Updated Growth Models for Bigeye Tuna (*Thunnus obesus*) in the Atlantic Ocean

By

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Abstract

The International Commission for the Conservation of Atlantic Tunas (ICCAT) concluded the Atlantic Ocean tropical Tuna Tagging Programme (AOTTP) in 2021. This project had the objectives of enhancing food security, stimulating economic growth, and improving management through research on tropical tuna resources in the Atlantic Ocean, including bigeye tuna (*Thunnus obesus*). Here, we combine tagging data and otolith data from the AOTTP program, Panama City Lab and the Pelagic Fisheries Lab at the University of Maine with historical tagging data and otolith data from ICCAT and other sources to fit integrated growth models with the goal of providing the most complete growth curve (in terms of data inclusion and validation of age-at-length) for bigeye tuna in the Atlantic Ocean. Both Richards and von Bertalanffy growth models were fitted. A variety of models were fitted to subsets of the data to investigate the consistency of growth information. In all cases for the integrated model, the Richards and von Bertalanffy models were very similar with the von Bertalannfy model being preferred for parsimony. The preferred model, based on fit to old fish, was the von Bertalanffy curve based on length-age pair data from multiple sources. The addition of tagging data to create an integrated model showed patterns of lack of fit to both the tagging and otolith data suggesting conflict between the tagging and otolith data. The preferred model (length-age pair data only) gave the estimates: asymptotic length L_∞ (fork length) equals 161.21 cm (95% bootstrap CI 154.39, 166.84), growth parameter K equals 0.392 yr^{-1} (95% bootstrap CI 0.355, 0.441), and the time-axis intercept t_0 equals -0.239 yr (95% bootstrap CI –0.306, -0.175). For the best fitting integrated model, the asymptotic length L_∞(fork length, in cm) was estimated to be 185.78 (SD 6.298), the growth parameter K was 0.252 yr^{-1} (SD 0.014), and the time-axis intercept t_0 was -0.524 yr (SE 0.025). The value for asymptotic length L_∞ from the integrated model was larger than the lengths of all the old fish in the sample whereas the value for the curve based on otoliths passes through the cloud of points for old fish.

Keywords: Validated age, life history, otolith, Scombridae, growth model, tagging

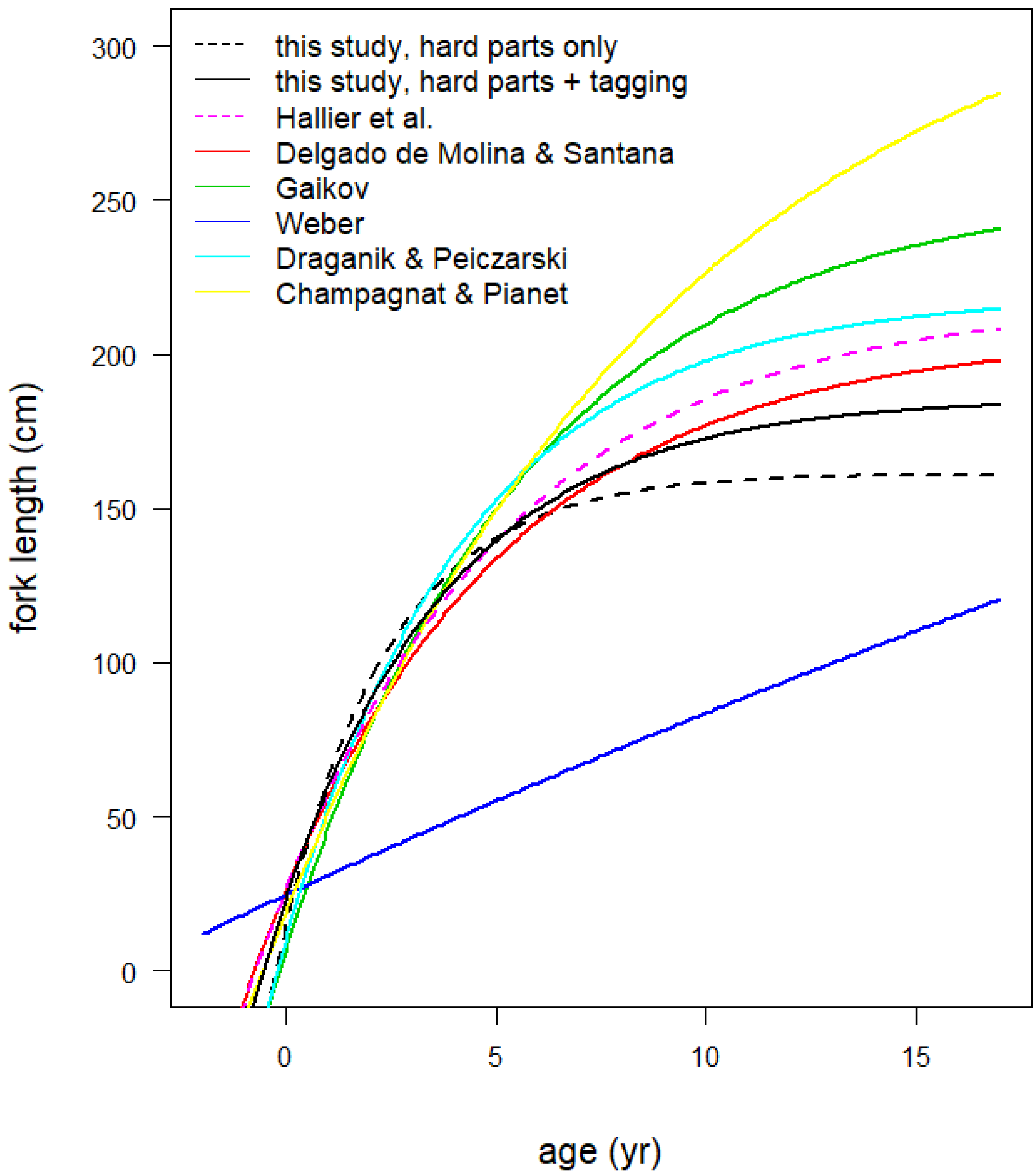
1. Introduction

Bigeye tuna, *Thunnus obesus*, are distributed in the warm waters of the Atlantic, Pacific, and Indian Oceans where they are commercially and recreationally fished. They can grow up to 230 cm in length and weigh up to 250 kg (Collette and Nauen 1983, Cayré et al. 1993). As a commercially valuable species fished in international waters by international parties, there is multi-national interest in keeping the fishery at a sustainable level. Accurately estimating the relationship between length and age provides critical information for assessment models. This paper focuses on the growth of bigeye tuna in the Atlantic Ocean.

Prior work for bigeye tuna in the Atlantic Ocean resulted in a variety of growth estimates, with values for the asymptotic maximum length, L_∞, ranging from ~200 to ~500 cm (Figure 1, Appendix 1). These models relied on a variety of data sources to estimate growth including tagging, otoliths, spines, and length frequency data, all of which lacked old individuals and long-term tag recapture data. The 2021 International Commission for the Conservation of Atlantic Tunas (ICCAT) assessment of bigeye tuna utilized estimates from the Hallier et al. (2005) formulation of the Richards growth model, reparameterized using Schnute (1981) as required by the Stock Synthesis (SS3) assessment platform. The resulting parameters were: L_∞ = 178.6 cm fork length (FL), the growth parameter K = 0.42 yr^{-1} and the Richards coefficient p = -0.00034 (Anon. 2021).

Figure 1. Comparison of estimated growth curves for bigeye tuna from the literature and the current study. The curve by Hallier et al. was used in the most recent stock assessment by ICCAT. The two curves from the current study are without the age 1 and age 2 fish in the Pelagic

Fisheries Lab dataset.



New data collected on Atlantic bigeye tuna now allows the growth curve to be revisited. ICCAT concluded the Atlantic Ocean Tropical Tuna Tagging Programme (AOTTP) in 2021, a five-year program with the goal of tagging at least 120,000 tropical tunas with a variety of tag types (Beare et al. 2019). During this time, nearly 25,000 bigeye tuna were tagged and released with just over 5,000 recoveries. Around the same time, laboratories across the Atlantic worked in collaboration to develop and validate age reading protocols for the species and increase the collection of hard parts for ageing purposes.

A goal of this work is therefore to estimate growth of Atlantic bigeye tuna using all available data for the stock. Of particular interest was to combine multiple data sources (i.e., tagging data and otolith data, including validated ages) in order to develop the most comprehensive and up-to-date growth model for the species. This included tagging data from three different sources (AOTTP, the ICCAT historical database, and a study by Hallier et al. (2005)) and otolith data from four different sources (AOTTP, Hallier et al. (2005), and age readings from the Pelagic Fisheries Lab (PFL) and the Panama City Lab (PCL) whose protocols have been validated using bomb radiocarbon dating (Andrews et al 2020)).

With so many sources of information, it was clear from the outset that issues related to data quality would have to be addressed. Ailloud et al. (2014) found that ICCAT tagging data for Atlantic bluefin tuna contain useful information about growth rates if, and only if, the data are subjected to extensive quality control procedures. Such procedures have not been applied to the ICCAT bigeye tuna tagging data but have been applied to the tagging data from AOTTP (see Anon. 2021). In the present study, measurement error was estimated from short-term recapture data for the ICCAT and AOTTP tagging data as well as those of Hallier et al. (2005). It was also noted that different age reading protocols were used: Hallier et al. (2005) age estimates were based on daily growth rings while most other samples were aged using annual growth rings. While daily growth rings can provide accurate and precise age estimates in young fish, the procedure has been shown to progressively underestimate age for bigeye older than one year (Williams et al. 2013, Ailloud et al. 2019). As such, the data analysis considered several subsets of the full dataset.

In order to estimate growth simultaneously from tag-recapture data and otolith age-length data, the tag-recapture data must be modeled in a way that is consistent with age-length data (Francis 1988a and 1988b; Laslett et al., 2002). That is, for age-length data, there is variability in length about age, so instead of modeling tag-recapture data as a function of length (i.e., using length increment data and times at liberty (Fabens 1965)) we model the lengths at release and recapture while treating the unknown age at release as a random variable (Francis et al., 2016; Aires-da-Silva et al., 2015; Eveson et al. 2004; Laslett et al. 2002). This modeling approach allows for the growth information from both sources of data to be modelled as a function of age, allowing for a common set of growth parameters to be derived.

2. Methods

2.1. Tagging Data

AOTTP Tagging Data

This analysis is based on AOTTP database version 'aottp_cisef_20210228'. Details of the AOTTP tagging program can be found in Beare et al. (2019). In the AOTTP database there are 24,252 releases of bigeye tuna (identified as bigeye in the release species code) representing 24,078 unique fish. Of those tagged fish there were 5,018 recoveries (note, some of these represent fish recovered more than once from fish that were released post recovery).

Of the 5,018 recoveries identified as bigeye during their release, 340 were identified during recovery as yellowfin (YFT), blackfin (BLF), little tunny (LTA), or skipjack (SKJ) (Table 1).

Table 1. Breakdown of species identifications during recovery of the 5,018 identified as bigeye during release (BET = bigeye, BLF = Bluefin, LTA = Little Tunny, SKJ = Skipjack, YFT = Yellowfin, UNK = unknown).

BET	BLF	LTA	SKJ	YFT	UNK	Total
2,243	1	1	22	316	2,435	5,018

For the purpose of this analysis, we assume that the fish are bigeye if they were identified as bigeye during biological sampling. We also include fish that were identified as bigeye during release and recovery or bigeye during release and unknown during recovery. There are 4,678 bigeye once this filter is applied (Table 2).

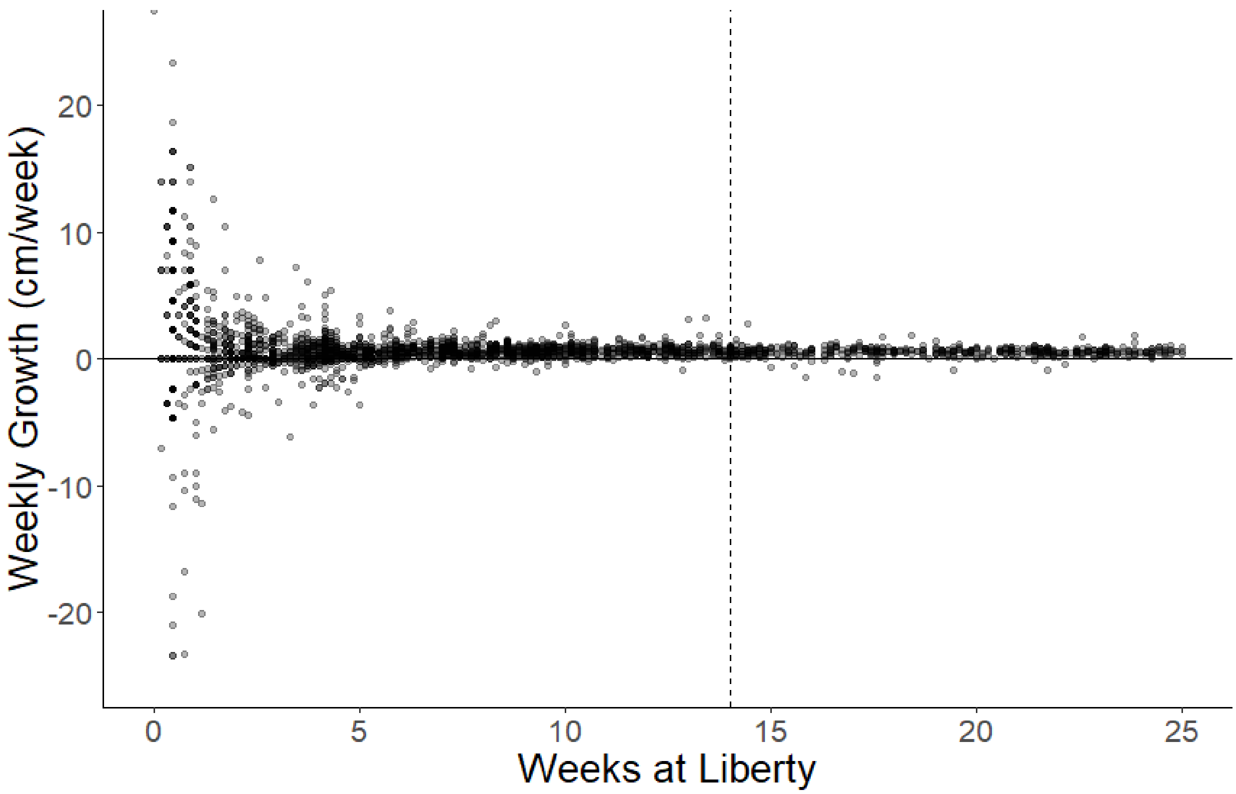
The release length type (relentype) and recovery length type (rclentype) were (straight) fork length (FL), blank, unknown (UNK), curved fork length (CFL), lower jaw to 1st dorsal (LD1), standard length (SL), or total length (TL). We retained fish which had length CFL (and converted them to FL, see Appendix 2 for details) and FL. We use the terms straight fork length and fork length interchangeably and distinct from curved fork length. There were 4,356 bigeye tuna pairs left after this filter. After eliminating those fish with negative time at liberty we had 4,280 pairs. There were 4,227 remaining fish after those with missing lengths were removed; some had times at liberty up to 150 weeks.

Table 2. Sample size from AOTTP database for bigeye tuna data after each step in the data processing to ensure only appropriate pairs of data were used in the assessment work.

Initial number of releases in database	*24,252*
Initial number of paired (release-recapture) records in the database	*5,018*
Justification for removal	**# paired records remaining**
I – Initial data processing	
Recovery length unknown or unable to convert to FL	4,678
Missing time at liberty	4,356
Time at liberty is negative	4,280
Missing release length	4,277
II – Further exclusion criteria	
Removed all records with time at liberty ≤97 days	1,626
Removed outliers in growth	1,592

Over short times at liberty the observed growth increments largely represent measurement error rather than somatic growth (Ailloud et al. 2014). We examined the distribution of unreasonable growth increments (negative weekly growth) as a function of time at liberty to determine a threshold time at liberty at which measurement errors are minimal while retaining as great a sample size as possible. In order to match what was done across other datasets, 98 days was used as the cutoff for determining the time at liberty that represents real growth rather than measurement error. This left 1,626 records (Table 2). In an attempt to eliminate outliers due to data entry and measurement errors, we removed records with the fastest and slowest 1% absolute growth per day (i.e., below the 0.01 and greater than the 0.99 quantiles). This resulted in 1,592 records for analysis.

Figure 2. Plot of weekly growth (cm/week) versus time at liberty (weeks) based on straight fork length (FL) measurements at time of tagging and recapture from 4,256 bigeye tuna in the AOTTP database. Only records for fish at liberty for up to 25 weeks are shown (maximum time at liberty is 161 weeks). The dashed vertical line is at 98 days. Due to the amount of data the circles have been made slightly transparent; circles that appear black (rather than grey) indicate multiple data points at this value.



The resulting dataset for bigeye consisted of 1,592 records with lengths at tagging ranging from 33 cm FL to 140 cm FL, lengths at recapture ranging from 28 cm FL to 150 cm FL (Figure 3) and times at liberty ranging from 98 to 1,127 days (median= 239 days). The releases peaked in March and then July to November, while the majority of the recoveries occurred May to August with a peak in July (Figure 4).

Figure 3. Histogram of lengths (cm) for the 1,592 bigeye tuna used in this analysis at release (top) and recovery (bottom) from the AOTTP database.

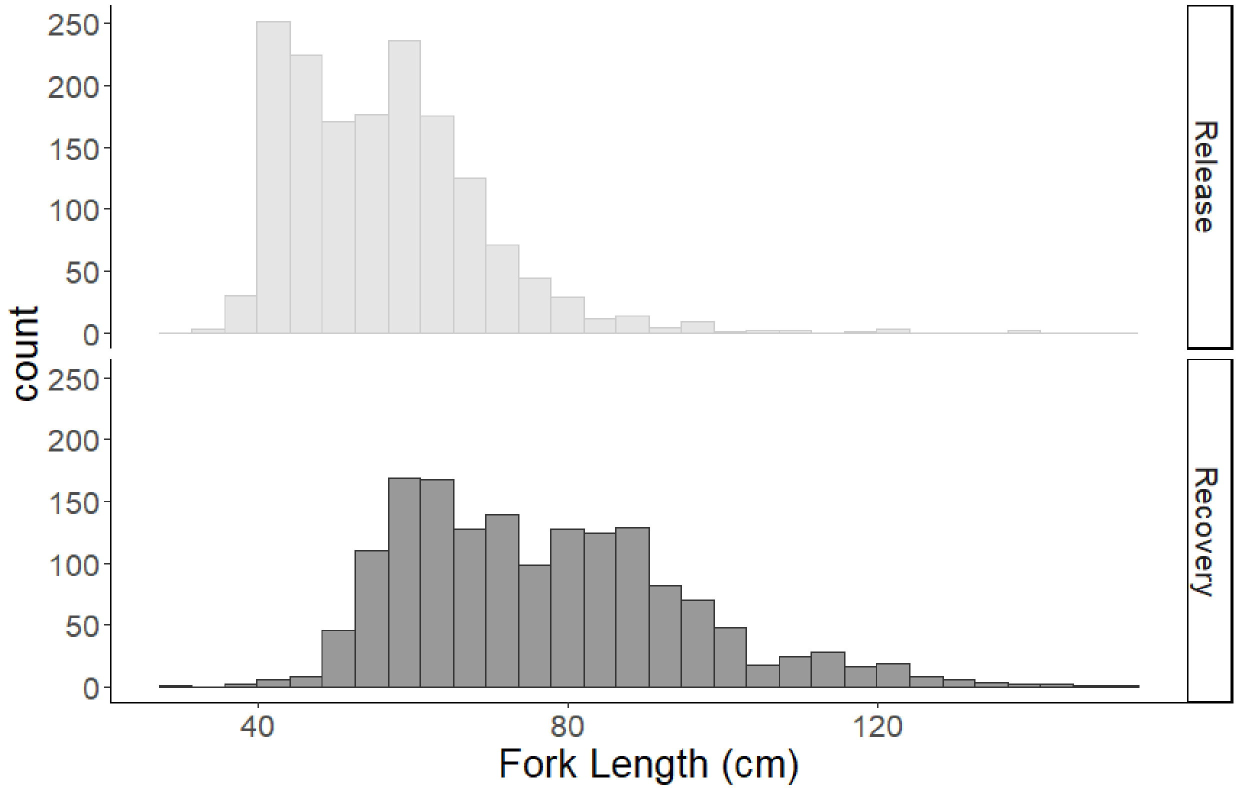
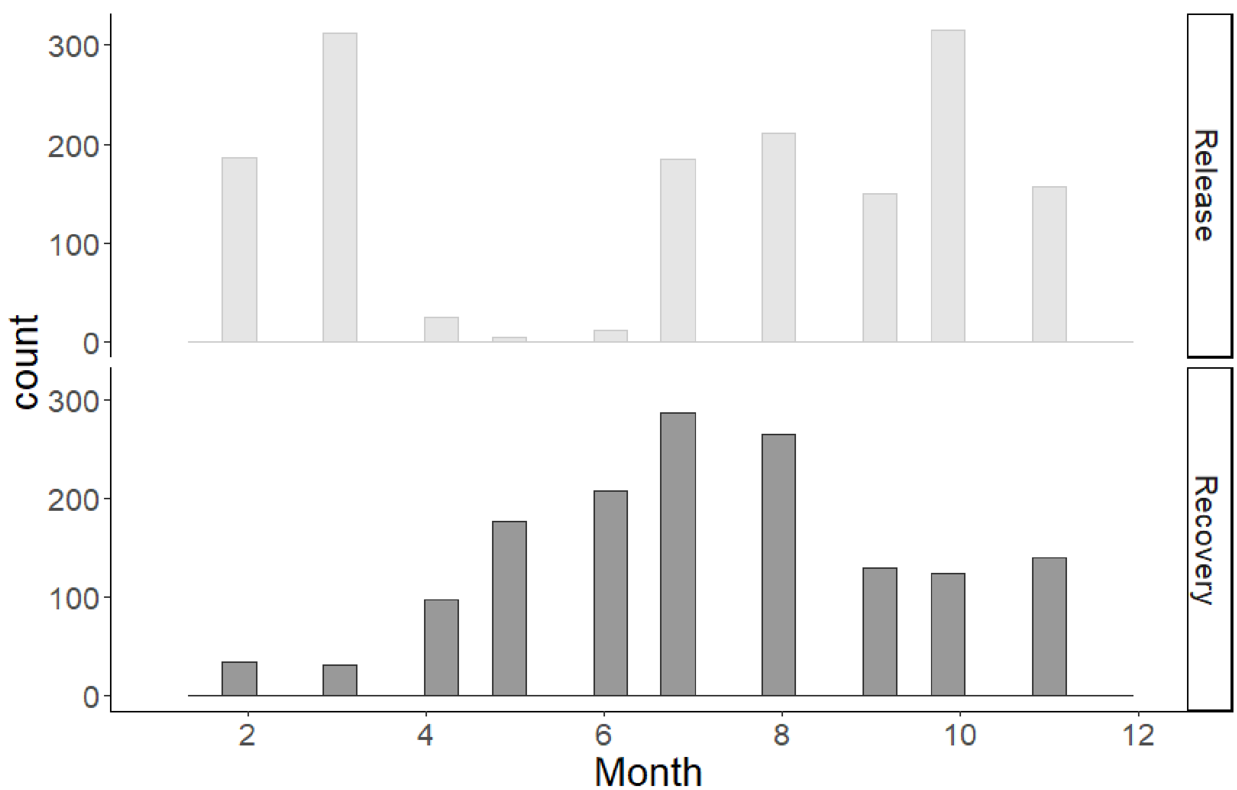


Figure 4. Histogram of month of release (top) and recovery (bottom) for the 1,592 bigeye tuna from the AOTTP database used in this analysis.



ICCAT Tagging Data

The ICCAT tagging database (ICCAT Secretariat n.d.) begins in 1960 for bigeye tuna and has releases or recaptures for 54 years (through 2020, which overlaps with the AOTTP tagging program). The tagging database has a total of 35,462 releases and 7,996 recoveries, although many of these (24,212 releases and 5,115 recoveries) are part of the AOTTP database (Table 3). A further 55 records have unknown release years and 115 records had missing recovery years. There are 2,108 pairs of release and recoveries with known dates of release and recovery and known lengths at release and recovery.

Of the 2,108 pairs of release/recovery, only 45 had both pairs with known measurement unit (either FL or LJF), and the rest were unknown. We treated LJF (lower jaw fork length) as equivalent to FL and thus all 45 lengths were retained. After removing those fish with negative time at liberty we had 44 pairs.

Table 3. Sample size from ICCAT database for bigeye Tuna data after each step in the data processing to ensure only appropriate pairs of data were used in the assessment work.

Initial number of releases in database	*35,462*
Initial number of paired (release-recapture) records in the database	*7,996*
Justification for removal	**# paired records remaining**
I – Initial data processing	
Part of AOTTP database	2,881
Recovery date is missing	2,826
Release date is missing	2,826
Release or recovery length is unknown	2,108
Release or recovery measurement unit (e.g., FL or LJF) is unknown	45
Time at liberty is negative	44
II – Further exclusion criteria	
Removed all records with time at liberty ≤97 days	19
Removed any record that could overlap with Hallier	18
Removed growth outlier	17

The majority of the tagged bigeye from the ICCAT database were tagged in the months of July and August with recoveries throughout the year, but with a peak in August (Figure 5). The release FL ranged from 56 to 129 cm and the recovery FL ranged from 12.5 to 203 cm (Figure 6).

Figure 5. Histogram of month of release (top) and recovery (bottom) for the 18 bigeye tuna used in this analysis (prior to the removal of the growth outlier), from the ICCAT database.

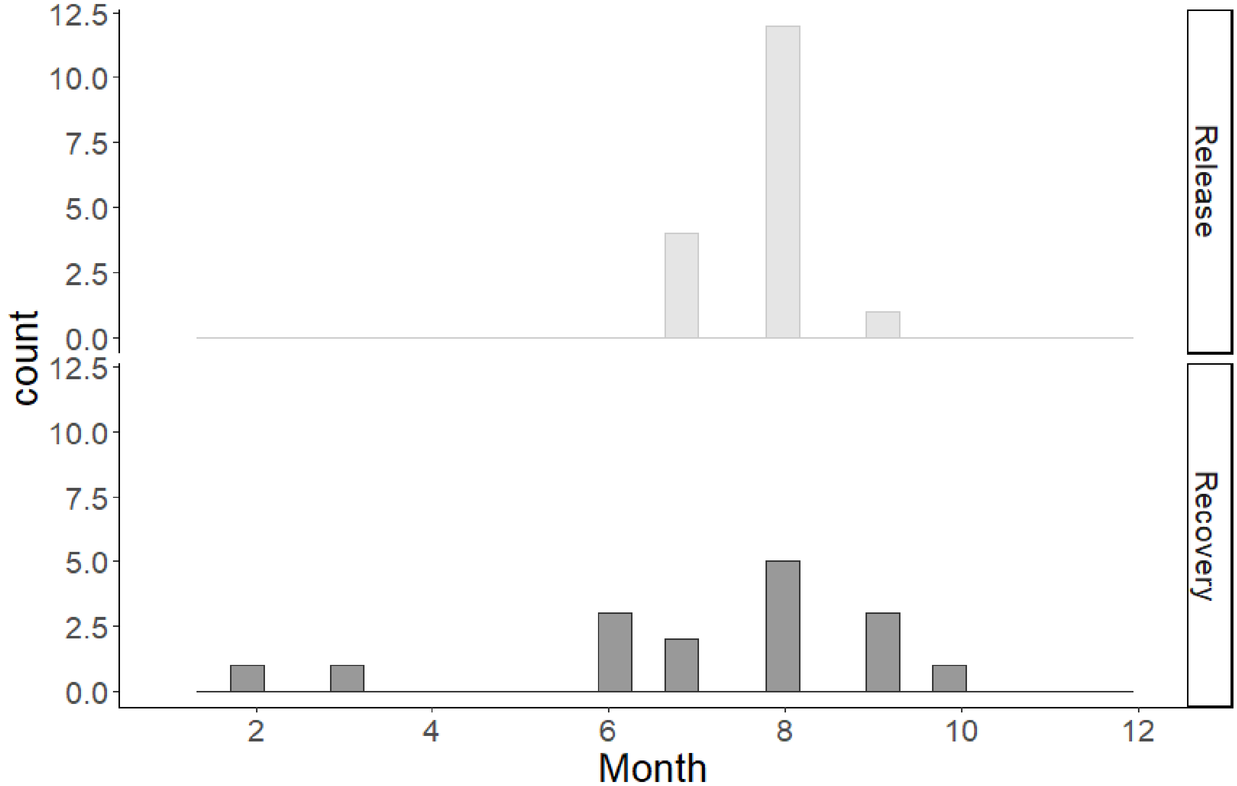
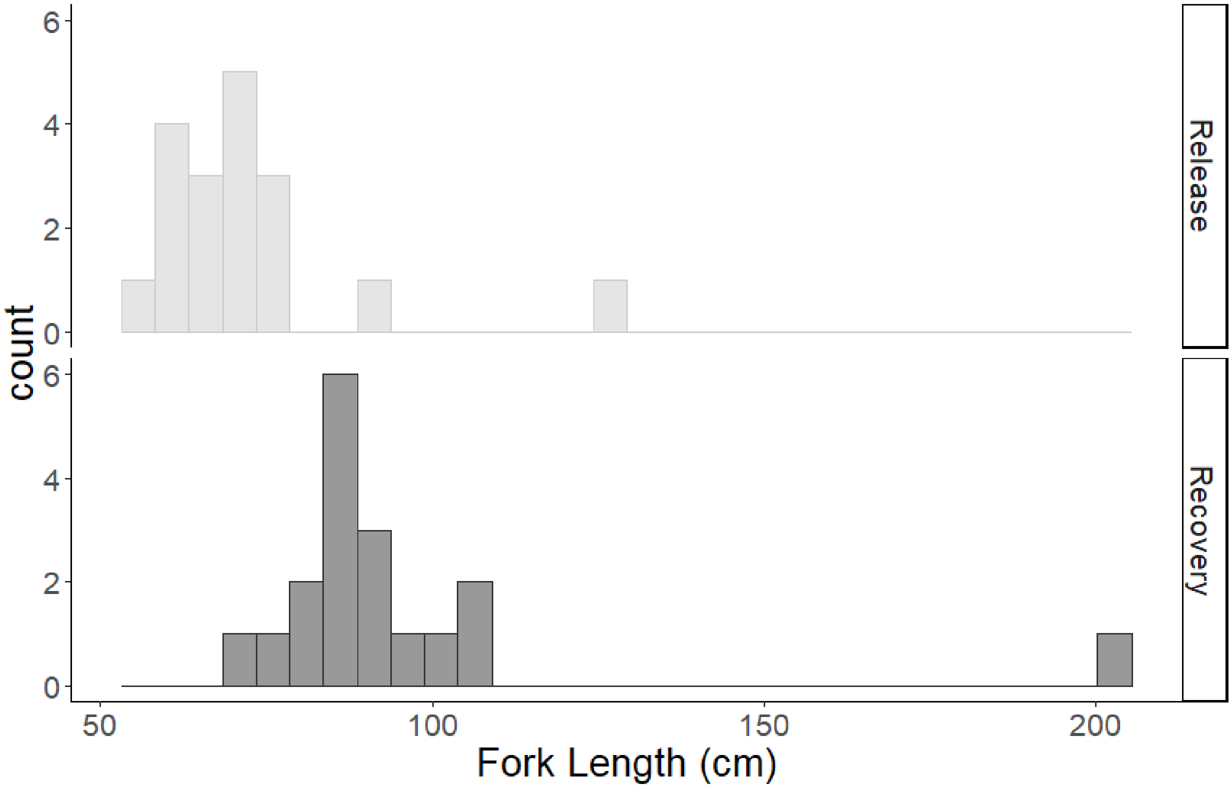


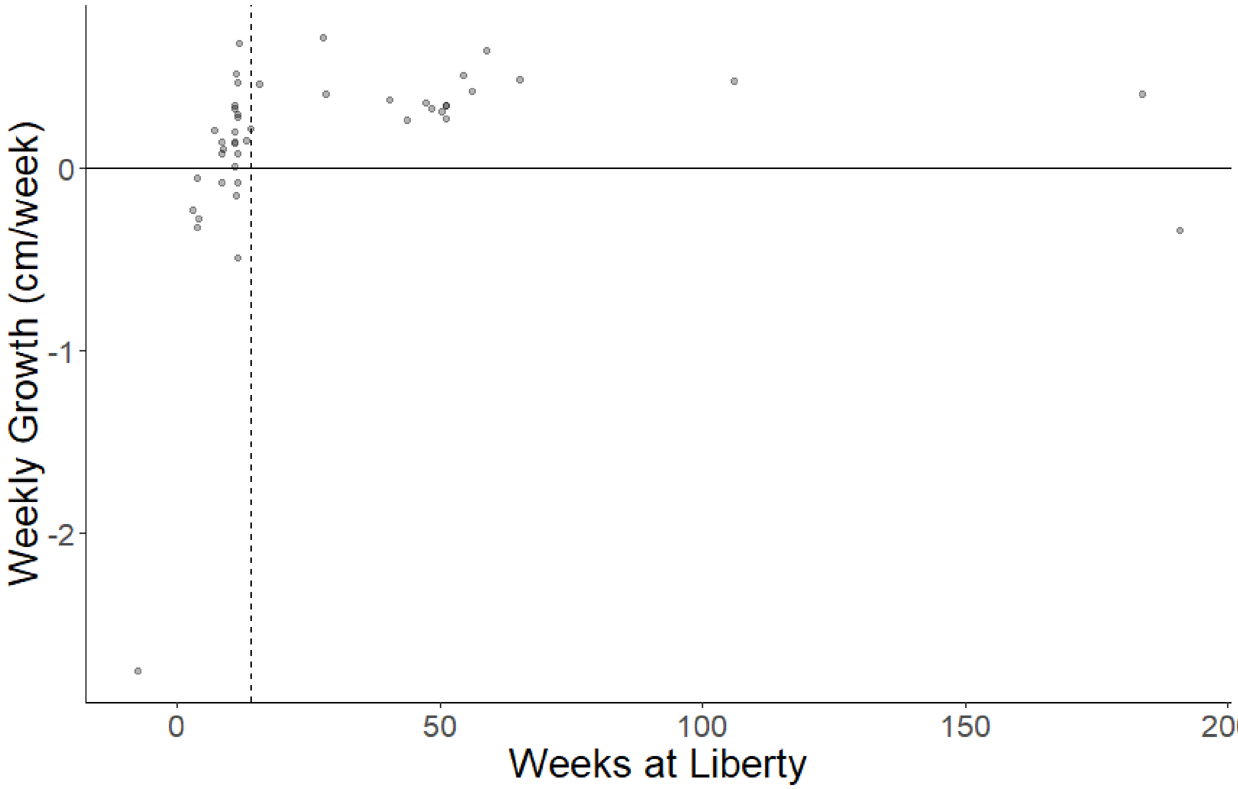
Figure 6. Histogram of lengths (cm) for the 18 bigeye tuna used in this analysis at release (top) and recovery (bottom) from the ICCAT database. The fish with recovery length of 203 cm is an

apparent outlier and was discarded (see Figure 10).



In order to avoid including records where observed growth rates most likely reflect measurement error or tagging effects, only data for fish at liberty >97 days were retained, leaving 19 data pairs to analyze (Figure 7). Of these 19 pairs, 16 had lengths that were measured at both release and recovery; 2 pairs had unknown (either estimated or measured) measurement type at release and recovery; and 1 pair had estimated measurement type at release and unknown at recovery. One additional record was removed to avoid overlapping with the Hallier et al. (2005) data (discussed below), as those data occur in the ICCAT database, but we were unable to uniquely identify the records. The one removal was a release from 2000 and this overlaps with the time frame of the Hallier data (releases in 1994 to 2000). Another record has an unreasonable growth trajectory (see Figure 10) and was removed. This resulted in 17 usable records from the ICCAT database.

Figure 7. Growth per week (recorded growth divided by weeks at liberty) versus time at liberty for bigeye tuna from the ICCAT database. The dashed vertical line denotes the 98 day time at liberty cutoff used in this study.



Tagging Data from Hallier et al. (2005)

We obtained data from a previous study in the eastern Atlantic Ocean (Hallier et al. 2005) that included 625 bigeye tagged and recaptured with FL ranging from 37 to 124 cm (Figure 8). When 98 days is used as the time at liberty cutoff (to be consistent with AOTTP and ICCAT tagging data), 146 bigeye release and recoveries remain (Figure 9). Originally Hallier used 14 days as the cutoff.

Figure 8. Frequency of recovery fork lengths (cm), top panel, and release lengths (cm), bottom panel, for bigeye tuna from the tagging data of Hallier et al.

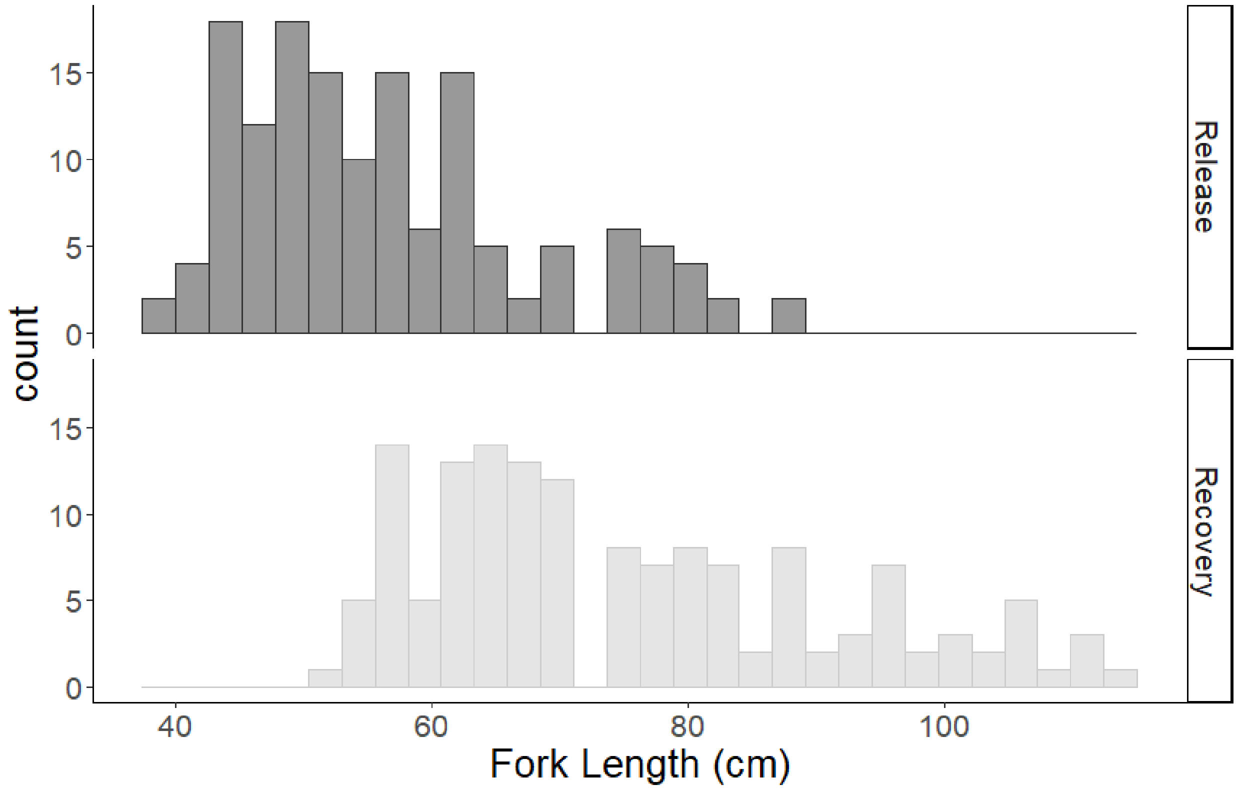
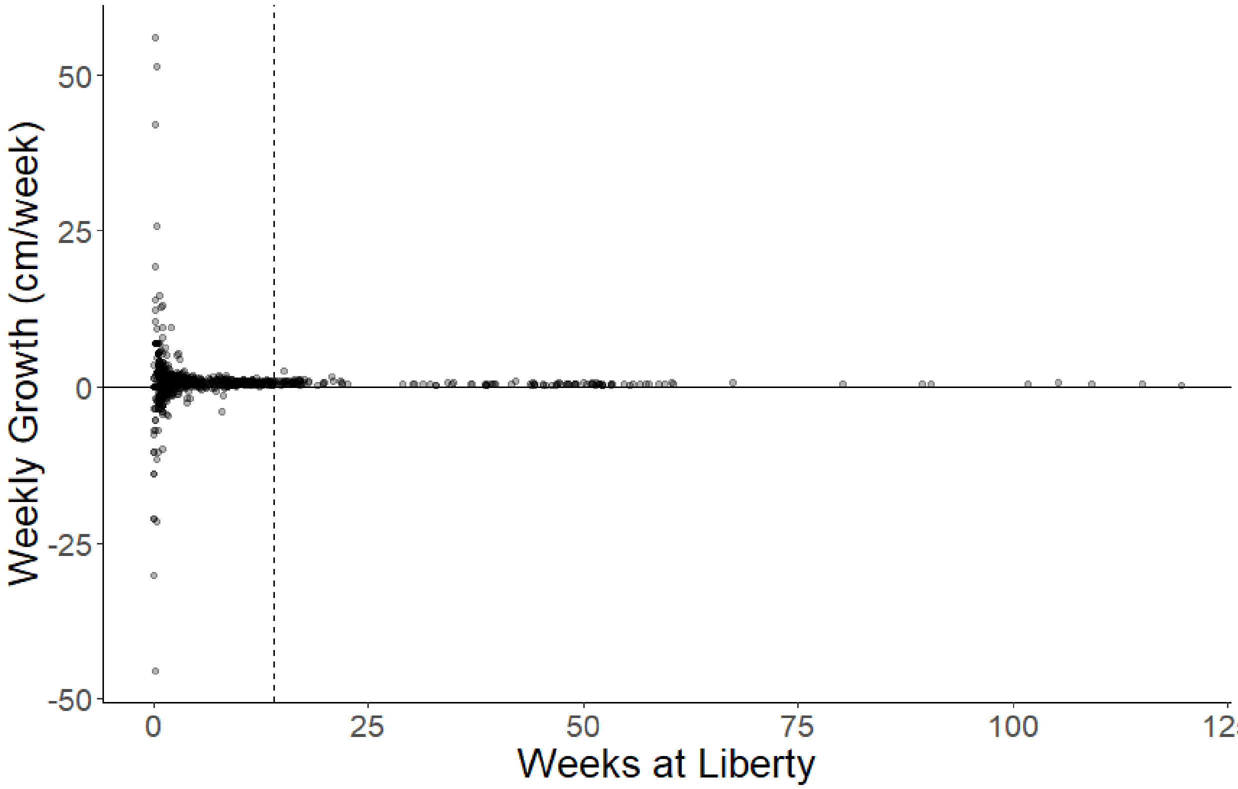


Figure 9. Growth per week (recorded growth divided by weeks at liberty) versus time at liberty for bigeye tuna from the tagging data of Hallier et al. The dashed vertical line denotes the 98 day time at liberty cutoff used in this study.



2.2. Otolith data

The otolith data comprised samples aged using two different reading protocols: one based on daily increment counts and the other on annual ring counts. Results from blind counts of micro-increments in chemically marked bigeye tuna have found that micro-increment counts tend to underestimate true times at liberty (Ailloud et al. 2019; Farley et al. 2020), indicating that daily counts are likely to underestimate true age. Additional work by Williams et al. (2013) has shown that age counts of presumed daily growth increments can lead to an underestimation of age in fish older than 1 year (Williams et al., 2013). As such, for all hard part data utilized in this analysis, daily readings were restricted to bigeye less than 1 year of age. The ageing protocol based on annual ring counts (Allman et al. 2020) that was used for all samples described below has been validated through bomb radiocarbon dating (Andrews et al. 2020) and preliminary results from AOTTP fish marked with oxytetracycline support the hypothesis that the larger growth increments are deposited on an annual basis (Ailloud et al. 2019).

AOTTP Otolith Data

A total of 63 pairs of otolith age and length was obtained through the AOTTP from fish sampled across a large area of the Atlantic Ocean. Twenty-six of those samples were read by a single expert using annual growth increment counts, while the remaining 37 (the 'reference collection') were aged by three independent readers who counted daily rings (Figure 10; Beare et al. 2019).

Whole otoliths were imaged and weighed prior to processing. Each core was marked prior to embedding in embedding in polyplex clear ortho casting resin (Allnex©). Transverse sections were cut through the center of each otolith using an Isomet 1000 low-speed saw with diamond edged wafering blades. Sections were then mounted on microscope slides (76.2 x 25.4mm) using thermoplastic resin (Cystalbond 509 ©) with the side of the section furthest away from the core facing up. Each section was ground to a thickness between 320 – 350 µm using wet/dry sandpaper (800 and 1200 grit), lubricated with distilled water. A small drop of microscope immersion oil (Cargille © -TYPE A) was added prior to imaging to help clear up the ground surface of the otolith and aid in the imaging process.

Otolith sections were imaged under transmitted light. Annual ages were assigned to individuals based on the number of fully formed opaque zones (i.e., presence of translucent otolith material between the outer edge of the last opaque zone and the otolith margin). All age readings were made without knowledge of fish size, otolith weight, sex, location of capture or time at liberty. Methods for the annual age reading followed those developed for other tuna species (Farley et al., 2013, 2006; Gunn et al., 2008; Lang et al., 2017). Ageing protocols developed for Atlantic bluefin tuna (Neilson and Campana, 2008; Rodríguez-Marín et al., 2014, 2007; Secor et al., 2014) were also used as a basis to aid interpretation of what may constitute an annual growth zone in Atlantic tunas.

Micro-increment counts were conducted at various magnifications ranging between 400 and 1000x. The method for the interpretation of the microstructure was consistent with those methods published for reading transverse sections (Lehodey and Leroy, 1999; Sardenne et al., 2015; Shuford et al., 2007). After a count of between 150-180 the internal micro-structure becomes increasingly difficult to interpret. For subsections of the otolith where increments were either difficult to interpret or not present, an interpolation method based on the zone pattern immediately before and after the difficult area was applied.

2.1.5. Otolith Data from Pelagic Fisheries Lab

A total of 229 sets of otoliths was extracted from bigeye tu,na landed by commercial pelagic longline vessels and recreational rod and reel fisheries along the east coast of the United States between June and November of 2018-2020. Catch locations include the Gulf Stream, along the continental shelf, and slope canyons from Cape Hatteras to the Hague Line. FL (cm) of individuals sampled from recreational fisheries and CFL from commercial longline fisheries were recorded. To standardize length across gears tunas measured in CFL were converted to FL using a regression equation developed by Farley et al. (2006). Fish ranged in size from 69.7 to 174.7 cm SFL. The minimum length in US waters for bigeye is 27 inches (68.58 cm) curved fork length, resulting in only large age 1 and 2 fish being retained. After extraction, sagittal otoliths were rinsed with water, dried, and stored in vials.

Otolith processing was based on methods developed by Busawon et al. (2015) and modified by Rodrigues-Marin (2019) for Atlantic bluefin tuna (*Thunnus thynnus*). All otoliths were cleaned in a jewelry sonicator to remove any remaining residual tissue that dried after extraction. Whole sagittal otoliths (left and right) were weighed and imaged, then embedded using Epothin 2 Epoxy hardener and resin at a 17:40 ratio respectively. Transverse sections were cut using an Isomet 1000 low-speed saw with diamond edged Buehler blades. Four transverse sections, 0.8 mm in width, were cut beginning with a rostral 'V-section' that included the origin.

Sections were mounted to glass slides using *QuickStick* Mounting Wax with the side closest to the origin facing down. After mounting, sections were polished using 180, 320 and 600 grit sandpaper to a width of roughly 0.3-0.5mm. A final polish with a felt pad containing a light coating of water mixed with *MicroPolish 2* Alumina powder was applied to each section. Otolith sections were imaged under transmitted light with a compound microscope and features such as contrast and brightness were adjusted for each section in Adobe Photoshop. A 1mm scale bar was created and placed at the first inflection point on the ventral arm of each bigeye section image to provide the reader guidance on the approximate location of first annulus formation based on mean distances in Farley et al. (2006).

All four sections were read twice by the same reader with no *a priori* information about the section (e.g., fish size, weight, previous age estimates). After analysis, only the two sections closest to the origin were used for age final estimation and reading error estimates. If age estimates from the first and second read were not identical, the section was aged again and assigned a final age based on that third reading. A readability score on a scale from 1-5 (1 = unreadable, 5 = excellent) was established and sections with low readability scores (mean score ≤ 2.5) were not included in final age estimates. Annual ages were assigned to individuals based on the number of fully formed opaque zones.

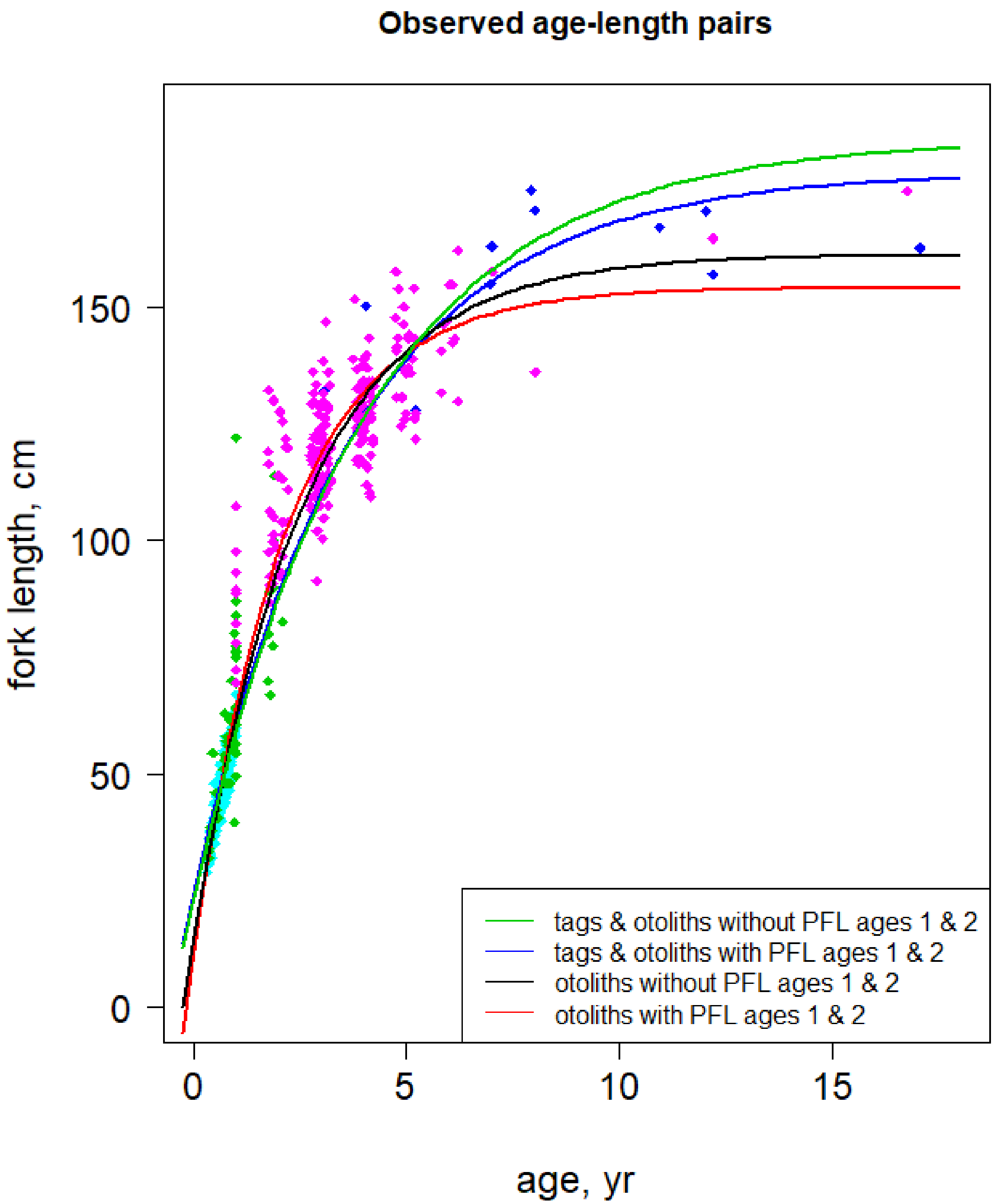
2.1.6. Otolith Data from Hallier et al. (2005) (Daily readings)

Data from a 2005 study published by Hallier included 255 bigeye tuna otoliths read for daily age (Hallier et al. 2005). The lengths ranged from 20 to 190 cm (FL) and the ages (in days) ranged from 116 to 3,324. A light microscope was used for readings from fish with FL less than 74 cm and a scanning electron microscope for fish with FL equal to or bigger than 74 cm. The otolith preparation and reading protocols are described in detail in Hallier et al. (2005). Hallier's original study retained 83 of the 108 otoliths from Dakar, Senegal, and 147 from Abidjan, Ivory Coast. Given concerns regarding potential underaging of fish, in the current study the dataset was restricted to 153 age-length pairs from fish under 1 year old (Figure 10). Fork lengths for this subset ranged from 29 to 67 cm.

2.1.7. Otolith Data from the Panama City Lab

Twelve otoliths prepared and read by the Panama City Lab (PCL) were included in this study. Detailed protocols are described in Pacicco et al. (2021) and are aligned with the abovementioned annual ageing protocols (Allman et al. 2020). Ages determined by counting purported annual growth zones in these twelve Bigeye otolith cross sections were validated with bomb radiocarbon dating (Andrews et al 2020). The valid age-at-length data for Bigeye were 3–17 years for fish lengths of 128.0–175.0 cm FL (n = 12) (Figure 10).

Figure 10. Plot of all the length-age pair data (excluding fish greater than one year of age in the dataset of Hallier et al. (2005)). Blue symbols represent data from Panama City Lab; cyan = ages from daily ring counts by Hallier et al. (2005), green symbols = AOTTP readings of annual rings in otoliths, magenta = data from Pelagic Fisheries Lab (PFL). Integer ages >1 have been jittered to reduce overprinting. Four fitted von Bertalanffy curves are shown which differ in whether age 1 and age 2 fish from the PFL dataset are included and whether tagging data is used in addition to the otolith data.



2.2. Growth Curve Analyses

We fitted two different growth models to the tag-recapture data and counts of growth rings in otoliths: the Richards and the von Bertalanffy models. The Schnute (1981) parameterization was used as it allows for both models to be expressed using a single equation where the shape parameter, p, controls the level of curvature and reverts the function to a classic von Bertalanffy model when p is equal to 1.0.

All computations (except for the integrated analyses) were done using the R program language (R Core Team 2020). Models based on just the otolith data were fitted using the R package 'FSA' (Ogle et al. 2020). For the integrated analyses, we used the "Aires da Silva-Maunder-Schaefer-Fuller with correlation" (AMSFc) framework (Francis et al. 2016). This approach models the release and recapture lengths of fish as functions of age by treating age at tagging as a random effect. It also accounts for correlation between the measurements of an individual through the parameter ρ, which models correlation as a simple decreasing function of time at liberty (Δt; Francis et al. 2016). The objective function is the sum of the bivariate normal log-likelihood of the release and recapture lengths, the lognormal log-likelihood of the random effects and the log-likelihood of the otolith data. Computer code in AD Model Builder (Fournier, D.A. et al. 2012) was used that was based on the Bluefin tuna work of Ailloud et al. (2017).

For the Schnute (1981) model, the following equations are used:

$$L_a = \left((L_1)^p + ((L_2)^p - (L_1)^p)\frac{(1-exp(-K(a-A_1))}{(1-exp(-K(A_2-A_1))}\right)^{\frac{1}{p}} \quad \text{(Equation 1)}$$

$$L_{a+\Delta t} = \left((L_1)^p + ((L_2)^p - (L_1)^p)\frac{(1-exp(-K(a+\Delta t-A_1))}{(1-exp(-K(A_2-A_1))}\right)^{\frac{1}{p}} \quad \text{(Equation 2)}$$

$$L_\infty = \left(\frac{exp(KA_2)(L_2)^p - exp(KA_1)(L_1)^p}{exp(KA_2) - exp(KA_1)}\right)^{\frac{1}{p}} \quad \text{(Equation 3)}$$

$$t_0 = A_1 + A_2 - \frac{1}{K}ln\left(\frac{exp(KA_2)(L_2)^p - exp(KA_1)(L_1)^p}{(L_2)^p - (L_1)^p}\right) \quad \text{(Equation 4)}$$

$$t^* = A_1 + A_2 - \frac{1}{K}ln\left(p\frac{exp(KA_2)(L_2)^p - exp(KA_1)(L_1)^p}{(L_2)^p - (L_1)^p}\right) \quad \text{(Equation 5)}$$

where:

a is age,

L_a is the expected length of a fish of age a, thus $L_{a+\Delta t}$ is the expected length of a fish tagged at age a and recaptured at age $a + \Delta t$,

L_∞ is the asymptotic length,

K is the growth coefficient,

t_0 is the theoretical age at size 0 in the von Bertalanffy growth model ($p = 1$),

t* is age at which the inflection of the Richards growth curve occurs ($p \neq 0$),

A_1 is age of youngest fish in sample,

A_2 is age of oldest fish in sample,

L_1 is the expected length of fish age A_1,

L_2 is the expected length of fish age A_2.

In fitting the model, there are three types of parameters: those fixed by the user (A_1 and A_2), those estimated when maximizing the likelihood (L_1, L_2, and the parameters defining the error structure (see below)), and those derived from the other parameters (L_∞, t_0, and t^*(see above) and a* and b* (see below)). The parameters of the error structure are:

k_ρ steepness of slope ($k_\rho > 0$) defining relationship between correlation coefficient (ρ) and time at liberty (higher value means the faster the correlation coefficient declines to zero),

ρ_0 correlation (ρ) between length at tagging and length at recovery when time at liberty is zero ($0 < \rho_0 < 1$, and note that $\rho = 1 - \frac{1-\rho_0}{1-\rho_0-\rho_0 e^{(-k_\rho \Delta t)}}$ where Δt is time at liberty),

σ_{L_1} variability in length for fish at age A_1 ,

σ_{L_2} variability in length for fish at age A_2,

$\mu_{logA_{tag}}$ - mean for random effects for age at tagging (follows lognormal distribution),

$\sigma_{logA_{tag}}$- standard deviation for random effects for age at tagging (follows lognormal distribution),

The derived parameters are:

a^* intercept for true variability around mean curve (variability in length at age) - linear model,

b^*slope for true variability around mean curve (variability in length at age) - linear model, (note - $\sigma_{L_a} = a^* + b^*$).

When p = 1, the model reverts to a von Bertalanffy model. Otherwise, the model assumes a Richards form.

2.3. Measurement Error

It is possible to estimate the measurement error from short-term recaptures for fish with measured or estimated lengths (Ailloud et al. 2014). 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 for any fish at liberty for less than Δ days 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

$$Var(I) = Var(L_r - L_t) = Var(L_r) + Var(L_t) = 2\sigma^2 \quad \text{(Equation 6)}$$

where Var(L_r) and Var(L_t) refer to the variance of repeated measurements of the same fish and 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. If Δ is a short period of time, there is high assurance that growth while at liberty is close to zero at the cost of a smaller sample size compared to using a larger Δ. We Use Δ = 25, 50, 75 and 98 days.

3. Results

3.1. Length measurement error

The Hallier et al. (2005) data have the lowest measurement error for length (4.7 or 4.9 cm depending on whether the cutoff Δ is set to 25 or 50 days) based on more than 500 paired measurements. The AOTTP data have slightly higher but similar measurement error (6.8 cm for both 25- and 50-day cutoffs, based on more than 900 paired measurements). The ICCAT database is extensive but there are very few short-term recaptures. With a cutoff Δ of 50 days, there are only 5 measurement pairs. With the 98-day cutoff, there are 26 pairs and the estimated measurement error is 10.9 cm. However, the mean size of the tagged fish increased by about 2 cm while at liberty so some of the estimated measurement error might be due to unaccounted growth. With such a small sample size, this estimate is sensitive to outliers and the removal of a single datapoint reduces the estimated measurement error to 3.9 cm.

3.2. Growth Curves Fitted to Otolith Data

The nonlinear least squares estimates for models fitted to just otolith data are given in Table 4 along with non-parametric bootstrap estimates from 999 resampled datasets using the package 'nlstools' (Baty et al. 2015). Goodness of fit of the von Bertalanffy growth model can be judged from Figure 10. The otoliths for the six oldest fish, four from the PCL data and two from the PFL data, are above the fitted growth curve when age-1 and age-2 fish from the PFL data are included in the study (red line). A sensitivity analysis was conducted on the influence of age-1 and age-2 fish from the PFL dataset. Those age-1 and age-2 fish had larger lengths than other age-1 and age-2 fish, indicating a potential sampling bias. All of the age-1 and age-2 fish from the PFL data were removed from the analysis (n=41). Once these data points were removed the von Bertalanffy model was refit to the length-age pair data (Table 4, Figure 10). The removal of the large age-1 and age-2 fish caused the estimate of asymptotic length to increase, the estimate of the time-axis intercept to decrease, and the estimate of K to decrease. When the larger age-1 and age-2 fish are removed, five of the oldest fish fall above the line and one below (Figure 10, black line). Because the number of old fish in the dataset is limited, we fit the von Bertalanffy model while fixing the value of L_∞ (between 145 and 200) to provide plausible pairs of K and L_∞ for use in population models (see Table 1of Appendix 5).

Table 4. Parameter estimates from fitting von Bertalanffy models to the otolith data and also the von Bertalanffy results from the integrated model applied to the otolith and tagging data. Also shown are the parameter estimates when age-1 and age-2 fish were removed from the PFL otolith data for both models. The 95% Bootstrap confidence interval is given in parentheses for the parameter estimates from the otolith data only model. The standard deviation is given in parenthesis for the parameter estimates from the otolith and tagging data.

	Otolith Data only		**Integrated Model, Otolith data + Tagging**	
Parameter	**All otoliths**	**PFL age 1 and 2 otoliths removed**	**All otoliths and tagging data**	**PFL age 1 and 2 otoliths removed and tagging data**
K	0.464 (0.403, 0.543)	0.392 (0.355, 0.441)	0.271 (0.015)	0.252 (0.014)
L_∞	154.148 (147.081, 161.491)	161.206 (154.389, 166.835)	178.700 (5.906)	185.780 (6.298)
t_0	-0.163 (-0.250. -0.085)	-0.239 (-0.306, -0.175)	-0.537 (0.028)	-0.524 (0.025)

Figure 11a. Vector plot of the tagging data from AOTTP, Hallier et al. (2005) and ICCAT. The vector plot is made by computing the predicted age for the length at tagging using the estimated von Bertalanffy growth parameters, and then assuming the age at recapture is the predicted age at tagging plus the time at liberty. The von Bertalanffy curve is based on the growth model from the otolith data only without the data for age-1 and age-2 fish from the PFL dataset. The fastest growing 1% and the slowest growing 1% (in cm/wk) of the records have been eliminated from the AOTTP data. One obvious outlier is seen among the 18 records from ICCAT.

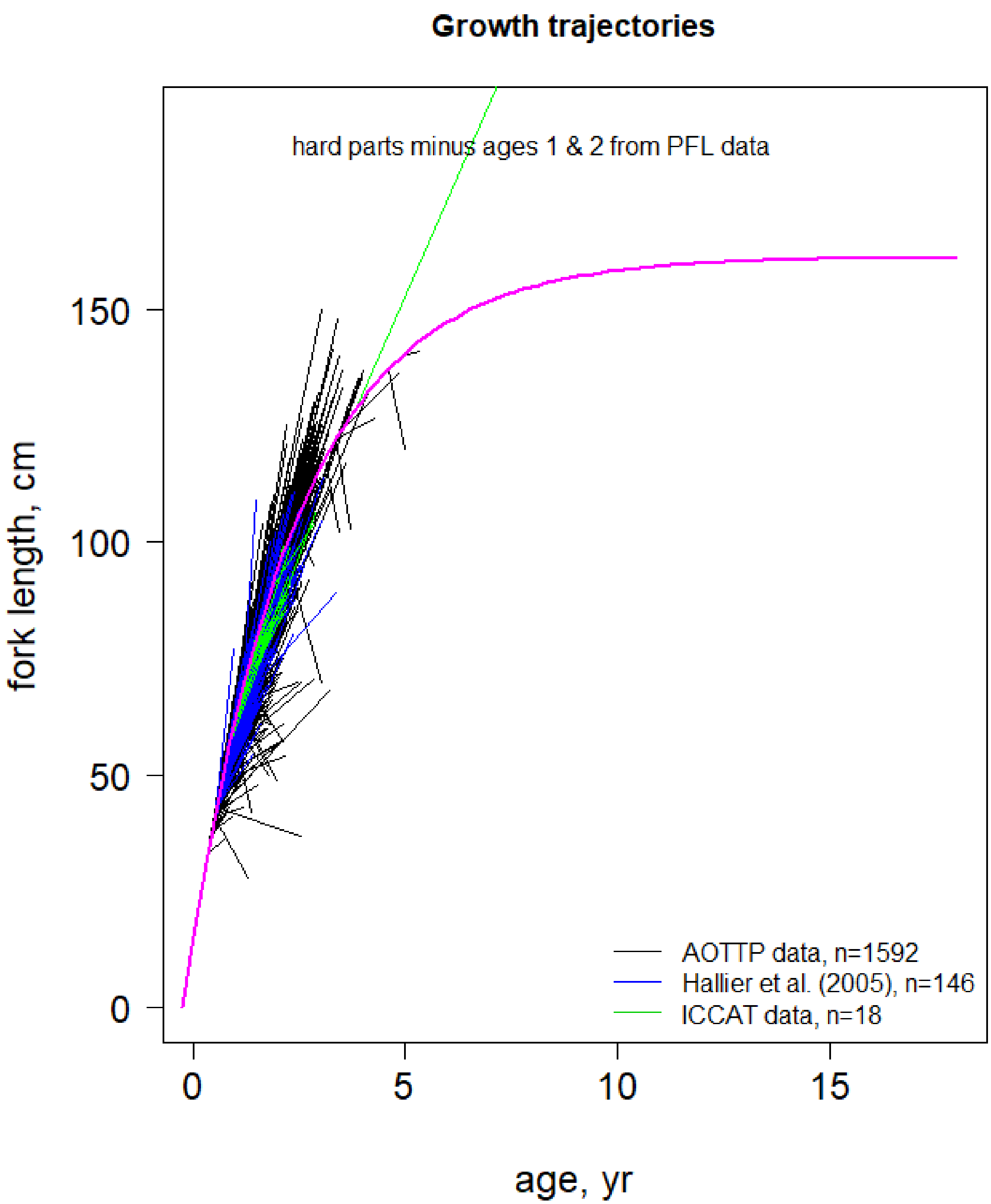
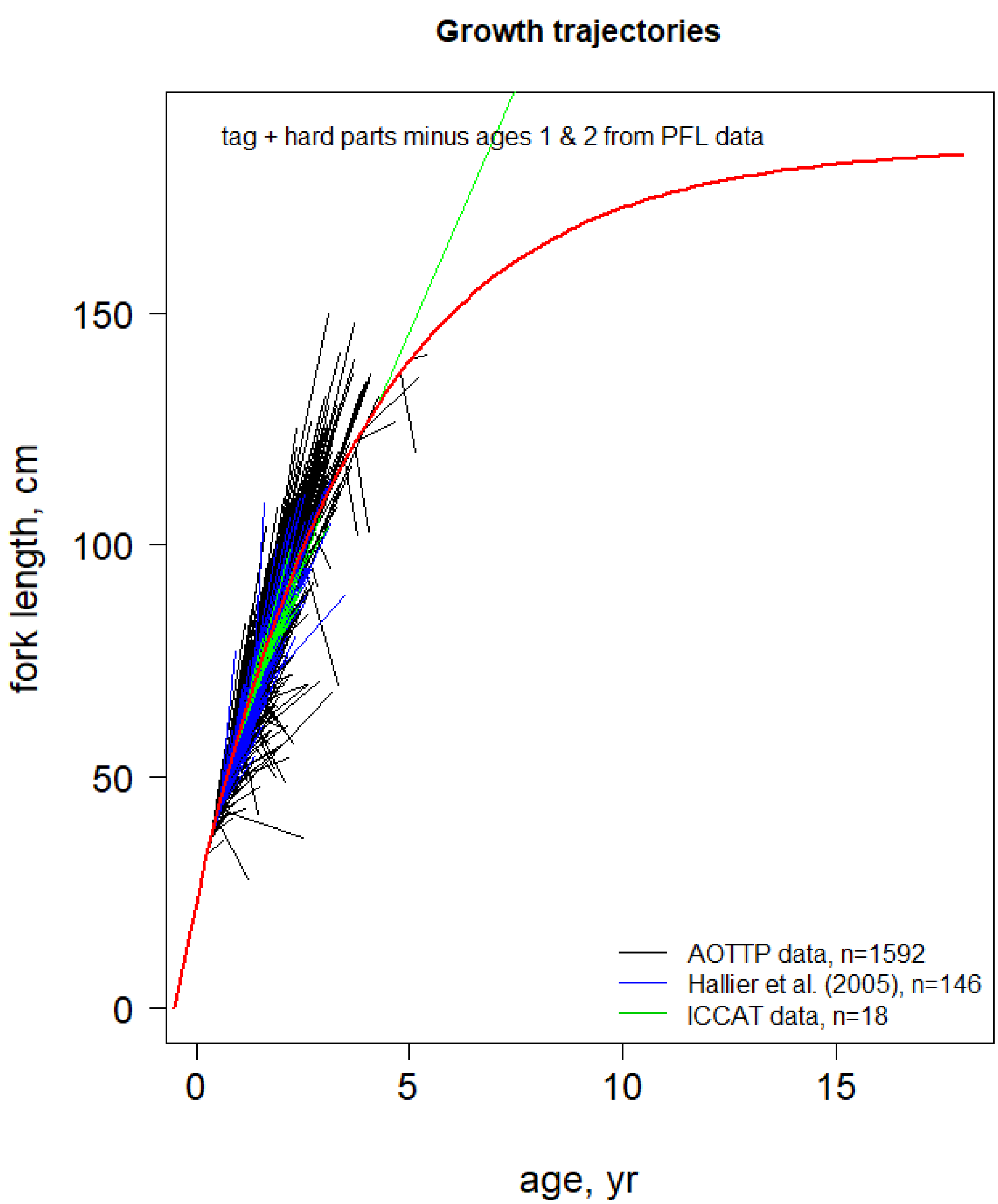


Figure 11b. Vector plot of the tagging data from AOTTP, Hallier et al. (2005) and ICCAT. The vector plot is made by computing the predicted age for the length at tagging using the estimated von Bertalanffy growth parameters, and then assuming the age at recapture is the predicted age at tagging plus the time at liberty. The von Bertalanffy curve is based on the integrated model applied to the data without age-1 and age-2 fish from the PFL otolith dataset. The fastest growing 1% and the slowest growing 1% (in cm/wk) of the records have been eliminated from the AOTTP tagging data. One obvious outlier is seen among the 18 records from ICCAT tagging data; this record was not used to fit the von Bertalanffy model.



3.3. Integrated Analysis Results

The dataset consists of 1,592 tag-recovery pairs from the AOTTP database, 18 tag-recovery pairs from ICCAT data, 146 tag-recovery pairs from Hallier dataset, 63 length-age pairs from AOTTP otoliths, 153 length-age pairs from otoliths from the Hallier dataset, 229 length-age pairs from PFL otoliths, and 12 length-age pairs from the PCL otoliths. Complete results with estimates for all of the parameters (fixed, estimated, and derived) can be found in (Table 1 of Appendix 3). The results from the Richards (Schnute with $p < 1$) and Von Bertalanffy (Schnute with $p = 1$) models were identical, and the Richards model estimated $p = 1.000$ (Table 1 of Appendix 3).

A sensitivity analysis was conducted on the influence of the 41 large age-1 and age-2 fish from the PFL dataset. The integrated model was fitted to the otolith data minus the 41 PFL fish (Table 4, Figure 10, and Table 2 of Appendix 3). The integrated models, with or without the deletion of PFL's age 1 and age 2 fish, had higher aymptotic sizes than the corresponding models based just on the otolith data. All six of the oldest fish were below the integrated model curves. Similar to the results from the otolith only data, the removal of the large age-1 and age-2 fish from the integrated model caused the estimate of asymptotic length to increase and the estimate of K to decrease. However, in the integrated model, the estimate of the time-axis intercept became less negative when the age-1 and age-2 PFL fish were removed (Table 4).

Goodness of fit of the von Bertalanffy growth model from the integrated analysis with PFL age-1 and age-2 fish removed can be observed in Figure 10 (green line) and Figure 11. The integrated model describes the growth of young bigeye well but the growth of older fish tends to be above the predicted line (Figure 11b). Otoliths for the six oldest fish, four from the PCL data and two from the PFL data, are below the fitted growth curves with and without the 1 and 2year olds from PFL's data (Figure 10). The vast majority of the data (nearly 100% of tagging and ~95% of length-age pairs) come from fish age-5 or younger.

The von Bertalanffy curve from just the otolith data (with age-1 and age-2 fish from PFL's otolith data removed) was plotted with the tagging data (Figure 11a). This model fits the fish tagged at an older age better than the integrated model, but overestimates the growth for fish tagged at a young age with short times at liberty.

4. Discussion

By utilizing data from both tagging studies and length-age pairs we were able to estimate several models for growth of bigeye tuna in the Atlantic Ocean. We incorporated multiple datasets to estimate a comprehensive growth model for the species.

The estimates of length measurement error in the AOTTP tagging data (roughly 7 cm) are similar to those found by Ailloud et al. (2014) for Bluefin tuna, i.e., roughly 5 cm. Measurement error in the tagging study of Hallier et al. (2005) was about 4.8 cm, slightly better than that in the AOTTP bigeye tuna data and the Bluefin tuna data. Unfortunately, the ICCAT tagging database for bigeye tuna contains very few short-term recaptures making it difficult to assess measurement error. Visual examination of the ICCAT tagging data (Figure 11) showed one obvious outlier and slightly slower growth than the tagging data of Hallier et al. (2005) and the ICCAT tagging data. There was no justification why these 17 records (after removal of the outlier) were invalid so they were retained in the analysis.

The integrated model runs yielded similar results between Richards and Von Bertalanffy when using the same datasets, i.e., the estimated value of the shape parameter p was close to or equal to the value of 1.0 at which the Schnute model reverts to a von Bertalanffy curve. The integrated model run using the von Bertalanffy model and all of the data (Table 4) estimates an L_∞ of 178.70 cm FL (SD 5.906) and K of 0.271 yr^{-1} (SD 0.015). The integrated model run removing PFL's age-1 and age-2 fish estimates an L_∞ of 185.78 cm FL (SD 6.298) and a $K$of 0.252 yr^{-1} (SD 0.014). These results are similar to those found in previous studies (Figure 1 of Appendix 1). It is worth noting that there was only one other integrated study completed for bigeye using tagging and otolith data (Hallier et al. 2005). The integrated results from that study yielded a larger estimate of L_∞ (217.28 cm FL) and a smaller estimated K (0.180 yr^{-1}). One explanation is that Hallier used daily ring readings for the otoliths beyond 1 year, a practice which has been shown to be unreliable for bigeye (Williams et al. 2013, Krusic-Golub and Ailloud n.d.). The Hallier study also used a much shorter time at liberty cutoff (14 days) versus the 98 days used here, had few old fish, and few long-term recaptures. Our results are more similar to the SS3 fits to the Hallier et al. 2005 data used by the 2018 ICCAT bigeye stock assessment (Anon. 2019) $L_\infty = 179.9$ and $K = 0.281$.

Of particular note is that we were able to extend the maximum age used in the analysis up to 17 years compared to the maximum age of approximately 9 years used by Hallier et al. (2005) to estimate the growth parameters currently used in the stock assessment and the maximum age of 8 found in the study by Delgado de Molina and Santana (1986). The importance of this is amplified by the lack of tag returns from either very large fish or fish at liberty for a very long time, i.e., from old fish.

Normally, it would be prudent to analyze different data sources independently to identify any conflicts among data sources. However, when fitting an asymptotic growth model, it is essential to have a wide contrast in the independent variable, age. It is impossible to judge the rate of curvature with change in age if age does not change (much) among observations. Lack of old animals in a growth study often leads to extremely high estimates of asymptotic size whereas lack of young animals can lead to very large, negative estimates of the t_0 parameter. In the case of bigeye tuna, the use of multiple datasets captured a broad size spectrum of the population but the use of just the tagging data resulted in very few large, old fish.

The study of Hallier et al. (2005) used otoliths and tagging data while the study of Delgado de Molina and Santana (1986) used growth rings in dorsal spines. The latter authors noted problems with remodeling of the central cavity of the spine which resulted in the loss of rings representing the first years of life. Given the current study utilized several datasets over more than two decades, contained the widest range of sizes, and included validated ages beyond those currently assumed by ICCAT, this new curve should represent the most realistic estimates of bigeye tuna growth in the Atlantic to date.

The new curve with tagging and otolith data is similar to the curve used in the last stock assessment but with a lower estimated asymptotic size (Figure 1). The six oldest fish in the study are below the estimated growth curve which suggests that the addition of additional old fish (> 7 yr, implying an effort to sample fish > 150 cm FL) to the analysis might bring the asymptotic size down and increase the growth coefficient *K* estimate.

Additional old fish should be collected (both from tagging and length-age data) in order to better estimate the model. The curve based on otolith data (without PFL's age 1 and age 2 fish) goes through the cloud of six old fish on the right. In the absence of adequate samples of old (large) fish, one can artificially assign greater weight to the existing samples of old fish to force the curve to go through the cloud of data points of old fish (e.g., Maunder et al. 2018). We estimated the growth parameters K and t_o with L_∞ held fixed at various values (Appendix 5). This shows that the asymptotic size is not well determined, with fits having L_∞ fixed anywhere between 155 and 170 cm FL having similar residual standard errors when age 1 and age 2 PFL fish are removed from the dataset.

All of the tagging data appear to be in some conflict with the otolith data (Figure 11a, 11b). When the vector plot is made with the curve fitted to just otolith data (Figure 11a), the young fish appear to grow slower than predicted by the growth curve as evidenced by the observation that there are more termini of the vectors to the right (below) the fitted line than to the left (above); fish recaptured at an older age (age > 2) tend to be to the left (above) the fitted line. This suggests a conflict between the tagging and otolith results. When the curve is fitted to tagging and otolith data, a different pattern appears in the vector plot (Figure 11b). Now, the vectors for fish tagged at age 0 and age 1 appear to be symmetric about the regression line, but the lack of fit for fish recaptured at age > 2 is worse than in Figure 11a.

It is not clear why the tagging and otolith data are in disagreement. We propose the model based on otolith data provides the most realistic estimates of bigeye tuna growth because it predicts the size of old fish through the fitted value of L_∞ and it avoids patterns in the residuals from the tagging data (Appendix 4). If tagged bigeye tuna with longer times at liberty are recaptured in the future it could resolve the apparent discrepancy between the tagging and otolith data. The inclusion of additional otoliths and tag returns from old fish would improve both models as the sample size for old fish remains limited.

Acknowledgements

We thank members of the AOTTP tag and recovery teams, including biological samplers, for doing the meticulous work of otolith extraction in recovered fish. We thank Captains Billy McIntyre of the F/V Shady Lady, Dan Mears Jr. of the F/V Monica, and their respective crew who were vital for longline sampling efforts and personal communications regarding fishery dynamics. Officials and participants in the Oak Bluffs Bluewater Classic, Mid-Atlantic Tuna, Ocean City Tuna, White Marlin Open, and Mid-Atlantic Billfish tournaments were also crucial for obtaining samples. Graduate students and lab technicians, Kelsey Moon, Isabelle See, Samantha Nadeau, and Brenda Rudnicky assisted with field and lab work for this project as well. Funding to support biological sampling of tunas, age estimation and radiocarbon analysis was provided by NOAA CRP # NA17NMF4540140 to Walt Golet in the School of Marine Sciences at the University of Maine. This work was also supported by the European Union (DCI-FOOD/2015/361-161). Additional financial support from ICCAT Contracting Parties and Cooperating non-Contracting Parties is gratefully acknowledged. Funding provided for L. Waterhouse and J. Hoenig by International Commission for the Conservation of Atlantic Tunas under fiscal identification number N4001546C. The anonymous reviewers and Beth Matta provided helpful comments.

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Appendices

Appendix 1

Appendix 1, Table 1. Estimates of growth parameters for bigeye tuna in the Atlantic Ocean. L_∞ and Length Range pertain to fork length in cm; K is in units of yr^{-1} and t_0 is in yr.

Growth Function	Linf	K	t_∞	Length Range	Method	Reference
VB	161.21	0.392	-0.239	29 – 175	Otoliths	This study
VB	185.78	0.252	-0.524	28 - 175	Otoliths, tagging	This study
Peterson's method	338.53	0.10497	-0.5425	58 - 140	Length Frequency (predorsal)	Champagnat & Pianet 1974
VB	199.77	0.1970	-0.71		Spines, males (n=245)	Delgado de Molina & Santana 1986
VB	214.54	0.1669	-0.77		Spines, females (n=239)	Delgado de Molina & Santana 1986
VB	206.14	0.1822	-0.74	50 - 180	Spines, both sexes (n=540)	Delgado de Molina & Santana 1986
VB	253.75	0.173	-0.15		Spines	Gaikov et al. 1980
VB	491.6	0.0135	3.808	40 - 180	Length Frequency	Weber 1980
VB	218.8	0.23	-0.20	56 - 190	Spines (n=77)	Draganik & Peiczarski 1984
VB	195.54	0.206		37 – 124	Tagging (n=625)	Hallier et al. 2005
VB (solved in excel)	207.43	0.202	-0.613	29 -190	Otoliths, daily (n=230)	Hallier et al. 2005
VB (FAO vonbit)	206.976	0.203	-0.616	29 -190	Otoliths, daily (n=230)	Hallier et al. 2005
Gompertz	179.13	0.4088	(A= 1.7268)	29 -190	Otoliths, daily (n=230)	Hallier et al. 2005
Richards	178.63	0.424	(b= -7.185, m= 2280.4)	29 -190	Otoliths, daily (n=230)	Hallier et al. 2005
VB	217.28	0.180	-0.709	37 – 124 & 29 -190	Tagging (n=625) & Otoliths, daily (n=230). Used in last stock assessment.	Hallier et al. 2005
VB	264.02	0.12	-0.68	44 – 179	Caudal vertebrae (n=175)	Alves et al. 2002
VB	285.3745	0.1127			Tagging (n=243)	Cayre and Diouf 1984
VB / Petersen's method	249.6	0.0124	-4.78		Length frequency	Marcille et al. 1978

Appendix 2

Appendix 2, Table 1. Modified from Table 1 in IOTC Secretariat 2006 *and* Scida et al. 2001. *Definition of length measurements used in conversions for tuna lengths (Table 2 of Appendix 2).*

Length	Type	Description
CFL	Curved fork length	
CKL	Cleithrum-Keel length	Projected straight distance between the point on the cleithrum that provides the shortest possible measurement to the anterior portion of the caudal keel. The cleithrum is the semicircular bony structure at the posterior edge of the gill opening.
EYF	Eye to fork	
FL	Fork Length	Projected straight distance from the tip of the upper jaw (snout) to the shortest caudal ray (fork)
FLT	Curved Fork Length	Projected curved-body distance from the tip of the upper jaw (snout) to the shortest caudal ray (fork).
LD1	Lower jaw to 1st dorsal	
LJF	Lower Jaw Fork Length	**Equivalent to fork length for tropical tuna species.
PFL	Pectoral-fork length	Projected straight distance between the most anterior insertion of the pectoral fin and the fork of the tail.
PFLT	Curved Pectoral-fork length	Projected curved-body distance between the most anterior insertion of the pectoral fin and the fork of the tail.
SFL	Straight fork length	**Equivalent to fork length for tropical tuna species.
SL	Snout (preorbital) length	
STD	Standard length	
TLE	Total length	
UNK	Unknown	

Appendix 2, Table 2. Length conversions used to convert between different length standards. Acronyms and definitions are given in Table 1 of Appendix 2.

L	a	b	R2	Standard Length (Y = a+b*L)	Area	Range (cm)	n	Ref
PFL	18.191	1.2129	0.8988	FL	Atl.	33-141	3174	1
CKL	-5.5109	0.6215	0.9255	FL	Atl.	29-110	570	1
PFLT	-2.287	1.4572	0.9564	FL	Atl.	44-110	59	1
PFLT	7.1818	1.3418	0.9733	FLT	Atl.	44-110	59	1
FLT	*0.9082*	*0.9676*	*0.9891*	*FL*	*Atl.*	*63-169*	*304*	*1*

Appendix 3.

Complete results from fitting the integrated model to all of the data (Table 1 Appendix 3) and to the data with age-1 and age-2 fish from PFL data removed (Table 2 Appendix 3).

Appendix 3, Table 1. Results from Richards and Von Bertalanffy models fitted to the full data set consisting of tagging data from AOTTP, ICCAT, and the Hallier et al. (2005) study plus hard part data from AOTTP, Hallier (only ages < 1 yr), PFL data, and PCL data. Symbols are defined in the main text. Note that p is fixed at 1.0 in the von Bertalanffy model and estimated to be 1.000 in the Richards model.

	Richards (Schnute with $\lvert p \rvert < 100$)		**Von Bertalanffy** (Schnute with $p = 1$)	
	Value	**S.E.**	**Value**	**S.E.**
Fixed parameters				
A_1	0	-	0	-
A_2	17	-	17	-
p	-	-	1	-
Estimated parameters				
L_1	24.364	0.765	24.364	0.765
L_2	178.910	5.560	178.910	5.560
K	0.266	0.015	0.266	0.015
p	1.00	8.867e-08	-	-
k_ρ	1.381	0.232	1.381	0.232
ρ_0	0.887	0.015	0.887	0.015
σ_{L_1}	2.220	0.387	2.220	0.387
σ_{L_2}	26.713	1.063	26.713	1.063
$\mu_{logAtag}$	-0.187	0.020	-0.187	0.020
$\sigma_{logAtag}$	-1.068	0.034	-1.068	0.034
Derived parameters				
L_∞	180.590	6.046	180.590	6.046
t_0	-	-	-0.544	0.028
t^*	-0.544	0.028	-	-
a^*	-1.641	0.500	-1.641	0.500
b^*	0.158	7.711e-03	0.158	7.711e-03
b	-1.000	7.679e-08	-	-
Negative log-likelihood	9238.97945		9238.97945	

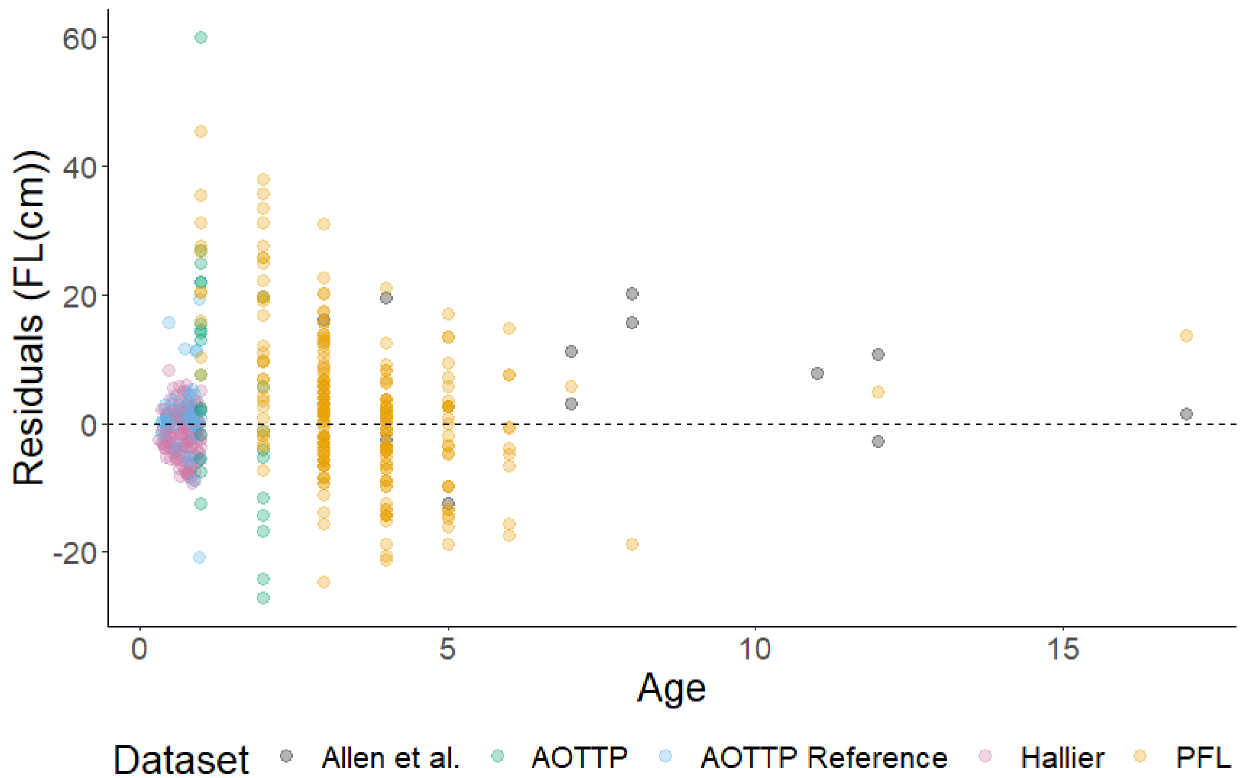
Appendix 3, Table 2. Results from Richards and Von Bertalanffy models fitted to the full data set consisting of tagging data from AOTTP, ICCAT, and the Hallier et al. (2005) study plus hard part data from AOTTP, Hallier (only ages < 1 yr), PFL data, and PCL data. Symbols are defined in the main text. The age-1 and age-2 fish have been removed from PFL (n=41) to avoid *probable sampling bias. Note that p is fixed at 1.0 in the von Bertalanffy model and estimated to be 1.000 in the Richards model.*

	Richards (Schnute with $\|p\| < 100$)		**Von Bertalanffy** (Schnute with $p = 1$)	
	Value	**S.E.**	**Value**	**S.E.**
Fixed parameters				
A_1	0	-	0	-
A_2	17	-	17	-
p	-	-	1	-
Estimated parameters				
L_1	23.127	0.642	23.127	0.642
L_2	185.450	5.790	185.450	5.790
K	0.247	0.014	0.247	0.014
p	1.000	1.317e-07	-	-
k_ρ	1.434	0.253	1.434	0.253
ρ_0	0.864	0.019	0.864	0.019
σ_{L_1}	1.571	0.322	1.571	0.322
σ_{L_2}	26.297	1.074	26.297	1.074
$\mu_{logAtag}$	-0.132	0.017	-0.132	0.017
$\sigma_{logAtag}$	-1.076	0.031	-1.076	0.031
Derived parameters				
L_∞	187.900	6.455	187.900	6.455
t_0	-	-	-0.531	0.025
t^*	-0.531	0.025	-	-
a^*	-1.952	0.429	-1.952	0.429
b^*	0.152	7.055e-03	0.152	7.055e-03
b	-1.000	1.178e-07	-	-
Negative log-likelihood	9014.8878		9014.8878	

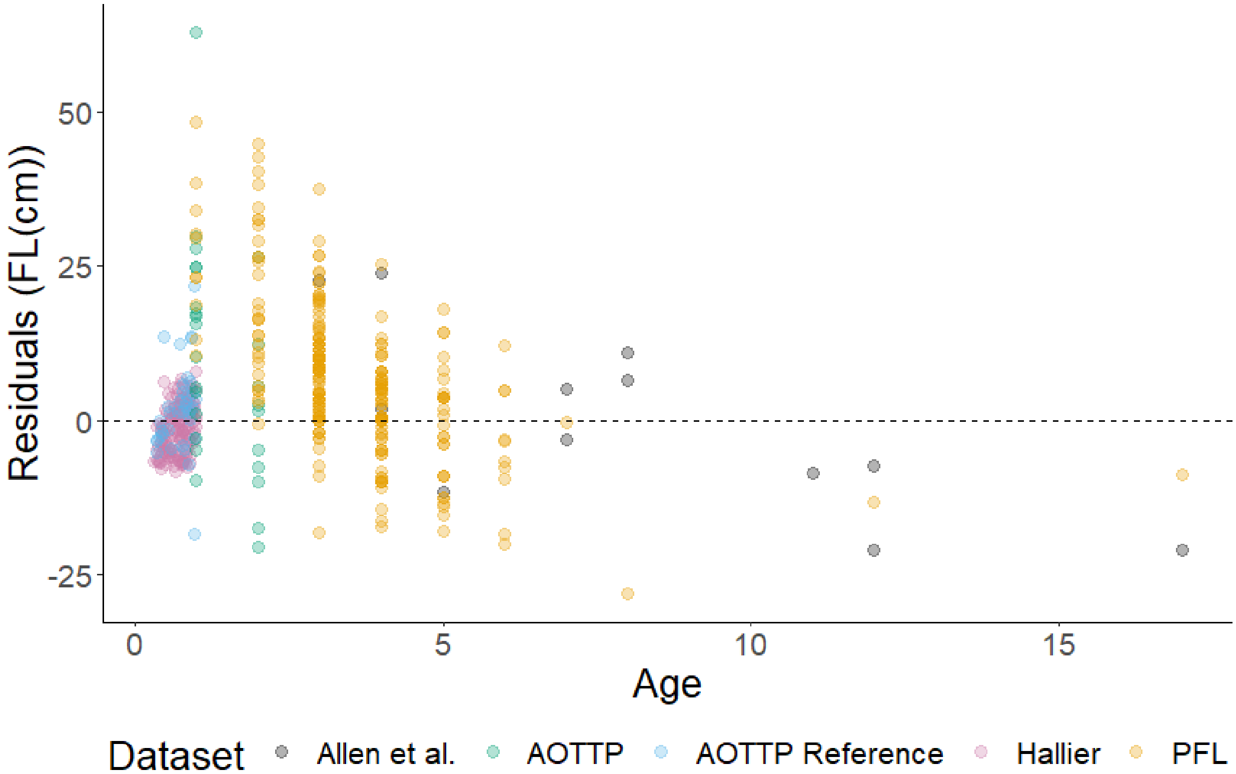
Appendix 4.

Residual plots from the preferred model (length-age pair data only) and the best fitting integrated model. For the preferred model (length-age pair data only), the asymptotic length L_∞ (fork length) equals 161.21 cm (95% bootstrap CI 154.39, 166.84), growth parameter K equals 0.392 yr^{-1} (95% bootstrap CI 0.355, 0.441), and the time-axis intercept t_0 equals -0.239 yr (95% bootstrap CI –0.306, -0.175). For the best fitting integrated model, the asymptotic length L_∞(fork length, in cm) was estimated to be 185.78 (SD 6.298), the growth parameter K was 0.252 yr^{-1} (SD 0.014), and the time-axis intercept t_0 was -0.524 yr (SE 0.025).

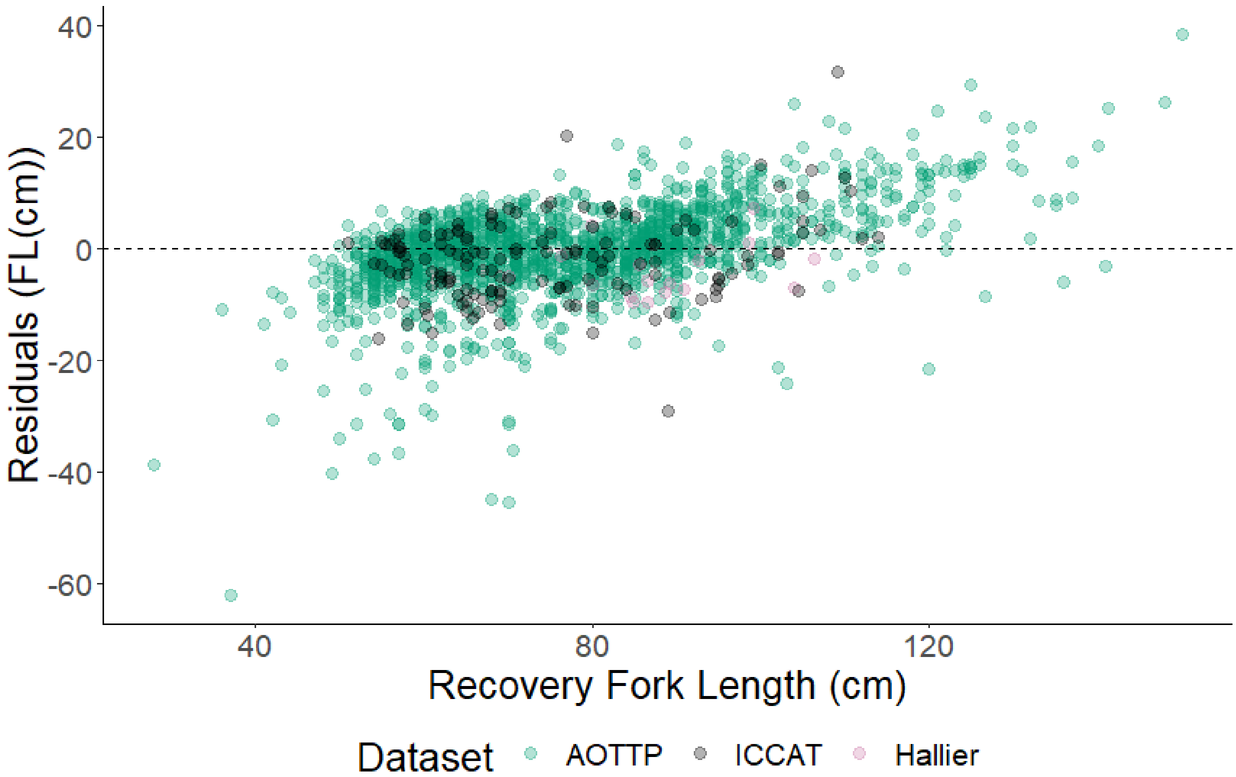
Appendix 4, Figure 1. *Residual plot by age from the preferred model (length-age pair data only).*



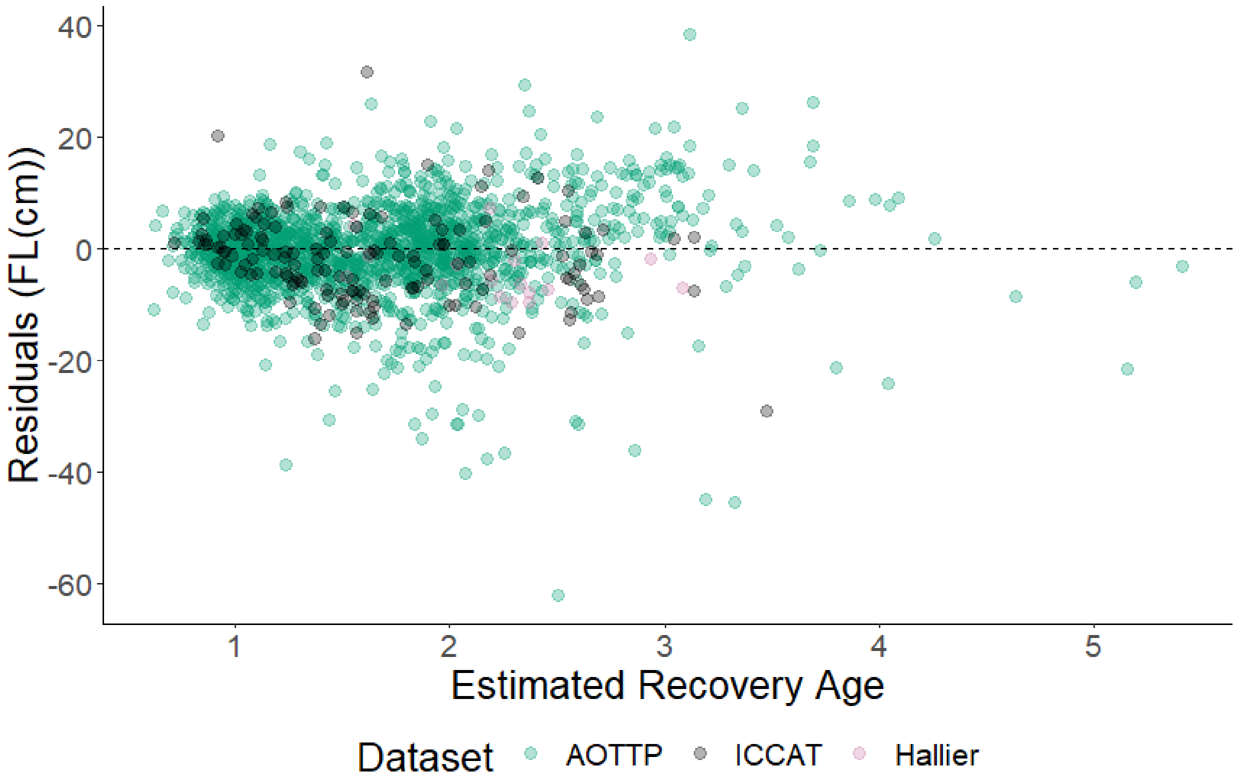
Appendix 4, Figure 2. *Residual plot by age from the integrated model for the length-age pair data only.*



Appendix 4, Figure 3. *Residual plot by recovery fork length (cm) from the integrated model for the tagging data only. A release age was calculated using the parameter estimates and the release fork length (cm). The recovery age was calculated by adding time at liberty to the calculated release age.*



Appendix 4, Figure 4. *Residual plot by estimated recovery age from the integrated model for the tagging data only. A release age was calculated using the parameter estimates and the release fork length (cm). The recovery age was calculated by adding time at liberty to the calculated release age.*



Appendix 5.

Parameter estimates for the von Bertalanffy growth model (length-age pair data only) were computed when the value of the asymptotic length L_∞ (fork length) was fixed. When the model is fit without setting a value for asymptotic length L_∞ and with PFL age 1 and 2 otoliths removed (Table 4), the asymptotic length L_∞ (fork length) equals 161.21 cm (95% bootstrap CI 154.39, 166.84), growth parameter K equals 0.392 yr^{-1} (95% bootstrap CI 0.355, 0.441), and the time-axis intercept t_0 equals -0.239 yr (95% bootstrap CI –0.306, -0.175). From Figure 10 the values of the asymptotic length L_∞ (fork length) that would best fit the oldest fish would be between 165 and 175, and this would result in a value of growth parameter K between 0.368 and 0.316 (when PFL age 1 and 2 otoliths are removed) or 0.380 to 0.325 (when all otoliths are included).

Appendix 5, Table 1. *Parameter estimates from fitting von Bertalanffy models to the otolith data when fixing the value of asymptotic length L_∞ (fork length). This was done with otolith data when the age-1 and age-2 fish were removed from the PFL otolith data and with all otolith data. Estimated values for growth parameter K and time-axis intercept t_0 and the residual standard error have been rounded to three decimal places.*

Set Value	PFL age 1 and 2 otoliths removed			All otoliths		
	Estimated Value		Residual	Estimated Value		Residual
L_∞	K	t_0	Standard Error	K	t_0	Standard Error
145	0.540	-0.078	9.292	0.564	-0.064	10.344
150	0.484	-0.130	8.987	0.505	-0.118	10.202
155	0.439	-0.180	8.817	0.456	-0.172	10.170
160	0.400	-0.228	8.752	0.415	-0.224	10.218
165	0.368	-0.274	8.769	0.380	-0.275	10.324
170	0.340	-0.319	8.850	0.351	-0.324	10.472
175	0.316	-0.362	8.980	0.325	-0.371	10.650
180	0.294	-0.403	9.147	0.302	-0.417	10.849
185	0.276	-0.443	9.341	0.283	-0.461	11.063
190	0.259	-0.481	9.555	0.265	-0.504	11.286
195	0.244	-0.519	9.782	0.249	-0.546	11.514
200	0.231	-0.555	10.018	0.235	-0.586	11.744

Appendix 5, Figure 1. *Estimated value of von Bertalanffy growth parameter K, and residual standard error, when the curve is fit to the data without the PFL age 1 and age 2 fish and with the value of* L_∞ *fixed.*