Age and growth of the sandbar shark, *Carcharhinus plumbeus*, from the Gulf of Mexico and the United States southern Atlantic Ocean

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Abstract

Age and growth analysis of the sandbar shark, *Carcharhinus plumbeus*, from the Gulf of Mexico and southern Atlantic Ocean was completed with vertebral samples primarily gathered from the sandbar shark research fishery (n = 1194). Three parameter von Bertalanffy growth curves were run for male and female sandbar sharks separately and growth parameters were estimated as a male L_∞ = 172.97 ± 1.30 cm FL, female L_∞ = 181.15 ± 1.45 cm FL, male k = 0.15 ± 0.005, female k = 0.12 ± 0.004, male t_0 = -3.09 ± 0.19, and female t_0 = -2.33 ± 0.16. The oldest aged sandbar shark was a 27 year old female. The age and growth analysis of the sandbar shark in this study represented a concerted effort to collect current samples from the commercial shark bottom longline fishery to better describe the age structure of the sandbar shark population based on recommendations from SEDAR 11.

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 in the U.S. waters are genetically of a single stock (Heist et al. 1985).

Research recommendations derived from the Stock Assessment Report for Large Coastal Sharks (SEDAR 11) 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. Herein, we report on a revised age and growth model for sandbar shark for data collected from 2005-2010.

Methods

Recent amendments to the Consolidated Atlantic Highly Migratory Species Fishery Management Plan based on updated stock assessments have eliminated the major directed shark fishery in the U.S. Atlantic (NMFS 2007). The amendments implemented a shark research fishery, which allowed NMFS to select a limited number of commercial shark vessels on an annual basis to collect life history data and catch data for future stock assessments. Samples of sandbar shark vertebrae (81.9%) were taken primarily from this fishery from 2005 through 2010 by at-sea observers from vessels in the Gulf of Mexico and southern Atlantic Ocean, and fishery independent sampling using gillnets and handlines (Figure 1).

Samples obtained by at-sea observers from the bottom longline commercial shark fishery (including the sandbar shark research fishery) had the following gear characteristics: an average length of the monofilament mainline of 15.1 km, an average number of hooks as 513.6 hooks, and the most common size and type of hook utilized was 18.0 circle hooks. Additional samples came from a variety of fishery-independent sampling sources in the Gulf of Mexico and South Atlantic. The South Carolina Department of Natural Resources (SCDNR) survey deployed a mixture of gillnets and longlines. The hydraulic longline was 275 m in length, with 40 gangions set with 15.0 offset circle hooks, the hand-deployed longline consisted of 306 m of mainline with 50 12/0 offset circle hooks, and the gillnet was 231 m long , 3 m deep, and had a stretch mesh of 10.3 cm. The Gulf States Shark Pupping and Nursery Survey (GULFSPAN) was strictly a gillnet survey with six 33 m panels of 7.6 - 13.9 cm stretch mesh. Two additional fishery-independent samples were collected by a survey using a hydraulic longline with 1.85 km set with 100 20.0 offset circle hooks in the Gulf of Mexico.

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. Vertebral centra were 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 NOAA Fisheries laboratory for processing.

Frozen vertebrae were thawed, excess tissue and neural and haemal arches were removed with a knife and/or scalpel, and individual vertebral centra were separated with a knife. These vertebrae were placed in a 3-6% sodium hypochlorite (bleach) solution until all extraneous tissue was dissolved. In some cases, multiple applications of the bleach were necessary to remove all tissue. Cleaned vertebrae were then rinsed for 30 seconds under running water, and stored in 70% ethanol. One vertebral centrum from each sample was selected at random for age analysis. The centra were affixed to a microscope slide with melted resin, positioned for longitudinal sectioning (Cailliet and Goldman, 2004). Slides were mounted on a Bueller isomet saw, and a 0.6 mm section was removed using two Norton Superabrasive Grinding Wheels, separated by a divider. One half of the ‘bowtie’ section was stained with crystal violet, and both sections were dried for 10 minutes 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 microscope. Concentric growth bands were considered to be one annulus (one opaque and one translucent band), with the first band associated with the change in angle being the 'birth mark' (Figure 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 viewed the sections digitally and concurrently 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. The 'age' of each shark was the number of band counts, less the first band, which was considered the birth mark: Age = Bands - 1.

To estimate growth coefficients, the von Bertalanffy growth model (vBGF) was fitted to the assessed age-at-length data for the sandbar shark based on vertebral annuli counts using a least-squares non-linear regression in R (R Development Core Team 2010). The von Bertalanffy growth equation used was

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

where L_t was the predicted fork length (cm) L at time t, L_∞ was the theoretical asymptotic fork length (cm), k was the growth coefficient (year^{-1}) and t_0 was the time when length theoretically equals zero (von Bertalanffy, 1957; Cailliet et al., 1983). A modified two-parameter von Bertalanffy growth model (2pvBGF) was fit to assessed age-at-length data using R (R Development Core Team 2010, Fabens 1965). The Fabens model sets $t_0 = 0$ and uses the known fork length at birth (L_0). The equation used was

$$L_t = L_\infty\left(1 - b * e^{-kt}\right) = L_\infty - \left(L_\infty - L_0\right)e^{-kt}$$
$$b = \frac{\left(L_\infty - L_0\right)}{L_\infty} = e^{kt_0}$$

where L_0 is the disc width at birth and all other parameters are as in the three-parameter von Bertalanffy growth model (Fabens 1965). The L_0 used for this model was 46 cm fork length based on the average fork length of the largest in utero near-term pups plus the fork length of smallest neonates captured (Baremore and Hale 2010).

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

Indices of precision were employed to determine how variable the readers were in their ages. The percent agreement (PA) between readers and the PA ±1 year between readers was determined by dividing the number of assessed ages agreed upon by readers by the total number of vertebrae examined (PA = (No. agreed/No. read)*100; Cailliet & Goldman, 2004; Goldman, 2004). Additionally, the average percentage error (APE, Beamish and Fournier 1981) was calculated for the consensus counts to indicate the between-reader error

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

where N is the number of animals aged, R is the number of readings, Xij is the count from the jth animal at the ith reading and Xj is the mean age of the jth animal from i readings. A Bowkers 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).

Results

A total of 1194 sandbar sharks (n = 701 females, n = 493 males) were analyzed for age and growth analysis. Fork lengths (cm) of sandbar sharks sampled ranged from 39 cm to 202 cm, with an average of 152.4 cm FL for females and 149.9 cm FL for males (Figure 3). Ages ranged from 0 to 27 years old, with the oldest female estimated to be 27 yr and the oldest male estimated to be 22 yr (Figure 4).

Overall APE was low (3.49%) and PA and PA ± 1 was high between readers and between the two readers and the final agreed-upon (Table 1). Bias between and among readers was not systematic, however older age fish showed more error between readers based on age-bias plots (Table 1, Figure 5).

The likelihood ratio test showed that there was a significant difference between sexes (χ^2 = 545.8 (vBGF), 537.8 (2pvBGF), d.f. = 3, $p < 0.001$), so growth curves were run for each sex separately. The von Bertalanffy growth function and the Fabens' modified two-parameter von Bertalanffy growth function both fit the data well, but the three-parameter model had the lowest residual sums of square error and the lowest AIC. The three-parameter von Bertalanffy growth function for male sandbar sharks estimated a L_∞ of 172.97 cm FL, a k of 0.15, and a t_0 of -2.33, with randomly distributed residuals (Figure 6, Table 2), whereas the three-parameter von Bertalanffy growth function for female sandbar sharks estimated a L_∞ of 181.15 cm FL, a k of 0.12, and a t_0 of -3.09, also showing a randomly distributed residual plot (Figure 7, Table 2). The modified two-parameter von Bertalanffy growth function for male sandbar sharks estimated a L_∞ of 178.29 cm FL, and a k of 0.14, with randomly distributed residuals (Figure 8, Table 2), whereas the modified two-parameter von Bertalanffy growth function for female sandbar sharks estimated a L_∞ of 172.13 cm FL, and a k of 0.16, also with randomly distributed residuals (Figure 9, Table 2).

Discussion

Overall, both the three-parameter and modified two-parameter von Bertalanffy growth functions provided good fits to the data. Utilization of the average birth size of 46 cm FL in the Fabens' model might provide a better biological description of the growth of the sandbar shark, even though the fit of the model was less parsimonious in comparison to the three parameter model. Other growth models, such as the Gompertz growth model and the Schnute growth model, were considered but not run due to limited applicability to these data. The Gompertz growth model uses weight to model growth, and since the majority of samples were from at-sea observers on commercial boats, sampling large animals that were gutted before returning to the dock, weights were not available. Alternatively, the Schnute model removes the assumption of asymptotic growth from the modeling contraints; however due to the reported sizes of sandbar sharks and the subsample of the population from this study, it is reasonable to believe that sandbar sharks do not continue to grow in length over their lifetime, and do indeed reach an asymptote in growth at some point. . Observations from this study and others (Casey et al. 1985, McAuley et al. 2006) noted that growth bands in the vertebrae of sandbar shark appear to be stacked on the edge in older aged animals, indicating that vertebrae and the correlated length of the shark reach a point at which the age is increasing, but the length is not.

The parameters estimated by the growth models in this study were within the range of parameters estimated by other studies (Table 3). The L_∞ estimates were lower than the largest shark aged in this study (202 cm FL) but the majority of the larger sharks in the study were in the 150 cm – 180 cm fork length range. The k value, an estimation of the growth rate, was higher than what was found in most other studies. We attribute this to having a large enough sample size that appropriately subsampled the population, as well as having good representation in all size bins. Most other studies relied on samples from multiple gears as well as protracted periods of sampling. In addition, some studies used back calculated length at age instead of directly ageing each shark, which can lead to an underestimation of mean length-at-age unless validated (Campana 1990, Francis 1990, Goldman and Musick 2006). The focus on directly ageing each sample as well as sampling the fishery in a finite time frame eliminates any potential bias related to back-calculation or fishery-dependent changes in length or age composition.

The age and growth analysis of the sandbar shark in this study represented a concerted effort to collect current samples from the commercial shark bottom longline fishery to better describe the age structure of the sandbar shark population based on recommendations from SEDAR 11.

Acknowledgements

The authors would like to thank the observers for sampling in tough conditions to make this study happen, and especially thank Assistant Observer Coordinator S. Gulak and A. Napier for all their help. The authors would also like to thank D. Bethea and D. Grubbs

(GULFSPAN), and B. Frazer (SCDNR) for providing additional samples that were essential for completing this study.

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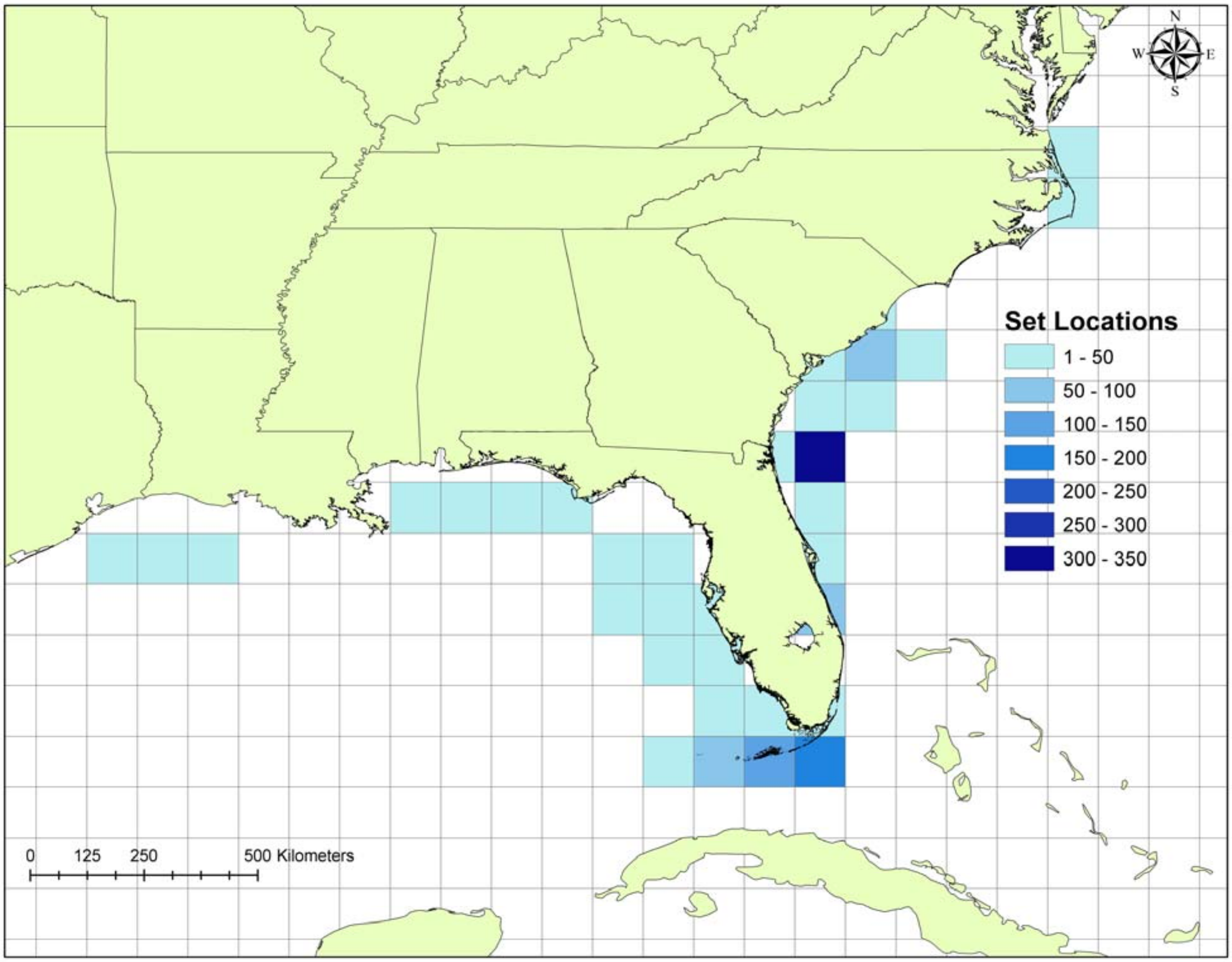

Figure 1. Map of set locations where vertebrae samples of sandbar sharks were taken.

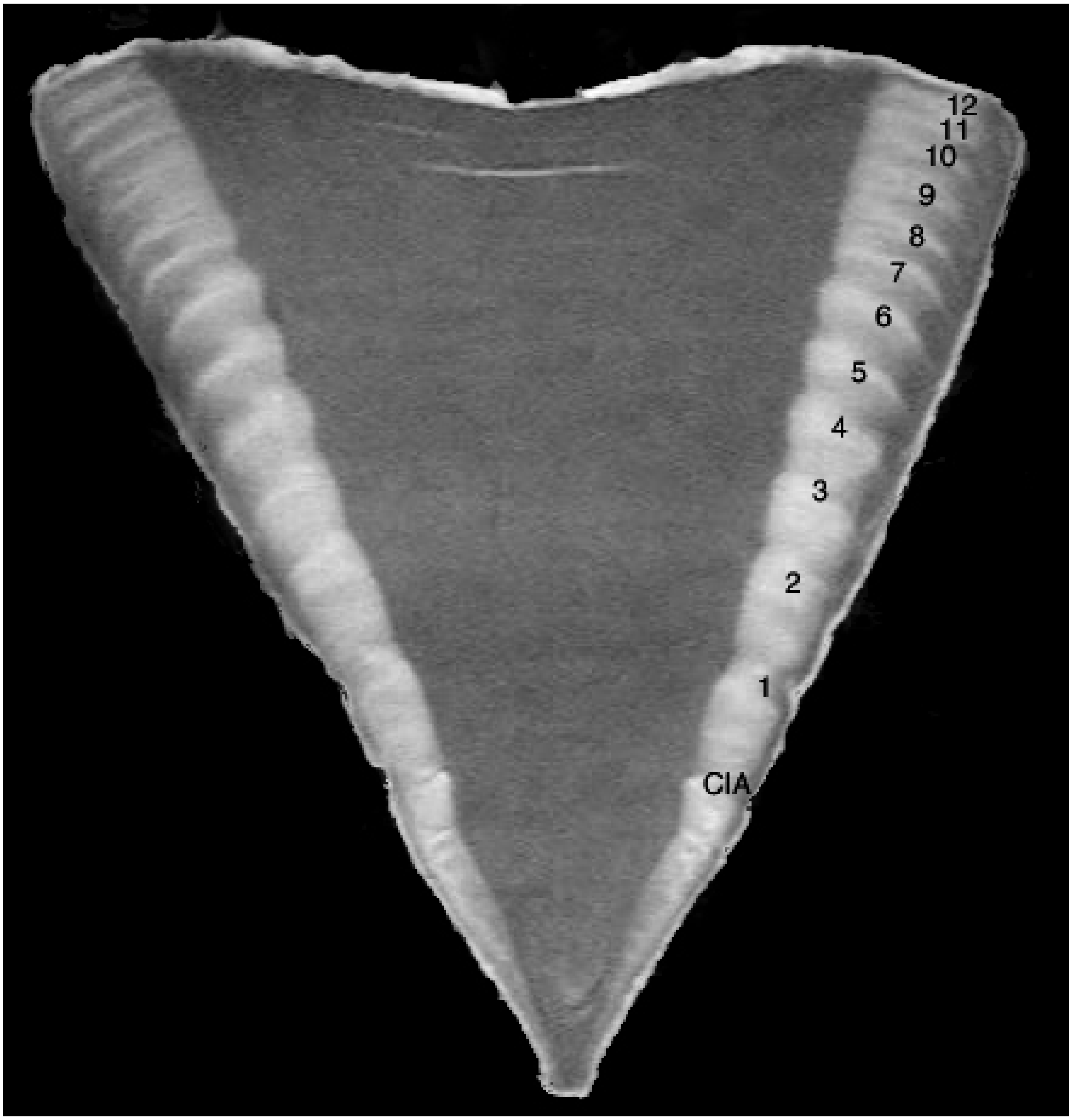

Figure 2. Image of vertebrae

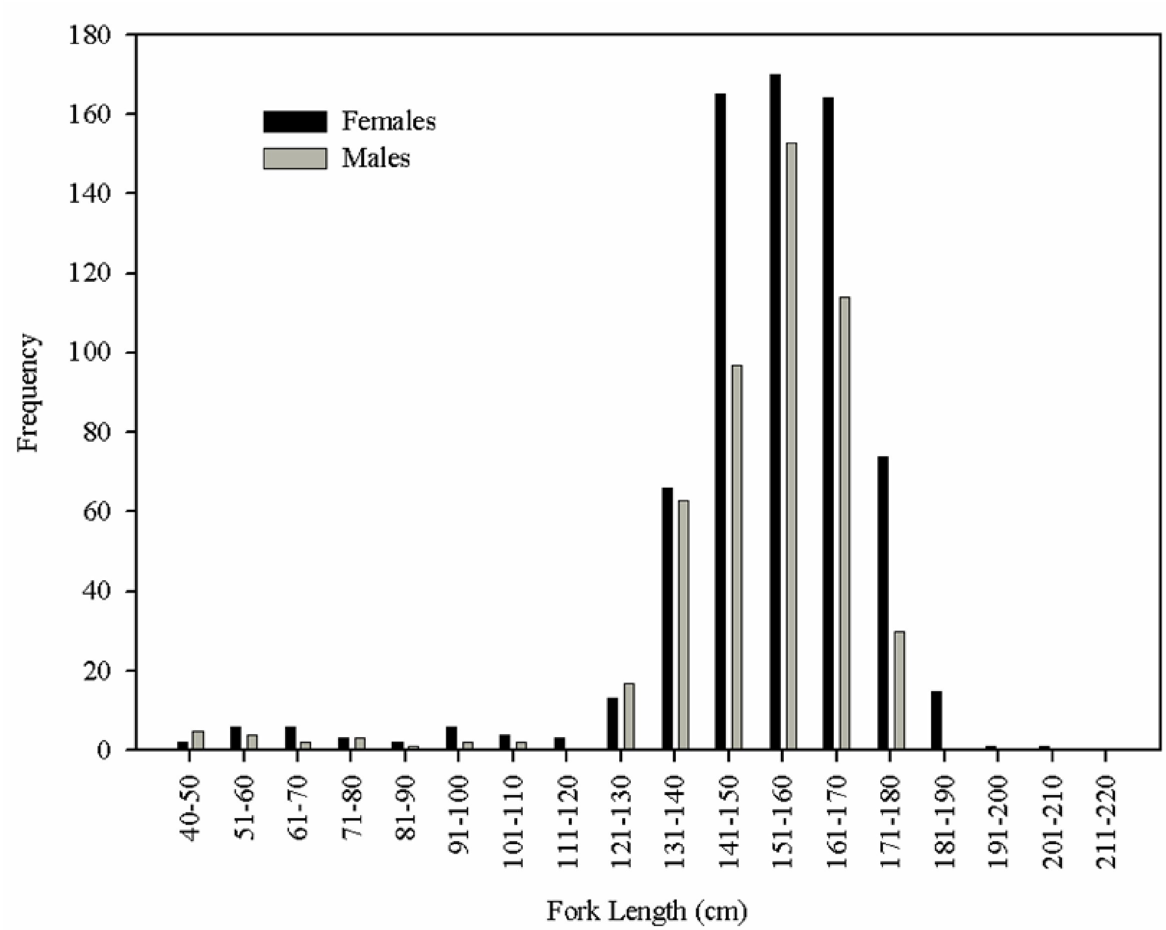

Figure 3. Fork length frequency of sandbar sharks used in age and growth analysis (n = 1194).

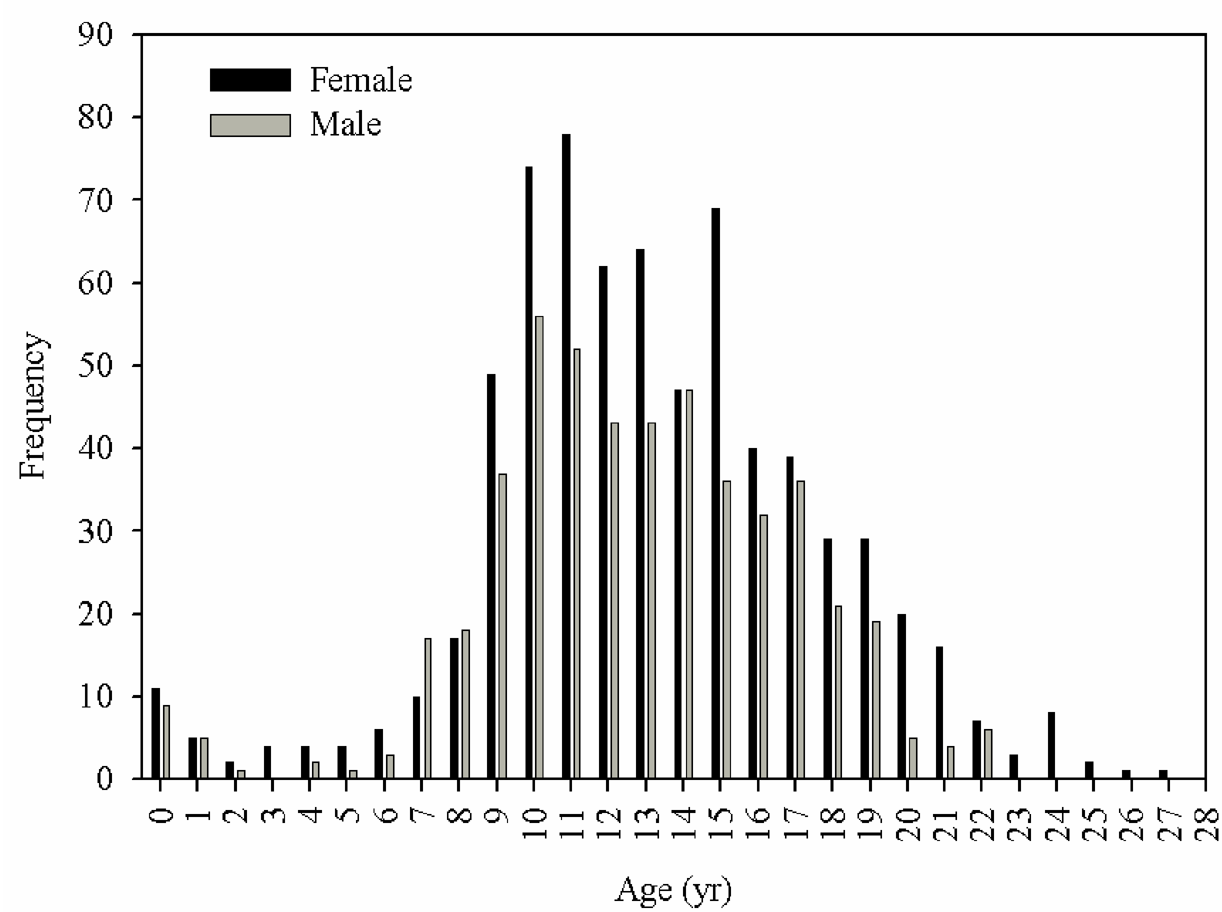

Figure 4. Age frequency of sandbar sharks used in age and growth analysis (n = 1194).

Table 1. Reader precision and bias analysis.

Reader Comparison	Percent Agreement (PA)	Percent Agreement ± 1 (PA ± 1)	Bowker's Test χ^2_{calc}	Bowker's Test degrees of freedom	Bowker's Test p value	McNemar's Test χ^2_{calc}	McNemar's Test degrees of freedom	McNemar's Test p value
Reader 1 vs Reader 2	48.35	82.04	86.91	68	0.06	0.46	1	0.49
Reader 2 vs Final	58.62	85.88	78.74	57	0.03	4.21	1	0.04
Reader 1 vs Final	60.14	90.08	76.46	62	0.10	4.95	1	0.03

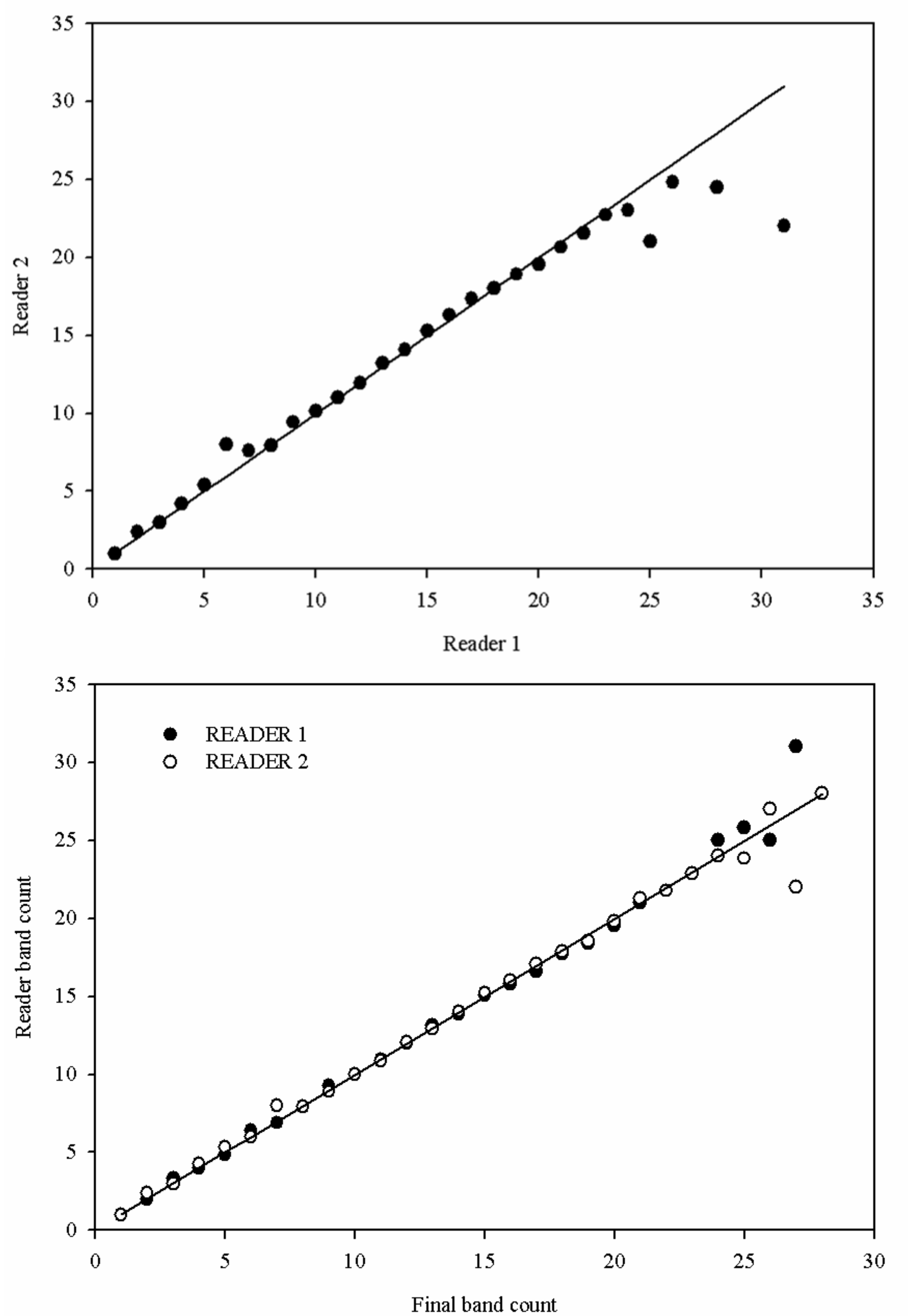

Figure 5. (a) Reader 1 to Reader 2 age bias graph, with 1:1 line. (b) Reader 1 (solid circles) and Reader 2 (open circles) to final band count age bias graph, with 1:1 line.

Table 2. Growth curve parameters estimated for the sandbar shark (fork length in cm).

Growth Curve	Sex	Sample Size	L∞ (± SE)	k (± SE)	AIC	Residual sums of squares
von Bertalanffy growth function	F	701	181.15 ± 1.45	0.12 ± 0.004	4899.28	44012
von Bertalanffy growth function	M	493	172.97 ± 1.30	0.15 ± 0.005	3343.15	25025
von Bertalanffy growth function	Combined	1194	177.89 ± 1.00	0.13 ± 0.003	8261.35	70231
2 parameter von Bertalanffy growth function	F	701	178.29 ± 1.17	0.14 ± 0.003	4929.27	46066
2 parameter von Bertalanffy growth function	M	493	172.13 ± 1.48	0.15 ± 0.004	3346.40	25293
2 parameter von Bertalanffy growth function	Combined	1194	175.97 ± 0.85	0.14 ± 0.003	8293.67	72278

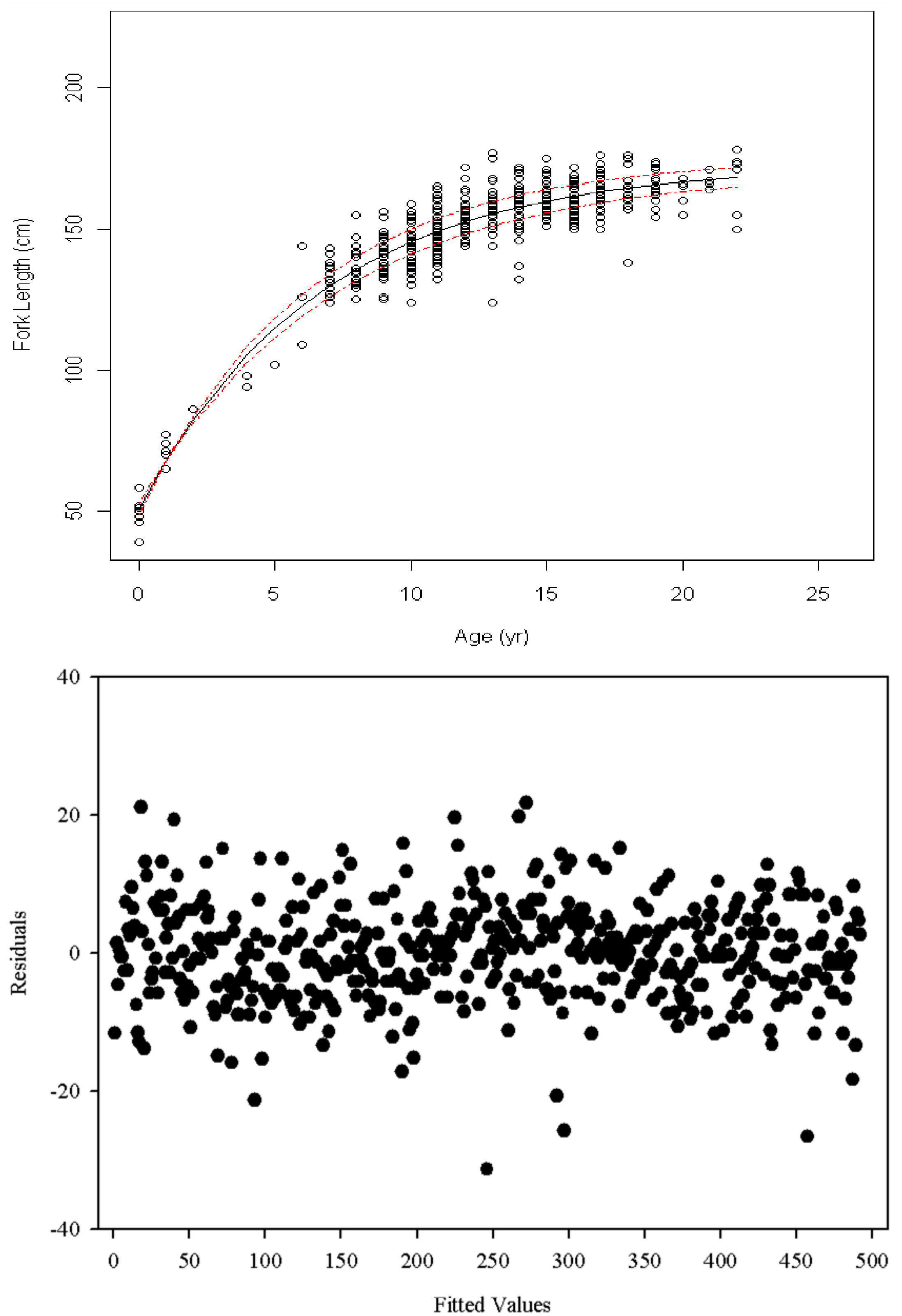

Figure 6. (a) von Bertalanffy growth curve for male sandbar sharks with 95% confidence intervals in red (n = 493, r^2 = 0.88, p<0.0001); (b) residuals of the von Bertalanffy growth curve for male sandbar sharks.

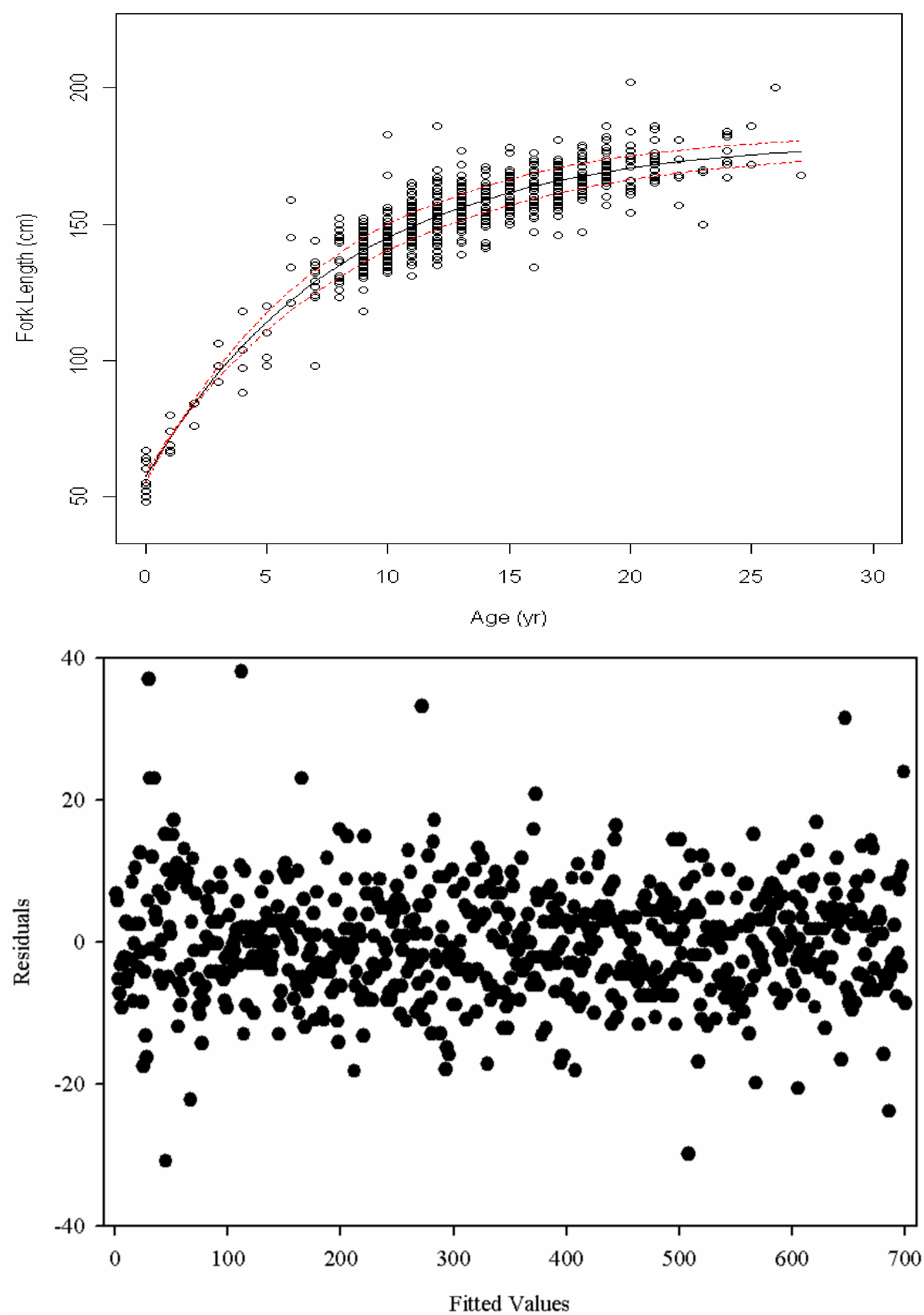

Figure 7. (a) von Bertalanffy growth curve for female sandbar sharks with 95% confidence intervals in red (n = 701, r^2 = 0.85, p<0.0001; (b) residuals of the von Bertalanffy growth curve for female sandbar sharks.

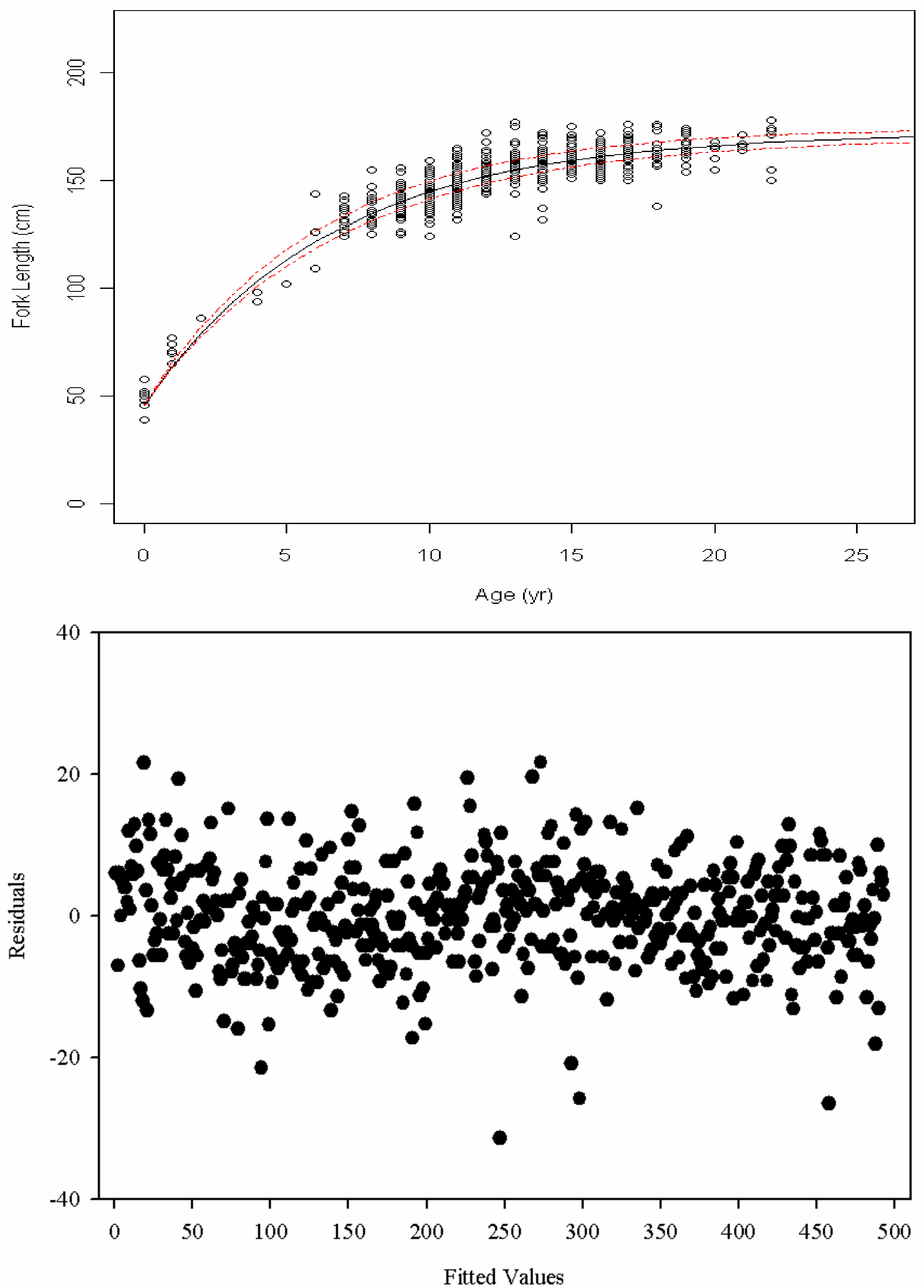

Figure 8. (a) Two parameter von Bertalanffy growth curve for male sandbar sharks with 95% confidence intervals in red (n = 493, $r^2 = 0.88$, p<0.0001); (b) residuals of two parameter von Bertalanffy growth curve for male sandbar sharks.

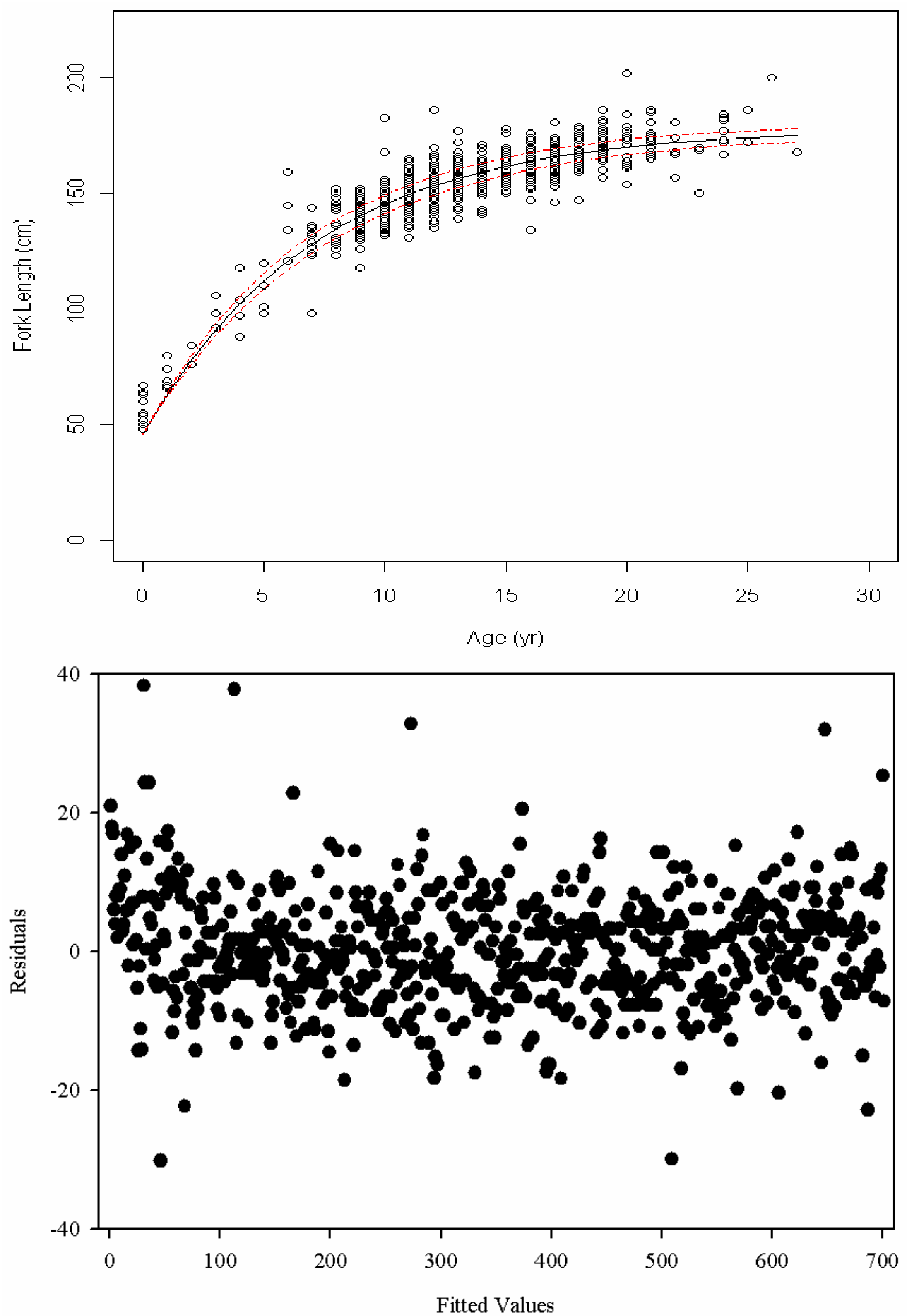

Figure 9. (a) Two parameter von Bertalanffy growth curve for female sandbar sharks with 95% confidence intervals in red (n = 701, $r^2 = 0.85$, p<0.0001); (b) residuals of two parameter von Bertalanffy growth curve for female sandbar sharks.

Table 3. Age and growth analysis estimates for the sandbar shark from various studies (all lengths are fork lengths in cm, converted using conversions calculated in each publication).

Study	**Growth Curve**	**Study Area**	**Sex**	**Sample Size**	**L_∞ (± SE)**	**k (± SE)**	**t_0 (± SE)**	**Length at birth (cm FL)**	**Oldest Aged**	**Age at Maturity**	**Size at Maturity**
Present study	von Bertalanffy growth function	GOM and SA	F	701	181.15 ± 1.45	0.12 ± 0.004	-3.09 ± 0.19	46	27	13.1	156
Present Study	von Bertalanffy growth function	GOM and SA	M	493	172.97 ± 1.30	0.15 ± 0.005	-2.33 ± 0.16	46	22	14.1	158
Present Study	von Bertalanffy growth function	GOM and SA	Combined	1194	177.89 ± 1.00	0.13 ± 0.003	-2.76 ± 0.13	46	27	—	
Present Study	2 parameter von Bertalanffy growth function	GOM and SA	F	701	178.29 ± 1.17	0.14 ± 0.003	—	46	27	13.1	156
Present Study	2 parameter von Bertalanffy growth function	GOM and SA	M	493	172.13 ± 1.48	0.15 ± 0.004	—	46	22	14.1	158
Present Study	2 parameter von Bertalanffy growth function	GOM and SA	Combined	1194	175.97 ± 0.85	0.14 ± 0.003	—	46	27	—	
Casey et al. 1985	von Bertalanffy growth function	SA	F	299	298	0.04	-4.9		21	12	203.4
Casey et al. 1985	von Bertalanffy growth function	SA	M	176	257.3	0.05	-4.5		15	13	153.9
Casey and Natanson 1992	von Bertalanffy growth function	SA	Combined	442	185.8	0.05	-6.45			30	186
Sminkey and Musick 1995 (1980-1981)	von Bertalanffy growth function	SA	F	150	217.7	0.06	-4.8			15-16	150.6
Sminkey and Musick 1995 (1980-1981)	von Bertalanffy growth function	SA	M	38	203.4	0.06	-5.4			15-16	149.5

Study	Growth Curve	Study Area	Sex	Sample Size	$L\infty$ (± SE)	k (± SE)	t_0 (± SE)	Length at birth (cm FL)	Oldest Aged	Age at Maturity	Size at Maturity
Sminkey and Musick 1995 (1980-1981)	von Bertalanffy growth function	SA	Combined	188	219.9	0.06	-4.9		25	15-16	150.6
Sminkey and Musick 1995 (1990-1991)	von Bertalanffy growth function	SA	F	191	182.5	0.09	-3.9			15-16	150.6
Sminkey and Musick 1995 (1990-1991)	von Bertalanffy growth function	SA	M	223	183.6	0.09	-3.8			15-16	149.5
Sminkey and Musick 1995 (1990-1991)	von Bertalanffy growth function	SA	Combined	412	181.4	0.09	-3.8		25	15-16	150.6
Joung et al. 2004	von Bertalanffy growth function	Taiwan	F	215	181.4	0.10	-4.5	66.1	20.8	7.5-8.2	140.5
Joung et al. 2004	von Bertalanffy growth function	Taiwan	M	233	162.8	0.14	-4.0	70.2	19.8	8.2	142.5
Joung et al. 2004	von Bertalanffy growth function	Taiwan	Combined	362	170.8	0.17	-2.3				
Romine et al. 2006	2 parameter von Bertalanffy growth function	Hawaii	F	105	153.4	0.10	___	47	22	8	
Romine et al. 2006	2 parameter von Bertalanffy growth function	Hawaii	M	82	169.1	0.12	___	47	12	10	
McAuley et al. 2006	von Bertalanffy growth function	Australia	F	130	245.8	0.039	-4.9		25	16.2	135.9
McAuley et al. 2006	von Bertalanffy growth function	Australia	M	105	226.3	0.044	-4.7		19	13.8	126.9
McAuley et al. 2006	von Bertalanffy growth function	Australia	Combined	238	239.6	0.040	-4.9				

Table 4. Age-length schedule for the sandbar shark.

Age	Average Length Female (cm FL)	SD	n	Average Length Male (cm FL)	SD	n
0	56.55	6.11	11	49.56	5.15	9
1	71.20	5.81	5	71.40	4.51	5
2	80.00	5.66	2	86.00	0.00	1
3	98.50	5.74	4	0.00	0.00	0
4	101.75	12.66	4	96.00	2.83	2
5	107.25	9.91	4	102.00	0.00	1
6	137.50	15.04	6	126.33	17.50	3
7	128.10	12.26	10	132.65	6.43	17
8	138.71	9.26	17	136.83	7.42	18
9	139.53	6.85	49	139.35	6.92	37
10	144.64	7.85	74	143.07	7.06	56
11	148.76	7.10	78	148.31	7.31	52
12	152.68	8.94	62	154.56	5.84	43
13	156.27	7.39	64	157.30	8.46	43
14	158.21	7.25	47	158.51	7.92	47
15	161.46	6.60	69	160.67	5.24	36
16	162.40	5.78	40	159.97	5.78	32
17	165.87	7.31	39	163.58	6.50	36
18	167.62	6.82	29	164.62	8.77	21
19	171.62	6.46	29	164.68	5.33	19
20	171.15	10.47	20	162.80	5.26	5
21	173.25	6.55	16	167.00	2.94	4
22	169.71	7.57	7	166.83	11.44	6
23	163.00	11.27	3	---	---	0
24	176.25	6.23	8	---	---	0
25	179.00	9.90	2	---	---	0
26	200	0.00	1	---	---	0
27	168	0.00	1	---	---	0