Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods

John K. Carlson
Ivy E. Baremore
Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
3500 Delwood Beach Road
Panama City, Florida 32408
E-mail address (for J. K. Carlson): john.carlson@noaa.gov

Abstract—The age and growth dynamics of the spinner shark (*Carcharhinus brevipinna*) in the northwest Atlantic Ocean off the southeast United States and in the Gulf of Mexico were examined and four growth models were used to examine variation in the ability to fit size-at-age data. The von Bertalanffy growth model, an alternative equation of the von Bertalanffy growth model with a size-at-birth intercept, the Gompertz growth model, and a logistic model were fitted to sex-specific observed size-at-age data. Considering the statistical criteria (e.g., lowest mean square error [MSE], high coefficient-of-determination, and greatest level of significance) we desired for this study, the logistic model provided the best overall fit to the size-at-age data, whereas the von Bertalanffy growth model gave the worst. For "biological validity," the von Bertalanffy model for female sharks provided estimates similar to those reported in other studies. However, the von Bertalanffy model was deemed inappropriate for describing the growth of male spinner sharks because estimates of theoretical maximum size (L_∞) indicated a size much larger than that observed in the field. However, the growth coefficient (k=0.14/yr) from the Gompertz model provided an estimate most similar to that reported for other large coastal species. The analysis of growth for spinner shark in the present study demonstrates the importance of fitting alternative models when standard models fit the data poorly or when growth estimates do not appear to be realistic.

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Virtually every study concerned with describing the growth of elasmobranchs uses the von Bertalanffy growth equation (von Bertalanffy, 1938), despite criticism of the model (Knight, 1968; Roff, 1980). A review of the existing literature from 1962 to 2002 indicates that only about 12% of the published papers concerned with elasmobranch age and growth provide or have examined an alternative model (I.E.B., unpubl. data). Most studies on elasmobranch age and growth have simply fitted the von Bertalanffy model to observed or back-calculated size-at-age data without much concern about goodness-of-fit. In addition, appropriate age-structured assessments require accurate measures of the growth coefficient (k) of the population when calculating, for example, indirect estimates of natural mortality. A complete study on the age and growth of a species may require the application of multiple growth models, especially when data do not appear to fit a given model (e.g., when there is no statistical significance or when there is poor goodness-of-fit) or when results do not appear to be biologically realistic.

The spinner shark (*Carcharhinus brevipinna*) is a cosmopolitan species occurring in warm-temperate areas of the Atlantic Ocean, the Indian Ocean, and the western Pacific Ocean (Compagno, 1984). Off the United States east and Gulf of Mexico coasts, the spinner shark is managed under a large coastal shark complex (NMFS, 1993). Sharks within this complex are considered to be relatively large, slow growing, long lived, and are currently overfished (Cortés et al.[1]).

Although Allen and Wintner (2002) recently examined the age and growth of the spinner shark off South Africa, the only existing information on spinner sharks from U.S. waters is from Branstetter (1987), who examined just 15 animals from the Gulf of Mexico. The purpose of the present study is to re-examine the age and growth dynamics of the spinner shark off the U.S. southeast and Gulf of Mexico coasts. We compare and contrast four growth models to determine the model that best describes the growth data of the spinner shark.

Materials and methods

Sharks (n=273) were collected from 1995 to 2003 in the U.S. Exclusive Economic Zone from Galveston, Texas to Key West, Florida, in the Gulf of Mexico and in the U.S. south Atlantic Ocean from Charleston, South Carolina, to West Palm Beach, Florida (Fig. 1). Precaudal (PC), fork (FL) or total (TL) length (cm) were measured, and sex and maturity state were determined for each shark. Total

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[1] Cortés, E., L. Brooks, and G. Scott. 2002. Stock assessment of large coastal sharks in the U.S. Atlantic and Gulf of Mexico. Sustainable Fisheries Division contribution SFD-02/03-177, 64 p. Southeast Fisheries Science Center, 3500 Delwood Beach Rd., Panama City, FL, 32408.

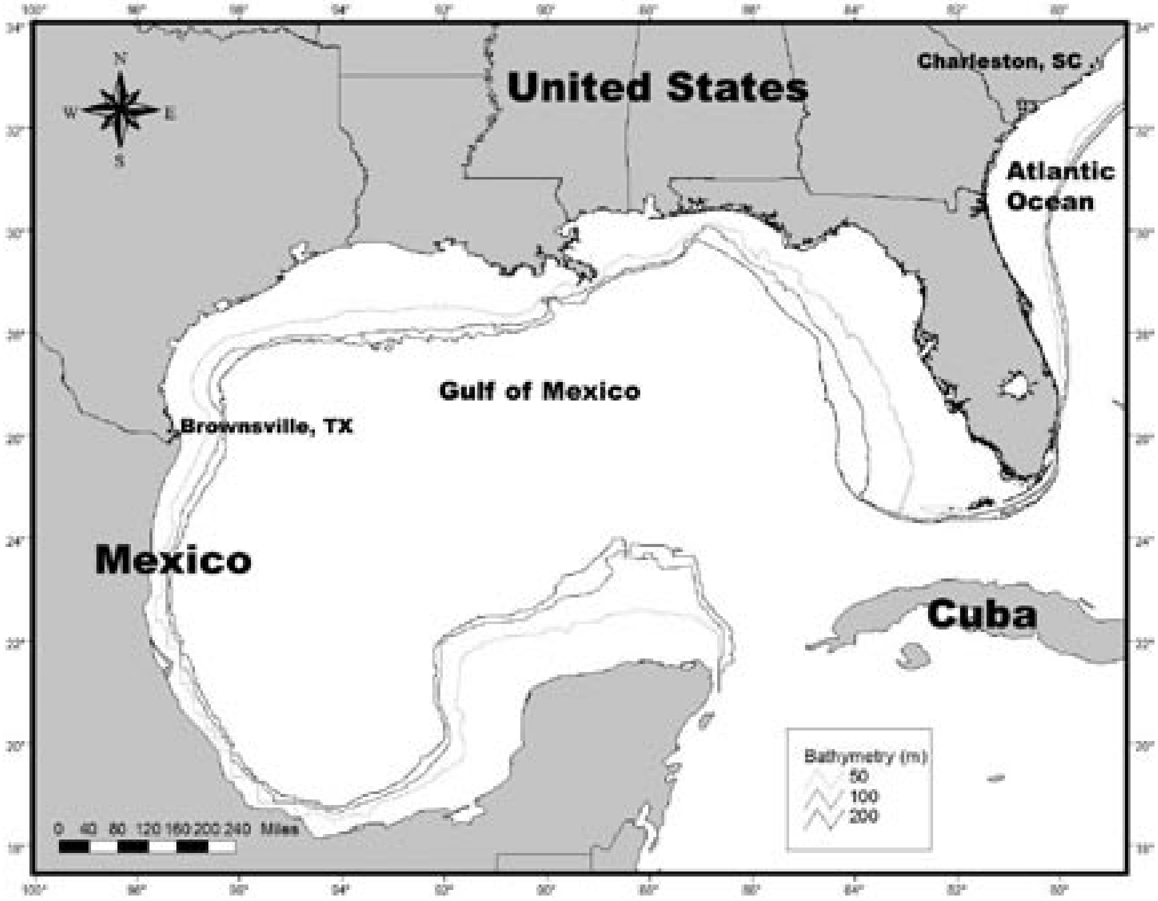

Figure 1

Map of the sampling area for spinner sharks (*Carcharhinus brevipinna*) showing areas and locations stated in the text.

length was measured as a straight line from the tip of the snout to the tip of the tail in a natural position. The weight (kg) of each shark was obtained when sampling conditions permitted. Vertebrae were removed from an area anterior to the first dorsal fin.

Vertebral sections were placed on ice after collection and frozen upon return to the laboratory. Thawed vertebrae were cleaned of excess tissue and soaked in a 5% sodium hypochlorite solution for 5–30 min to remove remaining tissue. After cleaning, vertebrae were soaked in distilled water for 30 minutes and stored in 95% isopropyl alcohol. Prior to examination, one vertebra from each shark was chosen at random, removed from alcohol, and dried. The vertebra was fixed to a clear glass slide with resin and sectioned with a Buehler 82 Isomet low-speed saw.

Sagittal sections of different thicknesses were cut from the vertebral centrum and stained with crystal violet, or alizarin red, or left unstained according to the methods of Carlson et al. (2003). Each vertebral section was mounted on a glass microscope slide with ProTex cytoseal (Lerner Laboratories, Pittsburg, PA) and examined by using a dissecting microscope under transmitted light. The banding pattern was found to be most apparent on unstained sagittal sections with a thickness of 0.3 mm.

Opaque bands representing summer growth and translucent bands representing winter growth were identified following the description and terms in Cailliet and Goldman (2004) (Fig. 2). Because no validation is available for this species, verification of the annual period of band formation was performed by using the relative marginal increment analysis (Branstetter and Musick, 1994; Natanson et al., 1995):

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where MIR = the marginal increment ratio;
VR = the vertebral radius;
R_n = distance to the outer edge of the last complete band; and
R_{n-1} = distance to the outer edge of the next-to-last complete band.

Mean MIR was plotted against month to determine trends in band formation. A single factor analysis of variance was used to test for differences in arcsine-transformed (Zar, 1984) MIR data among months.

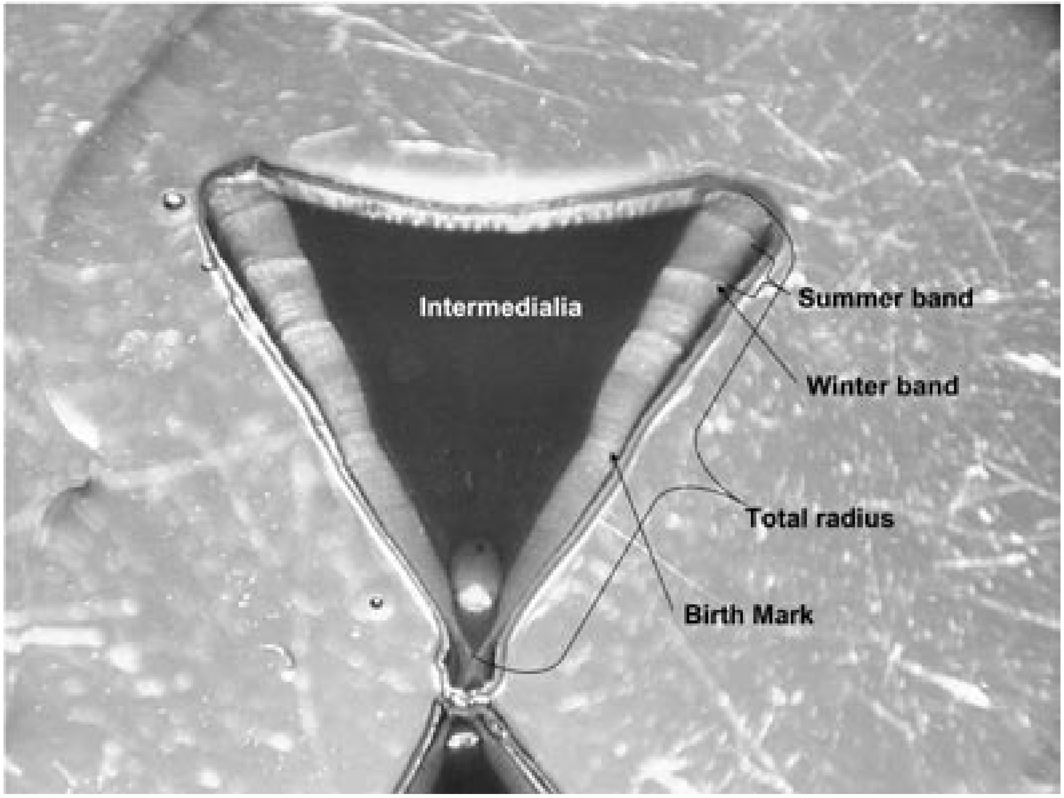

Figure 2

Sagittal section from a 3.5+ year-old spinner shark (*Carcharhinus brevipinna*) illustrating the banding pattern and winter marks (annuli) used to assign age.

Both authors randomly read vertebrae independently without knowledge of sex or length of specimens. Vertebral age estimates for which the readers disagreed were reread simultaneously by using a digital camera and software (Pixera Studio version 2, Pixera Corporation, Los Gatos, CA). If no agreement between readings was reached, samples were discarded.

Several methods were used to evaluate precision and bias among age determinations following the recommendations in Cailliet and Goldman (2004). Percent agreement (PA=number agreed/number read)×100 and percent agreement plus or minus one year were calculated for 10 cm (e.g. 76–85 cm FL) length intervals to evaluate precision (Goldman, 2002). The index of average percent error (APE: Beamish and Fournier, 1981) was calculated to compare the average deviation of readings from the means of all readings for each vertebral section:

$$IAPE = \frac{1}{n}\sum_{j=1}^{N}\left[\frac{1}{r}\sum_{i=1}^{R}\frac{\left|x_{ij}-x_j\right|}{x_j}\right],$$

where n = number of sharks aged;
r = number of readings;
x_{ij} = i^{th} age estimation of j^{th} shark at i^{th} reading; and
x_j = mean age calculated for the j^{th} shark.

Chi-square tests of symmetry following Hoenig et al. (1995) were used to determine if differences between readers were systematic or due to random error.

Several models were fitted to sex-specific observed size-at-age data to estimate the growth dynamics in spinner shark. Although back-calculated size-at-age length data would increase sample sizes for some ages (Cailliet, 1990), multiple back-calculated lengths-at-age are not independent samples and violate statistical assumptions in estimating parameters for a growth model (Vaughan and Burton, 1994). Vaughan and Burton (1994) pointed out that estimates of the model parameters may be biased because multiple back-calculated lengths cause an inaccurate number of degrees of freedom. Thus, we used data only from observed size-at-age.

In developing theoretical growth models, we assumed that 1) the birth mark is the band associated with a pronounced change in angle in the intermedialia, and we assigned an arbitrary birth date of 1 June, the approximate mid-point date when neonates were present in field collections, 2) translucent bands representing winter growth form approximately six months later (i.e., 0.5 years) and 3) subsequent translucent bands representing winter growth form at yearly intervals, thereafter. Thus, ages (yr) were calculated by following the algorithm of Carlson et al. (1999): *age = birth mark + number of translucent winter bands* − 1.5. If only the birth mark was present, the age was 0+ years. All age estimates from growth band counts were based on the hypothesis of annual growth band deposition (Branstetter, 1987).

The von Bertalanffy growth model (von Bertalanffy, 1938) is described by using the equation

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

where L_t = mean fork length at time t;
L_∞ = theoretical asymptotic length;
k = growth coefficient; and
t_0 = theoretical age at zero length.

An alternative equation of the von Bertalanffy growth model, with a size-at-birth intercept rather than the t_0 parameter (Van Dykhuizen and Mollet, 1992, Goosen and Smale, 1997; Carlson et al., 2003) is described as

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

where $b = (L_\infty - L_0)/L_\infty$; and
L_0 = length at birth.

Estimated median length at birth for spinner shark is 52 cm FL (Carlson, unpubl. data).

We also used the modified form of the Gompertz growth model (Ricker, 1975). The model is expressed following Mollet et al. (2002) as

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

where $G = \ln(L_0/L_\infty)$.

For the Gompertz model, the estimated median asymptotic length for spinner shark is 220 and 200 cm FL for females and males, respectively (Carlson, unpubl. data).

A logistic model (Ricker, 1979) was also considered in the form

$$W_t = W_\infty/(1 + e^{-k(t-a)}),$$

where W_t = mean weight (kg) at time t;
W_∞ = theoretical asymptotic weight;
k = (equivalent to g in Ricker, 1979) instantaneous rate of growth when $w \to 0$; and
a = (equivalent to t_0 in Ricker, 1979) time at which the absolute rate of increase in weight begins to decrease or the inflection point of the curve.

If weight was not available, length was converted to weight by using the regression: *weight* = $0.0000209 \times FL^{2.9524}$ (n=226, r^2=0.98, range: 1.1–66.1 kg).

Table 1

A summary of the number of spinner sharks (*Carcharhinus brevispinna*), by month and sex, used for our estimates of age.

Month	Male	Female
January	8	3
February	0	0
March	0	13
April	0	3
May	25	6
June	15	47
July	35	22
August	30	35
September	4	13
October	0	0
November	0	0
December	0	0

All growth model parameters were estimated with Marquardt least-squares nonlinear regression. All models were implemented by using SAS statistical software (SAS version 6.03, SAS Institute Inc., Cary, NC). The goodness-of-fit of each model was assessed by examining residual mean square error (MSE), coefficient-of-determination (r^2), F from analysis of variance, level of significance (P<0.05), and standard residual analysis (Neter et al., 1990).

Results

Morphometric relationships were developed to convert length measurements. Linear regression formulae were determined as PC=0.880(FL)+1.503, n=163, r^2=0.88, P<0.0001; and FL=0.847(TL)−3.497, n=260, r^2=0.99, P<0.0001.

Of the original 273 samples, 14 were deemed unreadable and were discarded (Table 1). The index of average percent error for the initial reading between authors was 10.6%. When grouped by 10-cm length intervals, agreement for combined sexes was reached for an average of 30.2% and 58.2% (±1 band) of band counts for sharks less than 115 cm FL (Table 2). Above 115 cm FL, agreement was reached for 33.5% and 74.0% (±1) of band counts for samples initially read. Hoenig's et al. (1995) test of symmetry indicated that there was bias between readers (χ^2=98.33, df=40, P<0.001).

Relative marginal increment analysis indicated that bands form annually during winter months (Fig. 3). The smallest relative increment was found in January and the greatest in July. The relative marginal increment ratio increased through spring months (March–May), peaked in summer (June–August), and then declined to fall. However, no statistical difference was found in MIR values among months (F=1.63, df=7, P=0.129), likely because of the large variation in increment by months.

Under the statistical criteria established in our study, all growth models fitted the data well (Table 3). For males and females, models were highly significant (P<0.001) and exhibited high coefficients of determination (r^2≥0.88). Residual mean square error (MSE) was lowest for the logistic models. Notably, MSE was much higher for the von Bertalanffy model males than for any other model. Plots of the residuals against predicted sizes indicated no pattern in the residuals for any model. The standard deviation of the residuals was lowest for the logistic models (Table 3).

Estimates of the asymptotic size varied depending on sex and model (Table 3; Figs. 4 and 5). For males, the highest asymptotic length was produced by the von Bertalanffy model (L_∞=421 cm FL), intermediate lengths came from the von Bertalanffy model with a size-at-birth intercept (L_∞=279 cm FL) and the Gompertz model (L_∞=200, G=1.38), and lowest length was produced by the logistic model (W_∞=60.2 kg, ~161 cm FL). For females, asymptotic sizes were highest and similar with the von Bertalanffy, von Bertalanffy model with a size-at-birth, and the Gompertz models (226, 202, and 220 cm FL, respectively) and lowest with the logistic model (62.6 kg or ~162 cm FL).

Among models with comparable growth coefficients, the von Bertalanffy model produced the lowest growth coefficient for both males and females (k=0.03 and 0.08/yr, respectively). Growth coefficients were higher and fairly similar for the other two length models. The growth coefficient from the logistic weight model was 0.44 and 0.37 for males and females, respectively.

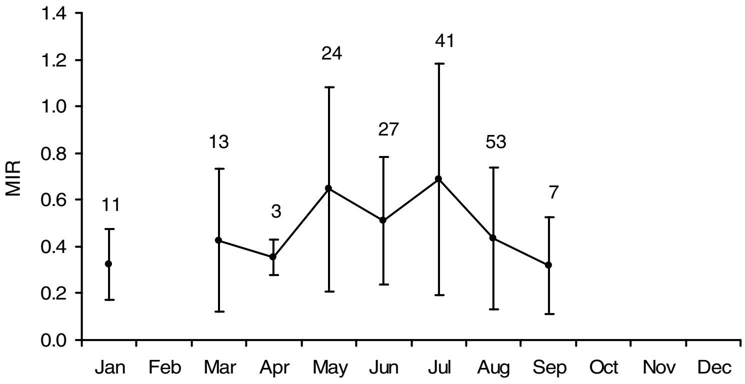

Figure 3

Mean marginal increment analysis (MIR) by month for combined sexes of spinner sharks (*Carcharhinus brevipinna*). Vertical bars are ± the standard deviation of the mean and numbers above each month represent the sample size.

Table 2

Percent agreement and percent agreement (±1 band) from the initial set of readings for spinner shark (*Carcharhinus brevispinna*).

	Sexes combined			Males			Females		
FL interval	Total read	Percent agreement	Percent agreement ±1 band	Total read	Percent agreement	Percent agreement ±1 band	Total read	Percent agreement	Percent agreement ±1 band
46–55	8	75.0	100.0	2	100.0	100.0	6	66.7	100.0
56–65	62	32.3	83.9	25	20.0	64.0	37	40.5	81.1
66–75	10	20.0	60.0	4	0.0	50.0	6	33.3	66.7
76–85	36	30.6	66.7	17	29.4	47.1	19	31.6	84.2
86–95	28	14.3	28.6	13	23.1	30.8	15	6.7	26.7
96–105	15	20.0	40.0	5	0.0	40.0	10	30.0	40.0
106–115	21	19.0	28.6	10	10.0	20.0	11	27.3	36.4
116–125	16	37.5	68.8	10	40.0	90.0	6	33.3	33.3
126–135	12	41.7	75.0	2	50.0	50.0	10	40.0	80.0
136–145	5	60.0	100.0	5	60.0	100.0	0	—	—
146–155	10	40.0	60.0	6	50.0	83.3	4	25.0	25.0
156–165	12	41.7	58.3	8	62.5	87.5	4	0.0	25.0
166–175	11	36.4	63.6	4	50.0	75.0	7	28.6	57.1
176–185	12	16.7	66.7	6	33.3	83.3	6	0.0	50.0
186–195	1	0.0	100.0	0	—	—	1	0.0	100.0

The Gompertz model estimated size-at-birth (61 cm FL) within the range reported for spinner sharks. Size-at-birth off the United States southeast and Gulf of Mexico coasts has been reported to range from 50 to 65 cm FL depending on the study (Branstetter, 1987; Castro, 1993; Carlson, unpubl. data).

Observed size-at-age and longevity were different between males and females (Table 4). For most ages, females were larger. The oldest animals aged were 17.5+ years (female) and 13.5+ years (male).

Discussion

Considering our statistical criteria (e.g., lowest MSE, high r^2, and level of significance), logistic models provided the best fits to the size-at-age data. The von Bertalanffy growth models, on the other hand, gave the worst fits. However, the criteria used to evaluate the models in this study may not be adequate. Because statistical fits have not been reported by other elasmobranch age and growth studies, we were not able to compare our criteria with other studies. Although not directly comparable, goodness-of-fit criteria used to select the best nonlinear gastric evacuation models have employed a combination of r^2, residual sum of squares, standard deviation, or coefficient of variation of residuals (review in Cortés, 1997). Until a more rigorous criterion is developed for growth models, efforts should continue to identify a best-fitting growth model.

We feel the von Bertalanffy model is inappropriate for describing the growth of male spinner shark. Asymptotic values indicated an unreasonable theoretical maximum size of 421 cm FL—much larger than sizes from recent fishery-dependent and fishery-independent sources (176–220 cm FL; Grace and Henwood, 1997; Morgan[3]; Carlson, unpubl. data). Asymptotic values from other models approach those actual values. Because of the relationship between k and L_∞, the von Bertalanffy growth coefficient was also much lower than expected. The growth coefficient from the Gompertz model was 0.14/yr, similar to those reported for other large coastal species in general (Cortés, 2000) and to those reported by Allen and Wintner (2002) for spinner sharks from South Africa.

The poor statistical fit and unrealistic biological estimates of the von Bertalanffy growth model for male spinner shark illustrates the importance of fitting alternative models to the data when estimates do not appear to be biologically real. Although sample size was well represented for most ages, the von Bertalanffy growth model did not reach an asymptote until well beyond the

Table 3

Estimates of growth and goodness-of-fit from four growth models fitted to observed size-at-age data for male and female spinner sharks (*Carcharhinus brevispinna*). Values in parentheses are standard errors. L_0 = size at birth. The standard deviation (SD) of the residuals is from standard residual analysis. MSE=mean square error. n/a=not available.

Model	Asymptotic size[1] (cm FL)	Growth coefficient (/yr)	t_0[2] (yr)	L_0 (cm FL)	F	P	r^2	MSE	SD of residuals
Male									
von Bertalanffy	421.0 (±157.6)	0.03 (±0.02)	−4.58 (±0.65)	—	543.91	<0.001	0.91	543.91	11.91
von Bertalanffy with size-at-birth	279.1 (±39.4)	0.07 (±0.02)	n/a	52	946.24	<0.001	0.89	163.65	12.49
Gompertz	200 (G=1.38±0.09)	0.14 (±0.02)	n/a	60.5 (±1.9)	557.83	<0.001	0.91	141.23	11.78
Logistic	60.2 (±39.4)	0.44 (±0.05)	6.75 (±0.47)		483.00	<0.001	0.93	47.44	6.83
Female									
von Bertalanffy	226.2 (±18.6)	0.08 (±0.02)	−3.84 (±0.40)	—	612.20	<0.001	0.90	150.70	12.19
von Bertalanffy with size-at-birth	202.7 (±10.9)	0.11 (±0.01)	n/a	52	1047.19	<0.001	0.88	173.07	12.78
Gompertz	220 (G=1.17±0.4)	0.16 (±0.02)	n/a	60.7 (±1.6)	609.09	<0.001	0.90	151.39	12.21
Logistic	62.6 (±3.2)	0.37 (±0.03)	7.62 (±0.43)		572.84	<0.001	0.93	43.82	6.57

[1] Asymptotic size for the von Bertalanffy, von Bertalanffy with size-at-birth, and Gompertz models are in cm, whereas asymptotic size for the logistic model is in kg.

[2] t_0 is the theoretical age at zero length for the von Bertalanffy whereas t_0 for the logistic model represents time at which the absolute rate of increase in weight begins to decrease.

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[3] Morgan, A. Personal commun. Program for Shark Research, Florida Museum of Natural History, Univ. Florida, P.O. Box 117800, Gainesville, FL, 32611.

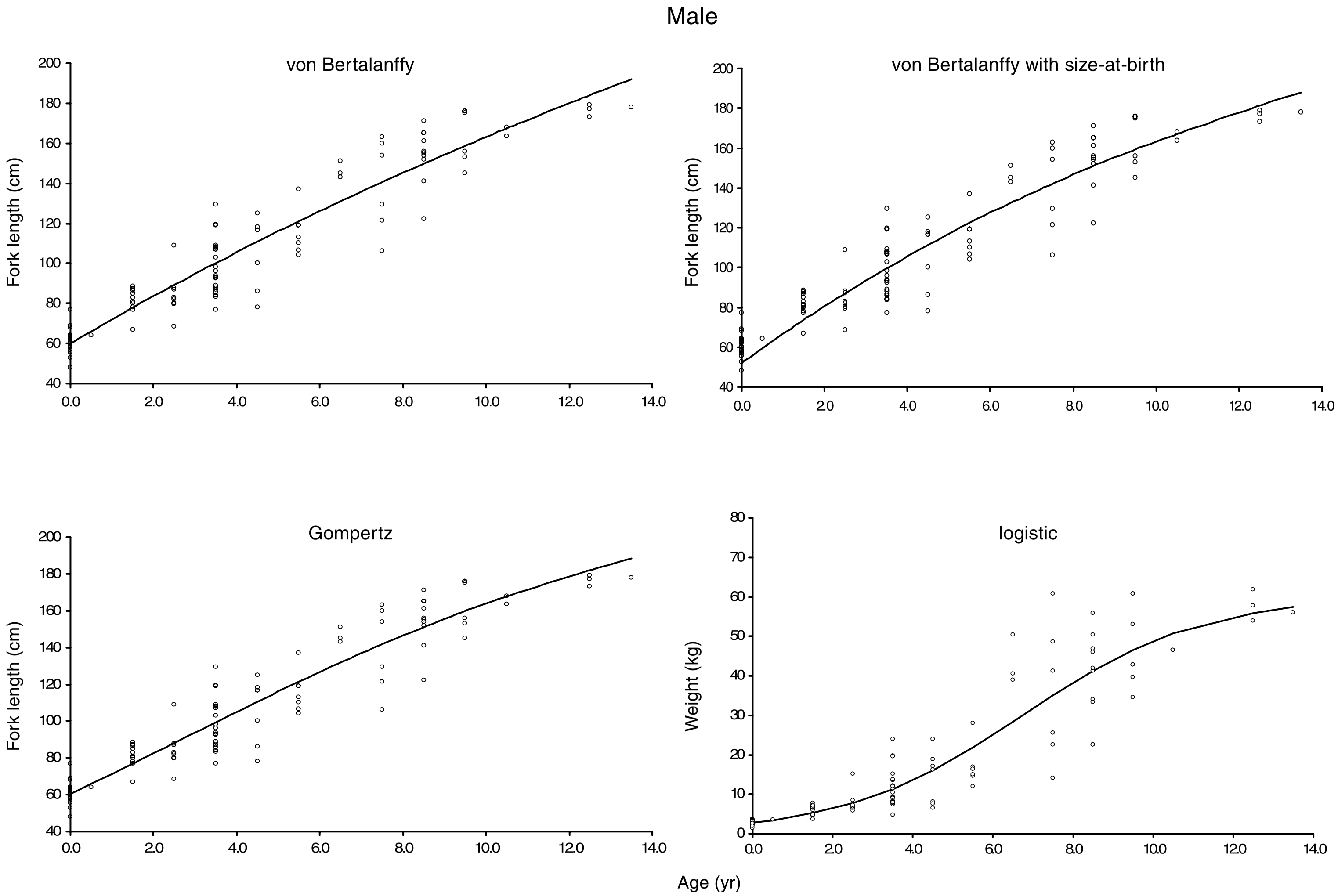

Figure 4

The von Bertalanffy, von Bertalanffy with a size-at-birth intercept, Gompertz, and logistic growth models fitted to observed size-at-age data for male (n=117) spinner sharks (*Carcharhinus brevipinna*) collected off the United States Southeast and Gulf of Mexico coasts.

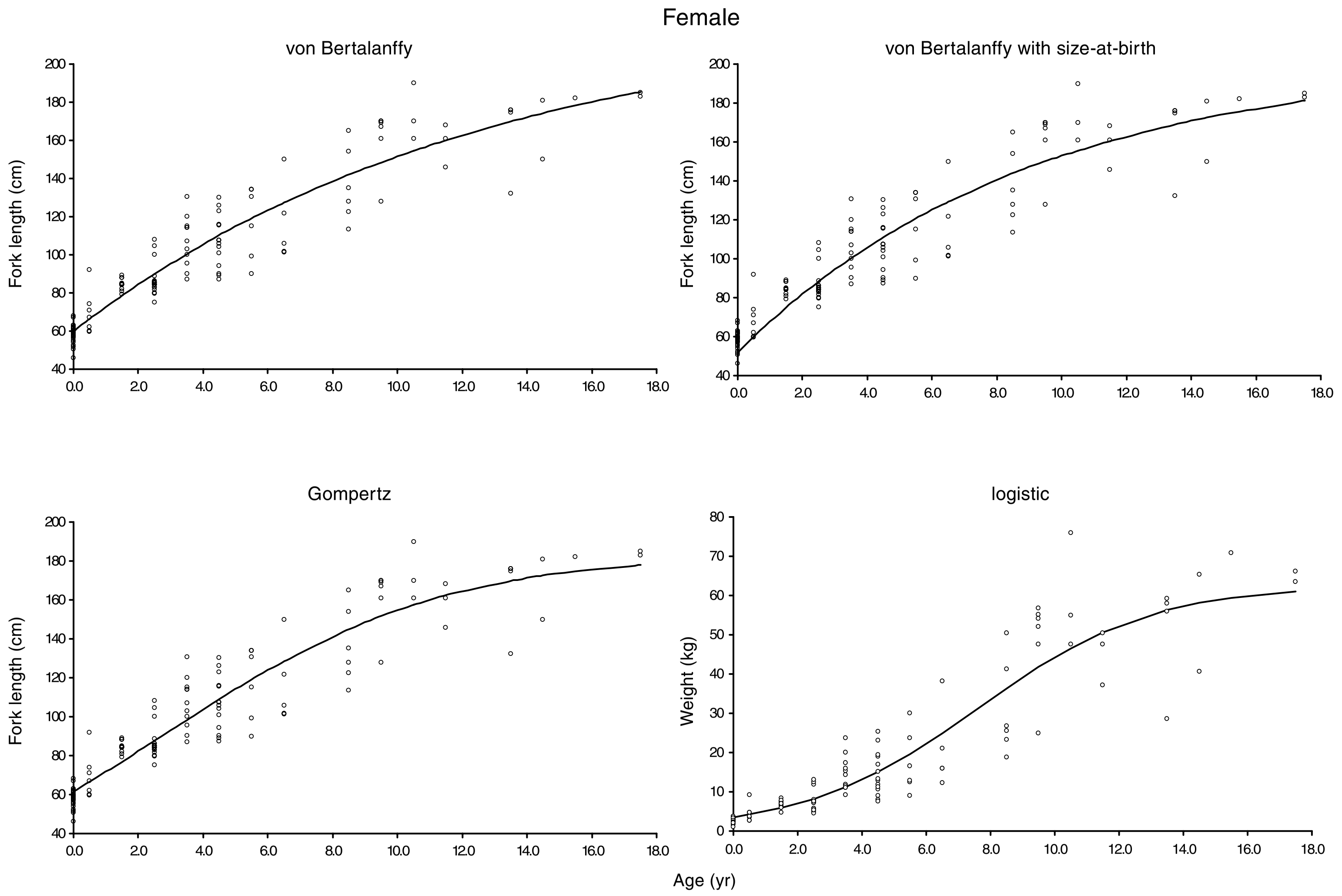

Figure 5

The von Bertalanffy, von Bertalanffy with a size-at-birth intercept, Gompertz, and logistic growth models fitted to observed size-at-age data for female (n=142) spinner sharks (*Carcharhinus brevipinna*) collected off the United States Southeast and Gulf of Mexico coasts.

Table 4

Mean size-at-age (cm FL) for male and female spinner sharks (*Carcharhinus brevispinna*). SD=standard deviation.

	Age (yr)																		
	0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5
Male																			
Size	60.7	64.1	81.2	84.6	99.9	105.8	115.5	146.3	138.9	154.2	165.3	165.9	—	176.3	178.0	—	—	—	—
SD	5.3		5.9	11.4	13.8	17.9	11.0	4.2	23.4	13.9	13.4	3.0	—	3.1		—	—	—	—
n	29	1	12	8	21	7	7	3	6	10	7	2	—	3	1	—	—	—	—
Female																			
Size	59.0	69.3	84.4	86.9	106.9	106.9	117.1	116.2	—	136.3	160.8	173.7	158.3	—	164.7	165.5	182.0	—	184.0
SD	4.1	11.5	2.9	8.7	13.3	13.9	19.1	20.7	—	19.6	16.4	14.8	11.2	—	21.7	21.9	—	—	1.4
n	42	7	12	18	11	14	6	5	—	6	6	3	3	—	4	2	1	—	2

expected maximum size, resulting in an inflated asymptote and low growth coefficient. Branstetter and Stiles (1987) also encountered this problem with bull sharks (*Carcharhinus leucas*) but rather than fit an alternative growth model, those authors hand-fitted a curve through the upper data points. Results such as these may seriously bias estimates of k and any resulting population models because several indirect estimates of natural mortality (M) and longevity rely heavily on accurate estimates of k from a growth model (Fabens, 1965; Pauly, 1980; Chen and Watanabe, 1989; Jensen, 1996). For example, the method of Jensen (1996) for estimating M yields values ranging from 0.05/yr (with results from the von Bertalanffy model) to 0.23/yr (with results from the Gompertz model). Similarly, theoretical longevity estimates determined by the method of Fabens (1965) are 115.5 years and 21.6 years from the von Bertalanffy model and the Gompertz model, respectively.

In general, our estimates of age and growth for female spinner sharks from the von Bertalanffy model were similar to those reported by Allen and Wintner (2002) for spinner sharks collected off South Africa. Growth coefficients in their study were about 0.13/yr, L_∞ was 250 cm FL, and observed longevity for females was up to 19+ years. Branstetter (1987), in his study on sharks collected in the Gulf of Mexico, reported an observed longevity up to 11+ years (combined sexes) and growth coefficients of about 0.21/yr. Because differences in life history traits (e.g., growth rates, size and age at maturity) between populations of blacktip and bull sharks from South Africa and United States waters have been proposed (Wintner and Cliff, 1995; Wintner et al., 2002, respectively), results from our study for spinner shark may be expected to be more similar to those of Branstetter (1987) rather than those of Allen and Wintner (2002). Although techniques (e.g., counting winter bands on sagittal vertebral sections) in Branstetter (1987) were similar to ours, the differences are likely a result of low sample size in the earlier study.

The index of average percent error (IAPE) in aging was at the higher end of the range of estimates provided in other studies that also used sagittal sections for aging. Values have been reported as low as 3.0% for the oceanic whitetip shark (*Carcharhinus longimanus*) (Lessa et al., 1999), and up to 13.0% for the blacktip shark (*Carcharhinus limbatus*) (Wintner and Cliff, 1995). Although IAPE indices are most commonly used to evaluate precision among age determinations, IAPE does not test for systematic differences and does not distinguish all sources of variation (Hoenig et al., 1995). In addition, comparing IAPE values among studies may not be valid unless the study species is the same and from the same geographic area (Cailliet and Goldman 2004).

Although bands were readily discernible in most samples, the inexperience of one of the authors (reader 2) in reading and counting vertebral bands likely led to the higher IAPE and systematic bias. Generally, most systematic bias is a shift to increasing or decreasing counts with age (Morison et al. 1998), yet the bias in this study was the result of reader 2 consistently over aging sharks from the final agreed age regardless of the band count of the sample. Percent agreement was similar for samples above 115 cm FL as it was for samples below this size. Although a reference collection was aged by reader 2 prior to beginning this study, finely honed skills through experience are key elements in the technique of aging.

The trend in marginal increment analysis indicated that band formation occurs once a year during winter months—a result common to most studies where relative marginal increment analysis is used for carcharhinid sharks (e.g., Natanson et al., 1995; Carlson et al., 1999; Carlson et al., 2003). However, high variance in marginal increment analysis (MIR) within each month resulted in months not being statistically different, which is a widespread occurrence when using this method. Marginal increment analysis has been criticized as one of the most abused methods for validation of band formation (Campana, 2001). Problems with differentiating bands on the vertebral edge and application to older age classes may provide misleading results (Campana, 2001). Other methods have been used recently to report yearly band formation in sharks, including oxytetracycline marking (Simpfendorfer et al., 2002; Skomal and Natanson, 2003; Driggers et al., 2004) and bomb radiocarbon methods (Campana et al., 2002). However, validation exists for relatively few elasmobranch species (Cortés, 2000).

Two-phase growth models may be more appropriate for describing the growth of sharks, especially those that are longer lived. Soriano et al. (1992) developed a biphasic growth model which they applied to the long-lived Nile perch (*Lates niloticus*) to better describe their change in growth from zooplanktivores as juveniles to piscivores as adults. Growth by sharks could be regarded as being found in two phases: a rapid juvenile growth followed by a slower adult growth. From a bioenergetic perspective, this would follow a change from energy devoted to growth to energy devoted to reproduction. The logistic model could be regarded as a two-phase model and may help to describe this change. The shift from juvenile to adult would correspond to the inflection point (t_0) of the curve, which approximates biological age-at-maturity. In spinner sharks, age at maturity was reported to be about 6–7 years for males and 7–8 years for females (Branstetter, 1987). This estimate of age-at-maturity is similar to the inflection points from our logistic model of 6.75 and 7.62 years for males and females, respectively. Although each species should be evaluated separately, future studies should investigate the use of two-phase models to provide a more accurate description of the growth of elasmobranchs.

There have been few other examples of fitting alternative growth models to size-at-age data when results from the von Bertalanffy model were biologically incorrect or when models did not fit the data well. The present study represents the first attempt to do so for a species of shark. Comparison of age and growth models by Mollet et al. (2002) and Neer and Cailliet (2001) for two species of rays revealed that the Gompertz model best described their respective data although all models they tested fitted the data fairly well. For pelagic stingray (*Dasyatis violacea*) the Gompertz model predicted a more reasonable size-at-birth and growth rate than the von Bertalanffy growth model (Mollet et al., 2002). Neer and Cailliet (2001) reported a slightly better statistical fit for the Pacific electric ray (*Torpedo californica*) when using the Gompertz model. However, because the difference in model parameters was negligible, results were reported only for the von Bertalanffy model.

The von Bertalanffy growth model is still the most common model used to describe growth in fisheries literature, despite criticism by Roff (1980) who recommended its retirement. As pointed out by Roff (1980), the choice of using another equation should be determined by the variables that are being investigated and the results that are produced by the equation; for example, if the results appear to be biologically unrealistic. Our analysis of the growth of the spinner shark clearly demonstrates the value of this approach. Use of the von Bertalanffy growth model should continue because it permits comparison of growth curves to information already published and in some cases adequately describes the growth of a given organism. However, the variety of statistical techniques and quality of each study make comparisons of von Bertalanffy growth curves between different populations difficult and results should be interpreted with caution regardless of what growth model is used (Roff, 1980).

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