Age and growth of sandbar sharks (*Carcharhinus plumbeus*) in US waters of the western North Atlantic Ocean, 2015-2025

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SEDAR101-DW-24

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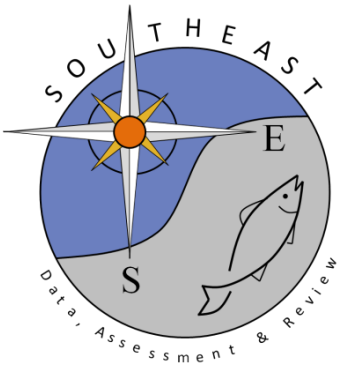

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Age and growth of sandbar sharks (*Carcharhinus plumbeus*) in US waters of the western North Atlantic Ocean, 2015-2025.

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Between 2015 and 2025, 1106 vertebral samples were collected from sandbar sharks (*Carcharhinus plumbeus*) by fisheries observers and biologists with the National Marine Fisheries Service. Vertebral samples were primarily collected from the cervical region of the vertebral column while onboard vessels operating in the shark research fishery or fisheries-independent surveys off the southeastern coast of the US and in the northern Gulf of America. The total sample was dominated by females (73.4%). Females and males ranged in size from 42-215 cm (mean = 151.0 cm, SD = 29.1) and 41-201 (143.5 cm, SD = 35.2), respectively (Figure 1). Cervical vertebrae were excised by at-sea and following collection, were cleaned using standardized protocols (e.g. Goldman 2005).

Based on an initial test to determine optimal thickness for elucidating growth bands, a 0.6 mm sagittal section, which included the focus, was removed from each vertebra using a low speed saw. Vertebrae comprising the sample set were sectioned in equal proportions at the NOAA Fisheries Pascagoula, MS, and Narragansett, RI, labs, as well as the South Carolina Department of Natural Resources lab in Ft. Johnson, SC. Sections were viewed under a dissecting microscope and when growth band resolution was deemed optimal a digital image was made at 10-15 X magnification. All samples were subsequently fixed in clear plastic resin.

A random subset of 52 vertebrae was selected and independently aged by four readers who are among the most experienced active US researchers in the field of shark age and growth. To evaluate among-reader reliability, the difference between each shark's mean age and each reader's estimate was calculated to obtain a standardized age. Variance components were estimated using a linear mixed model via the PROC GLIMMIX procedure (SAS Version 9.4; SAS Institute Inc., 2015), specifying the individual shark as a fixed effect and the reader as a random effect. An Intraclass Correlation Coefficient (ICC) was computed using the extracted reader and residual variance estimates to mathematically quantify agreement among the scientists. When evaluating between-reader reliability, the variance components estimated from the linear mixed model were 0.0138 for the rater effect and 0.5471 for the residual variance. Utilizing these components, the Intraclass Correlation Coefficient (ICC) was calculated to be 0.906. This high ICC value (close to 1) indicated strong agreement among the four scientists, demonstrating the raters were not a major source of variability and the vast majority of the variance in age estimates was attributable to actual differences among the sharks. Therefore, each reader aged approximately half of the total sample and data were combined once counts were complete.

Because of the difficulty associated with resolving growth bands on the periphery of the corpus calcareum and intermedialia, and the large number of samples with band counts higher than 10 (94%), paired band counts having a difference of two or less had a final count that was

the mean of the two counts (76% of samples). When the difference between two readers was three or more bands, the two readers conferred and final band count was made by consensus. Initial counts were identical for 37% of all counts, within one band for 76% of samples, within 2 bands for 92% of the sample and within 3 bands for 97% of samples. A total of 36 vertebrae had a difference between 4 and six bands between readers.

It was assumed that bands three and above were deposited annually and that the birthmark (first growth band) represented gestational growth and the second band was deposited six months after parturition. Therefore, 1.5 was subtracted from each band count and represented the age in years of each individual. The sample set lacked vertebrae from neonate sharks, therefore, in order to anchor the curve at a biologically meaningful position on the y-axis, length data were obtained from South Carolina Department of Natural Resources (B. Frazier, unpublished data) collected from 70 neonate sandbar sharks with umbilical remains or an open umbilicus collected in May, June and July within the coastal waters of South Carolina. Neonate shark data added to the age model included 39 females (42-53 cm FL) and 31 males (41-54 cm FL). The oldest aged female and male in the sample set were 27.5 and 24 years old, respectively.

Growth

Sandbar shark growth was modeled using the von Bertalanffy Growth Function (VBGF; von Bertalanffy, 1938), which describes the relationship between age (t) and length (L_t) as:

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

where L_∞ is the asymptotic mean length, K is the growth coefficient, and t_0 is the theoretical age at which length is zero. Growth parameters were estimated via maximum likelihood using the PROC NLMIXED procedure in SAS (Version 9.4; SAS Institute Inc., 2015). The model assumed a normal distribution of residuals [$L_t \sim N\left(\widehat{L_t}, \sigma^2\right)$]. Parameters were initialized using biologically plausible values to ensure convergence of the non-linear optimization algorithm.

To determine if growth patterns differed significantly between males and females, a Likelihood Ratio Test (LRT) was conducted (Kimura, 1980). A "Full Model," which estimated separate parameters (L_∞, K, t_0) for each sex, was compared with a "Reduced Model" (Combined Model), in which a single set of parameters was shared across both sexes. The test statistic was calculated as:

$$\Lambda = -2\ln(L_{\text{reduced}}) - 2\ln(L_{\text{full}})$$

where Λ follows a X^2 distribution with degrees of freedom (df) equal to the difference in the number of estimated parameters ($df = 3$). A p-value < 0.05 was considered indicative of significant sexual dimorphism in growth. Model fit was evaluated using a Pseudo R^2 statistic, calculated as 1 – (SSE/SST), where SSE is the residual sum of squares and SST is the total corrected sum of squares (Schabenberger & Pierce, 2001).

Ninety-five percent (95%) confidence intervals for the growth trajectories were generated using the delta method within the PREDICT statement of PROC NLMIXED. All visualizations, including observed vs. predicted length-at-age and comparative growth curves, were produced using PROC SGPLOT (SAS Version 9.4; SAS Institute Inc., 2015).

To test for differences in growth trajectories between SEDAR 54 and SEDAR 101, analyses were stratified into three specific groups: males, females, and combined sexes. For each group, a LRT was used to compare two nested models. The reduced model assumed the population-level parameters (L_∞, K, t_0) were identical across both datasets, whereas the full model allowed the parameters to be estimated independently for SEDAR 54 and SEDAR 101. The test statistic (X^2) was calculated as the difference in the -2 Log Likelihood between the reduced and full models, evaluated with three degrees of freedom to reflect the three parameters allowed to vary.

Results

Counts

Directly aged female and male sharks ranged in age between 0.5-27.5 years and 1.0-24.0 years, respectively (Figure 3). The mean coefficient of variation (CV = 4.49%) and the index of average percent error (IAPE = 3.44%) were quite low. This further reinforced the conclusion drawn from the high ICC, confirming strong agreement and minimal variance among the four readers. Visual inspection of the extended Bland-Altman plot revealed a slight but significant positive relationship between the mean age estimate and the standard deviation of the estimates ($p < 0.01$)(Figure 4). This indicated that, while overall agreement was high, the variance among readers increased marginally with shark age, a common phenomenon as growth bands become crowded in older individuals. Examination of the age-bias curve showed no severe systematic bias among the raters across the sampled age range. Deviations from the consensus mean were minimal: one rater exhibited a negligible tendency to underestimate ages (mean difference = -0.22 years), while another showed a similarly minor tendency to overestimate (mean difference = +0.14 years). The remaining raters exhibited negligible mean differences (+0.03 and +0.05 years), confirming a high degree of consistency and symmetry in age assignments among all four readers.

The VBGF provided a robust fit to the length-at-age data for both male ($N = 313$) and female ($N = 863$) sandbar sharks. For males, the asymptotic length (L_∞) was estimated at 170.6 cm (95% CI: 167.4–173.9 cm), with a growth coefficient (k) of 0.157 year^{-1} (95% CI: 0.142–0.172 year^{-1}) and a theoretical age at length zero (t_0) of -2.01 years (Table 1, Figure 5). Females attained a larger L_∞ of 178.9 cm (95% CI: 176.5–181.2 cm), but exhibited a k of 0.137 year^{-1} (95% CI: 0.129–0.145 year^{-1}) and a t_0 of -2.31 years (Table 2, Figure 6). When sexes were combined ($N = 1176$), the population-level parameters were $L_\infty = 177.0$ cm, $k = 0.141$ year^{-1}, and $t_0 = -2.22$ years (Table 3, Figure 7).

The VBGF demonstrated high explanatory power for both groups. The Pseudo R^2 values indicated the model accounted for 95.6% of the variance in male length-at-age and 91.8% of the variance in female length-at-age. The combined model also showed a high fit with a Pseudo R^2 of 0.930. Visual inspection of the growth trajectories and the 95% confidence intervals suggests that the models accurately represent the mean growth trend across the sampled age range.

The LRT revealed a highly significant difference in growth patterns between males and females ($\Lambda = 32.24$, $df = 3$, $p < 0.01$) (Figure 8). The significant test statistic indicates that the “Full Model,” which allows sex-specific growth parameters, provides a statistically superior fit to the “Reduced Model,” in which parameters are shared across sexes.

As illustrated in the comparative growth plot, females typically reach larger sizes than males at older ages, while males exhibit a slightly faster k toward their smaller asymptotic size. The divergence in growth trajectories becomes increasingly apparent after approximately age 10, as evidenced by non-overlapping 95% confidence intervals in higher age classes.

The LRT also revealed significant differences in growth parameters between the SEDAR 54 and SEDAR 101 datasets across all tested scenarios. For males, there was a significant difference in growth between the two datasets ($\Lambda = 38.83$, $df = 3$, $p < 0.01$) (Figure 9). Specifically, the male L_∞ in SEDAR 54 was estimated at 169.7 cm with a k of 0.164 year^{-1} and a t_0 of -1.14 years, whereas the SEDAR 101 males had a slightly higher L_∞ of 170.6 cm, a slower $k = 0.157$ year^{-1}, and a t_0 of -2.01 years. Female growth trajectories also differed significantly between the datasets ($\Lambda = 16.72$, $df = 3$, $p < 0.01$) (Figure 10). Females in SEDAR 54 exhibited a higher L_∞ (179.3 cm) compared to females in SEDAR 101 (178.9 cm). The k for SEDAR 54 females was estimated to be 0.132 year^{-1}, while SEDAR 101 females had a slightly higher k (0.137 year^{-1}). Finally, when pooling all sexes, the datasets remained significantly different ($\Lambda = 44.09$, $df = 3$, $p < 0.01$) (Figure 11). The overall population L_∞ was 176.3 cm in SEDAR 54 and 177.0 cm in SEDAR 101, and while overall growth rates were highly similar at $K = 0.141$ year^{-1} for both datasets, the theoretical age at length zero differed, with t_0 values of -1.81 years for SEDAR 54 and -2.22 years for SEDAR 101.

Theoretical longevity was calculated using the formula $5(\ln 2/k)$ using sex-specific growth coefficients and was calculated to be 22.07 year for males and 25.30 years for females; both values similar to the maximum aged individuals in this study.

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Parameter Estimates for Male Sandbar Sharks				
Parameter	*Estimate*	*Standard Error*	*95% Confidence Limits*	
L_∞	170.62	1.6451	167.38	173.85
k	0.1571	0.007454	0.1424	0.1717
t_0	-2.0058	0.1125	-2.2271	-1.7846
σ^2	54.3002	4.3406	45.7598	62.8406

Table 1. von Bertalanffy growth function parameter estimates for male sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean.

Parameter Estimates for Female Sandbar Sharks				
Parameter	*Estimate*	*Standard Error*	*95% Confidence Limits*	
L_∞	178.88	1.1982	176.52	181.23
k	0.1366	0.004106	0.1285	0.1446
t_0	-2.3148	0.1064	-2.5235	-2.1060
σ^2	69.2203	3.3323	62.6799	75.7607

Table 2. von Bertalanffy growth function parameter estimates for female sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean.

Parameter Estimates for Sandbar Sharks (combined sexes)				
Parameter	*Estimate*	*Standard Error*	*95% Confidence Limits*	
L_∞	176.97	0.9928	175.02	178.92
k	0.1407	0.003556	0.1337	0.1477
t_0	-2.2242	0.07973	-2.3806	-2.0677
σ^2	67.0628	2.7656	61.6367	72.4890

Table 3. von Bertalanffy growth function parameter estimates for female and male sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean.

Figure 1: Length distribution of sandbar sharks (Carcharhinus plumbeus) collected by observers and biologists and aged for use in SEDAR 101.

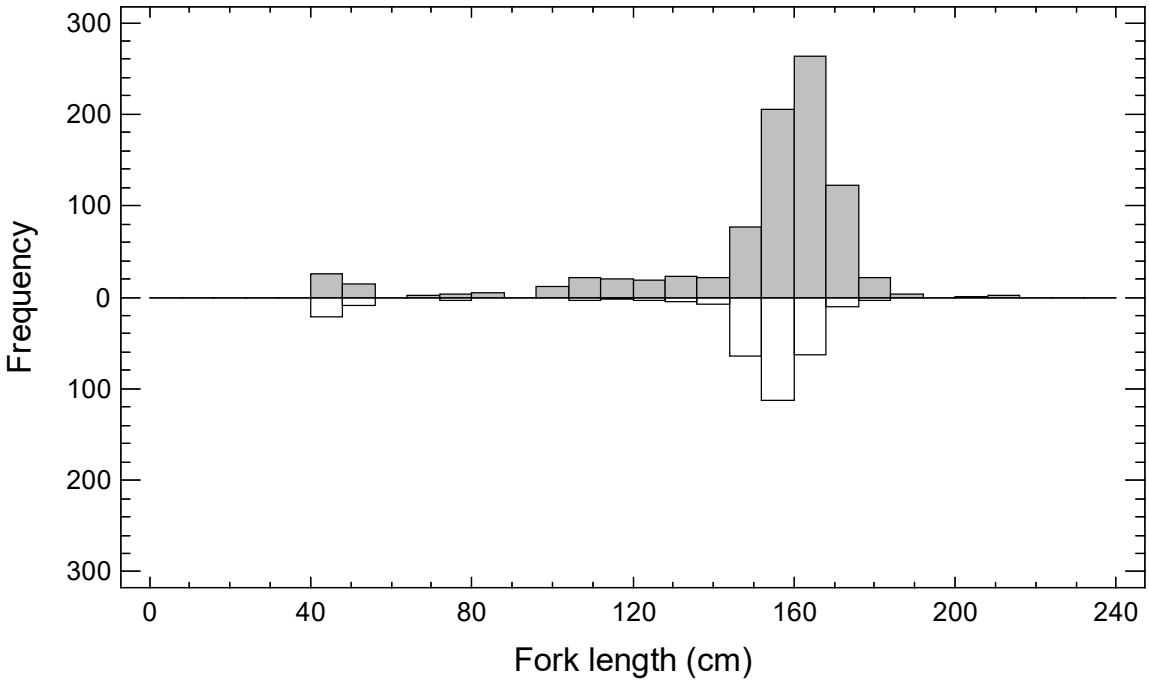

Figure 2: Vertebral section from a 155 cm fork length, male sandbar shark (*Carcharhinus plumbeus*) captured on March 16, 2024 in the Gulf of America. Total band count = 15, age = 13.5 years.

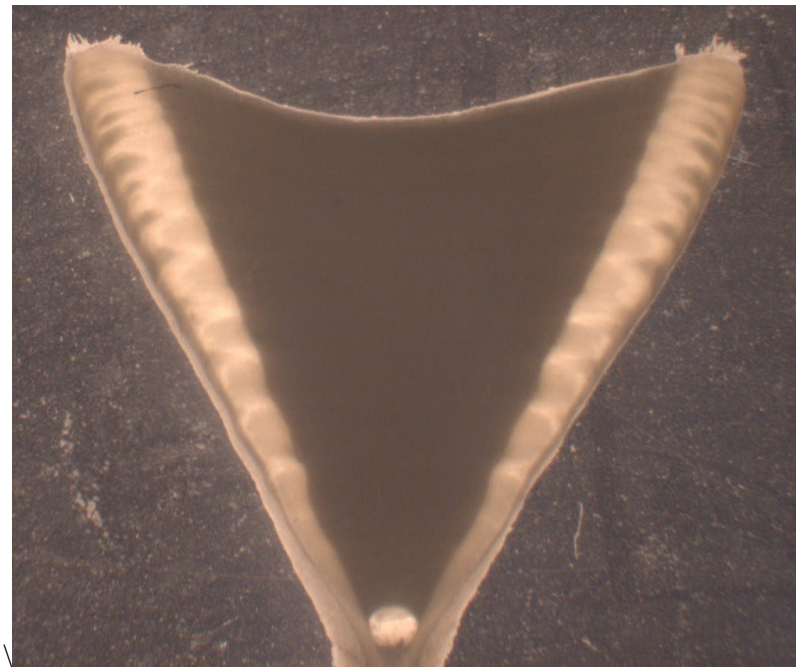

Figure 3: Scatterplot of ages assigned to each sandbar shark (*Carcharhinus plumbeus*) used to generate von Bertalanffy growth parameters (sexes combined).

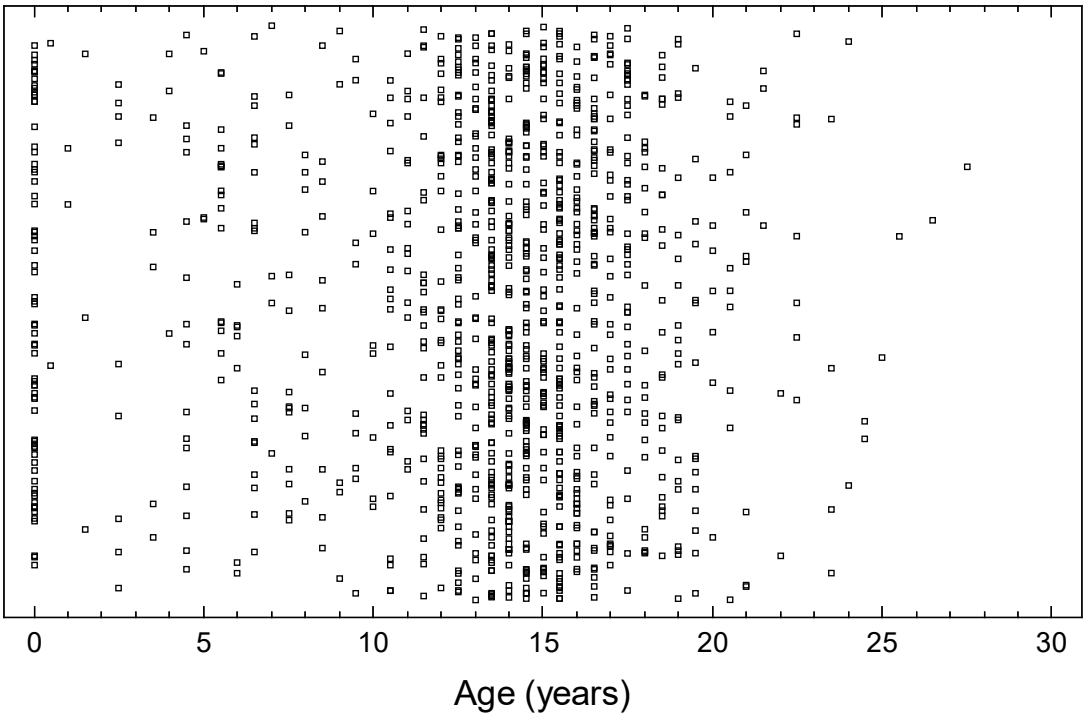

Figure 4: Bland-Altman plot showing increase in standard deviation among age estimates with increasing age for sandbar sharks (*Carcharhinus plumbeus*) aged in this study.

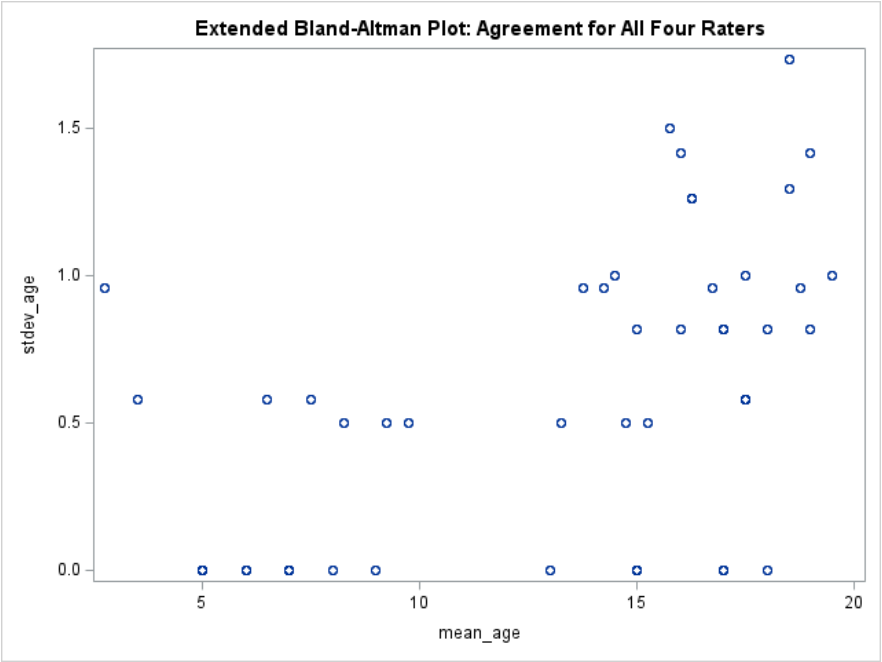

Figure 5: von Bertalanffy growth curve for male sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean.

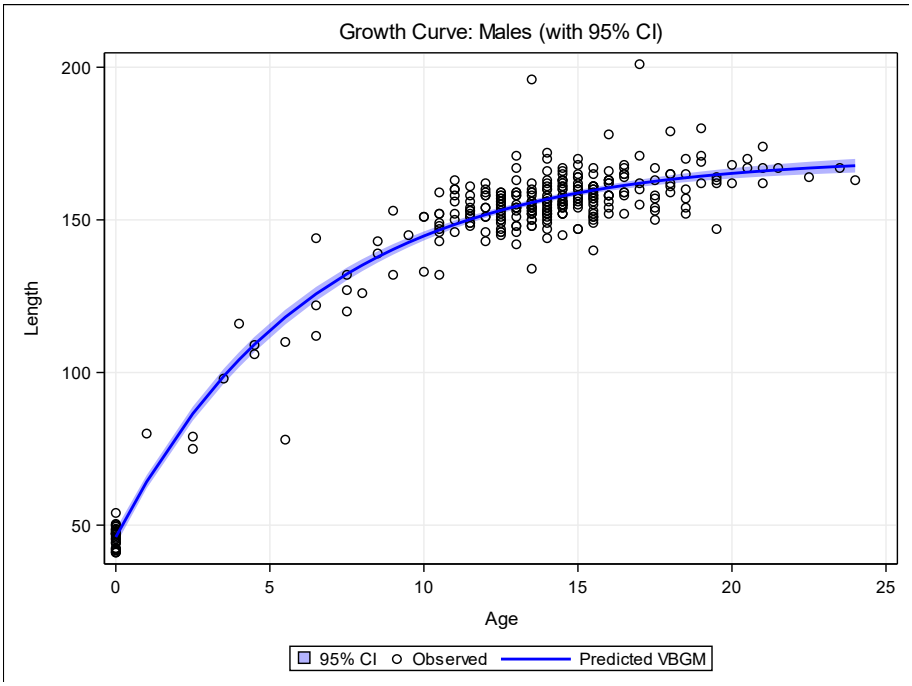

Figure 6: von Bertalanffy growth curve for female sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean.

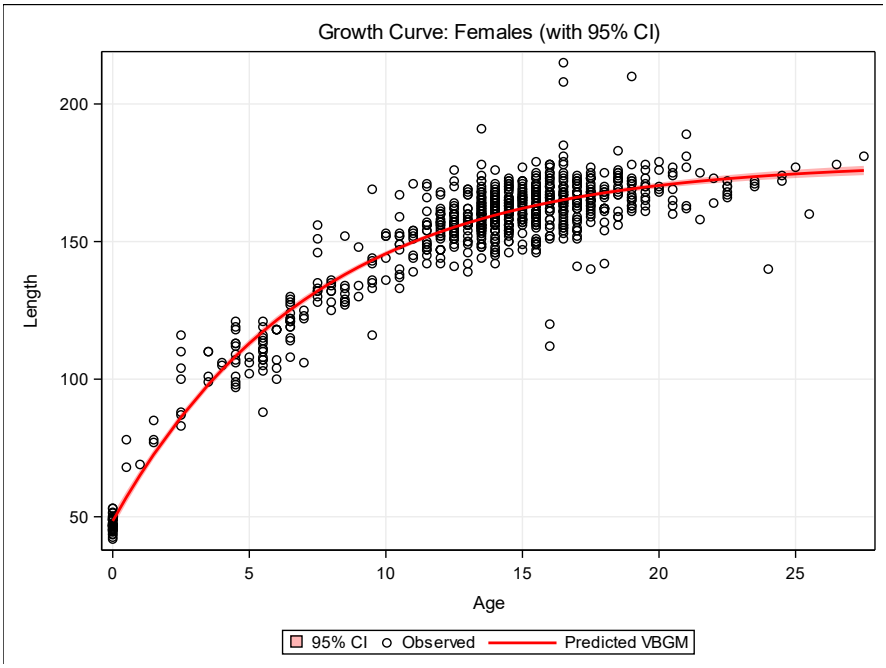

Figure 7: von Bertalanffy growth curve for female and male sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean.

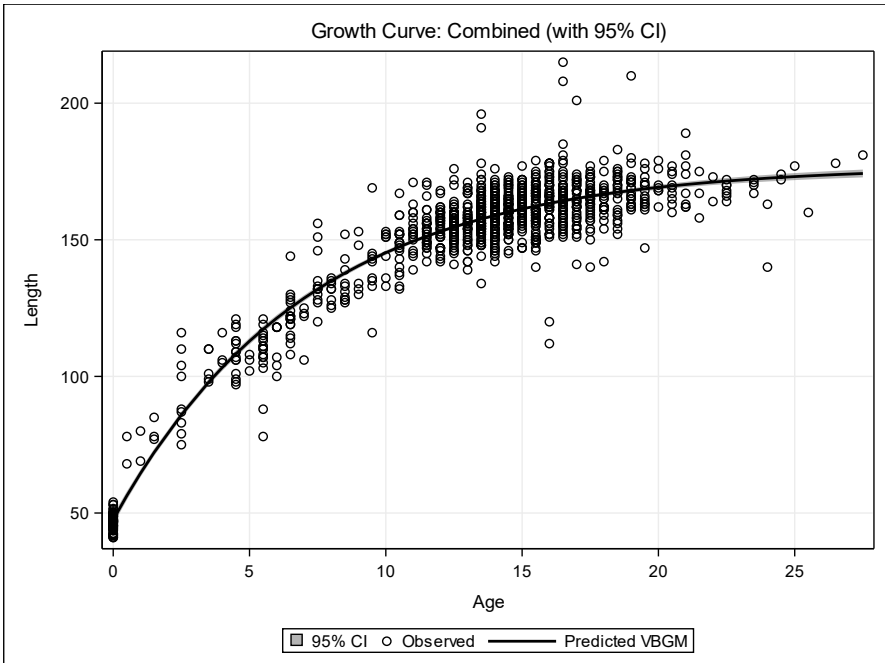

Figure 8: Comparison of von Bertalanffy growth curves for male sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean.

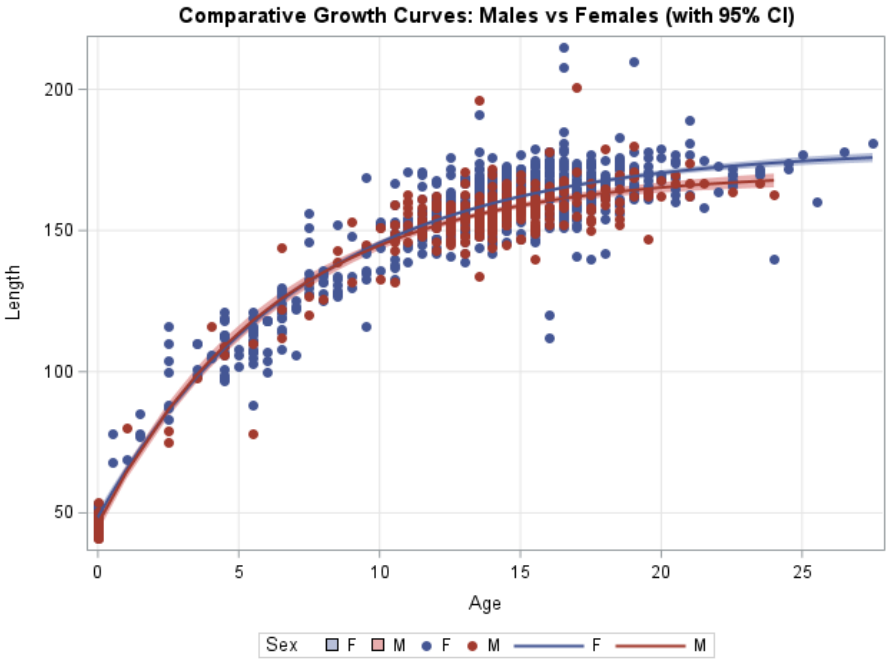

Figure 9: Comparison of von Bertalanffy growth curves for male sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean presented in SEDAR 54 and SEDAR 101.

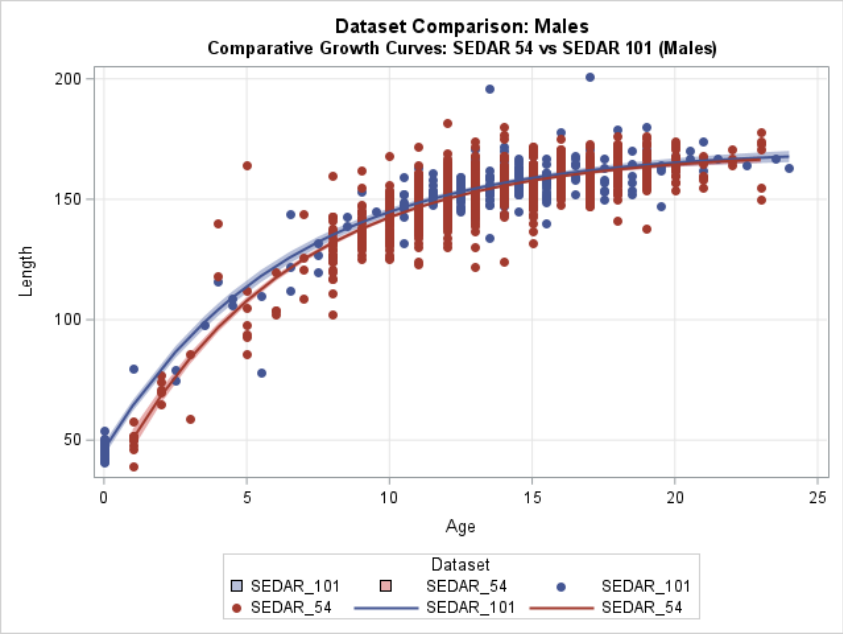

Figure 10: Comparison of von Bertalanffy growth curves for female sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean presented in SEDAR 54 and SEDAR 101.

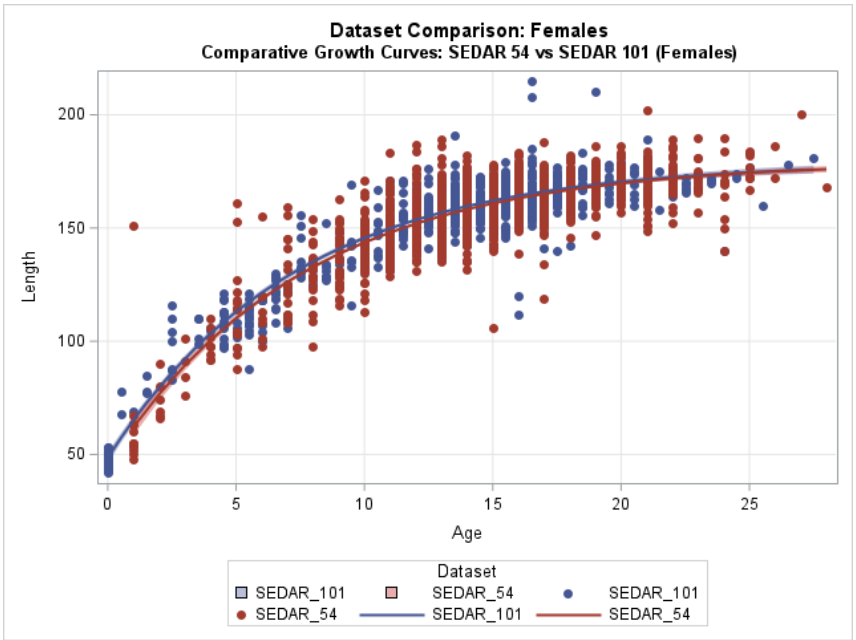

Figure 11: Comparison of von Bertalanffy growth curves for female and male sandbar sharks (*Carcharhinus plumbeus*) from the western north Atlantic Ocean presented in SEDAR 54 and SEDAR 101.