FEATURE ARTICLE

Age, growth, and mortality of Blackfin Tuna in the Gulf of Mexico

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Abstract

Objective: An otolith-based aging approach was used to evaluate age and growth relationships, sexual dimorphism in growth, and derive mortality estimates for Blackfin Tuna *Thunnus atlanticus* in the Gulf of Mexico (GOM).

Methods: Blackfin Tuna ($n = 395$) were sampled from recreational fisheries and aged from 0 to 13 years, representing an increase over previous estimates of longevity for the species.

Result: Rapid growth was exhibited during the first two years of life, and the Richards growth function provided a better fit ($L_\infty = 907\,mm$, $k = 0.112$/year, $a = 1.05$, $b = 0.25$) to the data compared with the von Bertalanffy growth model ($L_\infty = 824\,mm$, $k = 0.365$/year, $t_0 = -0.96$). Sexual dimorphism in growth was observed, with males (907 mm) reaching a larger L_∞ than females (857 mm), and otolith mass was a strong predictor of age in both sexes. Estimated instantaneous total ($Z = 0.532$/year) and natural ($M = 0.467$ year) mortality rates for Blackfin Tuna in the GOM were low relative to previous estimates in the southwestern Atlantic, where fishing mortality (F) is likely much higher.

Conclusion: Results represent critical baseline estimates of size-at-age, longevity, and natural mortality for Blackfin Tuna at relatively low levels of exploitation that can be used to inform future assessments.

KEYWORDS

Blackfin Tuna, maximum age, natural mortality, otolith, Richards growth function, sexual dimorphism, *Thunnus atlanticus*, von Bertalanffy

INTRODUCTION

Tuna *Thunnus* spp. are highly migratory species that serve an important role as predators in oceanic ecosystems around the world (Duffy et al. 2017; Miller et al. 2018). Because tunas are highly valued as a food source and sport fish, many tuna populations have been heavily exploited by commercial and recreational fisheries (Collette et al. 2011; Juan-Jordá et al. 2011; Pons et al. 2017). Atlantic Bluefin Tuna *Thunnus thynnus* and Southern Bluefin Tuna *Thunnus maccoyii*, Albacore *Thunnus alalunga*, Yellowfin Tuna *Thunnus albacares*, and Bigeye Tuna *Thunnus obesus* comprise some of the largest global fisheries (by landings and economic value), and their exploitation has led to population declines

in different parts of the world (Juan-Jordá et al. 2015; Bravington et al. 2016; Braun et al. 2023). In addition to direct removals, tuna populations are also threatened by the degradation of pelagic ecosystems due to pollutants, habitat alteration, and indirect changes in the functions and structure of ecosystems caused by overfishing and climate change (Nicol et al. 2022; Braun et al. 2023). While there is evidence to suggest that improved management actions over the past couple of decades have led to some recovery in tuna populations targeted by directed commercial fisheries (Juan-Jordá et al. 2022), many smaller tuna species remain data poor and lacking assessment, preventing the development of similar management plans (Lucena-Frédou et al. 2021).

Blackfin Tuna *Thunnus atlanticus* are the smallest of the eight true tunas and are distributed in tropical and subtropical waters of the western Atlantic Ocean (Doray et al. 2004; Bezerra et al. 2013; Cornic and Rooker 2018; Saillant et al. 2022), from the northeast coast of the United States to the southeastern coast of Brazil, including the Gulf of Mexico (GOM) and Caribbean Sea (Vieira et al. 2005). While Blackfin Tuna receive considerably less pressure from global fisheries than larger Atlantic tunas (Bluefin Tuna, Yellowfin Tuna, and Bigeye Tuna; Rooker et al. 2007; Lucena-Frédou et al. 2021), they support locally important commercial and recreational fisheries, particularly at lower latitudes, and make up most of the artisanal catch in South America (Freire et al. 2005) and the Caribbean (Taquet et al. 2000; Doray et al. 2004). Moreover, because Blackfin Tuna are an abundant tuna species throughout much of the tropical and subtropical western Atlantic Ocean (Cornic et al. 2018; Santos et al. 2023), the species has high fishery potential and is likely to become increasingly targeted as stocks of larger tunas decline. Still, our understanding of the biology of Blackfin Tuna remains relatively limited throughout the entirety of its range. There is a clear need for baseline life history information, such as age and growth, mortality, and reproduction, to develop stock assessments and more effectively manage this species (Santos et al. 2023).

Blackfin Tuna are the most abundant tuna found in the GOM, accounting for greater than 80% of the *Thunnus* larvae collected in long-term, fishery-independent sampling efforts in the region (Cornic and Rooker 2018). Still, the Blackfin Tuna fishery has received significantly less attention from stakeholders and scientists in the GOM, as commercial fisheries primarily target larger Yellowfin Tuna. Blackfin Tuna are commonly targeted by the recreational rod-and-reel fishery in the GOM (Adams and Kerstetter 2014; Fenton et al. 2015) because they are found closer to shore (Rooker et al. 2013) and are thus the most accessible tuna to coastal anglers. With growing threats of overfishing and stock depletion of larger tunas, increased fishing pressure on the Blackfin Tuna population is expected (Cornic and Rooker 2018), and indeed, recreational

Impact statement

Blackfin Tuna are the most abundant tuna found in the Gulf of Mexico; however, basic life history information on the species is limited. This study characterized age and growth of Blackfin Tuna in the Gulf of Mexico to obtain needed estimates of size at age, longevity, and natural mortality.

landings in the USA have increased by threefold since the 1980s (Saillant et al. 2022). Despite the GOM being classified as an essential spawning and nursery ground for the species (Muhling et al. 2017; Cornic and Rooker 2018), stock status for Blackfin Tuna remains uncertain, due in part to the lack of basic life history information (Cornic and Rooker 2018).

Here, an otolith-based aging approach was used to characterize age, growth, and mortality relationships for Blackfin Tuna in the northern GOM. Otolith-based aging methods have been used to develop growth curves for several tunas (Murua et al. 2017), including Atlantic Bluefin Tuna (Restrepo et al. 2010), Southern Bluefin Tuna (Ku et al. 2021), Yellowfin Tuna (Pacicco et al. 2021), and Albacore (Wells et al. 2013). While daily increment formation has been examined for Blackfin Tuna (Doray et al. 2004), otolith-based estimates of age and growth are limited throughout their range. As a result, our understanding of age–growth relationships for the Blackfin Tuna stock in the GOM remains relatively unknown. The primary objectives of this study were to use a multimodel approach to develop otolith-based age and growth relationships and mortality estimates for Blackfin Tuna in the GOM. Because tunas often exhibit sexual dimorphism (Freire et al. 2005; Vieira et al. 2005; Bezerra et al. 2013; Pacicco et al. 2021), sex-specific growth patterns in Blackfin Tuna were also examined. Given that otolith mass has been closely linked to age in other tunas and has great potential as a cost-effective alternative to counts of annual increments (Pacicco et al. 2021), we also examined the relationship between otolith mass and age for Blackfin Tuna. Growth parameters derived from best-fit models and longevity estimates were then used to empirically estimate natural mortality for Blackfin Tuna in the GOM. Information from this study will improve our understanding of Blackfin Tuna life history in the GOM and provide critical baseline data needed for stock assessment to enable management of this species.

METHODS

Blackfin Tuna were collected opportunistically in the north-central GOM from 2014 to 2019 ($n = 393$). All

samples were collected from fishery-dependent sources at offshore ports in in the north-central GOM, with fishing effort focused between 10 and 150 km offshore. Blackfin Tuna were primarily collected from the recreational charter fishery (rod and reel), although a small proportion of the sample was also collected from commercial (e.g., green stick) fisheries, where they are taken as bycatch. Biological information was recorded for each individual, including sex, weight, and curved fork length (CFL).

Sagittal otoliths were removed from each fish, cleaned with distilled water, stored dry in plastic centrifuge tubes, and inserted into a labeled coin envelope. Left otoliths from each fish were embedded in a 5:1 mixture of araldite and aradur (Huntsman) and sectioned transversely with diamond wafering blades on a Buehler low-speed Isomet saw. Two to three sections were cut to 0.5-mm thickness, mounted on slides (postrostrum side up) with Locktite UV glue cured under black lights for 15 min, and coated with Flotex mounting media to improve visibility. Images of each otolith section were taken under 20× magnification on an Olympus SZX12 dissection scope with a SeBaCam5C camera (5.1 megapixels) and viewed on the Laxco SeBaView software at the Louisiana Department of Wildlife and Fisheries Age and Growth Lab, Baton Rouge, Louisiana. Otolith sections were then analyzed using the ImageJ 1.52 K software to count annual increments and measure distance between annuli.

Age assignment

An annual growth increment (annulus) was defined as one successive translucent and opaque zone, and ages were estimated from counts of opaque zones. Counts were made starting from the core to the edge of the otolith along the inner margin of the otolith ventral branch, and an opaque zone at the otolith edge was only counted if complete. Because the first annulus is often difficult to identify in tunas, we developed a "yardstick" based on the mean distance from the otolith core to the first annulus measured by three independent readers from a random set of otoliths (Secor et al. 2014; Lang et al. 2017; Pacicco et al. 2021). This "yardstick" served as a guide in identification of the first annulus on subsequent otoliths. This measurement was compared qualitatively with measurements and daily increment counts from Doray et al. (2004) to identify the location of the first increment. While annual increment formation has not yet been directly validated for Blackfin Tuna, annual aging methods have been validated for several closely related congeners (Ishihara et al. 2017; Murua et al. 2017; Andrews et al. 2020), suggesting that age estimates are likely to be accurate.

Sections were read separately by at least two readers. To reduce biases, counts were made without the knowledge of fish size, sex, or previous counts. When counts differed between the two readers, the first reader conducted a third reading. For otoliths where an agreement between readers could not be immediately reached, the otolith was read by a third reader and a final increment count was agreed upon by all three readers. Edge codes were assigned to each otolith, where 1 indicated <0.33% of the next translucent zone had formed, 2 indicated 0.33–0.66%, and 3 indicated >0.66% of the zone had been formed. Index average of percent error (IAPE) was calculated to compare reproducibility of ages between readers (Beamish and Fournier 1981):

$$\text{IAPE} = \frac{1}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{N} \frac{|X_{ij} - X_j|}{X_j} \right],$$

where N is the number of fish aged, R is the number of readings for each fish, X_{ij} is the ith age determination of the jth fish, and X_j is the mean age calculated for the jth fish.

Measurements were taken from the core to the distal edge of the opaque zone of each annulus at the inner margin of the otolith ventral branch (Figure S1 in the Supplement available separately online). Marginal increment analysis was utilized to identify the seasonal pattern of opaque zone deposition, and the marginal increment ratio was added to the increment count to achieve a fractional age for each individual (Lang et al. 2017). Given the variation in birth date and potential asynchrony between birth date and timing of increment formation, resulting age estimates are approximate (Farley et al. 2006). Marginal increment ratio (MIR) was calculated using the following formula:

$$\text{MIR} = \frac{M_d - LA_d}{(LA_d - SLA_d)},$$

where M_d is the distance from the core to the otolith edge (margin), LA_d is the distance from the core to distal edge of the last annulus, and SLA_d is the distance from the core to the second to last annulus. Because growth is rapid and the distance between opaque zones decreases substantially across the first three annual increments, using the width of the previous increment as the denominator is likely to serially underestimate MIR in young fish. As a result, we used the third quartile distance (across all otoliths) between the first and second (215.15 μm), second and third (144.59 μm), and third and fourth (121.40 μm) opaque zones as the denominator in the MIR equation for age-1, age-2, and age-3 fish, respectively, based on Lang et al. (2017). Mean MIR ± SD was used to examine annual increment formation across quarters (seasons; Zaboukas and Megalofonou 2007; Koob 2020), where Q1 = the

months of January–March, Q2 = April–June, Q3 = July–September, and Q4 = October–December. Ages 1–5 were used in the model to reduce biases from older individuals, where the increment width is narrower (Gunn et al. 2008; Koob 2020).

Otolith mass

Sagittal otoliths were weighed to the nearest 0.0001 g to examine the relationship between otolith mass and biological age. Samples of age-0 fish with unknown sex ($n = 26$) were included in the models for both female and males to better anchor the relationship at younger ages. Using a linearized power function, otolith mass was plotted as a function of biological age to predict age following Pacicco et al. (2021):

$$\ln(\text{age}) = \ln(a) + b \cdot \ln(\text{otolith mass}),$$

where ln(age) is the natural log of the estimated age, ln(otolith mass) is the natural log of otolith mass (g), a is the scaling coefficient, and b is the allometric scaling exponent. Similarly, ln(CFL) was used to predict ln(age) using the same equation (substituting "CFL" for "otolith mass") to contrast the predictive ability of CFL and otolith mass on biological age. The Akaike information criterion corrected for small sample sizes (AIC$_c$; Sugiura 1978) was used to compare model fit for simple linear regressions of otolith mass and CFL to see which model was a better predictor of fish age. Sample size was restricted ($n = 245$) for both models (CFL and otolith mass) to include only those individuals for which an otolith mass was available. Analysis of covariance (ANCOVA) was used to test for sex-specific differences in the relationship between otolith mass and age. Significance was determined at $\alpha < 0.05$ for all tests.

Growth curves

Growth was evaluated with two different models: the von Bertalanffy growth model (VBGM; von Bertalanffy 1938) and the Richards growth function (Richards 1959). Length at age for Blackfin Tuna ($n = 393$) was first fitted using the VBGM due to its widespread use in modeling tuna age and growth (Shuford et al. 2007; Adams and Kerstetter 2014; Lang et al. 2017), which allowed for direct comparison of parameters among similar taxa. Additionally, separate growth curves were examined for each sex ($n = 270$ males, $n = 84$ females) to investigate sexual dimorphism. Immature age-0 individuals with unknown sex ($n = 26$) were included in both models to anchor each sex-specific growth curve at the origin, and AIC$_c$ was used to assess model fit. Sex-specific models were evaluated by comparing the AIC$_c$ value from the pooled curve data to the sum of the AIC$_c$ values from the sex-specific models (Williams et al. 2012). The VBGM followed the typical parametrization:

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

where t is the estimated age (years), L_t is the estimated mean CFL (mm) at age t, L_∞ is the mean maximum (asymptotic) CFL, k is the growth coefficient (year^{-1}), and t_0 is the theoretical age (years) when the fish had a length of zero.

While age and growth in tunas is typically characterized by the VBGM, recent studies indicate that the Richards model often better represents growth in a variety of taxa, including tropical tunas (Farley et al. 2020; Flinn and Midway 2021; Pacicco et al. 2021). Thus, the Richards growth function was also fitted to length at age for Blackfin Tuna ($n = 393$) in the current study. Sex-specific differences in age–growth relationships were also explored with the Richards growth function using the same methodology as the VBGM, where immature individuals ($n = 26$) were included in both models to "anchor" the curve. The Richards growth function has many parameterizations, and here we used a four-parameter model (Tjørve and Tjørve 2010):

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

where L_∞ is the mean maximum (asymptotic) CFL, k is the growth coefficient, and a and b are dimensionless parameters that control the horizontal (age) and vertical (size) inflection point position, respectively.

Growth parameters for both models were estimated using nonlinear least squares (nls) regression with the *Fisheries Stock Analysis* (FSA; Ogle 2018) and *minpack.lm* (Elzhov et al. 2016) packages in R version 4.1.1 (R Core Team 2021). Model fits were contrasted between the VBGM and Richards curve, as well as sex-specific versus pooled models for each method, using AIC$_c$. Bootstrapped resampling (999 iterations) was used to derive confidence intervals (95%) for parameters in each model using the *nlstools* package in R (Baty et al. 2015).

Mortality

The total instantaneous mortality rate (Z) was calculated from regression analysis of cross-sectional catch curves of age frequency data using the *fishmethods* package in R (Gary 2021). The natural-logarithm-transformed frequency at each age was plotted against age, and a linear regression was run on the descending limb of the catch

curve, beginning with the age with the highest frequency (Sanchez and Rooker 2021).

Several empirical methods were used to estimate natural mortality (M) based on recommendations outlined by Then et al. (2015). Longevity ($n = 2$) and growth-based ($n = 2$) methodologies were examined. Methods used based on maximum age (t_{max}) included the updated Hoenig (1983) method and the Hoenig$_{nls}$ equation described by Then et al. (2015), while methods based on growth parameters included the modified Pauly$_{nls-T}$ and modified one-parameter K estimator also described by Then et al. (2015). Hoenig's (1983) linear estimator (updated by Then et al. 2015) was calculated as follows:

$$\ln(M) = 1.717 - 1.01 \cdot \ln\left(t_{max}\right)$$

In contrast, the Then et al. (2015) equation (Hoenig$_{nls}$) using maximum age (t_{max}) is given as follows:

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

The modified Pauly$_{nls-T}$ equation described by Then et al. (2015) is modified from Pauly's (1980) equation and uses the parameters L_∞ and K:

$$M = 8.87 \, K^{0.73} L_\infty^{-0.33}$$

Finally, the one-parameter K equation described by Then et al. (2015) is based on the Beverton and Holt life history invariant equation (Beverton and Holt 1959; Charnov 1993):

$$M = 1.692 \, K$$

The modified Then et al. (2015) equation (Hoenig$_{nls}$) has been adopted by the International Commission for the Conservation of Atlantic Tunas (ICCAT) for tuna assessments and is generally recommended for empirical estimations of M. Because natural mortality is likely not constant throughout life, M estimated from the Then et al. (2015) equation was used as baseline M and scaled across age-classes using the VBGM parameters and Lorenzen (2005) methodology. This methodology for estimating baseline M and scaling across age-classes is currently used by ICCAT (ICCAT 2019; Pacicco et al. 2021) for other *Thunnus* species and was chosen here to be comparable to other tuna stocks in the Atlantic.

RESULTS

Blackfin Tuna were collected in all months, with approximately 95% of samples collected from the recreational rod-and-reel fishery ($n = 374$) and 5% ($n = 19$) from the commercial fishery. The sex ratio was skewed towards male fish, with males accounting for 69.7% ($n = 270$) of specimens, females accounting for 21.4% ($n = 84$), and unknown sex accounting for 9.9% ($n = 39$). This sex ratio was relatively consistent across months (Figure S2); however, the ratio of females and males was similar in younger age-classes (1–3 years old; chi-square: $p > 0.05$) (Figure S2). The observed size distribution for all Blackfin Tuna (combined sexes) in the sample ranged from 251 to 911 mm CFL, with a mean ± SE of 715.7 ± 7.2 mm. Male CFL ranged from 490 to 911 mm (mean ± SE = 764.5 ± 5.3 mm), while female CFL ranged from 434 to 870 mm (mean ± SE = 691.8 ± 12.1 mm) (Figure S3). Individuals of unknown sex ranged from 251 to 870 mm CFL (mean ± SE = 429.4 ± 27.0 mm); however, it should be noted that the vast majority of individuals (>82%) classified as unknown sex were young (age 0 or age 1) and likely immature.

Age determination

Age was estimated for a total of 393 Blackfin Tuna, comprised of 84 females, 270 males, and 39 unknown sex. The distance from the core to the first opaque zone represented the widest annulus, with distance between annuli decreasing with increasing age (particularly across the first 4 years). Similar to other tunas (Farley et al. 2006; Andrews et al. 2020; Pacicco et al. 2021), the first three opaque zones were relatively diffuse, becoming narrower and more clearly defined with age. Age estimates ranged from 0 to 13 years (for both sexes), although most individuals were younger than 9 years old, with 41.7% between 6 and 8 years old. Overall, age 6 and 7 were the most frequently observed age-classes (13.9% each), followed by age 8 (13.7%) and age 9 (10.4%). Agreement in annuli counts between readers was high (average percent error < 5.7%), and greater than 55% of otolith readings were identical, with over 88% differing by 1 year or less.

Edge type and MIR were used to identify seasonal patterns in annual increment deposition. The MIR differed across seasons (ANOVA: $F_{3,140} = 4.789$, $p < 0.05$) and was generally lowest in winter (quarter 1: January through March; Figure S4). While MIR increased throughout the year, variability was observed in all seasons. Similarly, the proportion of edge code 1 peaked during winter and decreased through subsequent seasons.

Growth models

The VBGM parameters for the pooled (both sexes) model were $L_\infty = 824$ mm CFL (95% CI = 813 to 835 mm),

$k = 0.365$/year (95% CI $= 0.329$ to 0.401), and $t_0 = -0.96$ (95% CI $= -1.16$ to -0.76) (Table 1). Sex-specific VBGMs were also explored, and separate models for male and female Blackfin Tuna resulted in an improved model fit (summed AIC_c) relative to a single pooled model ($\Delta AIC_c = 184.72$). The L_∞ estimates $\pm 95\%$ CI for males (832 ± 22.6 mm) exceeded that for females (776 ± 32.8 mm) by greater than 50 mm (Table 1; Figure 1); however, females exhibited a higher growth coefficient (0.47/year) than males (0.37/year) (Table 1).

Interestingly, the Richards growth function ($AIC_c = 4026.41$) was a better fit to the Blackfin Tuna data than the VBGM ($AIC_c = 4108.68$) (Figure 2). The overall parameterizations for the Richards growth function were $L_\infty = 907$ mm (95% CI $= 866$ to 965 mm), $k = 0.112$/year (95% CI $= 0.072$ to 0.167), $a = 1.05$ (95% CI $= 1.03$ to 1.07), and $b = 0.25$ (95% CI $= 0.23$ to 0.29). Similar to the VBGM, sex-specific growth models resulted in a better fit ($\Delta AIC_c = 31.57$), and the L_∞ estimate $\pm 95\%$ CI for males (907 ± 90.3 mm) exceeded that for females (857 ± 127.3 mm) by 50 mm (Figure 3; Table 1). In contrast to the VBGM, all other parameters for the Richards growth function were similar between females and males. Sex-specific differences in predicted length at age were minimal in the first few years of life and became more evident starting at age 3 (Table 2).

Otolith mass

A significant relationship was detected between the natural log of otolith mass and the natural log of age for both sexes when pooled together ($r^2 = 0.91$, df $= 243$, $p < 0.05$) (Figure 4A), suggesting that otolith mass was a strong predictor of age in Blackfin Tuna. The linearized power function for both sexes pooled was

$$\ln(age) = \ln(1.244) + 6.287 \cdot \ln(otolith\ mass),$$

where $a = 1.244 \pm 0.02$ (mean $\pm$ SE) and $b = 6.287 \pm 0.08$. Similarly, a significant relationship between otolith mass and age was also detected for separate regressions for females ($r^2 = 0.95$, df $= 60$, $p < 0.05$) and males ($r^2 = 0.92$, df $= 177$, $p < 0.05$) (Figure 4B,C). Sex-specific differences in the relationship between ln(age) and ln(otolith mass) were also observed (ANCOVA: $F_{1,244} = 46.69$, $p < 0.05$). The relationship between length and age was also examined in a linearized power function to contrast the predictive ability of length and otolith mass on age for Blackfin Tuna. The natural log of CFL was also a good predictor of the natural log of age for all individuals ($r^2 = 0.84$, df $= 243$, $p < 0.05$), with the linearized function as follows:

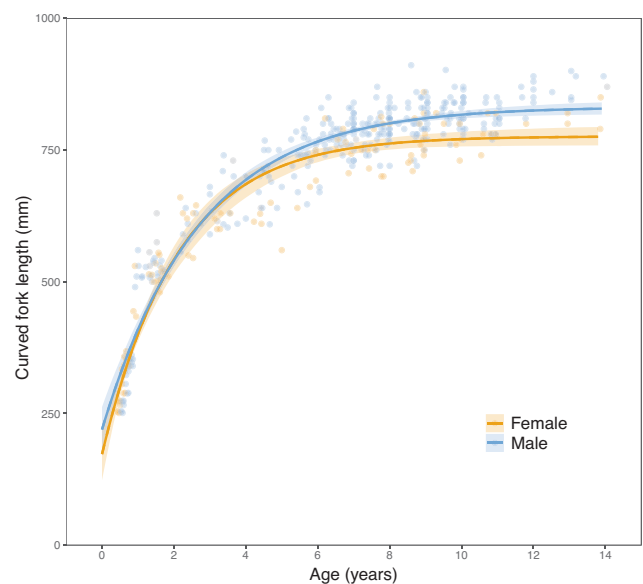$$\ln(age) = \ln(3.060) - 18.362 \cdot \ln(CFL),$$

FIGURE 1 Von Bertalanffy growth model fits and bootstrapped 95% confidence intervals (represented by the shaded polygons) showing length at age for female (orange; $n = 84$) and male (blue; $n = 270$) Blackfin Tuna in the northern Gulf of Mexico.

TABLE 1 Von Bertalanffy growth model (VBGM) and Richards parameter estimates for Blackfin Tuna in the Gulf of Mexico, as well as for females and males separately. Parameter abbreviations are as follows: L_∞ = average maximum asymptotic length (mm), k = growth coefficient (year^{-1}), t_0 = theoretical age (years) when the fish had a length of zero, and a and b are dimensionless parameters that control the horizontal (age) and vertical (size) inflection point position, respectively.

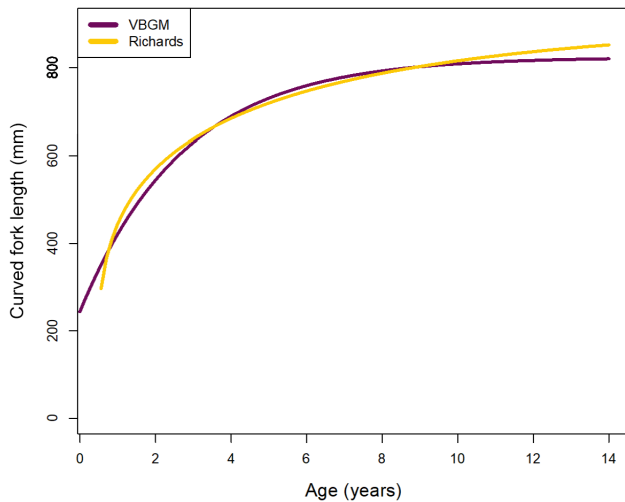| Growth model	Parameters	All ($n = 393$)	Females ($n = 84$)	Males ($n = 270$)
VBGM	L_∞	824	776	832
	k	0.365	0.474	0.371
	t_0	−0.960	−0.531	−0.825
Richards	L_∞	907	857	907
	k	0.112	0.123	0.123
	a	1.05	1.06	1.06
	b	0.25	0.26	0.27

FIGURE 2 Fits for the von Bertalanffy (VBGM; purple) and Richards (yellow) growth models of length at age for Blackfin Tuna in the northern Gulf of Mexico.
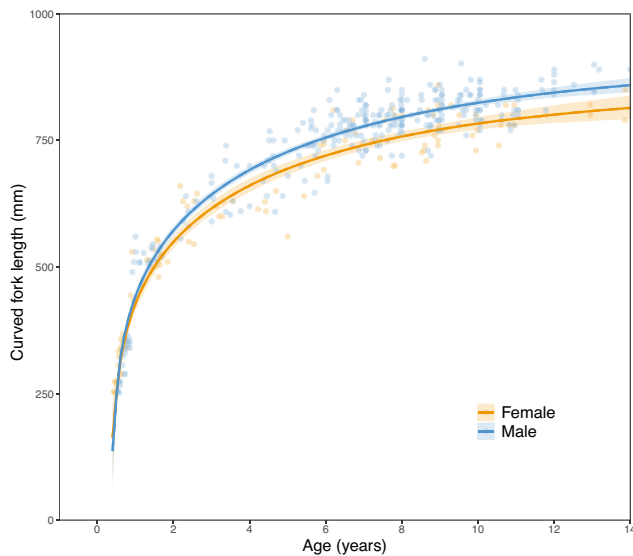

FIGURE 3 Richards growth model fits and bootstrapped 95% confidence intervals (represented by the shaded polygons) showing length at age for female (orange; $n = 84$) and male Blackfin Tuna (blue; $n = 270$) in the northern Gulf of Mexico.

where $a = 3.060 \pm 0.084$ (mean $\pm$ SE) and $b = -18.362 \pm 0.56$. Still, otolith mass explained about 7% more of the variance in age than did CFL ($r^2 = 0.91$ versus 0.84, $\Delta AIC_c = 145.95$).

Mortality

Total instantaneous mortality (Z) estimated from the descending arm of the catch curve was 0.532 (95% CI $= 0.382$ to 0.683) (Figure 5). Natural mortality (M) calculated using different empirical methods, based on either maximum age or growth parameters, was variable and ranged from

0.189 to 0.467 (Table 3). The t_{max} based estimators resulted in M estimates of 0.467 (modified Hoenig approach from Then et al. 2015) and 0.417 (Hoenig 1983 approach) based on a $t_{max} = 13$ from this study. The growth-based estimators resulted in the lowest M estimate of 0.189 (Pauly$_{nls-T}$ approach) and 0.190 (one-parameter K approach). The modified Hoenig estimate of 0.467 was used as the baseline value (baseline M) to scale Lorenzen M across age-classes using the VBGM parameters for all observations. Lorenzen M scaled across age-classes ranged from 1.02 at age 0 to 0.41 at age 13, with a sharp decline in M over the first 4 years of life (Figure 6; Table S1 in the Supplement available separately online).

DISCUSSION

Blackfin Tuna in this study were estimated to be over 13 years old, representing a substantial increase (~6 years) in maximum estimated age compared with previous estimates (Adams and Kerstetter 2014). Still, this is not surprising given that previous otolith-based age estimates for Blackfin Tuna are scarce and limited in sample size (Adams and Kerstetter 2014) and size distribution (Doray et al. 2004). Moreover, recent age validation analyses suggest that both temperate and tropical tunas have greater longevity than previously believed (Restrepo et al. 2010; Andrews et al. 2020), resulting in increased maximum age estimates for several tunas, including congeners in the GOM (Pacicco et al. 2021). While the longevity of Bluefin Tuna can exceed 30 years (Ailloud et al. 2017), estimates of maximum age for Blackfin Tuna from the current study (13+ years) are in accord with recent estimates for other *Thunnus* species, including Yellowfin Tuna (15–18 years; Andrews et al. 2020; Farley et al. 2020; Pacicco et al. 2021), Bigeye Tuna (15–18 years; Farley et al. 2006; Andrews et al. 2020; Farley et al. 2020; Waterhouse et al. 2022), Longtail Tuna *Thunnus tonggol* (18 years; Griffiths et al. 2010), and Albacore (13–15 years; Wells et al. 2013). Thus, this study provides a realistic estimate of longevity for Blackfin Tuna that is similar to other tunas of similar body size (i.e., Albacore) and reasonable relative to larger bodied congeners which might be expected to have longer lifespans.

Age and growth relationships for Blackfin Tuna in the GOM were best described by the Richards growth function. While the VBGM is still the most widely applied model to describe growth in *Thunnus* species (Murua et al. 2017), several recent studies have similarly demonstrated that the Richards model (or derivations of it) provides a better fit to length-at-age data for a range of taxa, including Yellowfin Tuna in the GOM (Pacicco et al. 2021), Bigeye Tuna in the western and

TABLE 2 Median curved fork length at age (CFL) from bootstrapped resampling ($n = 999$) and 95% confidence intervals (95% CI) for Blackfin Tuna pooled (general) and by sex (females and males) using the Richards growth function parameters.

	General		Females		Males	
Ages	CFL	95% CI	CFL	95% CI	CFL	95% CI
1	444	433–454	427	413–439	442	430–453
2	570	562–577	550	538–563	572	563–581
3	638	631–645	617	604–631	643	635–651
4	685	678–692	662	650–676	691	684–700
5	720	713–726	695	684–708	727	721–735
6	747	741–753	721	710–732	755	749–762
7	769	764–774	741	731–751	778	773–783
8	788	783–792	758	749–767	796	792–801
9	803	798–807	772	761–782	812	807–817
10	816	810–821	783	770–795	824	818–831
11	827	819–833	793	778–807	835	828–843
12	836	827–844	801	784–818	845	835–854
13	844	834–854	808	788–828	853	841–864

central Pacific (Farley et al. 2020), Bluefin Tuna in the Atlantic (Ailloud et al. 2017), and Longtail Tuna from the Indo-Pacific (Griffiths et al. 2010). Similar to other tunas, Blackfin Tuna exhibit rapid growth during the first year of life followed by slower growth after age 2, which is likely related to the onset of sexual maturity (Vieira et al. 2005). The Richards model allows for the possibility of multiple inflection points, which gives the model flexibility to account for younger individuals in the population and the fast-growing pattern at earlier stages that is typical of tuna life history, while the VBGM assumes a slower growing pattern at earlier stages of life resulting in a flatter curve (Griffiths et al. 2010). Similar to other studies, the Richards model also produced a higher and more realistic estimate of L_∞ for Blackfin Tuna (907 mm) that was within 1% of the largest fish in the study (911 mm), while estimates from the VBGM were considerably lower (832 mm). The finding that the Richards function also produced lower estimates of k than the VGBM is consistent with previous tuna studies that incorporated both models (Griffiths et al. 2010; Farley et al. 2020; Pacicco et al. 2021) and would be expected given that these parameters are negatively correlated (increase in L_∞ would be expected to result in a lower estimate of k).

Tunas are considered among the fastest growing marine fishes and are capable of reaching large body sizes (Murua et al. 2017). Although growth parameter estimates for Blackfin Tuna are limited, growth parameters from this study differed from previous work. Blackfin Tuna in the GOM exhibited slower growth ($k = 0.112$ versus 0.28/year) and reached a shorter

(albeit similar) mean asymptotic length ($L_\infty = 907$ versus 954 mm) relative to those in the Straits of Florida (Adams and Kerstetter 2014). Even smaller asymptotic lengths (559–785 mm) have been reported for Blackfin Tuna in the Caribbean, but these were estimated from primarily young fish using daily aging methods (<3 years old; Doray et al. 2004), which likely biased L_∞ estimates towards a smaller theoretical maximum. While a k of 0.112/year might seem relatively low for a tuna species, it should be noted that parameters estimated by Adams and Kerstetter (2014) were from the VBGM rather than Richards, and estimates of k from the VBGM in the current study ($k = 0.37$/year) were actually higher in comparison (resulting in a lower L_∞ estimate). In addition, similarly low growth coefficients have been reported for congeners in temperate and tropical areas, such as Atlantic Bluefin Tuna (0.06–0.20/year; reviewed in Ailloud et al. 2017; Murua et al. 2017), Southern Bluefin Tuna (0.11–0.19/year; Gunn et al. 2008; reviewed in Murua et al. 2017), Albacore (0.16/year; Wells et al. 2013), and Bigeye Tuna (0.18/year; Farley et al. 2006), suggesting that relatively slow growth is not uncommon in tunas. In contrast, growth coefficients for other tropical tunas such as Yellowfin Tuna (0.25–0.39/year; Lang et al. 2017; Farley et al. 2020; Pacicco et al. 2021), Bigeye Tuna (0.24/year; Farley et al. 2006), and Longtail Tuna (0.23/year; Griffiths et al. 2010) were considerably higher than those reported for Blackfin Tuna in the current study. This discrepancy could be explained by the fact that Yellowfin, Bigeye, and Longtail tunas reach larger theoretical maximum sizes (>L_∞) than Blackfin Tuna over a relatively similar (or slightly longer) lifespan. For example, Yellowfin Tuna in
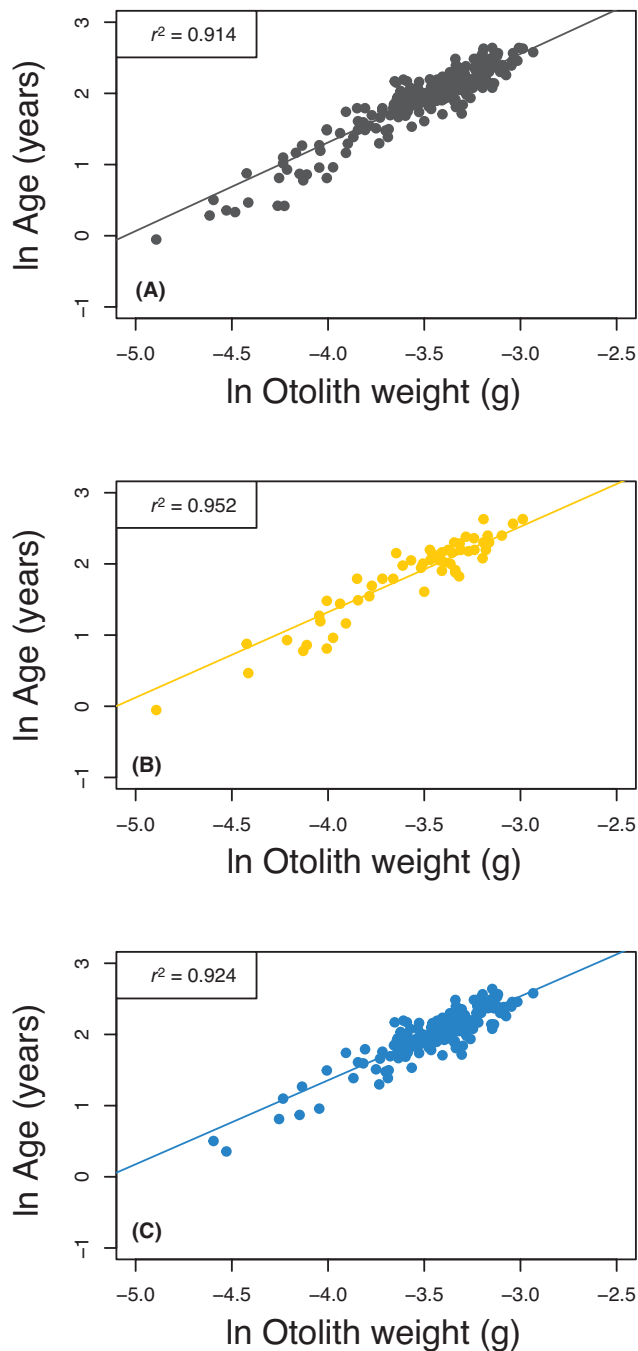
FIGURE 4 Biological age as a function of whole otolith weight for (A) all individuals (gray; $n = 245$; $r^2 = 0.91$; $p < 0.05$), (B) female Blackfin Tuna (orange; $r^2 = 0.95$; $p < 0.05$), and (C) male Blackfin Tuna (blue; $r^2 = 0.92$; $p < 0.05$).
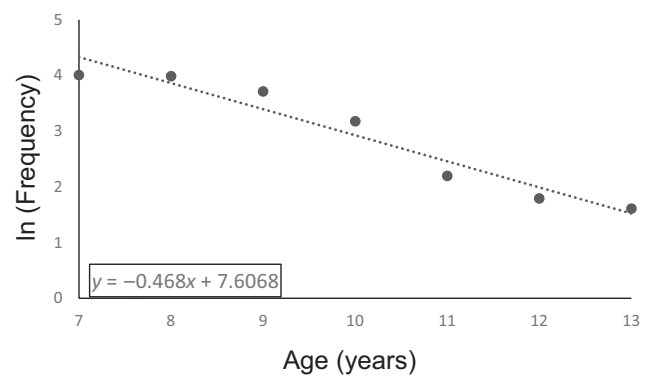

FIGURE 5 The natural log (ln) of catch frequency by age-class was regressed against age (years) for Blackfin Tuna sampled from fisheries in the northern Gulf of Mexico. Total instantaneous mortality (Z) was estimated from the descending arm of the catch curve and is represented by the slope ($Z = 0.53$).

the GOM achieve an L_∞ (1632 mm) almost double that of Blackfin Tuna in 18 years (compared to 13 years for Blackfin Tuna). Finally, it should be noted that VBGM is by far the most widely used model and often produces high estimates of k (see Griffiths et al. 2010; Farley et al. 2020; Pacicco et al. 2021). To that extent, estimates of k for Blackfin Tuna from the VBGM here (0.37/year) were actually quite similar to those estimated for

Yellowfin Tuna (0.35/year) and Bigeye Tuna (0.39/year) with the VBGM (Farley et al. 2020; Pacicco et al. 2021).

Sexual dimorphism is relatively common in marine fishes and has been documented in several tunas (Schaefer 2001; Gunn et al. 2008; Williams et al. 2012; Kolody et al. 2016; Pacicco et al. 2021). Male Blackfin Tuna in the current study reached greater mean maximum size than females, with size differences becoming apparent between age 1 and age 2 and increasing with age. Similar sex-specific differences in growth (males reaching larger sizes) have been documented for Blackfin Tuna in other age and growth studies from the Caribbean (Garcia-Coll et al. 1984) and the East Coast of the United States (Adams and Kerstetter 2014). Likewise, this pattern appears to be consistent across a range of tuna species, with males reaching larger sizes than females in Bigeye Tuna (Farley et al. 2006), Atlantic Bluefin Tuna (Rooker et al. 2007), Southern Bluefin Tuna (Gunn et al. 2008; Lin and Tzeng 2010), Albacore (Williams et al. 2012), and Yellowfin Tuna (Schaefer 1998; Pacicco et al. 2021). Several factors may drive sex-specific differences in growth, although it appears likely that this phenomenon is related to the onset of sexual maturity after which females invest more energy in reproduction relative to somatic growth (Glazier 1999; Lin and Tzeng 2010; Shih et al. 2014). Indeed, Blackfin Tuna become sexually mature between 1 and 2 years of age (Bezerra et al. 2013), which corresponded closely with the observed divergence in sex-specific length at age.

Blackfin Tuna collected from recreational fisheries in the northern GOM were predominately male (~3:1 sex ratio). While this could reflect a bias for males in the recreational fishery due to spatial segregation or sex-specific vulnerability to fishing gear (Maunder et al. 2016), similar male-dominated sex ratios (range of ~2:1 to 4:1) have been observed for Blackfin Tuna throughout their range in the western Atlantic Ocean (Brazil to the United

TABLE 3 Empirical estimates of natural mortality (M) for Blackfin Tuna based on maximum age ($n = 2$) and growth parameters ($n = 2$).

Natural mortality (M)	Equation	Parameters used	Source
0.467	$M = 4.899_{t_{max}}^{-0.916}$	Maximum age	Then et al. (2015)
0.417	$\ln(M) = a - b \ln(t_{max})$	Maximum age	Hoenig (1983)
0.189	$M = 8.87 K^{0.73} L_{\infty}^{-0.33}$	Growth parameters	Pauly (1980)
0.190	$M = aK$	Growth parameters	Beverton and Holt (1959)
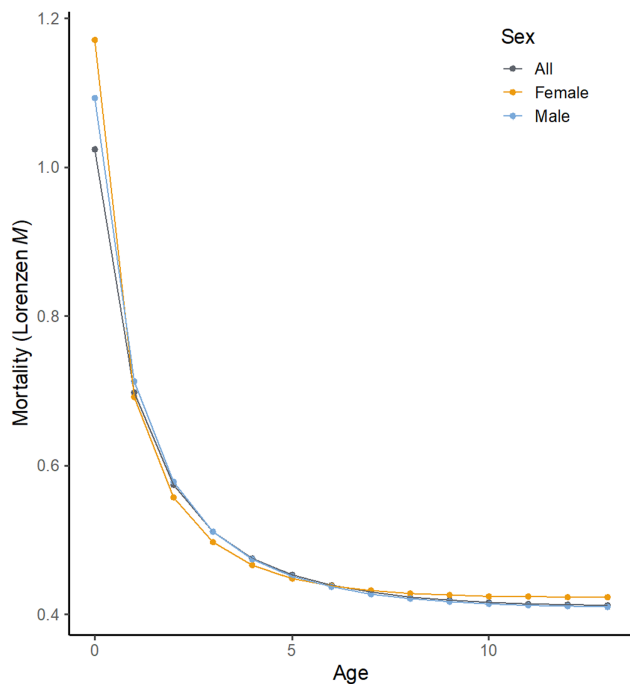
FIGURE 6 Natural mortality (M) for Blackfin Tuna scaled with Lorenzen natural mortality (Lorenzen M) for all observations (gray; $n = 393$) across age-classes and for females (orange) and males (blue).

States) (Freire et al. 2005; Vieira et al. 2005; Bezerra et al. 2013; Adams and Kerstetter 2014). Other tunas typically exhibit sex ratios close to 1:1 early in life, with an increasing skew towards male dominance at larger sizes (Schaefer 2001). Similarly, female Blackfin Tuna were more prevalent (~1:1) at younger ages (0–2) in the current study, with a shift towards male dominance beginning at age 3. Several factors may contribute to the increasing dominance of males with age in tunas, including female predation during spawning, vulnerability to fishing gear, higher natural mortality in females, male hostility during courtship, or sexual dimorphism (Garcia-Coll et al. 1984; Schaefer 1998). Given that female Blackfin Tuna reach smaller maximum sizes, it is possible that females have higher size-based natural mortality than males. Still, it seems likely that this discrepancy is related to spawning or sexual maturity, as the shift in sex ratio to male dominance occurred just after the expected onset of sexual maturity in Blackfin

Tuna (age 1–2; Bezerra et al. 2013). Blackfin Tuna are also smaller and reach sexual maturity earlier than larger tunas, which might explain why the observed shift in sex ratio occurs relatively early for Blackfin Tuna relative to congeners.

Seasonal patterns in MIR and edge type analysis observed here suggest that opaque (slow growth) zones are deposited during winter (January through March). While patterns in both MIR and edge type were not unequivocal, the observed pattern is corroborated by Adams and Kerstetter (2014), who also proposed that increments were formed during winter for Blackfin Tuna in the Straits of Florida. Winter deposition of the annual opaque zone has also been documented for Yellowfin Tuna in the GOM (Lang et al. 2017) and Bluefin and Bigeye tunas in other basins (Farley et al. 2006; Gunn et al. 2008), suggesting that periods of slow growth (in tuna otoliths) are likely more closely linked to cooler water temperatures rather than spawning (summer). Still, variability in marginal increment ratio patterns is not uncommon in tropical tunas and may simply reflect migratory behavior, prolonged spawning seasons, or individual variability in increment formation (Farley et al. 2006). For example, temporal patterns in annuli formation may vary among regions (subtropical versus tropical) and the mixing of migrants and residents could confound seasonal patterns. In contrast, variability could be a result of imprecision in measurements due to diffuse banding during the first few years (also observed here and in other tunas) or inconsistencies in resolution at the otolith edge (Campana 2001). Finally, increment analysis is best performed on younger individuals before annuli become more compressed, and the inclusion of older fish (up to age 5) to achieve appropriate samples sizes in this study could have also contributed to observed variability.

Otolith mass has been shown in multiple studies to be a reliable predictor of age in marine fishes (Cardinale and Arrhenius 2004; Gunn et al. 2008; Griffiths et al. 2010; Pacicco et al. 2021) and may provide a cost-effective alternative to increment counts in areas that lack the resources needed to conduct otolith-based aging (Cardinale and Arrhenius 2004; Williams et al. 2015). Linear (Griffiths et al. 2010) and curvilinear or linearized power functions (Gunn et al. 2008; Pacicco

et al. 2021) have been used to describe relationships between otolith mass and age in tunas, with the latter typically producing a better fit. Here, a strong relationship ($r^2 = 0.91$) between otolith mass and age was observed for Blackfin Tuna in the GOM using a linearized power function, suggesting that otolith mass could be an effective tool for estimating age for the species. Interestingly, the fit was nearly identical to those described for otolith mass and age for Southern Bluefin Tuna (0.90; Gunn et al. 2008) and Yellowfin Tuna (0.91; Pacicco et al. 2021) using either curvilinear or linearized power functions, which could indicate that otolith morphology may be a similarly useful predictor of age for a variety of tunas. The method was also a strong predictor of age for both females ($r^2 = 0.95$) and males ($r^2 = 0.92$) individually; however, similar to recent findings with Yellowfin Tuna (Pacicco et al. 2021), differences between the sexes appears to be biologically minimal. While the development of the otolith mass–age relationship is solely dependent on correct age determination through annuli counting (Cardinale and Arrhenius 2004), these findings provide support to the growing body of evidence that otolith mass and age are tightly coupled (Cardinale and Arrhenius 2004; Gunn et al. 2008; Sanchez and Rooker 2021). Given that many Blackfin Tuna are targeted in artisanal and subsistence fisheries in much of their range, the ability to estimate age from otolith mass could greatly improve existing information on growth, age composition, and mortality needed to assess stocks in regions where otolith-based aging techniques are not possible.

Estimates of mortality are important inputs for stock assessments and are extremely limited or nonexistent for Blackfin Tuna throughout most of the western Atlantic Ocean, including the GOM. Here, the total instantaneous mortality for Blackfin Tuna calculated from catch curves was 0.532/year. This appears to be the first estimate of Z for Blackfin Tuna in the GOM, and it was considerably lower than the Z (2.34/year) estimated for Blackfin Tuna in northeastern Brazil (Freire et al. 2005). This discrepancy could be explained by the fact that estimates by Freire et al. (2005) were based on younger fish (age 0–5 years) than in the current study (0–13 years) and collected in an area where the species is targeted directly in a substantial handline fishery (fishing mortality, $F = 1.40$/year). In contrast, Blackfin Tuna are not directly targeted by commercial fisheries in the GOM and are typically captured in recreational fisheries where the targeted catch is Yellowfin Tuna. Thus, we might expect total instantaneous mortality in the GOM to be more reflective of natural mortality than fishing mortality. Empirical estimation of natural mortality can be highly variable, and here the use of four empirical estimators produced estimates ranging from 0.189 to 0.467/year (mean = 0.316/year). In a recent evaluation of the predictive performance of empirical estimators, Then et al. (2015) recommended the use of an updated t_{max}-based estimator (Hoenig$_{nls}$; $M = 4.899 t_{max}^{-0.916}$) and suggested that computing a mean of multiple estimators offered little additional benefit. This methodology has also been adopted by ICCAT for other Atlantic tuna assessments (ICCAT 2019) and was recently used to estimate M for Yellowfin Tuna in the GOM (Pacicco et al. 2021). Thus, the M estimate for Blackfin Tuna of 0.467/year computed using the Then et al. (2015) equation is most compatible with statistical recommendations and practical application for assessments. Regardless of the method used, natural mortality estimates for Blackfin Tuna in the GOM were low relative to previous estimates from Brazil (0.90/year), which is likely reflective of the relatively young age distribution of fish (age 1–5) in their sample. Natural mortality is typically high in early life stages and estimates for M based on Lorenzen's methodology scaled across age were comparable over similar size ranges in the first few years of life (0.51–1.02/year). Finally, given that Yellowfin Tuna have longer life spans and reach larger sizes than Blackfin Tuna, it is not surprising that estimates of M for Blackfin Tuna (0.467/year) exceeded recent estimates of M for Yellowfin Tuna in the GOM (0.35/year) (Pacicco et al. 2021).

Age structure is often reflective of population sustainability (Berkeley et al. 2004), and the age composition of Blackfin Tuna captured in recreational fisheries in the northern GOM was dominated by older fish (63% > age 5). Blackfin Tuna are not directly targeted in commercial fisheries in the northern GOM, and the similarity between Z and M estimates described here indicate that F is likely minimal. Given that there is no size limit for Blackfin Tuna in the northern GOM recreational fishery, the abundance of older age-classes in the catch could simply be reflective of a healthy and sustainable population (Berkeley et al. 2004; Venturelli et al. 2009). Age truncation (absence of older individuals) is relatively common in exploited tunas (Secor et al. 2014), and the age structure of Blackfin Tuna catch in more directed fisheries in the southwestern Atlantic and Caribbean is dominated by younger fish (age 1–5; Vieira et al. 2005). The relatively low number of individuals in younger age-classes in the GOM suggests that, despite the lack of a size limit, there is also an angler preference or gear bias towards older (larger) individuals contributing to the observed age structure. This is likely explained by the fact that Blackfin Tuna often school with other tunas (Vieira et al. 2005; Bezerra et al. 2013) and are captured in recreational fisheries that primarily target Yellowfin Tuna in the northern GOM (size limit for Yellowfin Tuna = 686 mm).

Tunas are critical components of open ocean ecosystems and are among the most valuable and targeted taxa in global fisheries. This is the first study to examine the age, growth, and mortality for Blackfin Tuna in the GOM and provides needed baseline estimates of size at age, longevity, and natural mortality that can be used to inform future assessments. While Blackfin Tuna currently receive considerably less attention than larger tunas in the Atlantic, recent population declines in many large tunas could lead to increasing focus on smaller, more abundant tunas (Juan-Jordá et al. 2011). Given that Blackfin Tuna are the most abundant tuna in the GOM and Caribbean, such a scenario is certainly plausible. The results provide critical baseline life history information on a data-poor species at relatively low levels of exploitation that can be used as reference points for future studies. Still, comparable data from other regions are lacking, and future studies focused on reproduction, habitat use, and migratory patterns are needed to better identify critical habitats and improve our understanding of Blackfin Tuna population dynamics (e.g., stock boundaries, mixing).

CONFLICT OF INTEREST STATEMENT
The authors state that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data are available upon request from the corresponding author.

ETHICS STATEMENT
This study meets the ethical guidelines outlined by the American Fisheries Society.

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