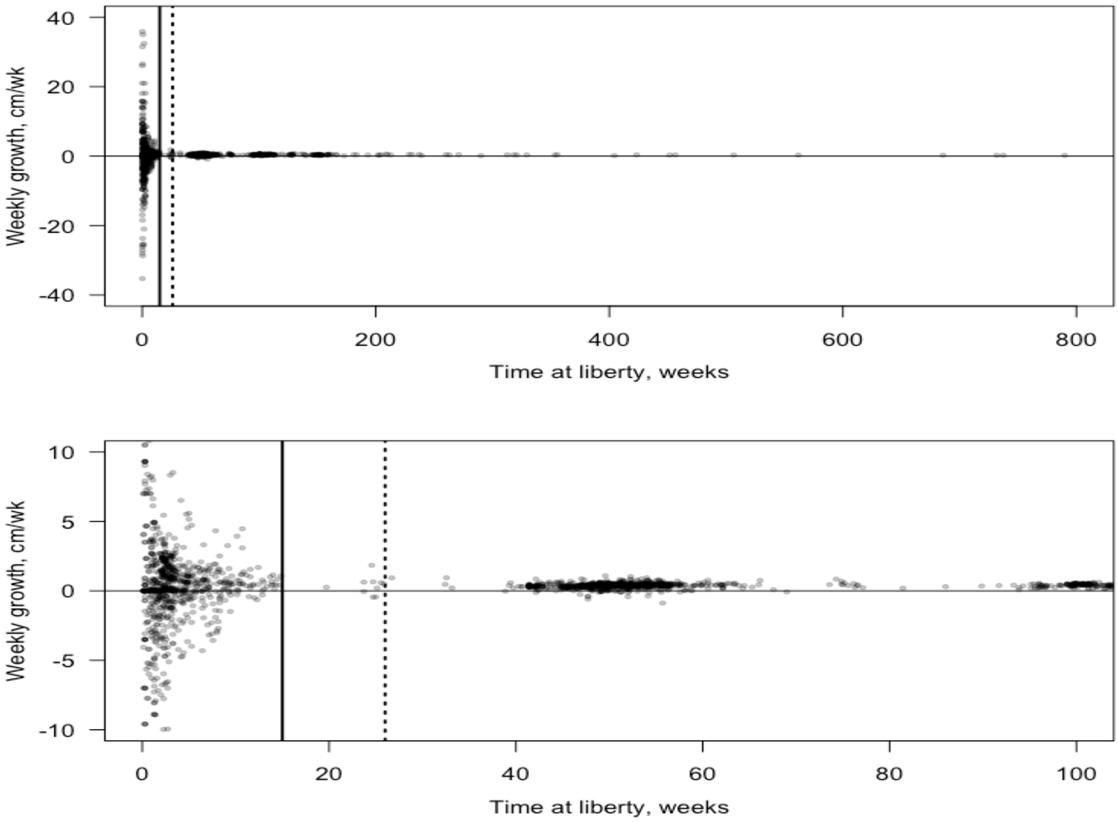

Figure 5. Growth per week (recorded growth divided by weeks at liberty) versus time at liberty. Top graph shows all fish; most of the large growth rates (whether positive or negative) are for fish at liberty for less than 105 days. Bottom graph eliminates the largest growth rates and times at liberty in order to expand the scales. It can be seen that for fish at liberty for more than 15 weeks almost all growth rates are positive. The solid and dashed black lines indicate the 105 day threshold used in our analysis and 180 day threshold recommended by ICCAT, respectively.

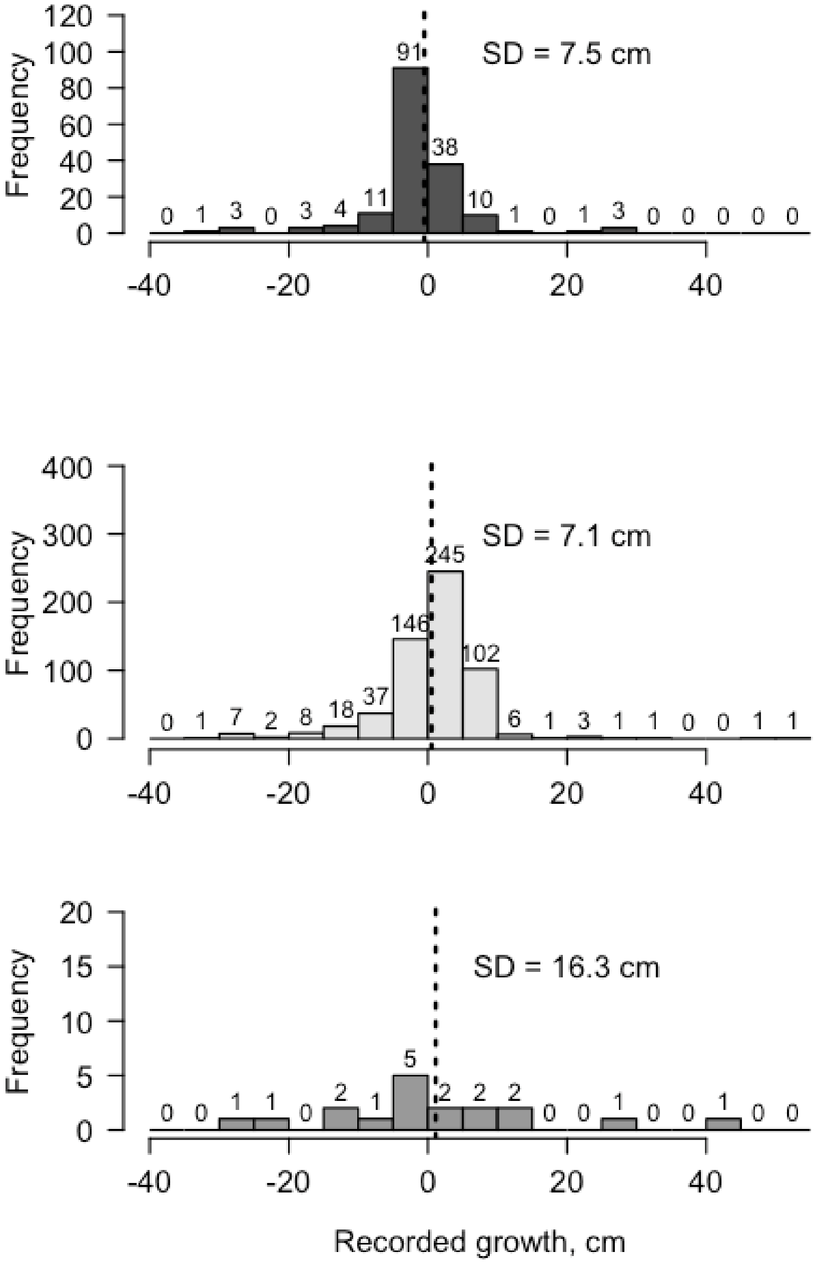

Figure 6. Growth increment frequencies for short-term recaptures of fish measured at both release and recapture (dark gray, n=166), estimated at both release and recapture (light gray, n=580) and estimated at either release or recapture (medium gray, n=18). Time at liberty was restricted to ≤ 5 weeks for fish ≤ 130 cm at time of recapture and ≤ 10 weeks for fish > 130cm at time of recapture. (The longer time at liberty is allowed for large fish because they grow more slowly and hence growth is not likely to be confused with measurement error.) Mean growth of the samples are represented by dashed vertical line and standard deviations (SD) are noted on the plots.

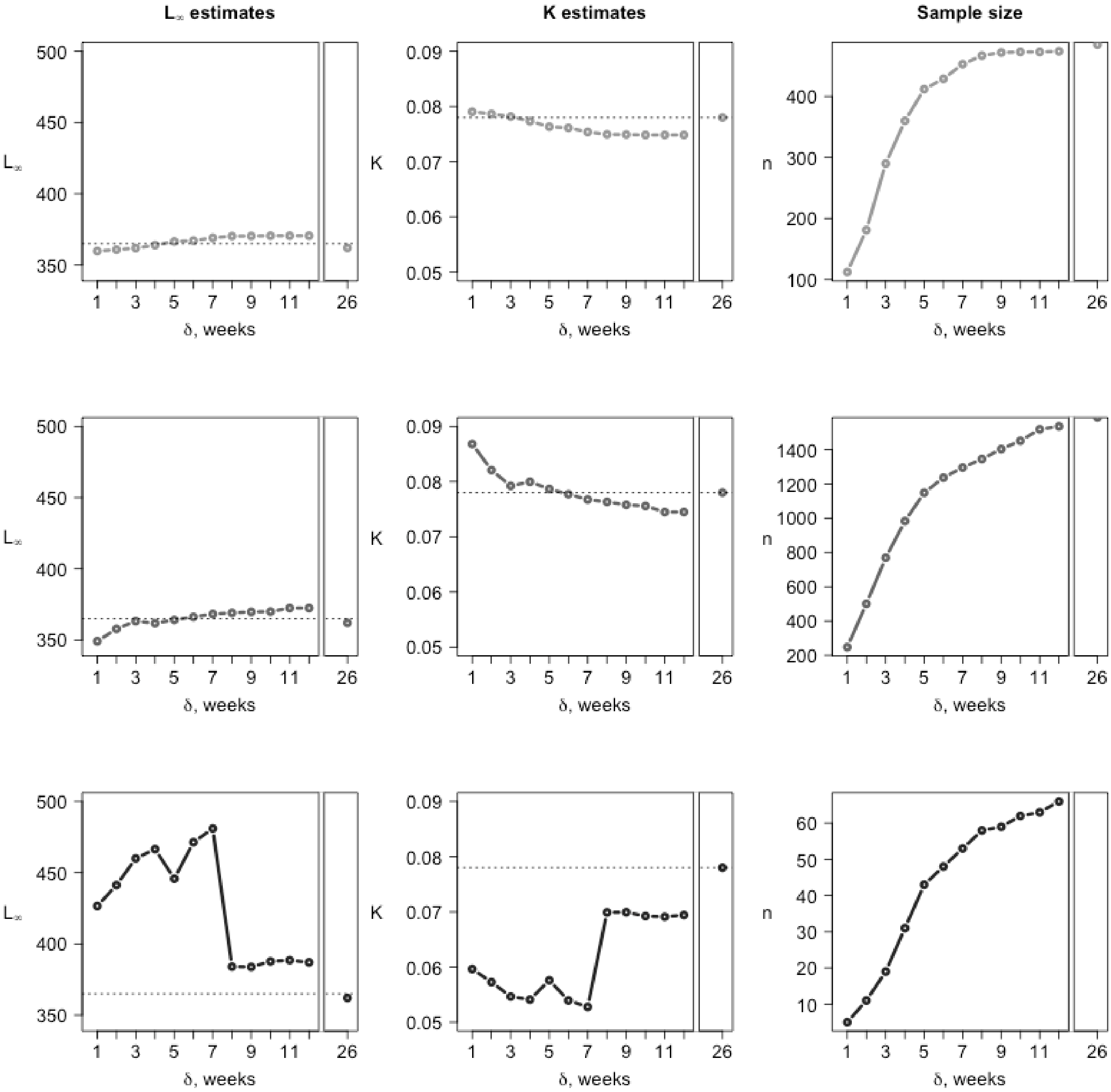

Figure 7. Effect of window size, δ, on the sample size and growth parameter estimates when the window criterion is applied to just small (top, light gray), medium (middle, medium gray) or large (bottom, dark gray) fish. Only fish at liberty for approximately a whole number of years are included in the analysis, meaning within δ weeks of a whole number of years, e.g., 3 years ± 5 weeks. Size categories are: small = length ≤ 70 cm FL, medium = 70 < length ≤ 130 cm FL and large = length > 130 cm FL. The dotted lines represent the final fitted values of the von Bertalanffy parameters.

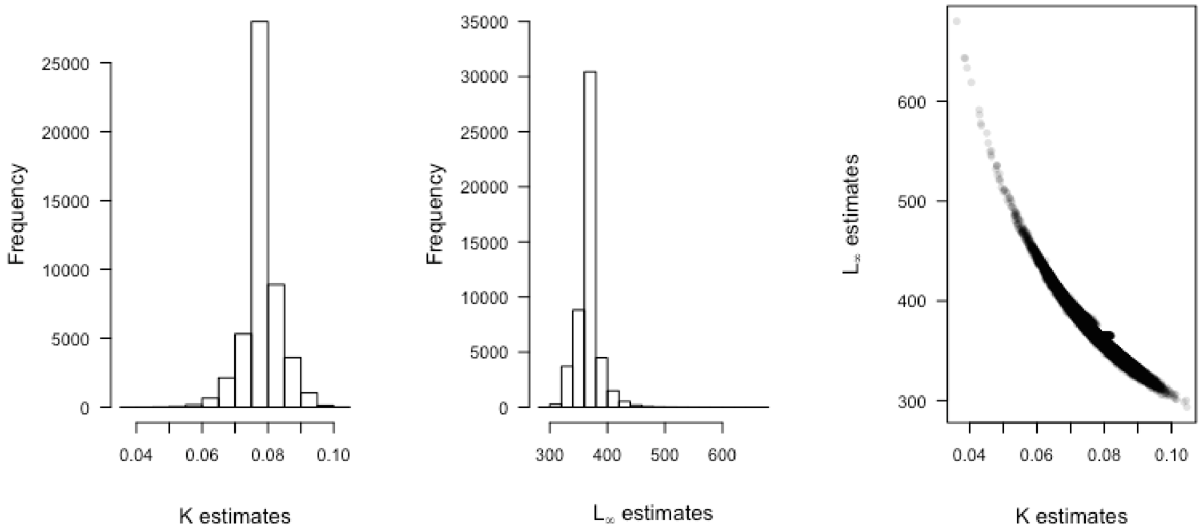

Figure 8. Frequency distributions of estimates of K and L_∞, and a scatterplot of K and L_∞ values, obtained from 50,000 bootstrap samples.

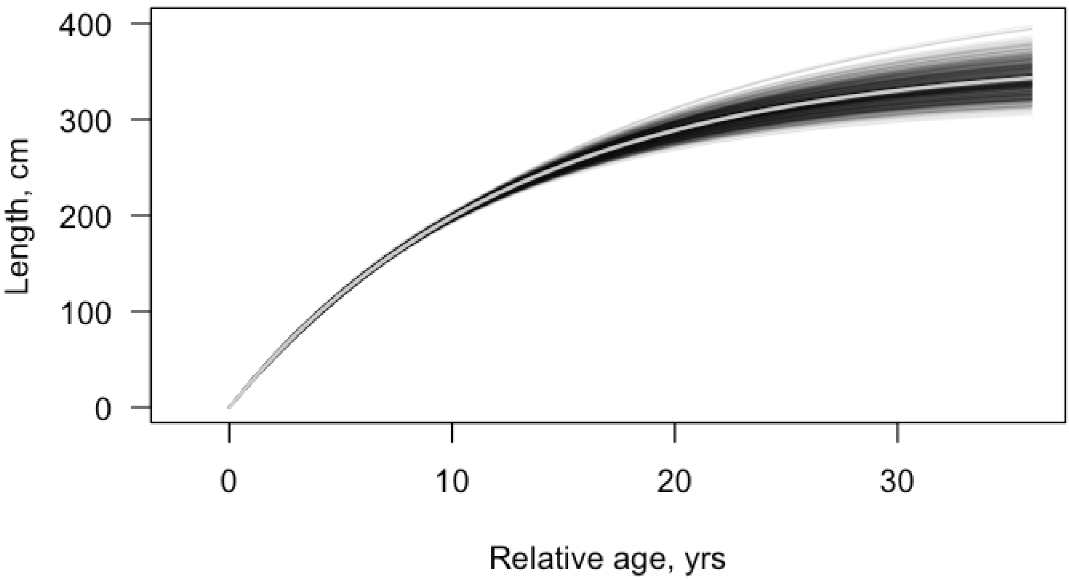

Figure 9. One thousand bootstrapped von Bertalanffy curves (dark gray) and the fitted von Bertalanffy curve (light gray) from our analysis.

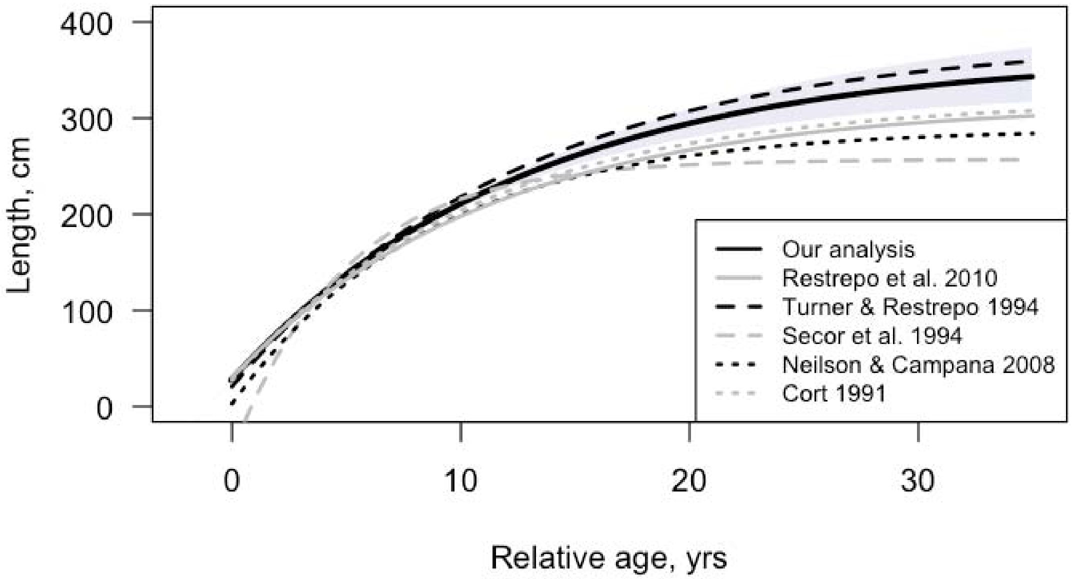

Figure 10. Graph comparing our results to published von Bertalanffy growth curves for Atlantic bluefin Tuna. The growth curves currently being used in stock assessment for Eastern and Western bluefin tuna are Cort (1991) and Restrepo *et al.* (2010), respectively. The shaded area indicates the 95% confidence envelope obtained by bootstrapping our analysis.

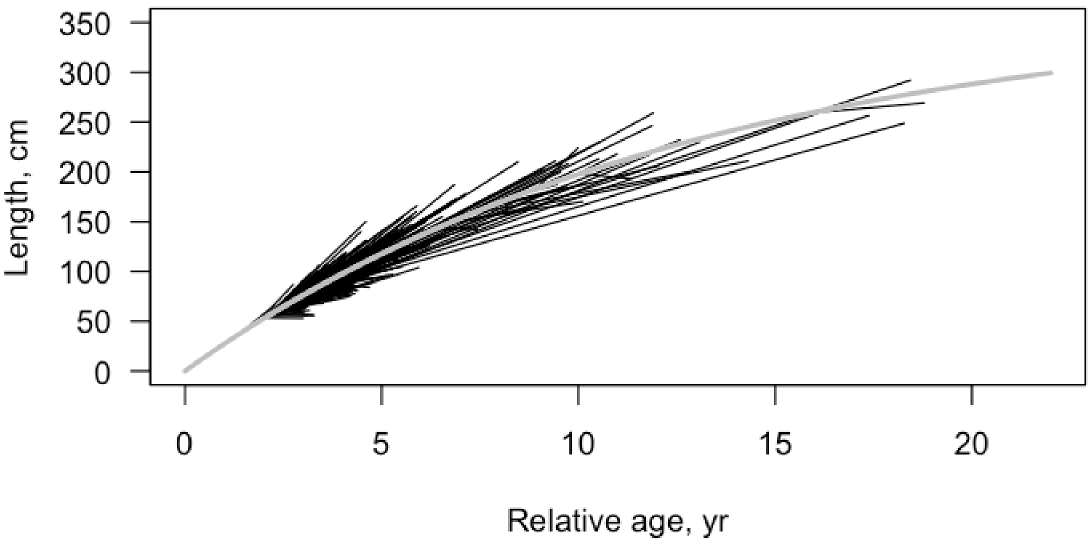

Figure 11. Vector plot of the growth increments. The relative age of each fish at the time of tagging, A_t, is estimated from the length at tagging, L_t, by inverting the von Bertalanffy growth equation. The age at recapture is then taken to be the age at tagging plus the time at liberty. Each growth trajectory starts on the fitted von Bertalanffy growth curve (shown in gray). The paucity of data for very young and very old fish is evident.

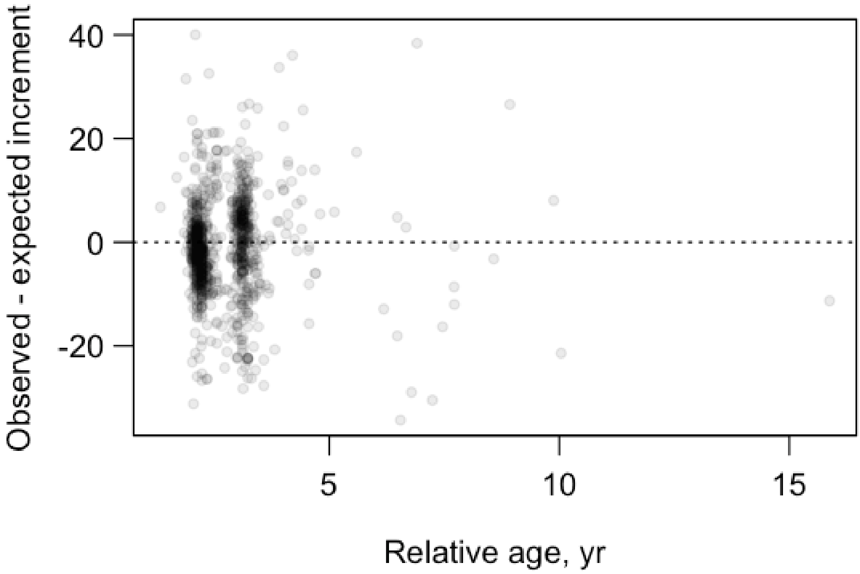

Figure 12. The difference between the observed and the expected (fitted) growth increment as a function of the estimated relative age at the time of tagging. Most animals were tagged at a relative age of 2 or 3 years. There is no evidence of a pattern to the residuals that would indicate an underlying biphasic growth model.