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Life history parameters of the sandbar shark, *Carcharhinus plumbeus*, in the Northwest Atlantic

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Introduction

Previous work on Age and Growth of the sandbar shark

Previous studies of the age and growth of the sandbar shark from the NWA have yielded mixed results. Lawler (1976) produced unrealistic values for maximum length (267 cm Total Length(TL)) and only produced von Bertalanffy growth parameters for female sandbar sharks due to a limited sample size of males. Casey et al. (1985) provided a more comprehensive study of the age and growth of the sandbar shark that consisted of a large sample size and included age validation studies, but also produced unrealistic maximum length estimates (303 cm Fork Length (FL)). Empirical maximum reported lengths are 234 cm TL and 226 cm TL for females and males respectively (Cortés 2000). Casey et al. (1985) lacked a representative sample from larger size classes, which is an inherent problem in conducting an age and growth study on long-lived species. The oldest male to be aged was 15 years old and the oldest female to be aged was 21 years old. Casey and Natanson (1992) provided new growth parameters based on tagging experiments and proposed age at maturity to be to 30 years and maximum size to be 186 cm FL. Sminkey and Musick (1995) reexamined age and growth of the sandbar shark from samples obtained a decade apart, 1980-1981 and 1991-1992. The sample set from 1991-1992 was the most robust sample size and had the greatest size range of any study conducted on sandbar shark to date.

Age and growth studies on sandbar sharks have been carried out in other regions as well. Joung et al. (2004) examined the age and growth of the sandbar shark from Taiwanese waters using vertebral centra from the caudal peduncle. Calculations from this study produced maximum lengths of 216.3 cm TL and 201.6 cm TL for females and males respectively. Estimated age at maturity was 9 yrs for females and 10.5 years for males at lengths of 170-175 cm TL for both sexes. This contradicts general trends in elasmobranch life history, males typically attain maturity at smaller sizes and younger ages (Cortés 2000). Annual formation of growth bands has not been validated for vertebral centra removed from the caudal peduncle and may be the cause for these discrepancies. Joung and Chen (1995) reported litter sizes ranging from 4-12 and a mean of 7.54. Size at birth was estimated as 60-65 cm TL following a 10-12 month gestation period. McAuley et al. (2006) examined the sandbar shark in Northwest Australian waters and reported von Bertalanffy growth parameters for females to be K=0.039 year^{-1} and L_∞=245.8. Male growth parameters were reported as K=0.044 year^{-1} and L_∞=226.3 cm FL. McAuley et al. (2006) also reported size at birth of 42.5 cm FL. Age at which 50% of the population was mature was estimated as 16.2 years for females and 13.8 years for males.

Protective nets off the west coast of South Africa provided the opportunity to conduct age and growth studies on the sandbar shark in the south western Indian Ocean. Cliff et al. (1988) reported size at maturity as 129 cm Pre-caudal Length (PCL) and 130 cm PCL for male and females respectively. Litter sizes averaged 7.2 pups and pups were 40-50cm PCL. The smallest free-swimming specimen from this area was 48 cm PCL reported by Bass et al. (1973).

Romine et al. (2006) provided estimates of growth for the sandbar shark in the Hawaiian Islands. Growth parameters estimated for the von Bertalanffy growth function were: K= 0.12 year^{-1} and L_∞=152.8 cm PCL for females and K= 0.10 year^{-1} and L_∞=138.5 cm PCL for males.

Methods

Data collection

Vertebral centra were obtained from sandbar sharks landed by the VIMS longline survey, Commercial Shark Fishery Observer Program (CSFOP), and NMFS shark longline survey. The VIMS long-line survey operated in Chesapeake Bay, Virginia coastal waters and North Carolina coastal waters. CSFOP and NMFS surveys operated from North Carolina south to Florida and into the Gulf of Mexico along Florida's western coast. Samples were collected during 1980-1983 and 2000-2004.

VIMS shark longline stations ranged in depth from five meters to 33 meters and were sampled once a month from May to October using longlines consisting of 100 9/0 J-hooks and 12/0 circle hooks on monofilament leader material. Hooks were baited with menhaden, *Brevoortia tyrannus*, and allowed to soak for 4 hours. Sharks landed by the VIMS longline survey were measured and euthanized. All measurements were straight line measurements. Pre-caudal length was the primary measurement used in this study and was defined as length from the tip of the snout to the deepest part of the pre-caudal notch. Once the shark was euthanized, vertebral centra were removed from directly below the first dorsal. Samples were labeled and placed in the vessel's freezer for return to the lab.

Samples were also obtained through trawl, gillnet, and recreational fishing gears within Chesapeake Bay and the Eastern Shore of Virginia during the 2000-2004 time period. Either the shark was sampled in the field using the aforementioned protocols or it was returned to the lab to be measured and sampled. Samples obtained through CSFOP were removed from the anteriorad of the "log" or carcass. Removal of centra from below the first dorsal was not practical in this commercial setting because such action would reduce the value of the shark at market. No significant differences in band counts between samples collected from both regions of individual sharks has been reported (Piercy et al. 2006).

Upon return to the laboratory, samples were thawed and excess muscle tissue was removed from the sample. The sample was then placed in 75% ETOH until it could be sectioned. Vertebral centra were sagitally sectioned through the focus of the centrum using an isomet rotary diamond saw. These sections were then set to dry for 24 hours. Once dry, the samples were mounted on a microscope slide via cover slip mounting medium. The samples were wet sanded using 300, 400 and 600 fine grit sand-paper progressively until light was readily transmitted through the sample and the annuli were distinguishable on a dissection microscope.

Male sharks were classified as mature if claspers were deemed fully calcified (i.e. hard) and could be rotated forward (Clark & von Schmidt 1965, Driggers et al. 2004). Maturity status of females was determined by examination of oviducal gland size, uteri width and appearance (Castro 1993). Pregnant and postpartum females were classified as mature.

Data analyses

The rings or annuli counted for age estimates were defined as a band pair consisting of an opaque zone combined with a wider translucent zone in the intermedialia, which continued on to the corpus calcareum (Casey et al. 1985, Sminkey & Musick 1995). The birthmark was determined as the first band that intersected the inflection of the corpus calcareum. Mounted vertebral sections were examined for age using a dissecting microscope and a video imaging system. The principal author and another reader conducted multiple blind readings of all vertebrae. Once all vertebrae were read, Hoenig's (1995) and Evans and Hoenig's (1998) tests of symmetry were conducted to test for systematic differences between readers using chi-square tests of symmetry that determine whether differences are systematic (biased) or due to random error.

Age estimates for vertebrae that were not consistent between readers were reexamined by both readers until a consensus was reached. The consensus estimate was used in the final analysis. If a consensus age estimate could not be reached the sample was removed from the study (Cailliet & Goldman 2004).

Following Carlson & Baremore (2005), we fitted five growth models to length-at-age data for male and female sharks. We fitted a modified version of the Gompertz model (Ricker 1975):

$$L_t = L_0(e^{G(1-e(kt))}),$$

where G=ln(L_∞ / L_0) (Bertalanffy 1938) where L_0 = mean length-at-birth (45 cm PCL), L_t = length at time t, L_∞ = theoretical asymptotic length, and k= coefficient of growth. The second model that was fitted was a model proposed by Galluci and Quinn (1979):

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

where ω=k*L_∞ . The third model fitted to the data was the logistic model (Ricker 1975):

$$L_t = L_\infty /(1+e^{-k(t-t_0)}).$$

Two forms of the von Bertalanffy growth model were also fitted to the data (von Bertalanffy 1938, Beverton & Holt 1957, Cailliet et al. 2006). The first form of the model (VB1) used the length-at-birth intercept rather than a theoretical age at zero length and is described as:

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt},$$

Length-at-birth was estimated from observed at-term embryos and free-swimming young-of-the-year during this study. The second form, a three-parameter von Bertalanffy model (VB2) incorporating the theoretical age-at-zero (t_0) term is described as:

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

where, t_0 = age or time when length theoretically equals zero.

All model parameters were estimated using the Marquardt least-squares nonlinear (NLIN) procedure in SAS statistical software (SAS V.9, SAS Institute, Inc). Final model selection was based on the model that produced the lowest value of Mean Square Error (MSE). The F-test statistic was used to determine which model provided a better description of the data. Homogeneity of variance across time periods was tested using Bartlett's Test in R. Model error was assumed to be independent, normally distributed, and homoscedastic. A Shapiro-Wilks test for normality was used to test the assumption of normality.

Size and age-based maturity ogives were developed for female sharks. Trippel and Harvey (1991) suggested the use of maximum likelihood or probit analysis to estimate age at which 50% (A50) of the population was mature in populations where there are successive increases in proportion of mature fish with increasing age. We used maximum likelihood (ML) methods to estimate A50. This method takes into account the sample size within each age class. The negative log-likelihood function that was minimized was:

$$-\ln(ML) = \sum_j [n_j * \ln[(1 + e^{(-b*(j-A50))})^{-1}] + (N_j - n_j) * \ln(1 - (1 + e^{(-b*(j-A50))})^{-1})],$$

where n_j= is the number of mature fish in age class *j*, N_j= the total number of fish in age class *j*, *b*=the instantaneous rate of fish maturation, and A50=the age at which 50% of the population is mature. A50 and *b* were estimated by minimizing the negative log-likelihood using AD model builder. Bias-corrected 95% confidence intervals were constructed using bootstrap methods of estimation (Haddon 2001). Confidence intervals were only estimated for the proportion mature. The steepness parameter, *b*, was held to the value estimated from the initial fit of the model.

Results

Over the time period of 2000-2004, 464 sandbar sharks were sampled. Of these 250 were females which ranged in length from 38 cm to 167 cm PCL and 206 were males that ranged from 40 cm to 162 cm PCL (Figure 1). The oldest estimated age for a female shark was 27 years and for males was 22 years. The relationship between cm FL and cm PCL for females and males was:

Females: FL=1.07(PCL) + 3.21 r^2=0.99
Males: FL=1.07(PCL) + 3.07 r^2=0.99

Percent agreement between readers was 64% for all samples. Reader estimates were within one year of each other for 95% of the samples and within two years for 98% of the samples. Results of between reader contingency tables revealed that differences between readers were due to random error rather than systematic error (X^2=41.20, *df*=33, *p*=0.154).

Based on MSE the VB2 model provided the best fit for the female data (Table 1, Figure 2). The logistic model provided the better fit for male data, but the logistic model underestimated empirical asymptotic length and returned a high growth coefficient value (Table 1, Figure 3).

The VB1 model estimated L_∞ to be 160.7 cm PCL for females and 155.8 cm PCL for males. Growth coefficient estimates from the VB1 model were 0.1148 for females and 0.1236 for males. The VB2 model growth parameter estimates were L_∞ =163.6 cm PCL for females and 158.8 cm PCL for males, *K*= 0.1055 for females and 0.1124 for males, and t_0= -3.26 for females and -3.16 for males. In all cases the VB2 model provided a better fit than the VB1 model based on an F-test at the 0.05 confidence level. The assumption of normally distributed error was not violated and skew and kurtosis were minimal for all model fits. ML estimation of age at 50% maturity for females was approximately 12.49 years, which corresponds to approximately 132 cm PCL (Table 2).

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Table 1. Model fits for males and females. Length values are cm PCL. (MSE=Mean square error, RSS= residual sums of squares, NA=not applicable)

Year 2000	Model	MSE	RSS	Linf	K	t0	ω
Female	Gompertz	36.2491	8881.03	150.734	0.19619	NA	NA
Female	GQ	31.8758	7777.70	NA	0.10611	-3.23893	17.3238
Female	Logisitc	33.7897	8244.68	149.902	0.23594	2.75959	NA
Female	VB1	32.9359	8069.29	160.582	0.11500	NA	NA
Female	VB2	31.8758	7777.70	163.260	0.10611	-3.23893	NA
Male	Gompertz	35.5325	7106.50	146.428	0.21053	NA	NA
Male	GQ	34.4020	6845.99	NA	0.11239	-3.16713	17.8476
Male	Logistic	31.0317	6175.31	145.127	0.25915	2.46751	NA
Male	VB1	35.8962	7179.24	155.755	0.12355	NA	NA
Male	VB2	34.4020	6845.99	158.797	0.11239	-3.16713	NA

Table 2. Proportion of females mature at age and length derived from maximum likelihood estimation methods. (LCL and UCL =lower and upper 95% confidence intervals)

Age (year)	Length (cm PCL)	Length (cm FL)	Proportion mature	LCL	UCL
0	47.48	54.02	0.0000	0.0000	0.0000
1	59.14	66.49	0.0000	0.0001	0.0000
2	69.62	77.71	0.0000	0.0003	0.0000
3	79.05	87.79	0.0001	0.0008	0.0000
4	87.53	96.86	0.0002	0.0019	0.0001
5	95.15	105.02	0.0004	0.0048	0.0002
6	102.01	112.36	0.0012	0.0120	0.0005
7	108.17	118.96	0.0034	0.0299	0.0012
8	113.72	124.89	0.0096	0.0725	0.0030
9	118.71	130.23	0.0265	0.1651	0.0075
10	123.19	135.03	0.0713	0.3337	0.0187
11	127.23	139.34	0.1778	0.5591	0.0460
12	130.85	143.22	0.3786	0.7625	0.1088
13	134.12	146.71	0.6319	0.8905	0.2362
14	137.05	149.85	0.8287	0.9537	0.4391
15	139.69	152.68	0.9316	0.9812	0.6647
16	142.06	155.22	0.9746	0.9925	0.8338
17	144.20	157.50	0.9908	0.9970	0.9270
18	146.12	159.55	0.9967	0.9988	0.9699
19	147.84	161.40	0.9988	0.9995	0.9879
20	149.39	163.06	0.9996	0.9998	0.9952
21	150.79	164.55	0.9999	0.9999	0.9981
22	152.05	165.90	0.9999	1.0000	0.9992
23	153.17	167.11	1.0000	1.0000	0.9997
24	154.19	168.19	1.0000	1.0000	0.9999
25	155.10	169.17	1.0000	1.0000	1.0000
26	155.92	170.05	1.0000	1.0000	1.0000
27	156.66	170.84	1.0000	1.0000	1.0000

Figure 1. Number of sharks sampled within five centimeter size classes.

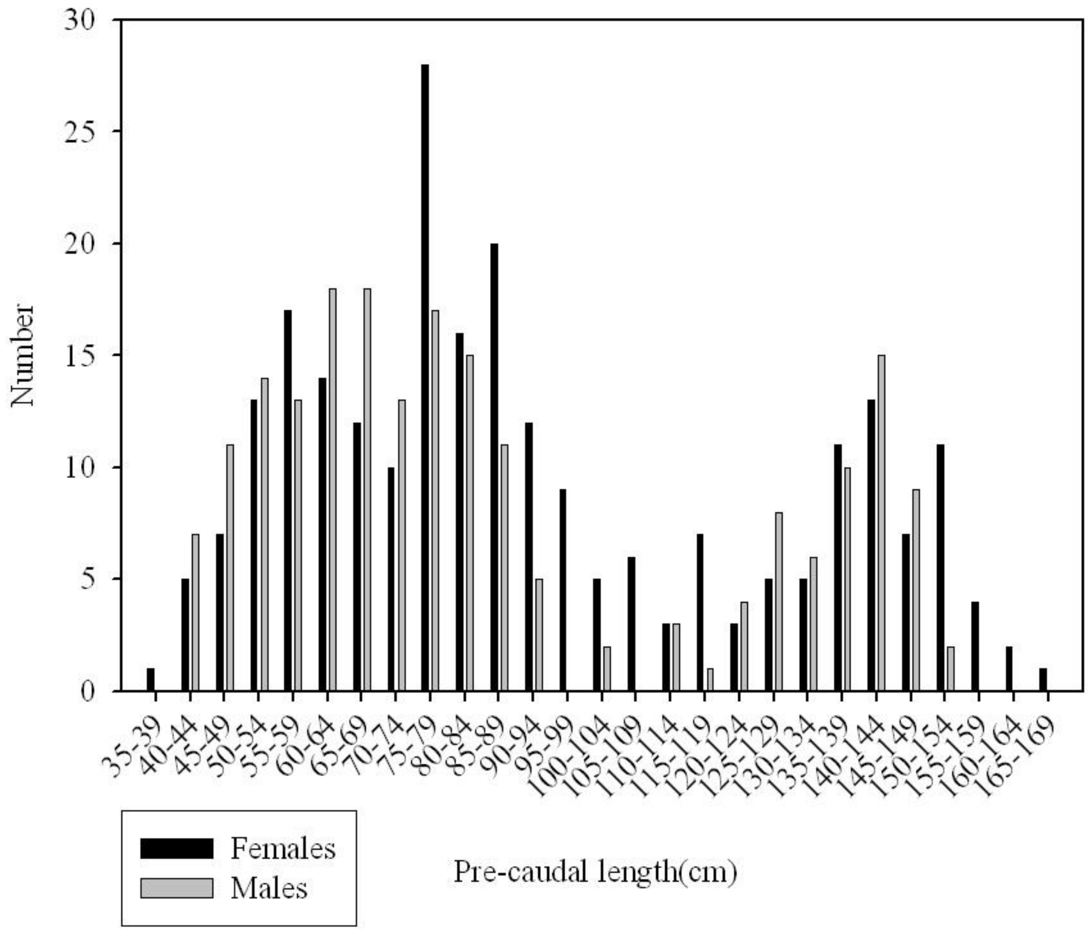

Figure 2. All model fits for female sandbar sharks.

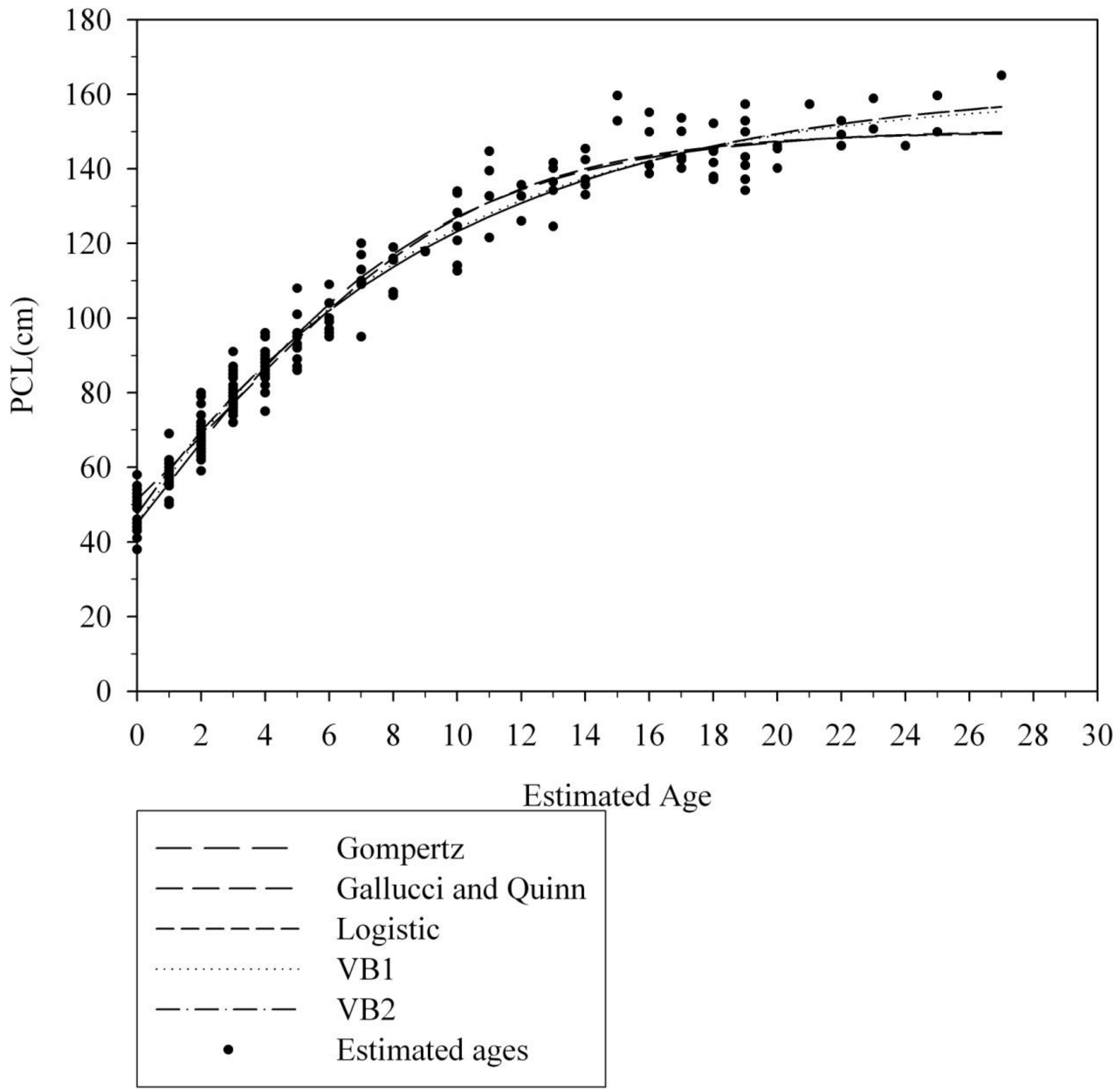

Figure 3. All model fits for male sandbar sharks.