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Age and Growth of the Sandbar Shark (*Carcharhinus plumbeus*) from the Northern Gulf of Mexico and the Western North Atlantic Ocean

Loraine F. Hale and Ivy E. Baremore

Age and growth analysis of the sandbar shark, *Carcharhinus plumbeus*, from the northern Gulf of Mexico and western North Atlantic Ocean was completed with vertebral samples (n = 1,194). Three parameter von Bertalanffy growth curves were run for male and female sandbar sharks separately, and growth parameters were estimated: theoretical maximum length (L_∞) = 172.9 ± 1.3 cm straight-line fork length [FL], growth coefficient (k) = 0.15 ± 0.01 yr^{-1}, x-intercept (t_0) = −2.3 ± 0.2 SE (male); and L_∞ = 181.2 ± 1.5 cm FL, k = 0.12 ± 0.01 yr^{-1}, t_0 = −3.1 ± 0.2 SE (female). The oldest sandbar shark was a 27-yr-old female, and the oldest male was 22 yr old. The age and growth parameters estimated during this study differed from those in previous studies. The differences in the age and growth parameters may indicate growth overfishing, or they may be due to the bias in sampling from a fishery that targets a limited size range of sharks.

Introduction

Sandbar sharks, *Carcharhinus plumbeus*, are large coastal sharks that inhabit temperate and subtropical waters worldwide (Compagno, 1984). In U.S. waters, they occur from Cape Cod, Massachusetts, to the Caribbean, including the Gulf of Mexico (Springer, 1960). Sandbar sharks have historically been an important component of commercial shark fisheries, and in the United States were harvested for meat and fins (Sminkey and Musick, 1995). Previous studies on the sandbar shark in this region have produced wide ranges in estimated age and growth parameters. Maximum ages of sandbar sharks were estimated from 15 to 30 yr, with a range in age at maturity of 12–30 yr (Casey et al., 1985; Casey and Natanson, 1992; Sminkey and Musick, 1995; Merson, 1998). Most of the investigations into age and growth of the sandbar shark have been conducted over a small spatial range and do not include individuals from all size classes.

Age and growth analysis of the sandbar shark by Sminkey and Musick (1995) had the most robust sample size and size range of any study on the species (SEDAR, 2006). Their examination of a proportion (Chesapeake Bay and coastal Virginia waters) of the U.S. Atlantic Ocean population of sandbar sharks from two distinct time periods (1980–81 and 1991–92) showed a decrease in theoretical maximum length (L_∞) and an increase in the growth coefficient (k) for the latter time period (k = 0.09, L_∞ = 181.4 cm straight-line fork length [FL] for the latter period, sexes combined). However, the age at maturity did not differ significantly (Sminkey and Musick, 1995) between the two time periods, remaining the same at 15–16 yr. The authors theorized that the increase in growth rate may have indicated some effects of reduced population density due to a decline in abundance, but that the long-term population-level consequences (evidenced by a reduction in age at maturity) had not yet been demonstrated due to the long generation time of the sandbar shark. Subsequent studies on the U.S. Atlantic Ocean population have not been conducted; therefore, the impacts of further fishing mortality have not been investigated.

In 2006, the sandbar shark was found to be overfished with overfishing occurring (SEDAR, 2006), and all landings were subsequently prohibited for commercial and recreational fishers (NMFS, 2008). Research recommendations derived from the Stock Assessment Report for Large Coastal Sharks in 2006 suggested that ''additional life history research into sandbar sharks'' be done to ''supplement or replace the available data'' used in the last sandbar shark assessment (SEDAR, 2006). Direct ageing of all fish was requested by industry representatives, because the ''change in stock status [to overfished with overfishing occurring] is mainly attributable to revisions to life history parameters'' (SEDAR, 2006). The age at maturity used in the 2006 assessment was 19.5 yr (Merson, 1998), and was a back-calculation of age at length using the growth curve from Sminkey and Musick (1995). Back-calculation can underestimate the age at length, which could lead to an inflated age-at-maturity estimate (Sminkey and Musick, 1995).

Reliable age and growth estimates are necessary to supply the best available information for

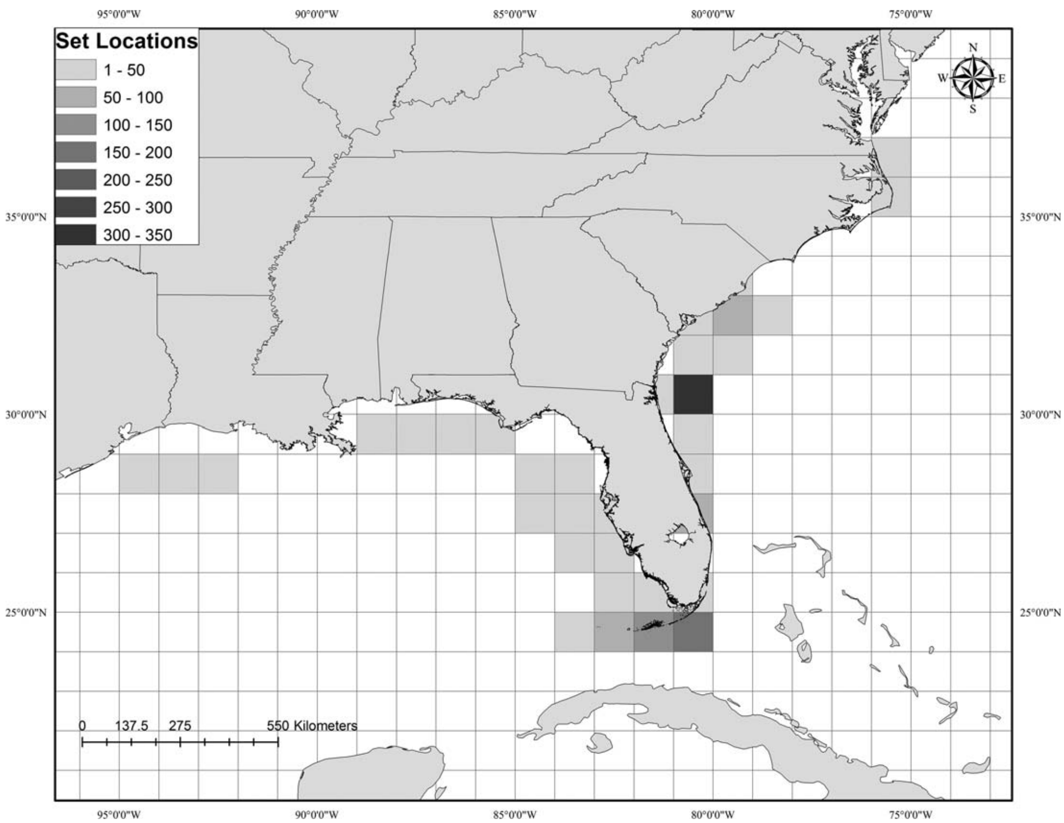


Fig. 1. Map of the number of sets per grid where sandbar sharks (*Carcharhinus plumbeus*) were sampled for age and growth analysis.

stock assessment (Siegfried and Sansó, 2006; Cailliet and Andrews, 2008). As such, amendments to the Consolidated Atlantic Highly Migratory Species Fishery Management Plan implemented a sandbar shark research fishery allowed the National Marine Fisheries Service (NMFS) to select a limited number of commercial shark vessels on an annual basis to collect life history and catch data for future stock assessments (NMFS, 2008). Therefore, the goal of this study was to provide revised age and growth estimates for sandbar sharks using data collected from 2005 to 2010.

Methods

Samples of sandbar shark vertebrae were taken, primarily from 2005 through 2010, by at-sea observers from vessels in the northern western North Atlantic Ocean, including the northern Gulf of Mexico. After the establishment of the research fishery in 2008, sampling protocols became more rigorous and observers were required to sample vertebrae from a minimum of five sandbar sharks per trip. The average hook used by the bottom longline commercial shark fishery (including the sandbar shark research fishery) was an 18/0 offset circle hook. Detailed description of the gear and deployment method can be found in Hale et al. (2010). Additional samples were collected during fishery independent sampling by the South Carolina Department of Natural Resources (SCDNR) and the Gulf States Shark Pupping and Nursery (GULFSPAN) survey using gillnets and longlines in the northeastern Gulf of Mexico and western North Atlantic in coastal waters (Fig. 1). The SCDNR survey deployed a mixture of gillnets and longlines, and the GULFSPAN survey employed only gillnets. Two additional fishery-independent samples were collected by a NMFS survey using a hydraulic longline.

At sea, each shark was sexed and a straight-line fork length (FL) measurement was taken from the tip of the snout to the fork in the caudal fin (±1 cm). A portion of the vertebral column was removed from behind the head anterior to the origin of the first dorsal fin (McAuley et al., 2006). Vertebrae were frozen and sent to the Panama City NMFS laboratory for processing.

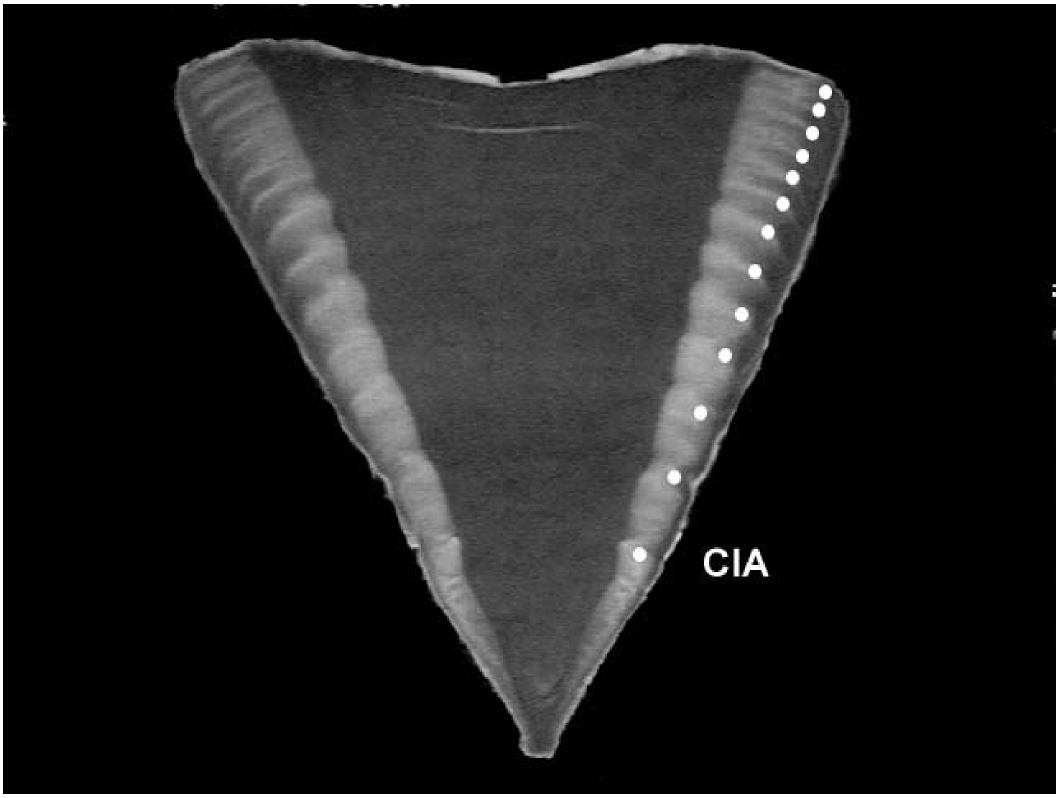


Fig. 2. Image of a 12-yr-old sandbar shark (*Carcharhinus plumbeus*) vertebra with dots marking the annuli. The CIA is the change in angle, also called the birth mark.

Frozen vertebrae were thawed, excess tissue and neural and haemal arches were removed with a knife and/or scalpel, and individual vertebrae were separated with a knife. These vertebrae were placed in a 3–6% sodium hypochlorite (bleach) solution until all excess tissue was dissolved. In some cases, multiple applications of the bleach were necessary to remove all tissue. Cleaned vertebrae were then rinsed for 30 sec under running water, and stored in 70% ethanol. One vertebral centrum from each sample was selected at random for age analysis. The selected centra were affixed to a microscope slide with melted resin and positioned for longitudinal sectioning (Cailliet and Goldman, 2004). Slides were mounted on a varying-speed IsoMet saw, and a 0.6-mm section was removed using two 4-inch Norton superabrasive grinding wheels, separated by a divider. One half of the ''bow-tie'' section was stained with crystal violet, and both sections were dried for 10 min before mounting to a labeled microscope slide using Cytoseal mounting medium. Slides were allowed to dry overnight and then stored in a slide box.

Sectioned vertebrae were aged using reflected light on a Meiji Techno dissecting microscope. Concentric growth bands were considered to be one annulus (one opaque and one translucent band in the corpus calcareum), with the first band associated with the change in angle assigned as the ''birth mark'' (Cailliet and Goldman, 2004) (Fig. 2). Vertebrae were read independently by two readers, without knowledge of the size or sex of the shark. If a section was considered too difficult to interpret by either reader, a second vertebral centrum was sectioned and reread. When independent ages differed, the readers concurrently viewed the sections digitally and read the bands until a consensus band count was reached. If an agreement could not be reached or if the section could not be read, the section was excluded from analysis. To keep ageing methodology consistent with previous studies, the ''age'' of each shark was the number of band counts, less the first band, which was considered the birth mark: age = band count − 1.

Indices of precision were employed to determine how variable the readers were when assigning ages. The percentage of agreement (PA) between readers and the PA ± 1 yr between readers was determined by dividing the number of assessed ages agreed upon by the total number of vertebrae examined (Cailliet and Goldman, 2004; Goldman, 2004). Additionally, the average percentage of error (APE) (Beamish and Fournier, 1981) was calculated for the consensus counts to indicate the between-reader error. The equation was

$$\mathrm{APE}=\left[\frac{1}{N}\sum_{j=1}^{N}\left(\frac{1}{R}\sum_{i=1}^{R}\frac{|X_i-X_j|}{X_j}\right)\times 100\right],$$

where N is the number of animals aged, R is the number of readings, X_{ij} is the count from the jth animal at the ith reading and X_j is the mean age of the jth animal from i readings. A Bowker's and McNemar χ^2 test of symmetry was used to test for systematic reader bias in the assessment of age (Hoenig et al., 1995; Goldman, 2002).

To estimate growth coefficients, the von Bertalanffy growth function (vBGF) was fitted to observed age and length data for the sandbar shark based on vertebral annulus counts using a least-squares nonlinear regression in R (R Development Core Team, 2009). The vBGF used was:

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

where L_t was the predicted fork length (cm) at time t, L_∞ was the theoretical asymptotic fork length (cm), k was the growth coefficient (yr^{-1}) and t_0 was the x-intercept (von Bertalanffy, 1938; Cailliet et al., 1983). A modified two-parameter von Bertalanffy growth function (2pvBGF) (Fabens, 1965) was fit to assessed age-at-length data using R. The 2pvBGF uses the known fork length at birth (L_0) for t_0. The equation used was the following:

$$L_t=L_\infty\left(1-be^{-kt}\right)$$

where $b = (L_\infty - L_0)/L_\infty$ and L_0 is the FL at birth. The L_0 value used for this model was 46 cm FL based on the average FL of the largest *in utero* near-term pups and the smallest neonates captured (Baremore and Hale, 2012). This value is similar to the range found by Springer (1960) in the U.S. Atlantic Ocean of 37–54 cm FL.

Males and females were analyzed separately and a likelihood ratio test ($\alpha = 0.05$) (Kimura, 1980) was used to determine whether there was a significant difference in growth coefficients between sexes. If no difference was found between the sexes, each model was rerun using pooled data between sexes. The goodness of fit of the growth models was evaluated by examining the residual sums of squares, the Akaike information criterion (AIC), and examination of the residual plots (Goldman, 2004; Carlson and Baremore, 2005).

Results

A total of 1,194 sandbar sharks (n = 701 females, n = 493 males) were analyzed for age and growth. The majority of vertebral samples (81.9%) were taken by at-sea observers from the Shark Bottom Longline Observer Program, including the Sandbar Shark Research Fishery. FLs of sandbar sharks sampled ranged from 39 to 202 cm, with an average of 152.4 cm FL for females and 149.9 cm FL for males (Fig. 3A). Age estimates ranged from 0 to 27 yr old, with the oldest female estimated to be 27 yr and the oldest male estimated to be 22 yr (Fig. 3B). The average age was 13.1 yr (±4.5 SD) for females and 12.6 yr (±4.1 SD) for males.

Overall APE was low (3.49%) and PA was high (90.1%) between readers and between the two readers and the final agreed-upon age (Table 1). Bias between and among readers was not significant; however, older fish (> 25 yr) showed more error between readers based on age-bias plots (Table 1, Fig. 4A,B). The increase in error between readers was likely due to an increase in difficulty of age interpretation of the bands on the edges of the vertebrae in the oldest fish (McAuley et al., 2006). Additionally, the low sample size of sandbar sharks older than 19 yr magnified the differences in age estimation between the readers (McAuley et al., 2006). The Bowker's and McNemar χ^2 test of symmetry showed no systematic ageing bias between readers (no consistent over- or underageing between readers); however, within readers there was a marginally significant difference (< 0.05) between the first read and the final age determination (Table 1).

The likelihood ratio test showed that there was a significant difference between sexes (χ^2 = 545.8 (vBGF), 537.8 (2pvBGF), df = 3, $P <$ 0.001); therefore, growth curves were reported for each sex separately. The vBGF and the 2pvBGF both provided good fits to the data, and the three-parameter function had the lowest residual sums of square and the lowest AIC. The vBGF parameter estimates were L_∞ = 172.9 cm FL, k = 0.15 yr^{-1}, and t_0 = −2.3 for males (Fig. 5a, Table 2), and L_∞ = 181.2 cm FL, k = 0.12 yr^{-1}, and t_0 = −3.1 for females (Fig. 5b, Table 2). Residual plots for the vBGF showed randomly distributed error for both sexes. The 2pvBGF parameter estimates were L_∞ = 172.1 cm FL, and k = 0.15 yr^{-1} for males (Fig. 6a, Table 2), and L_∞ = 178.3 cm FL and k =

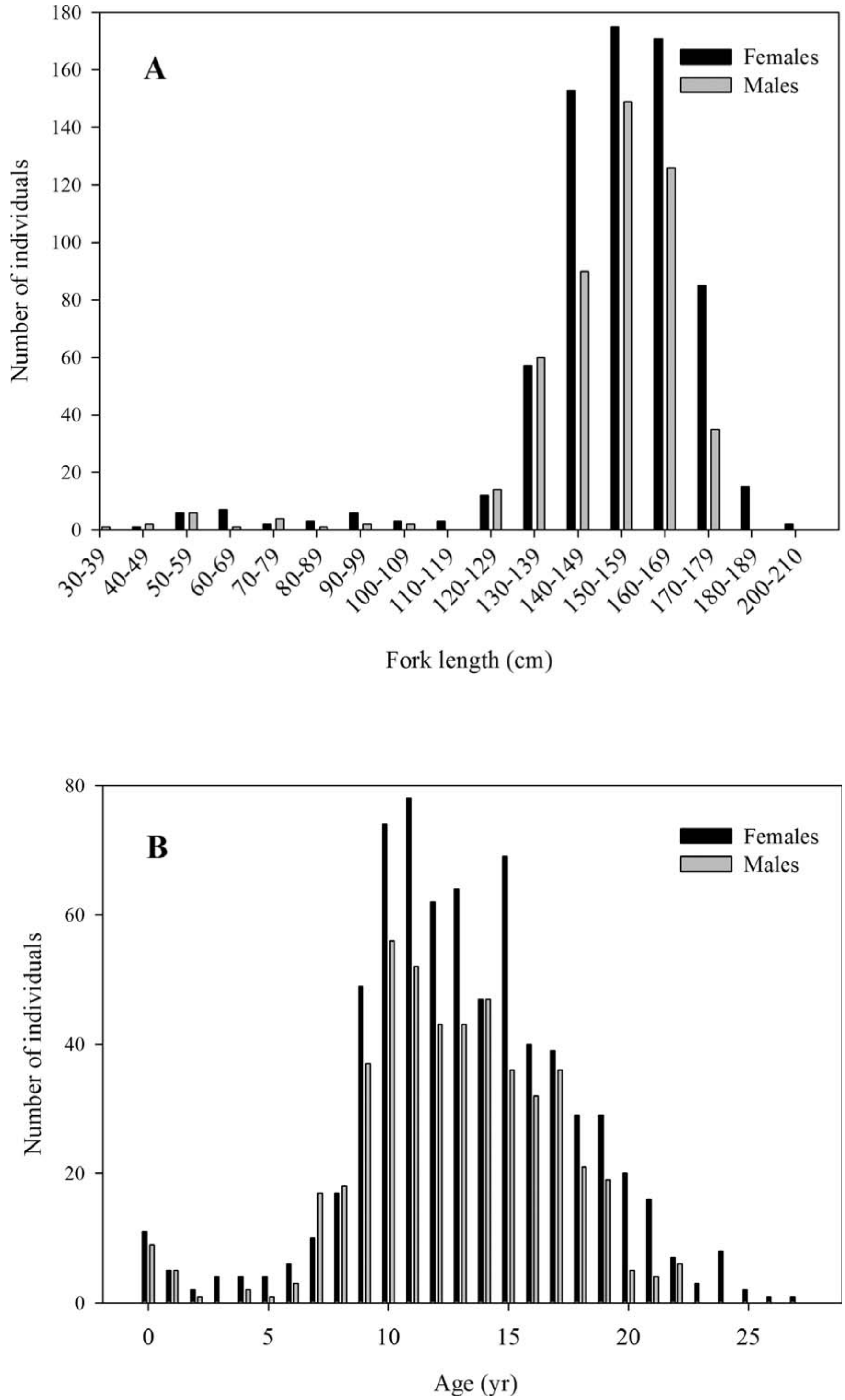


Fig. 3. Frequency of (A) fork length (n = 493 males and 701 females) and (B) ages of sandbar sharks (*Carcharhinus plumbeus*) (n = 493 males and 701 females) used in age and growth analysis.

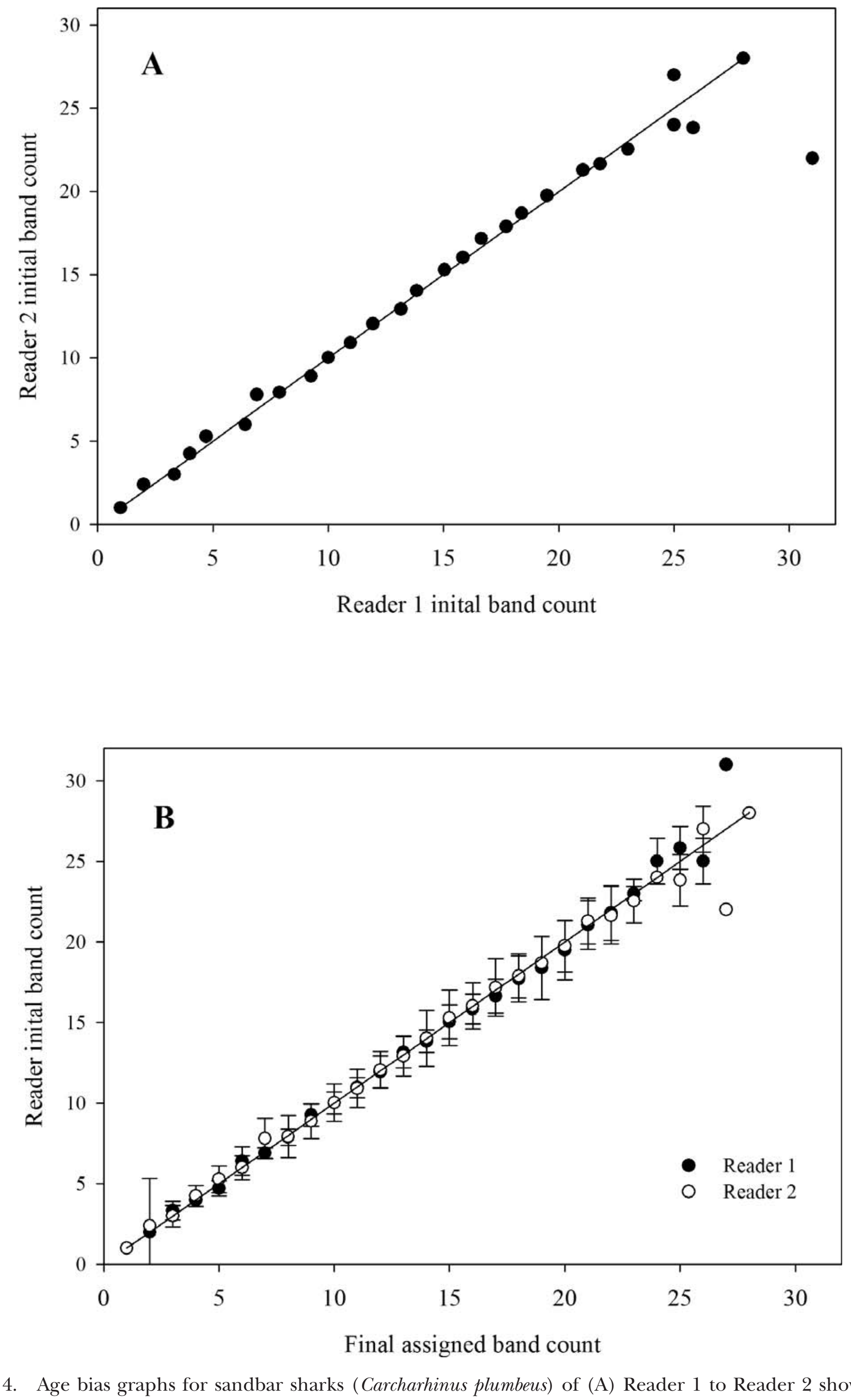


Fig. 4. Age bias graphs for sandbar sharks (*Carcharhinus plumbeus*) of (A) Reader 1 to Reader 2 showing no systematic bias between readers and (B) Reader 1 and Reader 2 vs final band count age bias graph. The solid line represents a 1:1 relationship, and error bars are standard deviation.

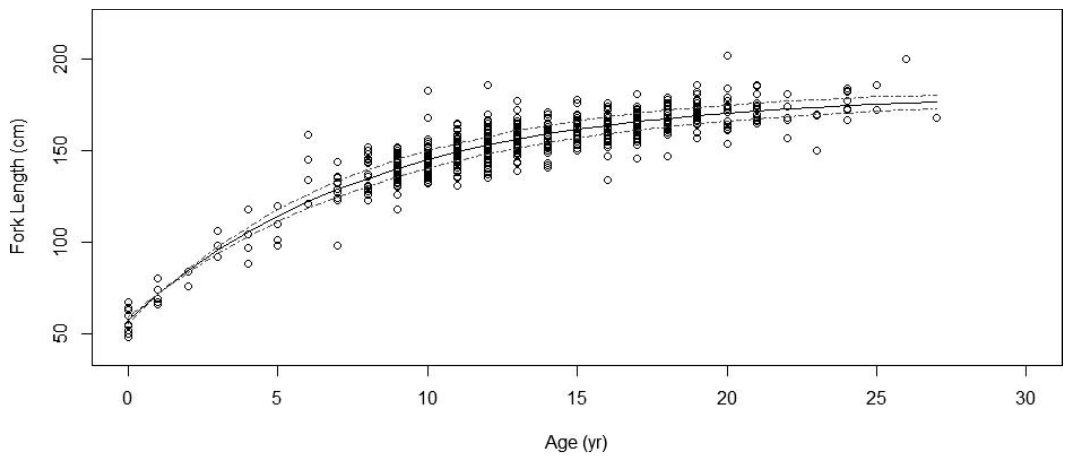
TABLE 1. Reader precision and bias analysis for sandbar shark (*Carcharhinus plumbeus*) age and growth analysis in the western North Atlantic Ocean and Gulf of Mexico.

Reader comparison	% Agreement	% Agreement ± 1 yr	Bowker's test χ^2_{calc}	Bowker's test df	Bowker's test P value	McNemar's test χ^2_{calc}	McNemar's test df	McNemar's test P value
1 vs 2	48.4	82.1	86.9	68	0.06	0.5	1	0.49
2 vs final	58.6	85.9	78.7	57	0.03	4.2	1	0.04
1 vs final	60.1	90.1	76.5	62	0.10	4.9	1	0.03

0.14 yr^{-1} for females (Fig. 6b, Table 2), both with randomly distributed residuals.

DISCUSSION

For this study, large numbers of sandbar sharks were sampled throughout the species' range in the United States (from North Carolina to the Florida Keys and the Gulf of Mexico) in a recent time period (2005–10). The results of this study provide valuable age and growth estimates for the sandbar shark in the U.S. Atlantic Ocean and Gulf of Mexico, which were used in the 2010 stock assessment for the species (SEDAR, 2010). The focus on directly ageing each sample, sampling in a finite time frame, and sampling



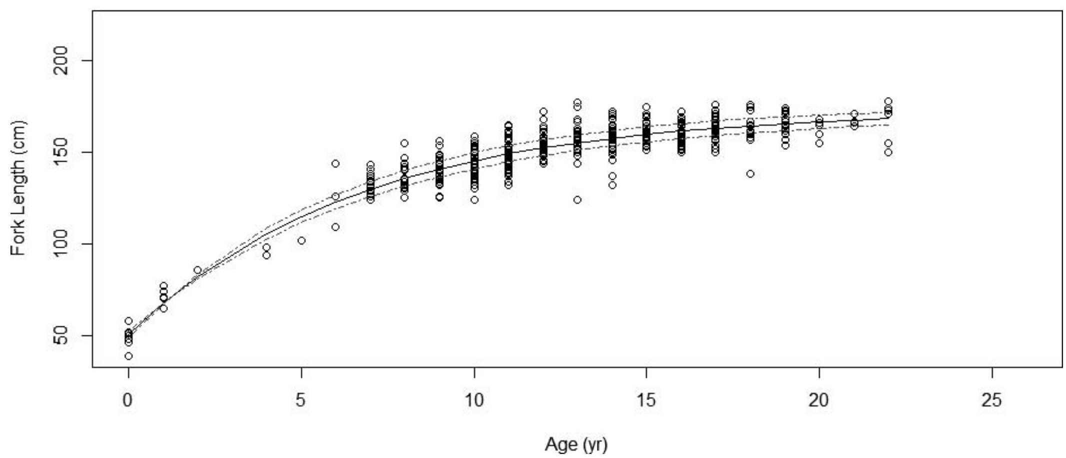


Fig. 5. von Bertalanffy growth curve for (A) male (n = 493, R^2 = 0.88, $P <$ 0.0001) and (B) female sandbar sharks (*Carcharhinus plumbeus*) (n = 701, R^2 = 0.85, $P <$ 0.0001). Model estimates are represented by black solid lines with dashed 95% confidence intervals.

TABLE 2. Growth curve parameters estimated for the sandbar shark (*Carcharhinus plumbeus*) in the western North Atlantic Ocean and Gulf of Mexico.

Growth curve[a]	Sex	n	L_∞ (cm FL) (± SE)	k (± SE)	AIC	Residual sums of squares
vBGF	F	701	181.2 ± 1.5	0.12 ± 0.01	4,899.3	44,012
vBGF	M	493	172.9 ± 1.3	0.15 ± 0.01	3,343.2	25,025
vBGF	Combined	1,194	177.9 ± 1.0	0.13 ± 0.01	8,261.4	70,231
2-parameter vBGF	F	701	178.3 ± 1.2	0.14 ± 0.01	4,929.3	46,066
2-parameter vBGF	M	493	172.1 ± 1.5	0.15 ± 0.01	3,346.4	25,293
2-parameter vBGF	Combined	1,194	175.9 ± 0.9	0.14 ± 0.01	8,293.7	72,278

[a] Abbreviations: vBGF, von Bertalanffy growth function; L_∞, theoretical maximum length; FL, straight-line fork length; k, growth coefficient; AIC, Akaike information criterion; M, male; F, female.

throughout the geographical range of the fishery reduced the inconsistencies that were faulted in earlier studies. Most other studies relied on samples from multiple gears, protracted periods of sampling, and/or limited geographical range of samples (Table 3). In addition, some studies used tag–return data or back-calculated length at age instead of directly ageing each shark, which

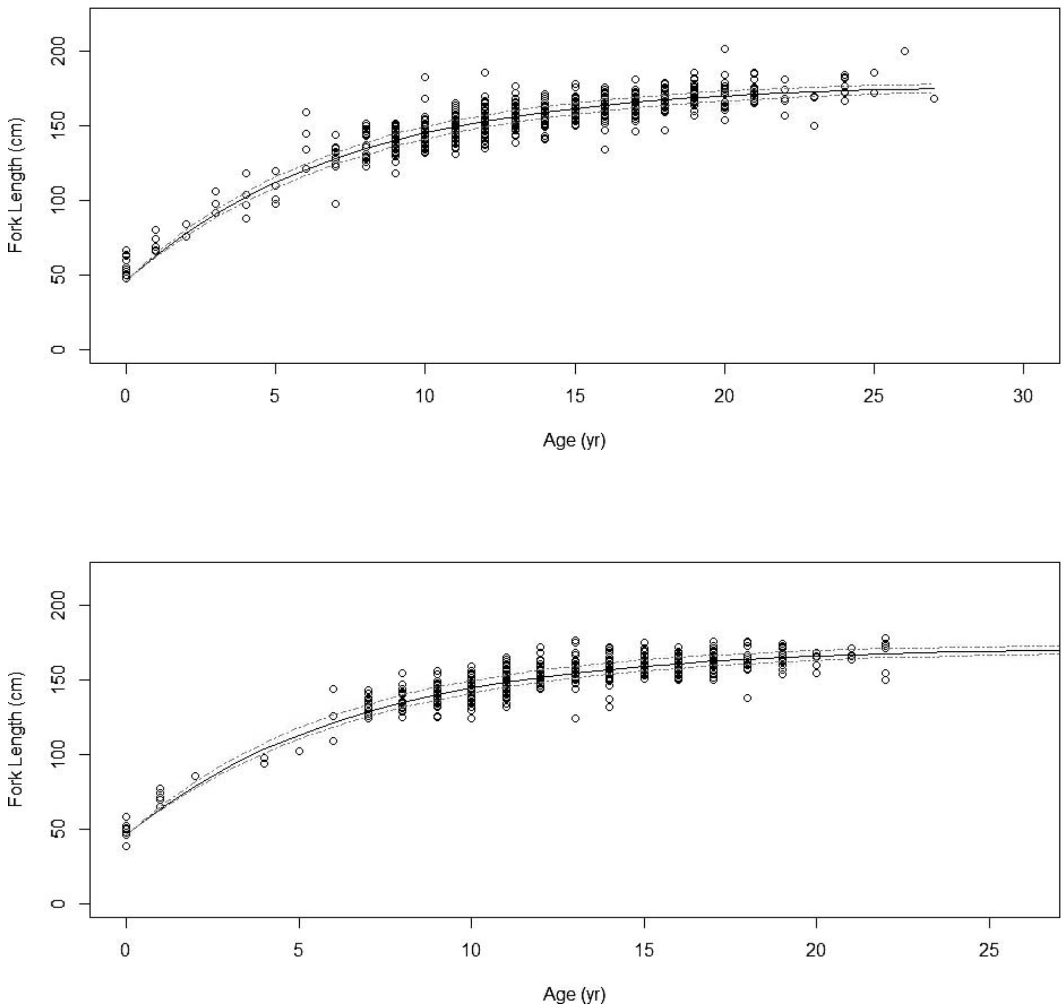


Fig. 6. Two-parameter von Bertalanffy growth curve for (A) male (n = 493, R^2 = 0.88, $P < 0.0001$) and (B) female sandbar sharks (*Carcharhinus plumbeus*) (n = 701, R^2 = 0.85, $P < 0.0001$). Model estimates are represented by black solid lines with dashed 95% confidence intervals.

TABLE 3. Age and growth analysis estimates for the sandbar shark (*Carcharhinus plumbeus*) from the current and previous studies (lengths were converted to straight-line fork length using conversions calculated in each publication). Blanks indicate data that were not reported.

Study	Sex	n	Size range (cm FL)	L_∞ (cm FL) ($\pm$ SE)	k ($\pm$ SE)	t_0 ($\pm$ SE)	Length at birth (cm FL)	Maximum estimated age	Age at maturity	Size at maturity
Present study	F	701		181.2 ± 1.5	0.12 ± 0.01	−3.1 ± 0.2	46	27	13.1	156
Present study	M	493		172.9 ± 1.3	0.15 ± 0.01	−2.3 ± 0.2	46	22	14.1	158
Present study	Combined	1194	39–202	177.9 ± 1.0	0.13 ± 0.01	−2.8 ± 0.1	46	27		
Casey et al., 1985	F	299	45–154	298	0.04	−4.9	47.7	21	12	203.4
Casey et al., 1985	M	176	44–204	257.3	0.05	−4.5	47.7	15	13	153.9
Casey and Natanson, 1992	Combined	442		185.8	0.05	−6.45	47.7	32–40+	30	186
Sminkey and Musick 1995 (1980–81)	F	150		217.7	0.06	−4.8			15–16	150.6
Sminkey and Musick, 1995 (1980–81)	M	38		203.4	0.06	−5.4			15–16	149.5
Sminkey and Musick, 1995 (1980–81)	Combined	188	57–190	219.9	0.06	−4.9		25	15–16	150.6
Sminkey and Musick, 1995 (1990–91)	F	191		182.5	0.09	−3.9			15–16	150.6
Sminkey and Musick, 1995 (1990–91)	M	223		183.6	0.09	−3.8			15–16	149.5
Sminkey and Musick, 1995 (1990–91)	Combined	412	48–178	181.4	0.09	−3.8		25	15–16	150.6

[a] Abbreviations: FL, straight-line fork length; L_∞, theoretical maximum length; k, growth coefficient; t_0, x-intercept; M, male; F, female.

can lead to an underestimation of mean length at age unless validated (Campana, 1990; Francis, 1990; Goldman et al., 2006). To date, validation for the annual periodicity of band formation is limited to neonates (Branstetter, 1987) and younger age classes in the U.S. Atlantic Ocean (Casey et al., 1985) and Australian sandbar sharks up to 8 yr old (McAuley et al., 2006). Other methods of band deposition verification were not considered for this study due to the paucity of animals with fewer than six band pairs: band pairs in older individuals were stacked and difficult to accurately measure. Centrum edges were similarly difficult to classify (Goldman et al., 2006). This study as well as most others assume that annual periodicity of band formation does not change with age (Sminkey and Musick, 1995; McAuley et al., 2006).

The oldest estimated age of a sandbar shark from this study was 27 yr; the maximum estimated age was 25 yr from Sminkey and Musick (1995) and McAuley et al. (2006). In this study, there were few sandbar sharks estimated to be older than 19 yr, and band elucidation in the oldest sharks led to uncertainty in age estimation (McAuley et al., 2006). However, it is not unreasonable to estimate that sandbar sharks could have longevities much longer than 20 yr based on our age estimations. Recent bomb radiocarbon dating of sandbar shark vertebrae indicated this species is longer lived than previously thought, and suggested that age may be underestimated using growth-band counting for sharks greater than 10–12 yr of age (Andrews et al., 2011). McAuley et al. (2006) reported that when estimated ages were extrapolated to the maximum reported size for sandbar sharks in Australian waters, maximum age could be as high as 41 yr for males and 36 yr for females. Casey and Natanson's (1992) revision of earlier age and growth estimates (Casey et al., 1985) suggested longevity estimates of over 50 yr based on individuals that were recaptured and aged after more than 17 yr at large. However, caution should be applied to estimates based on tag–recapture data because the variability in growth of tagged fish is not comparable to snapshot age growth estimates and should not be used for verifying length-at-age data (Francis, 1988).

The L_∞ for females was similar to estimations by Sminkey and Musick (1995) for the 1991–92 time period, but the L_∞ for male sandbar sharks in this study was lower. However, Sminkey and Musick (1985) theorized an L_∞ for males that was larger than females, which is rare in elasmobranch species (Cortés, 2004). The larger maximum size for males estimated by Sminkey and

Musick (1985) may have been skewed by fewer large male samples. The k estimated from this study was almost twice that estimated by Sminkey and Musick for the 1991–92 time period. The k and L_∞ parameters are inversely correlated in the growth model estimation; therefore, the higher k value in this study might indicate a more realistic asymptote in the model (Sminkey and Musick, 1995), rather than any population level changes in growth rate.

The maximum observed length for sandbar sharks in the study was a 202-cm FL female. Within the research fishery, the overall average length from all sandbar sharks caught and measured for females was 155.3 cm FL and 153.6 cm FL for males, and few sandbar sharks over 200 cm FL have been observed in the commercial shark fishery over the last 5 yr (Hale et al., 2010). McAuley et al. (2006) noted the scarcity of the very largest sandbar sharks in Australian waters. Historically, Springer (1960) found a mean length for sandbar sharks in the U.S. Atlantic Ocean of 199.9 cm FL for females (180.3–226.1 cm FL range) and 210.6 cm FL for males (182.9–236.2 cm FL range). The lack of observed large, old fish in this study or in the fishery as a whole is probably due to the bias length ranges sampled by the fishery, but could also indicate a lack of those larger, older fish in the population (McAuley et al., 2006; Cailliet and Andrews, 2008).

Baremore and Hale (2012) determined age at maturity and reproductive periodicity for the sandbar shark in the northern Gulf of Mexico and western North Atlantic Ocean concurrently with this study. The size and age at 50% maturity was 151.6 cm FL (12.1 yr) for males and 154.9 cm FL (13.1 yr) for females. Given that the average age of sandbar sharks in this study was 13.1 yr for females and 12.6 yr for males, landings data indicate the average sandbar shark caught in the sandbar shark fishery is at the cusp of maturity. Earlier age-at-maturity estimates from back-calculated length at age were much older (Merson, 1998), and may have inflated the age at maturity due to the tendency of back-calculation to underestimate age at length (Francis, 1990; Sminkey and Musick, 1995). The age at maturity in this study more closely matches that of Sminkey and Musick (1995), which was 1–2 yr older at a smaller length.

The differences in the age and growth parameters estimated by this study as compared to those estimated by Sminkey and Musick (1995) from the early 1990s may indicate growth overfishing, especially coupled with the reduction in maximum observed size as compared to historical records (Springer, 1960; Walker et al., 1998; Cailliet and Andrews, 2008). Recent management changes have prohibited commercial landings of the sandbar shark outside the research fishery, and have thus reduced fishing effort on the U.S. Atlantic Ocean sandbar shark population. However, with generation times of 20 yr or more, the effects of growth overfishing still remain difficult to elucidate. Analyses such as looking at changes in band radius could further elucidate whether growth differences are due to growth overfishing or another factor (Walker et al., 1998).

The differences found may also be a reflection of the relatively small number of sharks aged younger than 9 yr (n = 119) or aged older than 19 yr (n = 73) sampled in this study, even with the larger sample size and range utilized. Because the majority of samples came from the commercial shark bottom longline fishery, gear selectivity could have biased the results (Walker et al., 1998; Thorson and Simpfendorfer, 2009). However, the broad range of ages sampled, especially of animals > 20 yr, likely minimized the bias associated with gear selectivity. Ongoing sampling of the fishery will enable periodic reanalysis of the age structure of sandbar sharks in the fishery. This type of monitoring will allow for gear selectivity effects to be determined for future stock assessments.

The results of this study highlight the necessity for accurate and updated life history information for stock assessments of commercially important species such as the sandbar shark. Past life history studies of the species have led to contentious stock assessments, which could have decreased the confidence of stakeholders in the management actions as a result of the assessments (SEDAR, 2006). This study also demonstrates how novel approaches to management, such as the development of research fisheries that provide access to biological samples that are otherwise difficult to obtain, can produce valuable information that is otherwise nearly impossible to collect. The ongoing collaboration between scientists and the participating sandbar shark fishers will enable continued monitoring of the age structure of this stock to provide updates to stock assessment scientists in the future.

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National Oceanic and Atmospheric Administration–National Marine Fisheries Service, Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, Florida 32408. Present address (IEB): Mar Alliance, P.O. Box 283, San Pedro, Ambergris Caye, Belize. (LFH) Deceased. Send reprint requests to IEB.
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