

ARTICLE

Age and Growth of Yellowfin Tuna in the U.S. Gulf of Mexico and Western Atlantic

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Abstract

Age, growth, and mortality were estimated for Yellowfin Tuna *Thunnus albacares* from the U.S. Gulf of Mexico and western Atlantic Ocean. During 2004–2017, 3,443 Yellowfin Tuna were sampled, primarily from recreational landings off the coast of Louisiana (90%). Based on reading otoliths, ages ranged from 1 to 18 years, with younger fish (<4 years) representing the majority (78%) of the age-classes. Otolith weight was allometrically related to fish

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Received November 20, 2020; accepted April 20, 2021

age ($r^2 = 0.91$), which suggests that it may be a useful tool in indirectly estimating age given the challenges associated with directly aging tropical tunas. Based on Akaike's information criterion (AIC), the Richards growth model had the most parsimonious fit to the length-at-age data (average maximum length $L_\infty = 1,658$ mm, growth coefficient $k = 0.23 \text{ year}^{-1}$, $a = 1.04$, $b = 0.45$) compared to the von Bertalanffy growth model ($L_\infty = 1,589$ mm, $k = 0.36 \text{ year}^{-1}$, theoretical age at zero length $t_0 = -0.8$ year; AIC difference = 26.21), which had a relatively poor fit. The size-modified Richards model, which assumed a truncated error structure at the minimum size limit (686 mm curved fork length [CFL]) in fishery-dependent collections, improved the fit in the smallest individuals and was therefore the preferred model. Males and females had similar maximum ages (18 and 17 years, respectively) but showed significant differences in growth, with males reaching a larger L_∞ than females (size-modified Richards: 1,706 versus 1,568 mm CFL, respectively). Baseline natural mortality (M) using a maximum age of 18 years was 0.346 and was then scaled across age-classes. These growth and mortality estimates and the individual age data have been used in improving stock assessments for Yellowfin Tuna to support scientific management.

Yellowfin Tuna *Thunnus albacares* support some of the most profitable exploited fisheries worldwide (Campling 2012; Pecoraro et al. 2017). Average global landings of Yellowfin Tuna were 1.25 million metric tons/year in the last decade, making it the second most important tuna species in fisheries worldwide (Pecoraro et al. 2017). In the U.S. Gulf of Mexico (GOM), reported commercial landings from 1951 to 2017 reached a peak in 1988 at 7,781 metric tons but have since steadily declined to 595 metric tons in 2017 (NOAA Fisheries 2021). The recreational fishery in the GOM is also an important contributor to the total catch of Yellowfin Tuna in the region: catches have averaged around 380 metric tons/year since 2000 (ICCAT 2021), with a substantial contribution coming from waters covered by the Louisiana Recreational Creel Survey (LDWF 2021). A productive recreational fishery for Yellowfin Tuna exists off the coast of Louisiana near the mouth of the Mississippi River (Brown-Peterson et al. 2014; Lang et al. 2017). Landings from this area are often associated with oil platforms that act as fish aggregating devices (FADs; Edwards and Sulak 2006).

The International Commission for the Conservation of Atlantic Tunas (ICCAT) is responsible for assessing Atlantic Yellowfin Tuna, and the recent stock assessment indicated that the stock was not overfished but the current fishing mortality was near the overfishing threshold (ICCAT 2019b). Life history parameters, such as growth and mortality, are used in Yellowfin Tuna ICCAT stock assessment models to estimate maximum sustainable yield and the overall health of the stock relative to agreed biological reference points (ICCAT 2017, 2019b). Natural mortality (M) is often the most influential stock assessment parameter because it reflects much of the stock's overall productivity and, hence, its resilience to fishing (Then et al. 2015; Pecoraro et al. 2017). Often lacking empirical estimates of M , proxies based on maximum age in an unfished condition are used (Hoenig 1983; Then et al. 2015).

Despite various studies over the last 50 years, the reliability in determining the age and growth of Yellowfin Tuna has been debated (Wild 1986; Fonteneau and

Chassot 2013; ICCAT 2017, 2019a). A variety of approaches have been investigated to describe Yellowfin Tuna growth throughout their geographic range, including length frequency analysis (Le Guen and Sakagawa 1973), analysis of tag-recapture (Ortiz 2017), and direct aging from hard parts, including spines (annual age; Draganik and Pelczarski 1984; Lessa and Duarte-Neto 2004) and otoliths (daily or annual age; Wild 1986; Stequert et al. 1996; Driggers et al. 1999; Shuford et al. 2007; Shih et al. 2014; Lang et al. 2017; Farley et al. 2019, 2020). However, these methods present different challenges and potential sources of bias. Length frequency analysis is a potentially unreliable method in older age-classes due to an increase in overlapping length distributions (Everhart and Youngs 1992). Using length frequency analysis in a migratory tropical species like the Yellowfin Tuna is cautioned because individuals within the same age-class develop under varying environmental conditions, likely leading to differences in somatic growth (Driggers et al. 1999; Farley et al. 2006). Age estimates obtained from counting daily increments in otoliths are only considered a reliable aging method for larvae or fast-growing species (Brothers et al. 1976). In tunas, daily aging is generally restricted to juveniles. Williams et al. (2013) found that daily aging consistently underestimated the age of fish older than 1 year. Similarly, ages obtained from annulus counts in sectioned spines are only reliable for juveniles due to the reabsorption of spine annuli that also leads to underestimated ages of older individuals (Lessa and Duarte-Neto 2004). Reading otoliths from some tropical and subtropical species can also be challenging because of the limited seasonal variation in water temperature, resulting in less distinct annuli compared to temperate species that inhabit geographic locations with broader temperature ranges (Green et al. 2009; Sardenne et al. 2015). Less distinct annuli can cause errors in age assignment, including underestimation of individual age due to missing increments, falsely counting increments that are not true annuli (i.e., false checks), and misidentifying an increment on the otolith edge (Green et al. 2009). However, there have been

several studies estimating the growth of tuna species, such as South Pacific Albacore *T. alalunga* (Farley et al. 2013), Bigeye Tuna *T. obesus* (Farley et al. 2006; Schaefer and Fuller 2006), Pacific Bluefin Tuna *T. orientalis* (Ishihara et al. 2017), and western Atlantic Bluefin Tuna *T. thynnus* (Neilson and Campana 2008), using validated otolith-based annual aging methods. Additionally, the annual age-reading criterion currently used for Yellowfin and Bigeye tunas in the GOM was recently validated using ^{14}C bomb radiocarbon techniques (Andrews et al. 2020) and is recognized by ICCAT as an acceptable aging method (ICCAT 2019a, 2019b).

Using otolith morphometrics (i.e., otolith weight, width, and depth) to predict age has a reportedly high success rate (explaining at least 70% of the variation in age) in both temperate and tropical fish species (Lou et al. 2005; Williams et al. 2015). Preparing and reading otoliths for aging in tunas are time consuming, expensive, and require extensive training (Williams et al. 2015). Due to these difficulties, the relationship between otolith morphometrics relating to fish age and length may be a useful and cost-effective tool in predicting age (Lou et al. 2005; Williams et al. 2015). In particular, these relationships are worth exploring in younger fish due to the challenges associated with distinguishing the first few annuli (Pawson 1990). The use of otolith morphometrics as a tool to predict age has been explored in several tropical tuna species, including the Yellowfin Tuna (Driggers et al. 1999; Farley et al. 2020), the Southern Bluefin Tuna *T. maccoyii* (Gunn et al. 2008), and the closest relative of Yellowfin Tuna, the Longtail Tuna *T. tonggol* (Griffiths et al. 2010).

The von Bertalanffy growth model (VBGM) is often used to model length at age for Yellowfin Tuna (Stequert et al. 1996; Driggers et al. 1999; Shuford et al. 2007; Shih et al. 2014; Lang et al. 2017; Farley et al. 2020). However, the appropriateness of this growth model has been debated for Yellowfin Tuna due to overestimation of the VBGM parameters, including the growth coefficient (k) and the average maximum (asymptotic) length (L_∞), and failure to allow for more complex growth dynamics, such as multiple growth stanzas (Fonteneau and Chassot 2013; Murua et al. 2017). Those questionable parameters may be attributed to a myriad of factors, including sampling limitations, biases associated with various aging methodologies, and reader error associated with hard-part aging (Kolody et al. 2016).

For decades, ICCAT has used a two-stanza growth relationship from Gascuel et al. (1992) in stock assessments for Yellowfin Tuna, which assumes a growth slowdown between 350 and 650 mm curved fork length (CFL), followed by rapid growth (>650 mm CFL) based on the VBGM (Shuford et al. 2007; ICCAT 2017). However, the appropriateness of two-stanza growth for Yellowfin Tuna continues to be debated (Shuford et al. 2007; ICCAT

2012, 2019a, 2019b; Ortiz 2017). The Gascuel et al. (1992) growth relationship is derived using length frequency modal progression analysis and, hence, requires strong assumptions that fish have episodic birth events and similar growth trajectories, allowing for clear separation of growth models.

Since annual aging from otoliths of fish older than age 1 is considered the most accurate method for tropical tuna species (Williams et al. 2013; Farley et al. 2019) and has been recently validated for Yellowfin Tuna in the GOM (Andrews et al. 2020), there was a need to undertake a comprehensive aging study to improve the growth information for Yellowfin Tuna stock assessments. The goals of this study were to derive ages using annual growth increments in otoliths, to determine both pooled sex and sex-specific growth model parameters using a multi-model approach, to investigate otolith weight as a tool to predict age, and to estimate mortality of Yellowfin Tuna in the U.S. GOM and western Atlantic Ocean.

METHODS

Study site.—Sagittal otoliths were sampled from a total of 3,443 Yellowfin Tuna from 2004 to 2017 in the U.S. GOM ($n=3,232$) and the western Atlantic Ocean ($n=211$) from fishery-dependent (~99%) and fishery-independent sources (<1%; Figure 1). Most samples were collected from the GOM recreational fishery (90.2%) by Louisiana Department of Wildlife and Fisheries and National Marine Fisheries Service (NMFS) port samplers, with Atlantic recreational samples collected by Quantech, Inc., and by the NMFS Trip Interview Program. Recreational anglers in the U.S. GOM primarily reported fishing between 9.26 and 111.12 km (between 5 and 60 nautical miles) off the mouth of the Mississippi River. In the western Atlantic, recreational catches were most frequent in the U.S. mid-Atlantic region extending as far north as Massachusetts. Samples were also obtained by at-sea personnel aboard commercial vessels from the NMFS Pelagic Observer Program (5.31%) fishing from the West Florida Shelf to the central GOM and the NMFS Shark Bottom Longline Observer Program (<1%), which sampled in the U.S. South Atlantic. Among samples collected from a fishery-dependent source, 3.05% had an unknown fishing mode. Recorded gear types from fishery-dependent sources included rod and reel (RR; 93%) and pelagic longline (PLL; 7%); RR was the only gear type recorded by the recreational sector. Fishery-independent samples were collected from Yellowfin Tuna captured on PLLs deployed by personnel aboard the National Oceanic and Atmospheric Administration's (NOAA) RV *Oregon II* that sampled in the north-central U.S. GOM (1.4%). Analysis of variance was used to determine whether there were significant differences in length

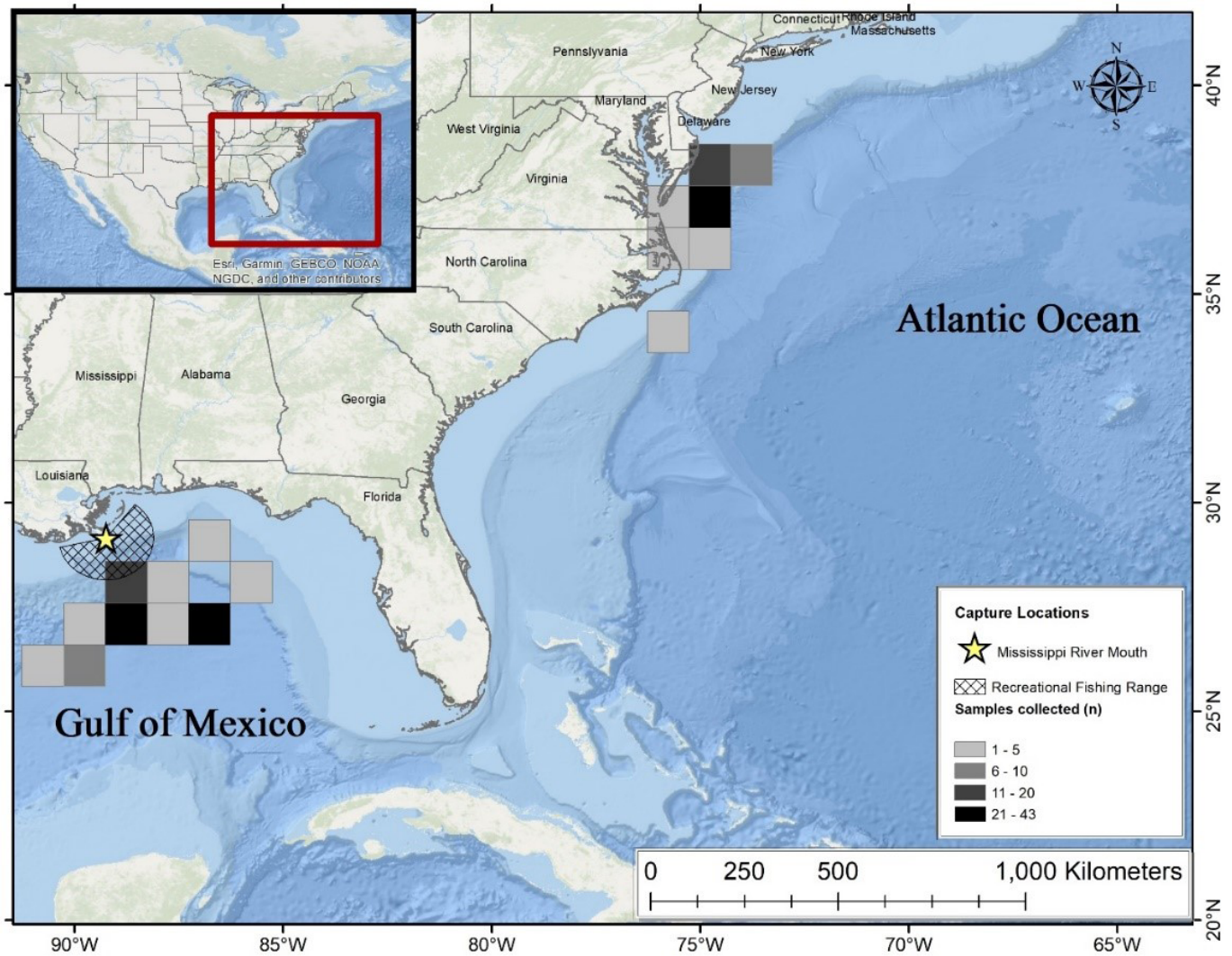


FIGURE 1. Yellowfin Tuna sampling areas in the U.S. Gulf of Mexico (GOM) and western Atlantic Ocean. Catch coordinates for the recreational and commercial sectors are denoted by the number of samples collected per 1° grid block. Recreational anglers in the U.S. GOM reported fishing between 9.26 and 111.12 km (between 5 and 60 nautical miles) off the Mississippi River mouth (yellow star), denoted by the checkered half-circle.

at age between the U.S. GOM and western Atlantic for the most common age-classes.

Biological sampling followed protocols given in the ICCAT Manual (ICCAT 2006–2016:chapter 4) and the Trip Interview Program user's guide (Saari and Beerkircher 2014). Straight fork length (SFL) was converted to CFL using the formula from Scida et al. (2001) for Yellowfin Tuna in the western north Atlantic: $CFL (mm) = (SFL - 8)/0.96$. This conversion was performed because CFL is the preferred length used by ICCAT.

Otolith preparation.—Yellowfin Tuna sagittal otoliths were rinsed with distilled water and stored dry. Otoliths were processed for aging following the methodology of Secor et al. (1991, 2014). Both the left and right otoliths were weighed if whole to the nearest 0.001 g. The left

otolith was processed for aging, but the right otolith was used if the left was unavailable. Each otolith was embedded in epoxy and was mounted in the arm of a low-speed saw with the sectioning plane encompassing the core positioned between two 102-mm (4-in), diamond-encrusted blades with a 0.5-mm spacer to produce a single transverse cut. Otolith sections were mounted with the post-rostrum side up using a thermoplastic adhesive on a glass slide. A liquid cover slip was applied over the section to fill in any grooves left by the saw blade and thereby improve the visibility of the annuli.

Age assignment.—The Yellowfin Tuna aging protocol followed the established criteria used for Atlantic Bluefin Tuna (Busawon et al. 2015). An annulus was identified as successive opaque and translucent zones under transmitted

light, and age was determined by counting the opaque zones. The ventral arm of the sectioned otolith was used for aging because the annuli were generally clearer and more widely spaced than those on the dorsal arm (Secor et al. 2014). The identification of the first annulus in tuna species is often challenging. To help verify the location of the first annulus in Yellowfin Tuna, daily increments were counted in juvenile otoliths ($n = 4$; Lang et al. 2017; Allman et al. 2020). The first annulus was evident around the 270th daily increment, which on average was 1 mm (4.5% critical value) from the core to the proximal edge of the first opaque zone (Lang et al. 2017). This distance was measured for each otolith using image analysis software and was used as a guide for identifying the first annulus.

Aging precision was estimated among readers by using the index of average percent error (APE; Beamish and Fournier 1981; Campana 2001). Before final ages were determined, each age reader completed a Yellowfin Tuna aging reference set ($n = 100$) to ensure standardization and precision of aging (Pacicco 2020). A reader was considered qualified to age when an APE of less than 10% was reached between the reader's ages and a consensus set of reference ages.

Each otolith section was read twice by each reader (independent of the first read) with at least 2 weeks between each reading and without knowledge of the fish length or capture date. If the first and second reads differed, a third read was conducted to determine the final age. During the third read, the first two age readings were made available to aid in determining a final age (Busawon et al. 2015). A readability code was assigned to each otolith on a scale of 1 to 4, with a score of 1 showing the least confidence in the age assignment and a score of 4 indicating high confidence (Busawon et al. 2015).

One of three otolith edge codes was assigned following Allman and Goetz (2009): opaque margin, narrow translucent margin (up to one-third complete), and wide translucent margin (over one-third complete). An opaque zone was counted on the otolith edge only if complete. To assign fish to a year-class, a calendar age was calculated (Vanderkooy and Guindon-Tisdell 2003). Opaque zone counts were advanced by 1 year if a wide translucent margin was assigned to a Yellowfin Tuna captured from January 1 to July 31. Otherwise, calendar age equaled the opaque zone count. Calendar ages were converted to decimal ages for use in growth curves. A biological birthdate of July 1 was assigned, which corresponded to the midpoint of the peak spawning season in the GOM (Brown-Peterson et al. 2014). The proportion of the year between the capture and birthdate of a fish was calculated using the equation

$$\text{Proportion of year} = \left| \frac{\text{capture date} - \text{July 1}}{365} \right|.$$

To determine a decimal age, the proportion of the year was added to the calendar age if the capture date was after July 1 or subtracted if before (Allman et al. 2020; Pacicco 2020).

Otolith weight.—Otolith weight was plotted as a function of decimal age using a linearized power function,

$$\ln(\text{Age}) = \ln(a) + b \cdot \ln(\text{OtoWt}),$$

where Age = predicted age (year), OtoWt = otolith weight (g), a = the scaling coefficient, and b = the allometric scaling exponent. Analysis of covariance was used to determine whether there were significant differences in otolith weight versus age by sex. Simple linear regression was also run to predict $\ln(\text{Age})$ from $\ln(\text{CFL})$, followed by a multiple linear regression predicting $\ln(\text{Age})$ using $\ln(\text{CFL})$ and $\ln(\text{OtoWt})$ as covariates to determine which model explained the most variance for all observations. Since most otolith weights were from a few age-classes, inverse-sample-size weighting (Beckman et al. 1990) was applied to provide a better fit to the low sample sizes for very young fish and older fish. The significance threshold was set at $P < 0.05$ for all statistical tests.

Growth models.—Most of the fish sampled for this study were above the minimum size limit of 686 mm CFL (27 in). In the absence of age-length data for smaller/younger Yellowfin Tuna (i.e., especially age 0) from the U.S. GOM, daily ages from juvenile Yellowfin Tuna (0.4–1.2 years) collected in the Gulf of Guinea on the west coast of Africa were supplied from the Shuford et al. (2007) study ($n = 23$) and by Fish Ageing Services ($n = 14$; www.fishageingservices.com) to help anchor the growth curves. These juveniles ranged from 304 to 721 mm CFL and were primarily captured by purse seine. Sex for these fish was not recorded.

The VBGM and the Richards model (Richards 1959) were fitted to the size-at-age data for Yellowfin Tuna ($n = 3,480$) by using nonlinear least-squares regression. Standardized residuals were plotted to check for normality and homoscedasticity in conjunction with observing each overall model fit. Growth model parameters were computed using R version 3.5.0 (R Core Team 2018) with the add-on package Fisheries Stock Analysis (Ogle et al. 2018).

The VBGM followed the typical parameterization (von Bertalanffy 1938),

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)} \right],$$

where L_t = the predicted average CFL (mm) at age t , L_∞ = the average maximum (asymptotic) CFL, k = the growth coefficient (year^{-1}), and t_0 = the theoretical age (years) when the fish had a length of zero. The Richards (1959) model followed the parameterization described by Tjorve and Tjorve (2010),

$$L_t = L_\infty \left[1 - ae^{(-kt)} \right]^b,$$

where k = the growth coefficient (the slope at the inflection point), a = a dimensionless parameter that controls the horizontal inflection point position (i.e., age), and b = a dimensionless parameter that controls the vertical inflection point position (i.e., size).

Akaike's information criterion (AIC; Akaike 1973) was used to test the fit of the candidate models to determine the most appropriate growth model for all observations and was calculated using the AICcmodavg package in R (R Core Team 2018; Mazerolle 2019).

Size-modified growth.—Additional growth models in which the assumed error structure was truncated at the minimum size limit (686 mm [27 in]) were run for the Richards model and VBGM following the methodology of Diaz et al. (2004). These models (hereafter referred to as size-modified models) accounted for potential bias when estimating mean length at age due to the presence of a minimum size limit in fishery-dependent collections (McGarvey and Fowler 2002; Diaz et al. 2004). The daily aged juvenile Yellowfin Tuna were included in these models to aid in predicting growth of individuals at sizes that were not collected by fishery-dependent sampling (Lombardi et al. 2013). Size-modified growth models were fitted to the length-at-age data by minimizing the least squares using the Solver tool in Microsoft Excel.

Sex-specific growth.—The VBGM and the Richards model were each fitted to length-at-age data individually for males ($n = 1,637$) and females ($n = 1,685$) to investigate sexually dimorphic growth, where the assumed error structure was truncated at the minimum size limit. The daily aged juveniles ($n = 37$) were included in each respective size-modified, sex-specific growth model to help anchor the growth curves. A likelihood ratio test was used to test for significant sex-specific differences in growth (Kimura 1980; Haddon 2001). Using a one-way ANOVA, differences in mean lengths at age between males and females were investigated for each age-class with at least 25 samples/sex.

Mortality.—Instantaneous total mortality rates (Z) were calculated using cross-sectional catch curves (i.e., assuming constant recruitment; Ricker 1975) for males, females, and all fish pooled that were captured by RR. The slope (Z) of each catch curve was determined by regressing the natural logarithm of the number of Yellowfin Tuna in each age-class (beginning with the first age that was fully recruited to the gear) as a function of calendar age. Age-classes with fewer than five observations were not included in the catch curve or in the estimation of Z (Chapman and Robson 1960). An ANCOVA was used to determine whether there were significant differences in Z between the sexes.

Baseline M was estimated using the equation from Then et al. (2015),

$$M = 4.899t_{max}^{-0.916},$$

where t_{max} = the maximum observed age-class. Since it is biologically unrealistic for M to be constant throughout a fish's life, baseline M was also scaled across age-classes by using the parameters from the VBGM and following the methodology of Lorenzen (2005). The corresponding sex-specific VBGM parameters were used when Lorenzen- M was scaled for male and female age-classes. This method for estimating M was chosen because it is the accepted method used by ICCAT and the results can be easily compared (ICCAT 2017, 2019b).

RESULTS

Sample Collection

Size distribution of individual Yellowfin Tuna (male, female, and unknown sex) from the U.S. GOM ($n = 3,232$) ranged from 628 to 1,981 mm CFL, and the size of individuals from the western Atlantic ($n = 211$) ranged from 609 to 1,481 mm CFL. Yellowfin Tuna below the current minimum size limit (686 mm CFL [27 in]) were rarely observed ($n = 23$) because the majority of samples were collected from fishery-dependent sources (99%). A χ^2 goodness-of-fit test showed that males ($n = 1,600$) were in significantly greater abundance than females in the two largest size-classes (1,500–1,599 mm CFL: $\chi^2 = 8.33$, $P < 0.01$; $\geq 1,600$ mm CFL: $\chi^2 = 24.02$, $P < 0.001$) when compared to the expected sex ratio of 1:1 (Table 1).

Yellowfin Tuna caught by RR were observed in all age-classes, with an average length of 1,122 mm CFL and an average age of 2.9 years ($n = 3,202$). Individuals captured on PLLs were observed beginning at age 2 and were on average larger and older: 1,408 mm CFL and 4.9 years, respectively ($n = 241$). There were no significant differences in mean length at age between Yellowfin Tuna caught in the U.S. GOM and those caught in the western Atlantic for the most common age-classes (1–3 years; ANOVA: $P < 0.05$). Therefore, ages were pooled together and treated as a single population for the remaining analyses.

Age Determination

The APE among age readers was 8.1% after completion of a reference set. Generally, the first through third opaque zones in otoliths were wide, becoming narrower as the age estimate increased (Figure 2). Yellowfin Tuna annual ages were estimated from 3,443 otoliths comprised of 1,648 females, 1,600 males, and 195 individuals of unknown sex (Figure 3). A χ^2 goodness-of-fit test showed

TABLE 1. Number (*n*) and percentage (%) of female and male Yellowfin Tuna in each 100-mm curved fork length (CFL) size-bin landed in the U.S. Gulf of Mexico and western Atlantic.

CFL (mm)	Females		Males		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
600–699	8	0.49	17	1.06	25	0.77
700–799	92	5.58	90	5.63	182	5.60
800–899	91	5.52	104	6.50	195	6.00
900–999	182	11.04	164	10.25	346	10.65
1,000–1,099	325	19.72	312	19.50	637	19.61
1,100–1,199	329	19.96	284	17.75	613	18.87
1,200–1,299	246	14.93	225	14.06	471	14.50
1,300–1,399	219	13.29	192	12.00	411	12.65
1,400–1,499	107	6.49	96	6.00	203	6.25
1,500–1,599 ^a	39	2.37	69	4.31	108	3.33
≥1,600 ^a	10	0.61	47	2.94	57	1.75
Total (<i>n</i>)	1,648	100	1,600	100	3,248	100

^aSex ratio was significantly different from the expected ratio of 1:1 ($P < 0.05$).

no significant difference in the number of males and females within any age-class from the expected sex ratio of 1:1. Due to low sample size, ages 10–18 were pooled together for comparison.

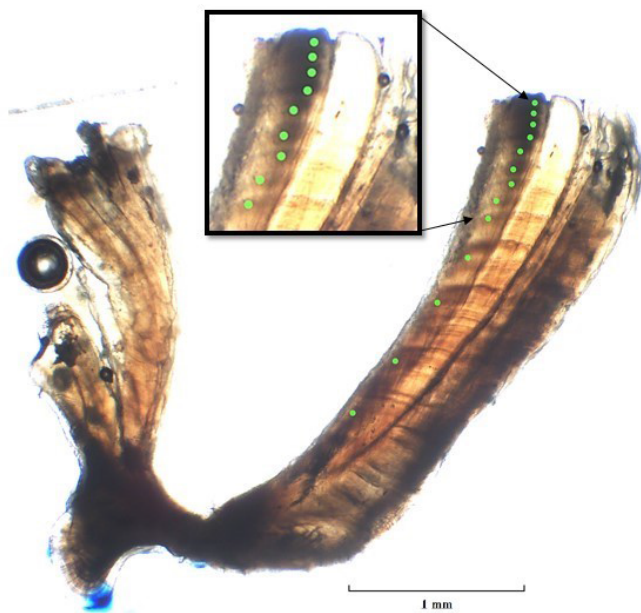


FIGURE 2. Transverse section of a sagittal otolith from a Yellowfin Tuna aged to 13 years, with an opaque edge. Annuli representing the first 3–5 years are typically broad and diffuse. The enlarged region shows the low-contrast banding pattern of the last nine annuli, which are thin and less diffuse. Annuli are annotated with green dots.

Ages ranged from 1 to 18 years, although a majority of both males and females were younger than 4 years. For all samples, age 2 was the most frequently observed age-class (40.7%), followed by age 3 (30.5%), age 4 (11%), and age 1 (6.7%). Edge type analyses revealed that the opaque zone formation began in March, with the highest percentage of opaque zones in June (40.1%). Since only one peak was observed throughout the 12-month period, increment formation was assumed to be annual. Readability codes were assigned for 1,623 otoliths. The most common readability code scored was a 2 (i.e., pattern was present in the otolith but uncertain in some areas; 49%), followed by a 3 (i.e., good pattern was present in the otolith but slightly uncertain in some areas; 32%). This indicated that Yellowfin Tuna were relatively difficult to age, especially for younger ages, when opaque zones were wide and diffuse.

Otolith Weight

There was no significant difference between mean left and right otolith weights (ANOVA: $F = 0.052$, $df = 827$, $P = 0.82$), which allowed the right otolith to be used if the left was missing or broken. The heaviest otolith (0.1831 g) corresponded to the oldest Yellowfin Tuna in the data set (18 years). Otolith weight was a significant predictor of fish age for all observations ($r^2 = 0.909$, $df = 827$, $P < 0.001$) as well as for females ($r^2 = 0.908$, $df = 364$, $P < 0.001$) and males ($r^2 = 0.892$, $df = 375$, $P < 0.001$) separately. The linearized power function for all observations was

$$\ln(\text{Age}) = \ln(4.84) + 1.216 \cdot \ln(\text{OtoWt}),$$

where $a = 4.84 \pm 0.04$ (mean \pm SE) and $b = 1.216 \pm 0.01$. A significant difference in the relationship between $\ln(\text{Age})$ and $\ln(\text{OtoWt})$ was observed between sexes (ANCOVA: $F_{1, 740} = 5.77$, $P = 0.02$), although it was minimal (Figure 4). Based on simple linear regression, $\ln(\text{OtoWt})$ explained about 27% more variance than $\ln(\text{CFL})$ alone when used to predict $\ln(\text{Age})$ ($r^2 = 0.909$ versus 0.641). A combined model that included both $\ln(\text{OtoWt})$ and $\ln(\text{CFL})$ as covariates to predict $\ln(\text{Age})$ increased the variance explained by less than 0.5% ($r^2 = 0.912$).

Growth Models

All models met the assumptions of nonlinear regression, as the standardized residuals were normally distributed (Figure 5). The Richards model resulted in the most parsimonious fit to the length-at-age data ($L_{\infty} = 1,658$ mm, $k = 0.23 \text{ year}^{-1}$, $a = 1.04$, $b = 0.45$), whereas the VBGM had a relatively poor fit ($L_{\infty} = 1,589$ mm, $k = 0.36 \text{ year}^{-1}$, $t_0 = -0.8$ year; AIC difference = 26.21) compared to the Richards model (Figure 6).

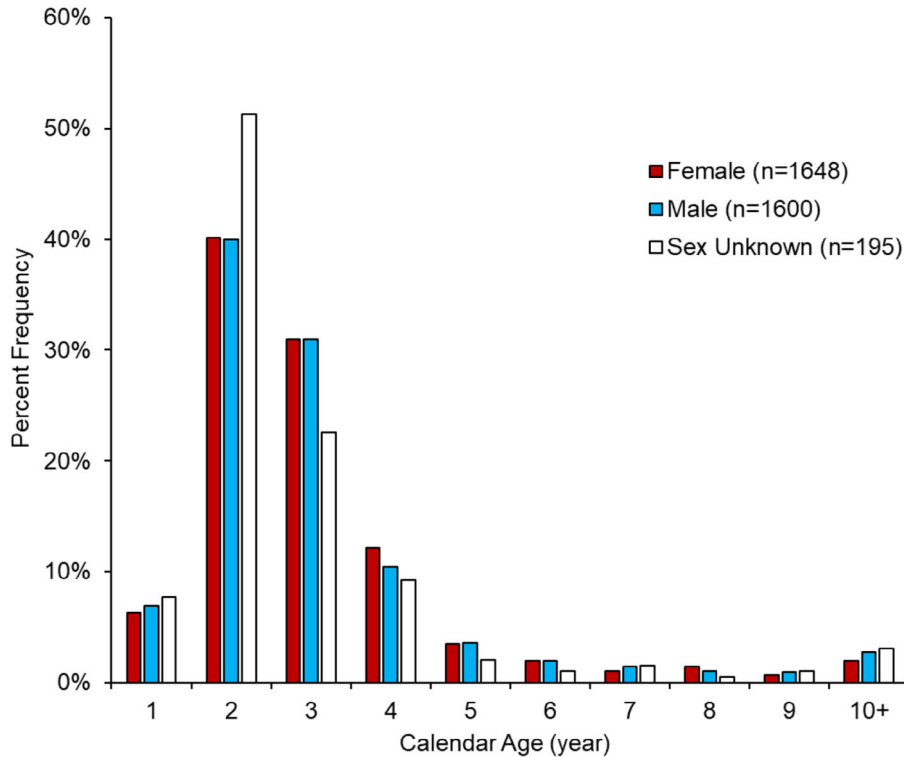


FIGURE 3. Age frequency distribution of Yellowfin Tuna females, males, and individuals of unknown sex. The 10+ group includes ages 10–18.

Size-Modified Growth

Yellowfin Tuna ages and observed CFL fitted to the size-modified Richards model marginally decreased L_{∞} , increased k , and had similar estimates in the additional two shape parameters ($L_{\infty} = 1,632$ mm, $k = 0.25$ year⁻¹, $a = 1.1$, $b = 0.44$). Similarly, the size-modified VBGM slightly decreased L_{∞} and t_0 values, which increased k ($L_{\infty} = 1,560$ mm, $k = 0.41$ year⁻¹, $t_0 = -0.48$ year; Table 2). Both size-modified models primarily showed an improved fit in individuals captured below the 686-mm CFL minimum size limit compared to the respective non-size-modified models (Figure 6).

Sex-Specific Growth

Likelihood ratio tests indicated that growth curves for males and females were significantly different in both size-modified models (Richards: $\chi^2 = 56.17$, $P < 0.001$; VBGM: $\chi^2 = 26.76$, $P < 0.001$; Table 2; Figure 7). The difference in L_{∞} estimates between male and female growth curves for both models exceeded 100 mm CFL. Sex-specific differences in mean CFL were observed for age 3 (ANOVA: $F_{1, 1,004} = 4.51$, $P = 0.03$), age 4 ($F_{1, 365} = 6.65$, $P = 0.01$), and age 6 ($F_{1, 62} = 9.59$, $P = 0.003$). Ages 7–18 were excluded from the analysis due to an insufficient sample size per age-class ($n < 25$).

Mortality

For all observations (male, female, and unknown sex) from the same gear type (RR), age-classes included in the catch curve ranged from 2 to 13 years ($n = 2,963$). The overall Z was 0.453. Age-classes used in the catch-curve regression ranged from 2 to 11 years for females and from 2 to 13 years for males, with corresponding Z -values of 0.512 and 0.411, respectively. There was no significant difference in Z by sex (ANCOVA: $F_{1, 19} = 0.13$, $P = 0.72$).

Baseline M for combined sexes resulted in an estimate of 0.347 when a maximum age (t_{max}) of 18 was used. Natural mortality was then scaled across age-classes by using the parameters from the size-modified VBGM for all observations ($L_{\infty} = 1,560$ mm, $k = 0.41$ year⁻¹, $t_0 = -0.46$ year). Baseline M was slightly higher for females ($M = 0.366$) because the oldest female observed in the data set was age 17 (1 year younger than the oldest male). Lorenzen- M scaled across age-classes for males and females showed a similar trend (Figure 8).

DISCUSSION

Yellowfin Tuna age and growth were successfully estimated in the U.S. GOM and western Atlantic Ocean using direct annual aging methods from otoliths that were

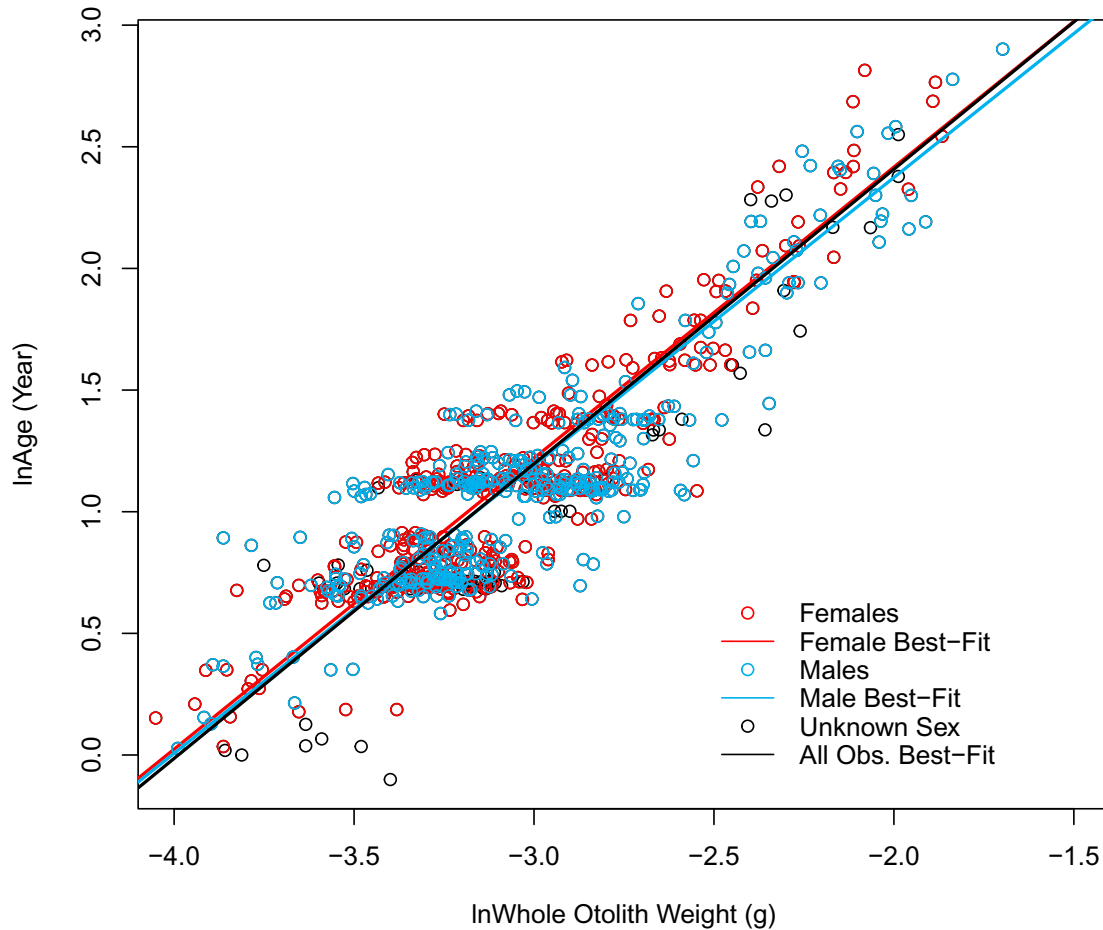


FIGURE 4. Yellowfin Tuna decimal age as a function of whole-otolith weight for females ($r^2 = 0.908$, $df = 364$, $P < 0.001$), males ($r^2 = 0.892$, $df = 375$, $P < 0.001$), and all observations combined (All Obs.; $r^2 = 0.909$, $df = 827$, $P < 0.001$). The equation represents the linearized power function for all observations.

largely obtained from fishery-dependent recreational sources. The aging criterion was supported by ^{14}C bomb radiocarbon validation (Andrews et al. 2020) and otolith edge analysis, and the APE among age readers (8.1%) was less than the threshold of 10% set for similar, difficult-to-age pelagic fish species, such as Atlantic Bluefin Tuna (Secor et al. 2014; Busawon et al. 2015). The ability to reliably age Yellowfin Tuna by using otoliths has resulted in the age-at-length data being used in the most recent ICCAT Yellowfin Tuna stock assessment (ICCAT 2019b).

A common difficulty in obtaining reliable growth parameter estimates stems from the challenge of collecting samples that represent an entire population, which is complicated by gear selectivity and minimum size limits (Haddon 2001; Kolody et al. 2016; Murua et al. 2017). The smallest (age-0) Yellowfin Tuna were captured primarily by purse seine in the eastern Atlantic. In the U.S. GOM and western Atlantic, Yellowfin Tuna captured by PLLs were on average larger and older than individuals landed

by RR, with the latter gear catching most of the observed age-classes. However, using multiple gears can aid in obtaining samples that are more representative and lead to improved parameter estimates used in estimating growth curves (Wilson et al. 2015). If possible, future studies should strive to age fish that have been landed from a variety of gear types representing both fishery-dependent and fishery-independent sources to limit gear bias and size limit effects.

Length at age was highly variable for Yellowfin Tuna in the U.S. GOM and western Atlantic, especially within the youngest age-classes. Large variation in length at age is common among tuna species and was also reported in Yellowfin Tuna in the Indian Ocean (Shih et al. 2014), Longtail Tuna in the central Indo-Pacific (Griffiths et al. 2010), and Bigeye Tuna off Australia (Farley et al. 2006). This variation is attributable to a myriad of factors, such as environment, spatial distribution, density dependence, and general individual variability (Maunder et al. 2015).

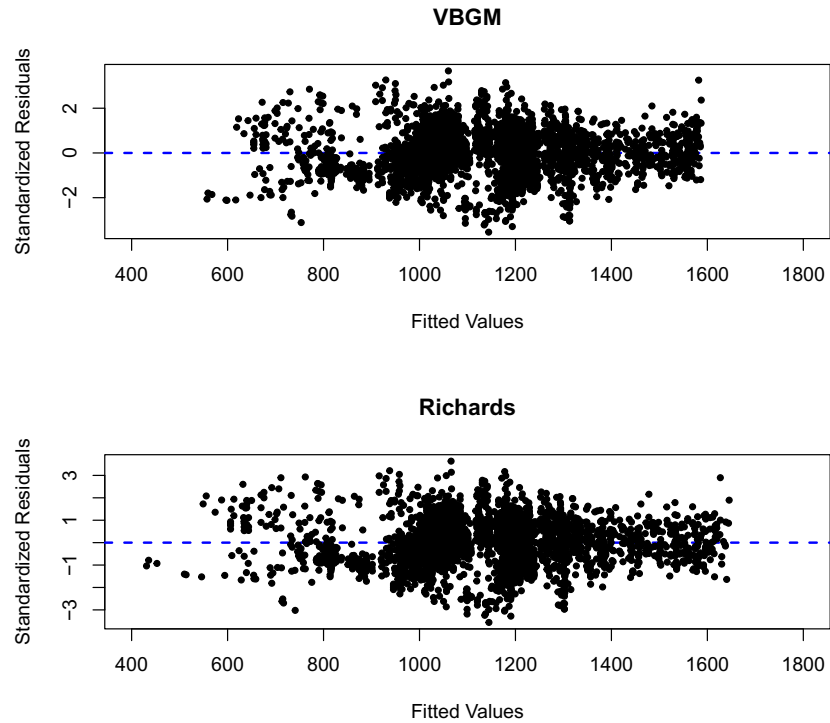


FIGURE 5. Standardized residual plots from fitting nonlinear least-squares regression for the von Bertalanffy growth model (VBGM) and the Richards growth model for Yellowfin Tuna. The y -axis represents the residual values, with the dashed reference line at 0, and the x -axis represents the predicted curved fork length (mm) values.

In addition to environmental factors, aging error, incorrect assignment of biological birthdate, and gear selectivity all may have contributed to the variability in size at age of Yellowfin Tuna in this study (ICCAT 2019b). Diffuse banding patterns in the first few annuli have been noted in other tuna species, such as Bigeye Tuna (Farley et al. 2006), Southern Bluefin Tuna (Gunn et al. 2008), and Atlantic Bluefin Tuna (Secor et al. 2014). Edge type assignment also presented difficulty among age readers due to the lack of consistency in opaque or translucent appearance along the entire otolith edge.

In tropical tunas, predicting age based on otolith weight has been explored using a variety of relationships. In Longtail Tuna, the linear relationship between otolith weight and age resulted in a relatively weak relationship ($r^2 = 0.55$; Griffiths et al. 2010). A significant curvilinear relationship between otolith weight and age was observed for Southern Bluefin Tuna ($r^2 = 0.90$; Gunn et al. 2008). With respect to Yellowfin Tuna in the western north Atlantic, a linear relationship between otolith weight and age was reported ($r^2 = 0.79$; Driggers et al. 1999), although ages were derived from daily increment counts that may have led to aging error in individuals older than 1 year. The significant allometric relationship of otolith weight as a predictor of age in our study suggests that otolith weight may be

an effective tool in estimating age for Yellowfin Tuna in the U.S. GOM. This would be beneficial because it could potentially reduce the costs associated with aging this species. Predicting age from otolith weight explained more variation ($r^2 = 0.909$) than length alone ($r^2 = 0.641$), but adding both variables did not substantially increase the predictability over using otolith weight alone ($r^2 = 0.912$). The statistically significant difference observed in this relationship between males and females was likely due to the influence of the variation in the most prevalent age-classes sampled (ages 2–4) being reduced, with the much fewer samples in the older age-classes (ages 5–18) carrying more weight. It was also in the older ages that the sexually dimorphic growth became obvious, with males being larger at any given age than females (Figure 7). However, the difference observed in otolith weight as a function of age between the sexes was biologically minimal (Figure 4). We recommend that future studies explore additional otolith morphometric relationships (i.e., otolith width and depth), as these are easy to measure, may provide a more precise estimate of age than otolith weight alone, and may also further distinguish differences between sexes in the otolith–age relationship.

The current ICCAT integrated assessment model for Yellowfin Tuna incorporates the annual ages from otoliths

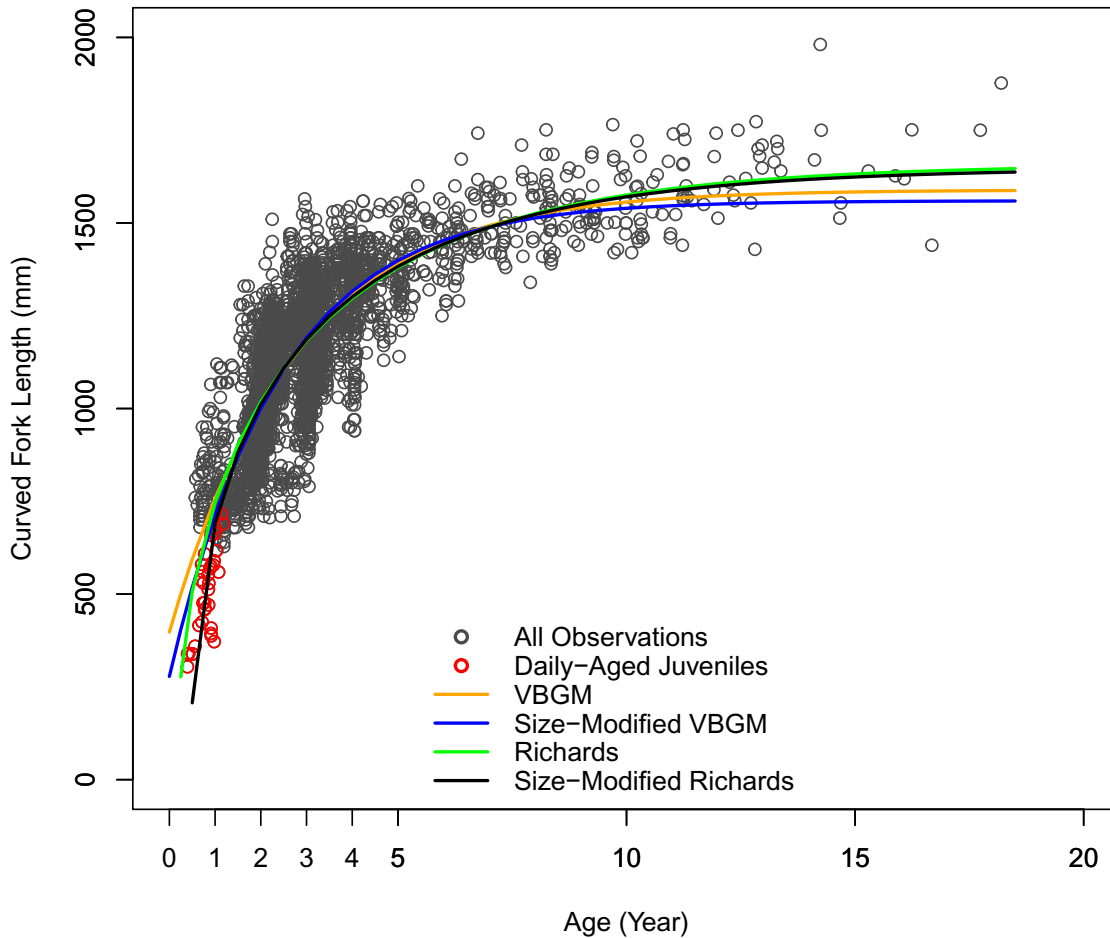


FIGURE 6. Model comparisons of Yellowfin Tuna predicted curved fork length as a function of decimal age for all observations ($n = 3,443$) and for the daily aged juveniles ($n = 37$). The open circles represent the observed length at decimal age (VBGM = von Bertalanffy growth model).

TABLE 2. Size-modified von Bertalanffy growth model (VBGM) and Richards model parameter estimates for all Yellowfin Tuna pooled (males, females, and unknown sex) and for sex-specific models (L_{∞} = average maximum length [mm]; k = growth coefficient [year^{-1}]; a , b = dimensionless parameters [defined in Methods]; t_0 = theoretical age [years] at zero length).

Size-modified model	Parameter	Pooled ($n = 3,480$)	Males ($n = 1,637$)	Females ($n = 1,685$)
Richards	L_{∞}	1,632	1,706	1,568
	k	0.25	0.21	0.27
	a	1.10	1.11	1.14
	b	0.44	0.41	0.40
VBGM	L_{∞}	1,560	1,599	1,478
	k	0.41	0.41	0.50
	t_0	-0.48	-0.37	-0.25

estimated in this study along with daily aged juveniles caught in the Gulf of Guinea to supplement for the few Yellowfin Tuna caught below the U.S. minimum size limit of 686 mm CFL (ICCAT 2019a, 2019b). Specifically, growth was estimated internally using the Richards

growth function (Richards 1959), which allowed the flexibility to mimic the two-stanza growth pattern of Gascuel et al. (1992) due to its additional shape parameter (ICCAT 2019a, 2019b). In this study, the Richards growth model provided the most parsimonious fit to the length-at-

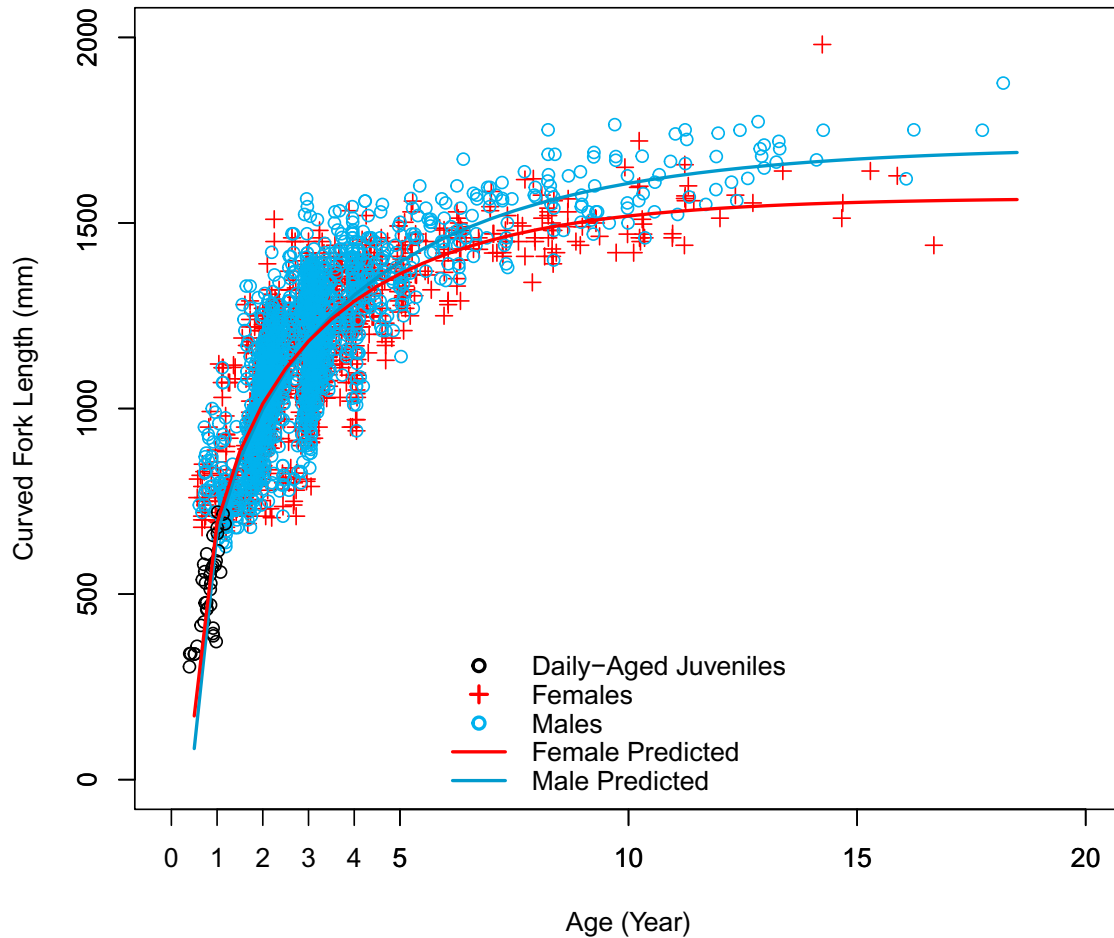


FIGURE 7. Predicted size-modified, sex-specific Richards growth curves for Yellowfin Tuna. The open blue circles and red crosses represent the observed length at decimal age for males ($n=1,637$) and females ($n=1,685$), respectively. The daily aged juveniles are represented by open black circles.

age data, followed by the VBGM. This suggests the possibility of two-stanza growth for Yellowfin Tuna in the U.S. GOM and western Atlantic, but more data from individuals in the first stanza (<650 mm CFL) collected directly from the U.S. GOM are necessary to explore this further. The only known data for young-of-the-year Yellowfin Tuna collected in the U.S. GOM were reported by Kitchens (2017) and Kitchens et al. (2018), but only the mean lengths of 42 young-of-the-year fish caught over a 3-year period off the coast of Louisiana were documented (size range of 342–383 mm FL for fish that were mostly 5–6 months old; i.e., ~0.4–0.5 year old). In general, the mean size and age ranges of these juveniles overlapped with those of the juveniles that were “borrowed” from the Gulf of Guinea in the present analysis (Figure 6). We recommend, however, that the specific fish data (i.e., length and capture date, which can provide decimal age) of each of the 42 young-of-the-year fish sampled by Kitchens (2017) be incorporated into the next ICCAT assessment to

further aid in informing the growth curve of the smallest/youngest individuals from the U.S. GOM. The Richards growth model has also been preferred to the VBGM for Yellowfin and Bigeye tunas in the western and central Pacific Ocean (Farley et al. 2020) and for western Atlantic Bluefin Tuna (Ailloud et al. 2017), as the additional shape parameter resulted in an improved fit to the length-at-age data. There was little disparity in the parameter estimates between the typical Richards model and the size-modified Richards model because there were very few fish captured below the minimum size limit, in addition to relatively large numbers of age-1 and age-2 fish observed. However, the size-modified Richards model further improved the fit of the individuals smaller than 650 mm CFL and overall provided the best fit to the length-at-age data. This model should be considered when sample collection is impacted by the minimum size limit to account for selection of the fastest growing age-0 and age-1 fish by fishery-dependent gear. Given that peak selectivity of the Yellowfin Tuna

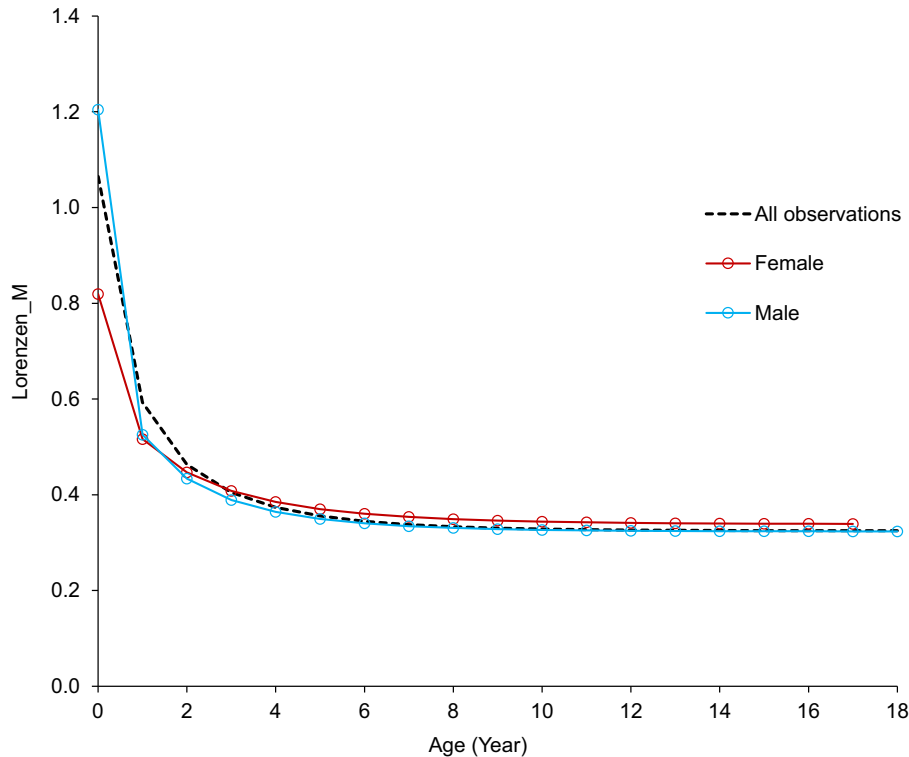


FIGURE 8. Lorenzen natural mortality (Lorenzen- M) estimates for Yellowfin Tuna females ($n=1,667$), males ($n=1,618$), and all observations ($n=3,480$; including individuals of unknown sex) scaled across age-classes using the parameters estimated from each respective size-modified von Bertalanffy growth model.

FAD fishery is 500 mm CFL, extra attention is needed in improving growth estimates of individuals in this size range (ICCAT 2019a).

Due to the frequent application of the VBGM, the estimated parameters from this study were compared to previous Yellowfin Tuna growth studies that estimated ages from otoliths or spines (Table 3). Daily age enumeration from otoliths (Stequert et al. 1996; Shuford et al. 2007) and annual aging of spines (Lessa and Duarte-Neto 2004) resulted in extremely high L_{∞} estimates (2,307–2,727 mm SFL), an implausible situation given that L_{∞} is intended to represent the average maximum (asymptotic) length—not the maximum length of the largest individual observed in the population (ICCAT 2019a). The high extrapolated L_{∞} estimates were likely caused by using aging methodologies (i.e., daily otolith increments and spines) that are known to underestimate the ages of older individuals (Williams et al. 2013; Andrews et al. 2020). In the current study, the L_{∞} estimated from the VBGM was 1,589 mm CFL (1,533 mm SFL), which was reasonable given that the standardized residuals were normally distributed around L_{∞} . Similar estimates of L_{∞} were reported for Yellowfin Tuna aged primarily from annual aging methods in the western and central Pacific Ocean (1,505 mm SFL; Farley et al. 2020) and the Indian Ocean (1,669 mm

SFL; Shih et al. 2014). The estimated rate of growth towards L_{∞} was generally faster ($k=0.39 \text{ year}^{-1}$) compared to values reported from other investigations (between 0.18 and 0.44 year^{-1}). It is likely that both the extended age range (0–18 years) and the lower L_{∞} seen in this study contributed to a higher observed k .

Differences in sex-specific growth among tuna populations is well documented (Kolody et al. 2016). The number of male and female Yellowfin Tuna in this study did not significantly deviate from the expected sex ratio of 1:1 in any age-class (1–10+ years), which is an indicator that they have equal survival (ICCAT 2019a). Males were prevalent in the largest sizes (>1,500 mm), which has also been documented for Yellowfin Tuna in the Atlantic Ocean (Arocha et al. 2000; Fonteneau and Chassot 2013; Diaha et al. 2016), the Indian Ocean (Stequert et al. 1996; Shih et al. 2014), and the Pacific Ocean (Schaefer 1998). Sexually dimorphic growth of Yellowfin Tuna in the U.S. GOM and western Atlantic was also observed in the current study, with males reaching a larger L_{∞} than females (>100-mm difference). There was no significant difference in mean length at age between sexes for age-1 and age-2 Yellowfin Tuna. Around age 3, males began to diverge from females and reached a greater L_{∞} . The lack of a significant difference observed between sexes at age 5 may be

TABLE 3. A comparison of studies that estimated von Bertalanffy growth model parameters derived from hard parts of Yellowfin Tuna (L_{∞} = average maximum length [mm]; k = growth coefficient [year^{-1}]; t_0 = theoretical age [years] at zero length; GOM = Gulf of Mexico). The L_{∞} estimate and the range of observed lengths from this study were converted from curved fork length to straight fork length (SFL; Scida et al. 2001) in order to allow comparison with other studies.

Study	L_{∞}	k	t_0	Method (structure)	Region	n	SFL (mm)	Maximum age (years)
Current	1,533	0.36	-0.8	Annual (otolith)	U.S. GOM, Atlantic Ocean	3,480	593–1,910	18
Farley et al. 2020	1,505	0.44	-0.24	Annual and daily (otolith)	Western and central Pacific Ocean	1,567	300–1,600	15
Shih et al. 2014	1,669	0.21	-2.7	Annual (otolith)	Indian Ocean	386	660–1,650	10.5
Shuford et al. 2007	2,455	0.28	0.04	Daily (otolith)	Atlantic Ocean	132	54–1,790	5.5
Lessa and Duarte- Neto 2004	2,307	0.27	-0.08	Annual (spine)/ LFA ^a	Western equatorial Atlantic Ocean	380/ 6,758	450–1,910	6.5
Stequert et al. 1996	2,727	0.18	-0.27	Daily (otolith)	Indian Ocean	151	280–1,350	4

^aLength frequency analysis.

attributable to the relatively low sample size ($n=114$) compared to age 3 ($n=1,006$) and age 4 ($n=367$), although a significant difference was observed at age 6 ($n=64$). Shih et al. (2014) also observed sexually dimorphic growth for Yellowfin Tuna in the Indian Ocean, with males reaching a greater L_{∞} (1,629 mm SFL) than females (1,236 mm SFL). However, no significant sex-specific differences in growth were observed for Yellowfin Tuna in the western and central Pacific Ocean (Farley et al. 2020). Differences in growth for Yellowfin Tuna are likely correlated to when females reach sexual maturity and begin to put more energy into ovarian growth and egg production than somatic growth (Shih et al. 2014).

The oldest Yellowfin Tuna observed in this study was estimated to be age 18, which represented a substantial increase (~ 7.5 years) in longevity for Yellowfin Tuna. It is unknown whether individuals reach similar longevity in the eastern Atlantic Ocean, although a preliminary annual maximum age of 18 years for a Yellowfin Tuna landed near Ascension Island has been reported (ICCAT 2019a, 2019b). Farley et al. (2020) reported a similar longevity of at least 15 years for Yellowfin Tuna in the western and central Pacific Ocean. Previous studies in the Atlantic by Lessa and Duarte-Neto (2004) and Shuford et al. (2007) reported maximum ages of 6.5 and 5.5 years, respectively, but those studies were based on age readings from spines and daily otolith increments, which are both known to underestimate ages of older fish. Using annual otolith increment counts, Shih et al. (2014) reported a maximum age of 10.5 years for Yellowfin Tuna in the Indian Ocean, with males reaching an older age (9.4 years) than females (6.5 years).

Instantaneous total mortality (Z) for all observations from RR gear was 0.453, and no significant difference was observed between males and females, indicating that fishing pressure is likely similar between the two sexes. This study presents the first estimate of Z derived from an age-based catch curve for Yellowfin Tuna in the U.S. GOM and western Atlantic. Natural mortality was estimated using a maximum age of 18, which was also adopted by ICCAT, largely as a result of the bomb radiocarbon validation (ICCAT 2019b; Andrews et al. 2020). Prior to the 2019 ICCAT assessment for Yellowfin Tuna, the maximum age used to estimate M was 11 years ($M=0.54$; ICCAT 2017), whereas our estimate of t_{max} (maximum age in the population) gives a lower estimate of M (0.35) derived from the Then et al. (2015) estimator. Natural mortality was highest at age 0 and age 1 when the M -estimate of 0.35 was scaled across age-classes following Lorenzen (2005). The 2019 ICCAT assessment noted a similar pattern of M across age-classes for Yellowfin Tuna following similar methodology (ICCAT 2019b). Sex-specific M was similar since longevity estimates were similar (ICCAT 2019a). Despite some growth differences, Yellowfin Tuna are not currently modeled as separate sexes in ICCAT stock assessments because sex is rarely recorded in landings data (ICCAT 2019a, 2019b). We recommend that sex-specific growth models be considered in future assessment models if these data become available.

Stock assessment models are influenced by estimates of growth and mortality, which ultimately affect model fit estimates of productivity and stock status benchmark calculations (i.e., overfished and overfishing status), stressing

the need for accurate and precise age and growth data (Maunder et al. 2015; Murua et al. 2017). Properly characterizing growth and mortality of Yellowfin Tuna less than 650 mm has become increasingly important given the extensive fishing mortality of juveniles associated with the FAD fishery in the eastern Atlantic (ICCAT 2019a). Overall, this study addressed key uncertainties and recommendations put forth by ICCAT (2017, 2019a) to improve basic biological data for future assessments. We recommend that sampling of otoliths be expanded throughout the range of Atlantic Yellowfin Tuna, especially in the eastern and southern Atlantic, where it is currently limited, to compare potential regional differences in growth (ICCAT 2019a). Future collaborations with scientists from other countries and institutions are necessary to improve sampling and ensure that otolith aging is standardized.

ACKNOWLEDGMENTS

We thank recreational port samplers Cijji Marshall (Louisiana Department of Wildlife and Fisheries), Joe Yurt (NMFS), and all of the biological sample collectors from Quantech, Inc. (contractor to NMFS), for their efforts in collecting otoliths. Our thanks go to the NOAA, Southeast Fisheries Science Center, Sustainable Fisheries Division, Highly Migratory Species Branch under the leadership of Craig Brown for support and to Derke Snodgrass for collecting otoliths while onboard commercial vessels. We wish to thank Rebecca Shuford (current affiliation: New York Sea Grant), Kyne Krusic-Golub (Fish Ageing Services), and the ICCAT Atlantic Ocean Tropical Tuna Tagging Programme (AOTTP) for sharing their juvenile Yellowfin Tuna age data. Funding for ICCAT-AOTTP samples was provided by the European Union (Directorate-General for International Cooperation and Development) and ICCAT contracting parties, cooperating non-contracting parties, entities, or fishing entities. Contributions made by the ICCAT-AOTTP tag and recovery teams are gratefully acknowledged. We thank the Sport Fish Restoration Program for partially funding the sampling in Louisiana. We are grateful to Guy Davenport (former director of the NMFS Panama City Laboratory) for his support throughout the duration of this project. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect those of NOAA or the Department of Commerce. Reference to trade names does not imply endorsement by the U.S. Government. As a standard practice when handling manuscripts submitted by an editorial board member of this journal, D.J.M. did not, at any stage, have access to the online system, processing, or peer review for this article. There is no conflict of interest declared in this article.

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