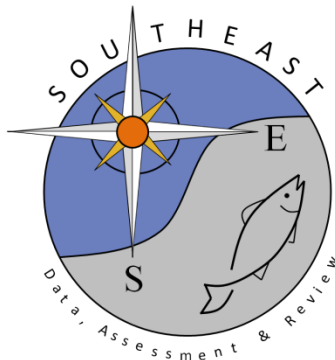


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Bryan S. Frazier, Ashley S. Galloway, Lisa J. Natanson, Andrew N. Piercy, and William B. Driggers III

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Age and growth of scalloped (*Sphyrna lewini*) and Carolina (*Sphyrna gilberti*) hammerheads in the western North Atlantic Ocean

Bryan S. Frazier¹, Ashley S. Galloway¹, Lisa J. Natanson², Andrew N. Piercy³, and William B. Driggers III⁴

¹Marine Resources Research Institute, South Carolina Department of Natural Resources
217 Fort Johnson Road Charleston, SC 29412

²53905 McBride Ave, Homer, AK 99603

³Valencia College 12350 Narcoossee Road Orlando, FL 32832

⁴National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southeast Fisheries Science Center, 3209 Frederic St. Pascagoula, MS 39567

Introduction

Vertebrae from Carolina (*Sphyrna gilberti*) and scalloped (*Sphyrna lewini*) hammerheads were collected from a variety of fishery dependent and independent sources. Contemporary samples were collected using longlines (bottom and pelagic), gillnets and shrimp otter trawls. When possible, fin clips were taken, and samples were identified to species (Carolina or scalloped hammerhead) using genomic techniques (Barker et al. 2021). Additionally, archived samples were provided by collaborators, including samples used by Piercy et al. (2007) to describe the age and growth of the scalloped hammerhead. As fin clips were not available for archived specimens, we could not determine if Carolina hammerhead samples were present. Despite extensive sampling, the Carolina hammerhead has not been detected in the Gulf of Mexico (GOM) but is known to occur along the U.S. east coast (hereafter, Atlantic) (Barker et al. 2021). Therefore, samples from the Atlantic were assumed to include both scalloped and Carolina hammerheads while samples from the GOM were assumed to be solely scalloped hammerheads.

Methods

Contemporary samples were measured to fork length and maturity was determined via gross morphology. A section of 8-10 cervical vertebrae were excised and excess muscle tissue was removed, and vertebrae were frozen prior to processing in the laboratory. Archived and contemporary samples from collaborators were received in various conditions (e.g. dry, submerged in ethanol, frozen and uncleaned). Individual vertebrae remained stored in their original state unless they had not been previously cleaned. Uncleaned vertebrae were thawed, separated into individual vertebrae, and excess tissue was removed using a scalpel. Vertebrae were then soaked in sodium hypochlorite (household bleach) to remove remaining peripheral tissue. Vertebrae were rinsed thoroughly and then stored in 95% ethanol.

Prior to sectioning, vertebrae were mounted to a glass slide using Crystalbond 509™ and a 0.5 mm sagittal section containing the focus was removed using a Buehler isomet low speed saw. The section was monitored while drying to ensure a preferred viewing state before being permanently mounted and preserved on a glass slide using Cytoseal™-XYL. Each mounted

vertebrae was examined using a Nikon SMT-2T dissecting microscope at 5-20X magnification with a transmitted light source.

Vertebral samples were selected at random and the number of translucent bands on the corpus calcareum were counted independently by two readers, each without knowledge of the other's reading or of the sex, size or date of capture of the shark from which the section was removed. Opaque bands representing summer growth and translucent bands representing winter growth were identified following the description and terminology of Cailliet & Goldman (2004). The birthmark, or change in angle of the corpus calcareum, was identified and counted as the first band. Following Piercy et al. (2007), we assumed a birth date of June 1 and that translucent bands representing winter growth formed 6 months later. Subsequent bands representing winter growth formed annually thereafter, therefore age = birthmark + winter bands -1.5. Marginal increment analysis previously conducted by Piercy et al. (2007) verified annual band formation and therefore was not completed for this working paper.

If there were discrepancies between readers band counts, the section was re-read simultaneously by both readers to resolve the difference. If no agreement was reached, the sample was discarded from all analyses. Reader precision and bias were determined using percent agreement, Beamish's index of average percent error (IAPE, Beamish & Fournier 1981), Bowker's test of symmetry (Hoenig et al. 1995) and age bias plots (Campana et al. 1995).

Growth models were generated using the three parameter von Bertalanffy growth model as adapted by Beverton and Holt (1957) $L_t = L_\infty(1 - e^{-k(t-t_0)})$ where L_t is length-at-age t and L_∞ (asymptotic length), k (coefficient of growth) and t_0 (theoretical age at which length equals zero) are fitted parameters. Confidence intervals for all model parameters were generated by bootstrapping (5,000 replicates). Models and confidence intervals were generated using the FSA (Ogle 2021) package in R (R Core Team 2021). Model fit was assessed by examination of residuals, Akaike Information Criterion (Akaike 1973) and residual sums of squares. To examine potential differences in growth parameters between males and females and regions, sex- and region-specific growth curves were estimated. Maximum likelihood ratio tests (Kimura 1980) generated using the fishmethods (Nelson 2021) package in R (R Core Team 2021) were used to detect if there were significant differences between sexes and regions.

Results

Samples from both species were pooled for assessment of precision and bias in age estimation. Of the 1,062 vertebrae received from contemporary and archived sources, 1,035 contained sufficient data (sex, and length) to include in growth models. Of these, four were discarded due to reader disagreement. Reader agreement (70.8%) and reader agreement ± 1 band (92.8%) were high. Bowker's test of symmetry results indicated no bias between Reader 1 and Reader 2, as well as between readers and consensus age estimates (Table 1). Results from Beamish's IAPE and Chang's C.V. indicate ages estimates were below the 5.5% and 7.6% thresholds suggested for age and growth studies (Campana 2001). Age bias plots for Reader 1 and Reader 2 revealed no systematic differences between readers among age classes (Figure 1).

Carolina hammerhead

A total of 76 vertebrae (Table 2) were available for construction of growth curves for Carolina hammerheads (all from the Atlantic). Unfortunately, insufficient samples were available

to generate robust estimates of growth in this species. The majority of collected specimens were young-of-the-year or juvenile animals (Table 3, Figure 2). Only one mature specimen, a male, was present in the dataset (observed age 21.5). Length data from young-of-the-year Carolina and scalloped hammerhead in SC nursery areas suggest Carolina hammerhead are born at a smaller length than scalloped hammerhead (SCDNR unpublished); however, how this difference in length-at-birth impacts species-specific life histories (e.g. growth and fecundity) remains unknown. Future efforts should focus on continuing to collect life history data from scalloped and Carolina hammerhead along with paired fin clips. These efforts will be necessary to develop an understanding of the life history data of this species.

As archived samples from the Atlantic likely include Carolina hammerheads and catch and fishery independent data are a mix of the two species, these samples were included in analyses of growth for scalloped hammerheads in the Atlantic and combined GOM and Atlantic growth models.

Scalloped Hammerhead

Vertebrae from 955 scalloped hammerhead plus 76 Carolina hammerhead were available for generation of growth curves. After initial model generation, the Life History Working Group determined 5 samples were outliers (likely incorrectly labeled samples or data errors) and removed them from subsequent analyses, leaving 1,026 samples for growth analyses (Table 4). Samples were pooled from the Atlantic and GOM and combined and sex-specific growth curves were generated (Figure 3, Table 5). There were significant differences in growth between females and males ($X^2 = 19.00, p < 0.001$); therefore, sexes were modeled independently for region-specific models. Maximum observed age for females was 29.5, and 39.5 for males for combined regions.

A total of 285 females were available from the Atlantic and 107 from the GOM (Table 4). The majority of samples were from young-of-year and juveniles, with low representation from mature individuals (Figure 4). Growth models were not significantly different between the Atlantic and GOM (Table 5, $X^2 = 1.02, p < 0.796$); however, given the small sample size from the GOM and lack of samples from large mature female scalloped hammerheads in this region, we do not have confidence that these results reflect true population parameters. Model results from this study were similar to those from Piercy et al. (2007) although maximum observed age in this study was slightly lower (Table 5).

A total of 423 males were available for the Atlantic and 184 from the GOM (Table 4) with representation of all size classes in the population (Figure 5). Growth models were significantly different between regions ($X^2 = 48.15, p < 0.001$) with scalloped hammerheads in the Atlantic reaching a larger asymptotic length and lower growth constant compared to individuals from the GOM (Table 5). Maximum longevity was similar between regions (39.5 years Atlantic, 37.5 years GOM). Model results from this study were significantly different than those from Piercy et al. (2007) with significant differences in all parameter estimates for combined regions. Results from this study suggest scalloped hammerhead males grow slower and to a greater average asymptotic length with greater longevity than previously thought; however, GOM specific results are not significantly different than those published in Piercy et al. (2007) although longevity is greater than previously published (Table 5).

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Tables

Table 1. Results for tests of precision and bias of scalloped (*Sphyrna lewini*) and Carolina hammerhead (*Sphyrna gilberti*) age estimation including: Percent agreement, Percent agreement plus or minus (\pm) one year 1, Bowker's Test (χ^2 , degrees of freedom and p-value), Beamish's Average Percent Error (I_{APE}) and Chang's Coefficient of Variation (CV).

Reader Comparison	Percent Agreement (PA)	Percent Agreement (PA \pm 1)	Bowker's Test	Bowker's Test degrees of freedom	Bowker's Test p value	Beamish's Average Percent Error (APE)	Chang's CV
Reader 1 vs. Reader 2	70.8	92.8	63.7	66	0.555	2.02	2.85
Reader 1 vs. Final	83.8	97.9	60.7	50	0.143	1.01	1.42
Reader 2 vs. Final	82.5	96.8	59.3	51	0.198	1.53	1.08

Table 2: Sample size and minimum/maximum fork lengths by sex for Carolina hammerheads (*Sphyrna gilberti*) collected off the U.S. east coast (Atlantic).

Sex	n	Min FL (cm)	Max FL (cm)
Female	39	27.0	104.1
Male	37	27.6	192.5
Combined	76	27.0	192.5

Table 3. Combined sex von Bertalanffy growth parameter estimates for Carolina hammerheads (*Sphyrna gilberti*) collected off the east coast of the U.S. (Atlantic). L_∞ = asymptotic length, k = growth constant, t_0 = theoretical age at size zero, MOA = maximum observed age.

Sex	L_∞ (cm)	k	t_0 (years)	n	MOA
Combined	192.0	0.211	-0.987	78	21.5

Table 4. Sex and capture location of scalloped hammerhead (*Sphyrna lewini*) and Carolina hammerhead (*Sphyrna gilberti*) specimens used to examine potential growth differences between individuals collected off the U.S. east coast (Atlantic) and in the northern Gulf of Mexico. A limited number of individuals (n=11 Female, n=16 Male) had no known region and are included in the areas combined only.

Sex	n	Atlantic		Gulf of Mexico			Areas Combined		
		Min FL (cm)	Max FL (cm)	n	Min FL (cm)	Max FL (cm)	n	Min FL (cm)	Max FL (cm)
Female	285	27.0	245.0	107	30.0	235.0	403	27.0	245.0
Male	423	27.6	287.0	184	35.0	223.0	623	27.6	287.0
Combined	708	30.8	287.0	291	30.0	236.0	1026	30.0	287.0

Table 5. Sex-specific, combined sex, and region-specific von Bertalanffy growth parameter estimates with 95% confidence intervals for scalloped hammerheads (*Sphyrna lewini*) and Carolina hammerheads (*Sphyrna gilberti*) collected off the east coast of the U.S. (Atlantic) and scalloped hammerheads in the northern Gulf of Mexico (GOM). L_{∞} = asymptotic fork length (FL, cm), k = growth constant, t_0 = theoretical age at size zero, MOA = maximum observed age.

Region	Sex	L_{∞} (cm FL)	k	t_0	n	MOA
Atlantic	Female	225.8 (219.6-240.8)	0.089 (0.077-0.096)	-2.290 (-2.579 · -2.143)	285	29.5
	Male	242.1 (235.5-249.8)	0.081 (0.074-0.087)	-2.33 (-2.551 · -2.129)	423	39.5
GOM	Female	234.5 (213.6-266.8)	0.084 (0.067-0.101)	-2.407 (-2.778 · -2.100)	107	24.5
	Male	210.5 (203.9-219.6)	0.122 (0.106-0.139)	-1.818 (-2.214 · -1.501)	184	37.5
Combined	Female	229.2 (219.6-240.8)	0.086 (0.077-0.096)	-2.352 (-2.579 · -2.143)	403	29.5
	Male	230.1 (225.1-236.0)	0.092 (0.086-0.099)	-2.166 (-2.356 · -1.986)	623	39.5
	Combined	232.2 (227.7-237.6)	0.088 (0.083-0.092)	-2.262 (-2.416 · -2.132)	1026	39.5
Piercy et al. 2007 [#]	Female	233.1 ± 11.5	0.09 ± 0.01	-1.62 ± 0.24	116	30.5
	Male	214.8 ± 4.2	0.13 ± 0.01	-2.22 ± 0.20	191	30.5
	Combined	219.8 ± 4.1	0.12 ± 0.01	-1.84 ± 0.15	307	30.5

[#]Standard error is reported for Piercy et al. (2007), and estimates are for the Atlantic and GOM combined.

Figures

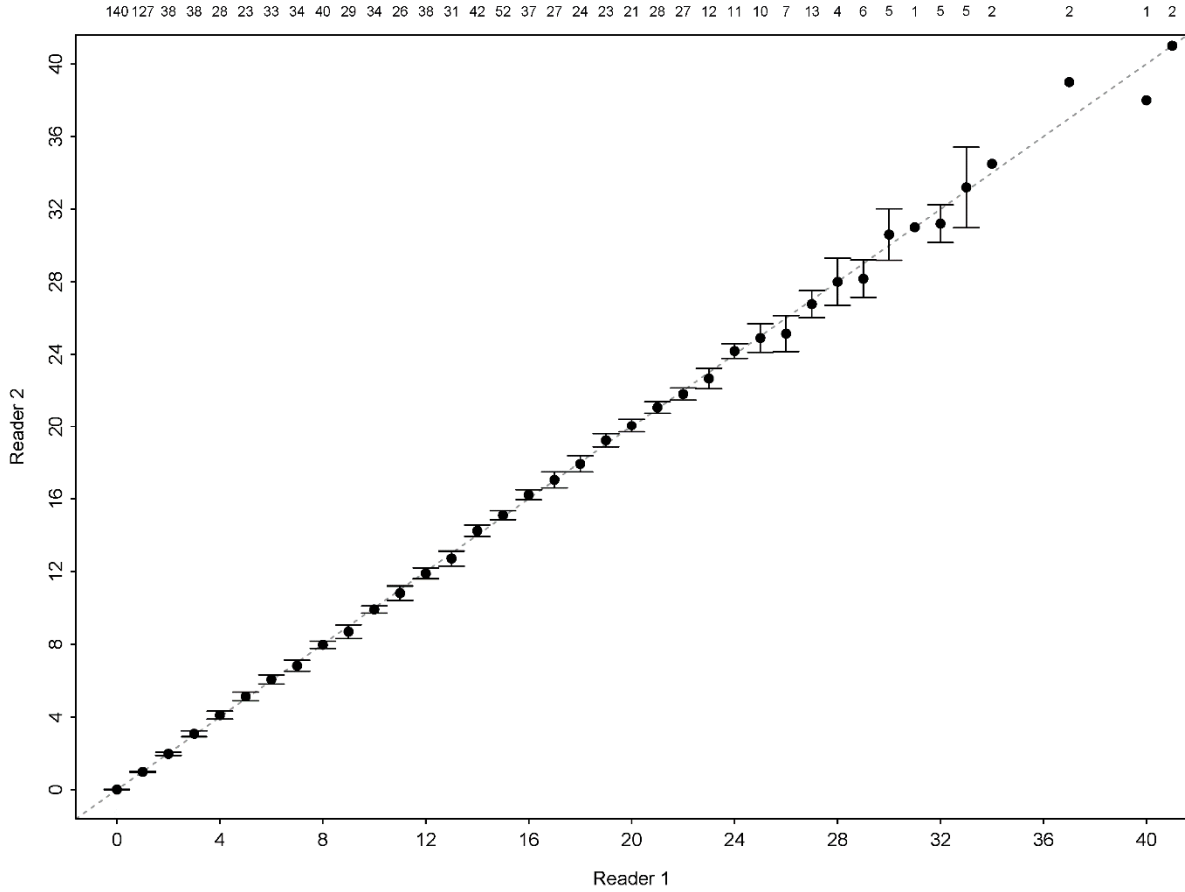


Figure 1. Intra-reader age bias plot for Reader 1 versus Reader 2 band counts with confidence intervals. The dashed line indicates 1:1 reader agreement. Numbers above the plot indicate sample size by band count.

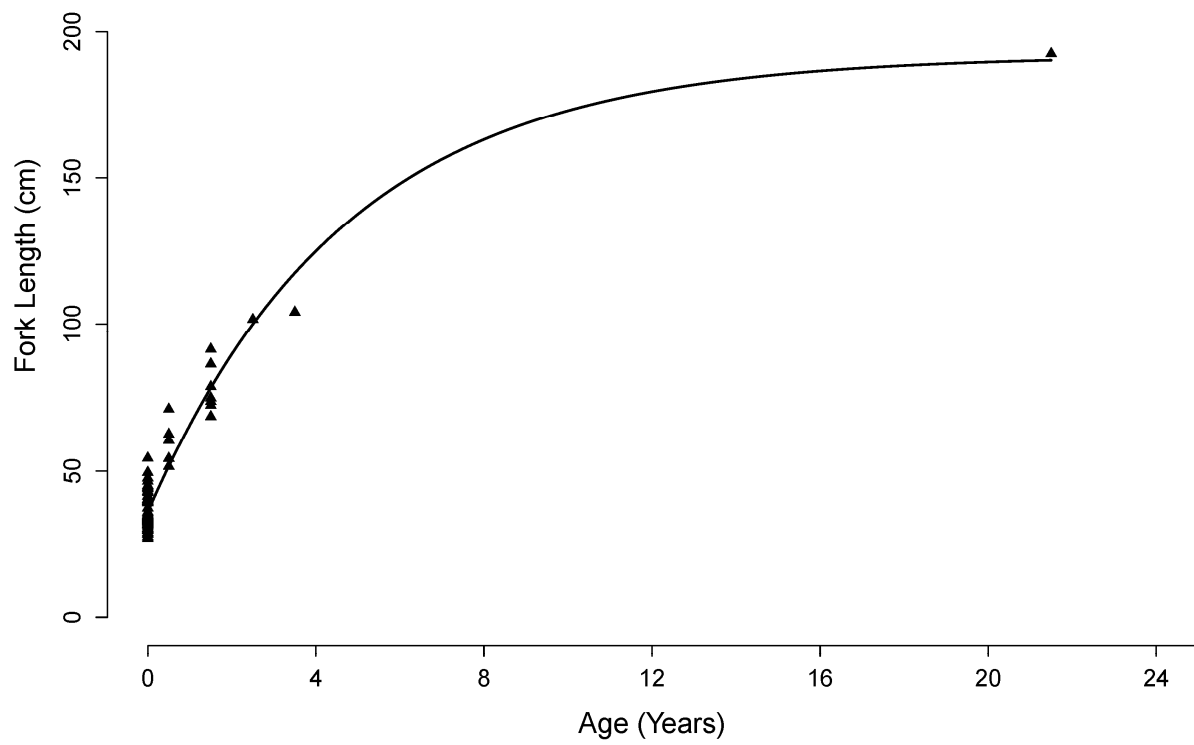


Figure 2. von Bertalanffy growth curve for combined male and female Carolina hammerheads (*Sphyrna gilberti*) sampled off the east coast of the U.S. (Atlantic).

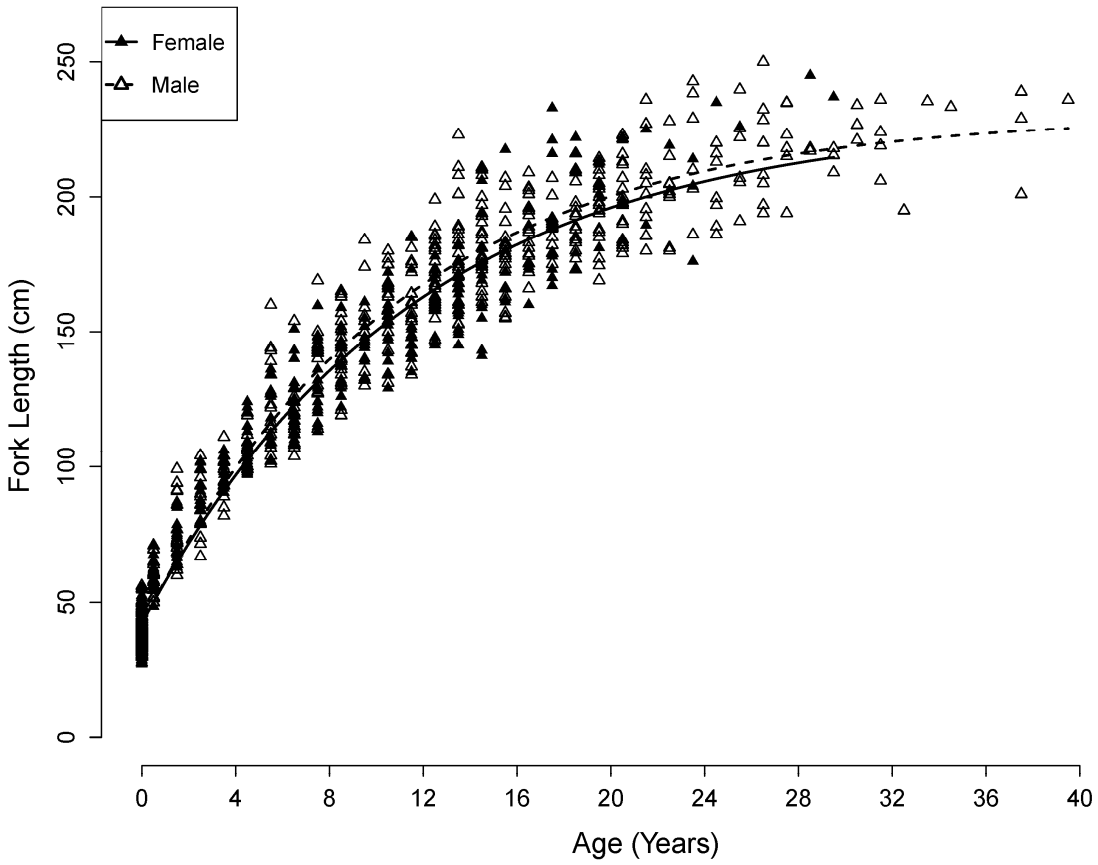


Figure 3. Comparison von Bertalanffy growth curves for female and male scalloped hammerheads (*Sphyrna lewini*) and Carolina hammerheads (*Sphyrna gilberti*) sampled off the east coast of the U.S. (Atlantic) and scalloped hammerheads from the northern Gulf of Mexico (GOM).

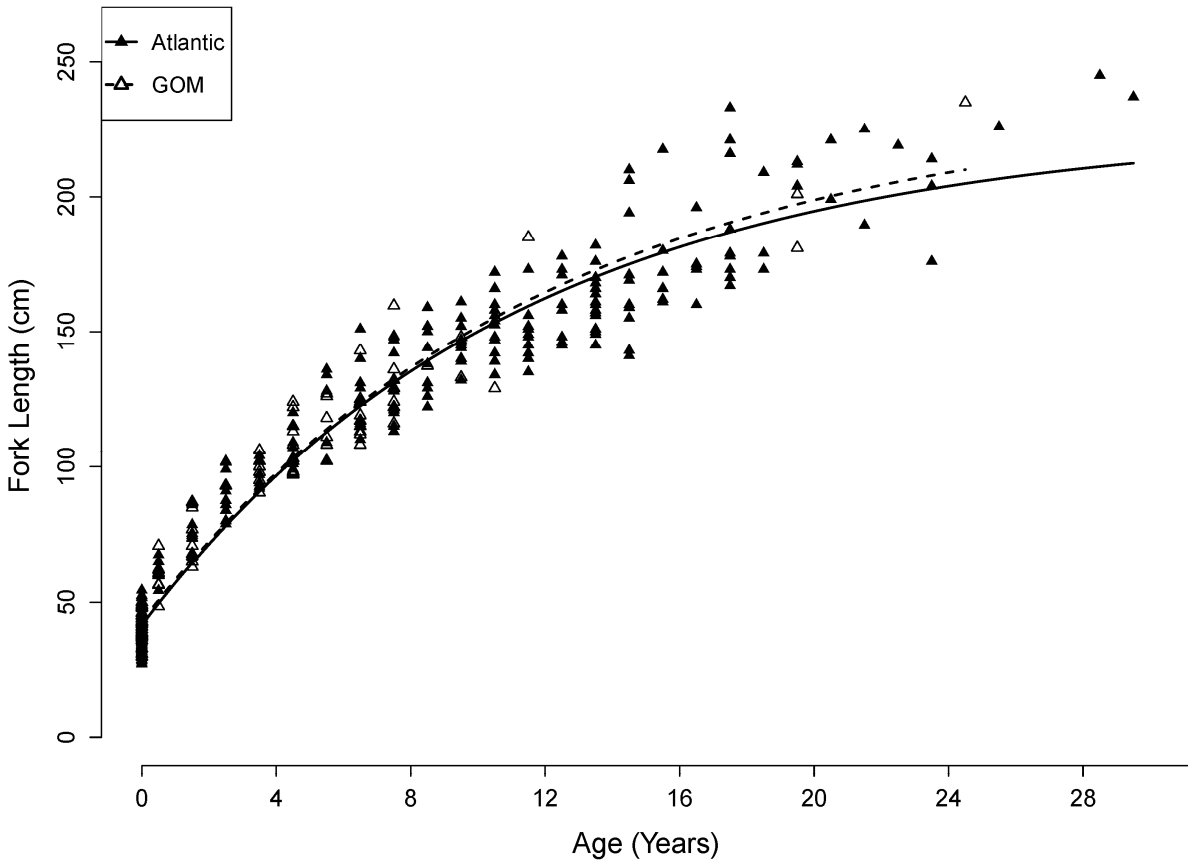


Figure 4. von Bertalanffy growth curve for female scalloped hammerheads (*Sphyrna lewini*) and Carolina hammerheads (*Sphyrna gilberti*) sampled off the east coast of the U.S. (Atlantic) and female scalloped hammerheads from the Gulf of Mexico.

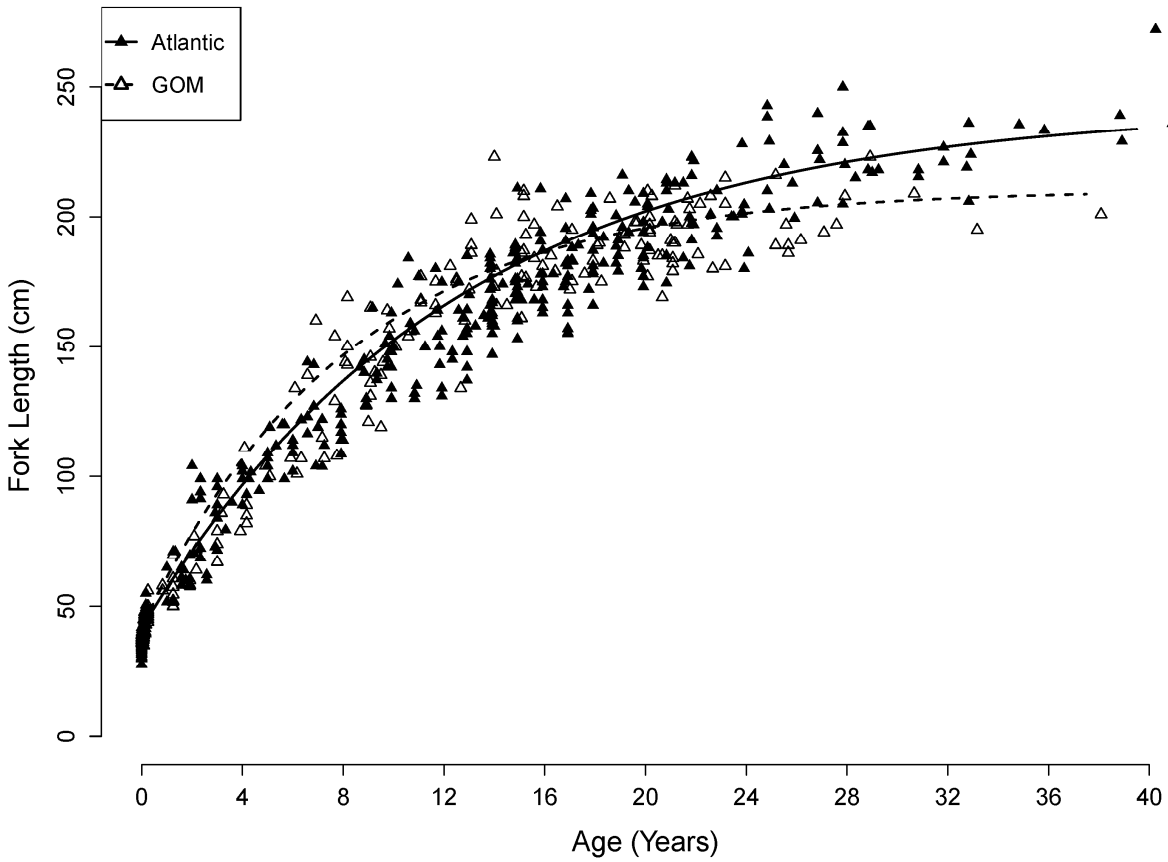


Figure 5. von Bertalanffy growth curves for male scalloped hammerheads (*Sphyrna lewini*) and Carolina hammerheads (*Sphyrna gilberti*) sampled off the east coast of the U.S. (Atlantic) and male scalloped hammerheads from the Gulf of Mexico.