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A Revised Age and Growth Model for Blacknose Shark, *Carcharhinus acronotus*, from the Eastern Gulf of Mexico Using X-Radiography

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SHORT PAPERS AND NOTES

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A REVISED AGE AND GROWTH MODEL FOR BLACKNOSE SHARK, *CARCHARHINUS ACRONOTUS*, FROM THE EASTERN GULF OF MEXICO USING X-RADIOGRAPHY.—Understanding the age structure of a population forms the basis for calculations of growth rate, mortality rate, and productivity, ranking it among the most influential of biological variables (Campana, 2001). Modern fisheries management is often dependent upon demographic or stock assessment models, and incorrect estimates of age can bias management decisions if these models are sensitive to inaccurate age determinations (Cailliet and Goldman, 2004). It is essential that accurate age estimates be obtained to facilitate proper species management.

The blacknose shark, *Carcharhinus acronotus*, is a small coastal species found in the western North Atlantic Ocean from North Carolina to Florida, and throughout the Caribbean Sea and the Gulf of Mexico (Compagno, 1984). Blacknose sharks are harvested commercially and recreationally with estimated U.S. landings of 43.07–90.53 metric tons and 2,890–11,831 animals from 1995–2000, respectively (Cortés, 2002). A stock assessment from the western North Atlantic Ocean and Gulf of Mexico found that the biomass in 2002 was above that producing maximum sustainable yield (MSY) and all values of fishing mortality were below that producing MSY (Cortés, 2002). However, the results were equivocal because of the uncertainty of available age and growth estimates.

A previous study on the age and growth of blacknose shark in the eastern Gulf of Mexico utilized vertebral half-sections (Carlson et al., 1999). Utilizing half-sections can be problematic because of difficulty in discerning bands on the edge and thus underestimating age (Cailliet and Goldman, 2004). Carlson et al. (1999) reported maximum observed age as 4.5 yr using half-sections, yet the recent return of a tagged specimen indicates an age of at least 9 yr in the Gulf of Mexico (Carlson, unpublished data).

X-radiography has been used as a successful ageing method for white shark, *Carcharadon carcharias* (Wintner and Cliff, 1999), school shark, *Galeorhinus galeus* (Ferreira and Vooren, 1991), and pelagic thresher shark, *Alopias pelagicus* (Liu et al., 1999). Carlson et al. (1999) suggested that an alternative technique such as x-radiography may be required to elucidate bands and derive more accurate age estimates for the blacknose shark. Our objectives for this study were to develop revised age estimates utilizing x-radiography and an updated age and growth model on the basis of these estimates for the blacknose shark in the eastern Gulf of Mexico.

Materials and methods.—We obtained 57 of the original vertebrae used by Carlson et al. (1999). These samples were supplemented with 97 additional vertebrae collected from 1996 to 2001 by the National Marine Fisheries Service Panama City Laboratory and Mote Marine Laboratory. A 0.5-mm sagittal section was taken from each sample using a Buehler 82[1] Isomet low-speed saw. The sagittal sections were x-rayed at 3 mA sec^{-1} with exposure times of 40–45 sec and a voltage of 25 kV. X-radiographs were viewed under a Meijo Techno R2[1] dissecting microscope with transmitted light, and vertebral bands were counted in the intermedialia following Martin and Cailliet (1988). Before band counting, two authors (AMM and JKC) read a subsample of x-radiographs to determine the definition of bands for ageing. Subsequently, these authors randomly read all 154 vertebrae independently without knowledge of sex or length of specimens.

Driggers et al. (2004) and Driggers (NOAA Fisheries Service, Mississippi Laboratories, personal communication) validated the ages of two blacknose sharks (ages 4 and 6 yr, respectively) using oxytetracycline (OTC) injection of specimens held in the South Carolina Aquarium. The periodicity of growth increment formation was determined to be 1 yr on the basis of the presence of one growth increment distal to the OTC mark on the corpus calcareum (Driggers et al., 2004). On the basis of annual band validation of these animals and the verification in Carlson et al. (1999), we assigned ages assuming that (1) the birth mark is associated with a pronounced change in angle in the intermedialia, (2) growth bands (one narrow light band and one broad dark band) are formed once a year, and (3) narrow light bands are deposited in winter. Ages were calculated using the algorithm: age = birth mark + number of winter marks − 1.5 (Carlson et al., 1999). If only the birth mark was present, age was assumed to be 0+.

[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Several methods were used to determine the precision among initial age estimates: the index of average percentage error (IAPE; Beamish and Fournier, 1981), percentage agreement (PA = (number agreed/number read) * 100), and PA plus or minus one band calculated for 10-cm fork length (FL) intervals (Goldman, 2004). Age estimates for which the readers disagreed were re-examined together. If no agreement was reached after consultation, samples were discarded.

The von Bertalanffy (1938) growth equation was fit to observed age data for males, females, and sexes combined and is described as:

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

where L_t = predicted length at age t; L_∞ = asymptotic maximum FL; K = growth coefficient; and t_0 = age when length theoretically equals zero.

A modified form of the von Bertalanffy growth model was also fitted to observed size-at-age data (Van Dykhuizen and Mollet, 1992; Carlson et al., 2003; Neer et al., 2005). This form expresses the three-parameter model with two unknown parameters (L_∞ and K) and known size at birth (L_0):

$$L_t = L_\infty \left(1 - be^{-Kt}\right) = L_\infty - (L_\infty - L_0)e^{-Kt},$$
$$b = (L_\infty - L_0)/L_\infty = e^{Kt_0},$$

where L_0 is the length at birth (360 mm FL, Carlson, unpublished 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 $G = \ln(L_0/L_\infty)$ with the mean maximum FL = 1,290 mm (A. Morgan, Florida Museum of Natural History, personal communication). All models were implemented using the PROC NLIN function in SAS statistical software[1] (SAS 8.0, SAS Institute, Cary, NC).

We compared the initial band count on vertebral half-sections (Carlson et al., 1999) with those determined using x-radiography using a two-tailed t-test. A likelihood ratio test (Kimura, 1980) was used to compare von Bertalanffy growth models between sexes and studies.

Results.—Age estimates were obtained for 150 of 154 vertebral samples. Although growth bands were visible in both corpus calcerum and intermedialia, our age estimates were obtained from the intermedialia (Fig. 1). The IAPE was 4.1%. When grouped by 10-cm FL intervals, average PA between readers for combined sexes was 97.7% total agreement and 100.0% agreement within one band for sharks less than 700 mm FL. Above 700 mm FL, total agreement was reached for 91.9% and 99.2% agreement within one band of samples initially read. Observed maximum age was 11.5+ yr for females and 9.5+ yr for males. We found significant differences (n = 57, t = −11.51, $P < 0.001$) in the two-tailed t-test of band counts among comparable samples between our study and that of Carlson et al. (1999).

The traditional von Bertalanffy growth equation produced parameter estimates for blacknose sharks of L_∞ = 1,363 mm FL, K = 0.10 yr^{-1}, t_0 = −3.23 yr for females and L_∞ = 1,053 mm FL, K = 0.22 yr^{-1}, t_0 = −2.04 yr for males (Table 1). The modified von Bertalanffy growth equation predicted L_∞ = 1,266 mm FL, K = 0.12 yr^{-1} for females and L_∞ = 1,030 mm, K = 0.24 yr^{-1} for males (Table 2). The Gompertz model predicted growth rates between 0.20 yr^{-1} and 0.33 yr^{-1} for females and males, respectively. The Gompertz model also estimated size at birth (388 mm FL) within the range reported for blacknose sharks in the Gulf of Mexico (Carlson et al., 1999; Sulikowski et al., 2007). All growth curves were found to be significantly different between males and females ($P < 0.001$).

To allow for comparison with the original study of Carlson et al. (1999), we only compared von Bertalanffy growth models from age estimates derived using vertebral half-sections with those of x-radiographs. von Bertalanffy growth curves derived from age estimates from x-radiographs were different than those originally derived by Carlson et al. (1999; Fig. 2 and Fig. 3 for males and females, respectively). Using the original age estimates of Carlson et al. (1999), von Bertalanffy growth parameters were L_∞ = 1,209 mm FL, K = 0.29 yr^{-1}, t_0 = −1.70 yr for females and L_∞ = 1,024 mm FL, K = 0.53 yr^{-1}, t_0 = −1.18 yr for males. Significant differences in von Bertalanffy growth curves were found between studies (female, log-likelihood ratio = 153.4, $P < 0.001$; male, log-likelihood ratio = 84.0, $P < 0.001$).

Discussion.—The use of x-radiography in this study increased the observed maximum age of blacknose shark compared with that reported in Carlson et al. (1999). The increased longevity resulted in standard von Bertalanffy growth parameters with larger theoretical maximum sizes and corresponding lower estimates of

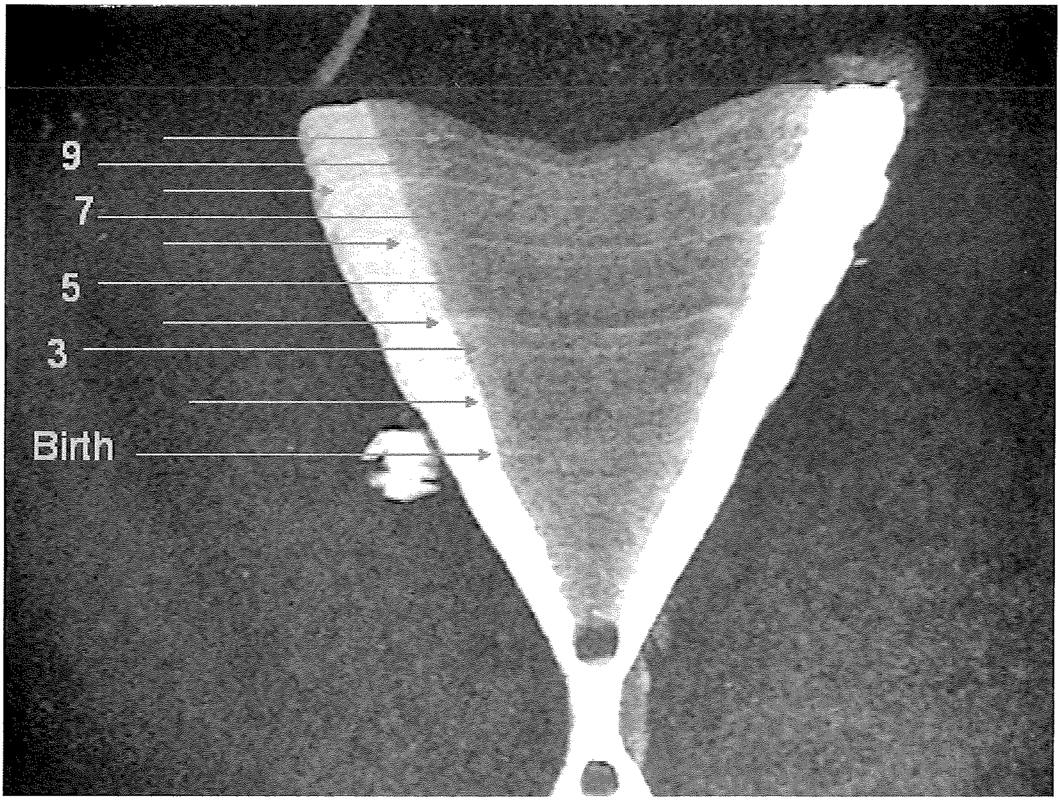

Fig. 1. X-radiograph from an 8.5+-yr-old blacknose shark illustrating the banding pattern and winter marks (annuli) used to assign age.

growth rate for both females and males. However, the updated von Bertalanffy growth parameter estimates suggest a larger theoretical maximum size and lower growth coefficient for females than was reported by Driggers et al. (2004) from the western North Atlantic Ocean. Schwartz (1984) found even larger estimates of maximum size (L_∞=1,650 mm FL) for female

TABLE 1. Parameters of the traditional von Bertalanffy growth model. Estimates are provided for models developed using band counts obtained for blacknose sharks from x-radiographs and from half-sectioned vertebrae by Carlson et al. (1999). In parentheses are 95% confidence limits (CL) (lower CL/upper CL).

Parameter	Female	Male	Combined sex
	X-radiographs		
L_∞ (mm)	1,363	1,053	1,174
	(933/1,791)	(867/1,240)	(977/1,372)
K (yr^{-1})	0.10	0.22	0.15
	(0.04/0.17)	(0.09/0.35)	(0.09/0.22)
t_0 (yr)	−3.23	−2.04	−2.59
	(−1.31/−2.16)	(−3.02/−1.07)	(−3.32/−1.87)
N	76	72	150
	Vertebral half-sections		
L_∞ (mm)	1,209	1,024	1,070
	(875/1,544)	(939/1,109)	(979/1,162)
K (yr^{-1})	0.29	0.53	0.44
	(0.06/0.52)	(0.34/0.73)	(0.30/0.59)
t_0 (yr)	−1.70	−1.18	−1.30
	(−2.54/−0.86)	(−1.57/−0.79)	(−1.63/−0.97)
N	49	76	125

TABLE 2. Growth parameter estimates from the modified von Bertalanffy growth model using a size-at-birth intercept (L_0) and the Gompertz growth model for blacknose shark. Models were fitted to x-radiography data only. In parentheses are 95% confidence limits (CL) (lower CL/upper CL).

Parameter	Female	Male	Combined sex
	von Bertalanffy growth model with L_0		
L_∞ (mm)	1,266	1,030	1,125
	(975/1,558)	(881/1,180)	(977/1,273)
K (yr^{-1})	0.12	0.24	0.17
	(0.06/0.18)	(0.13/0.36)	(0.11/0.23)
L_0 (mm)	360	360	360
	Gompertz		
L_∞ (mm)	1,290	1,290	1,290
	$G = 1.11$	$G = 0.94$	$G = 1.02$
	(0.95/1.27)	(0.79/1.09)	(0.91/1.12)
K (yr^{-1})	0.20	0.33	0.25
	(0.13/0.27)	(0.19/0.47)	(0.19/0.32)
L_0 (mm)	387	388	388
	(359/412)	(339/440)	(363/415)

blacknose sharks off North Carolina, but the lack of younger fish in his study probably led to the large L_∞ and low K values (Carlson et al., 1999).

Although female blacknose sharks up to 1,290 mm FL have been captured in the eastern Gulf of Mexico (A. Morgan, Florida Museum of Natural History, personal communication), we believe the theoretical maximum size predicted by the traditional von Bertalanffy growth equation (1,363 mm FL) is biologically unrealistic. Because of the unrealistic theoretical maximum size predicted for females and the consequent lower growth rate, we suggest that the growth parameter estimates determined using the Gompertz growth equation or modified von Bertalanffy growth equation more adequately describe the growth of the blacknose shark. Our results agree with a recent recommendation to use L_0

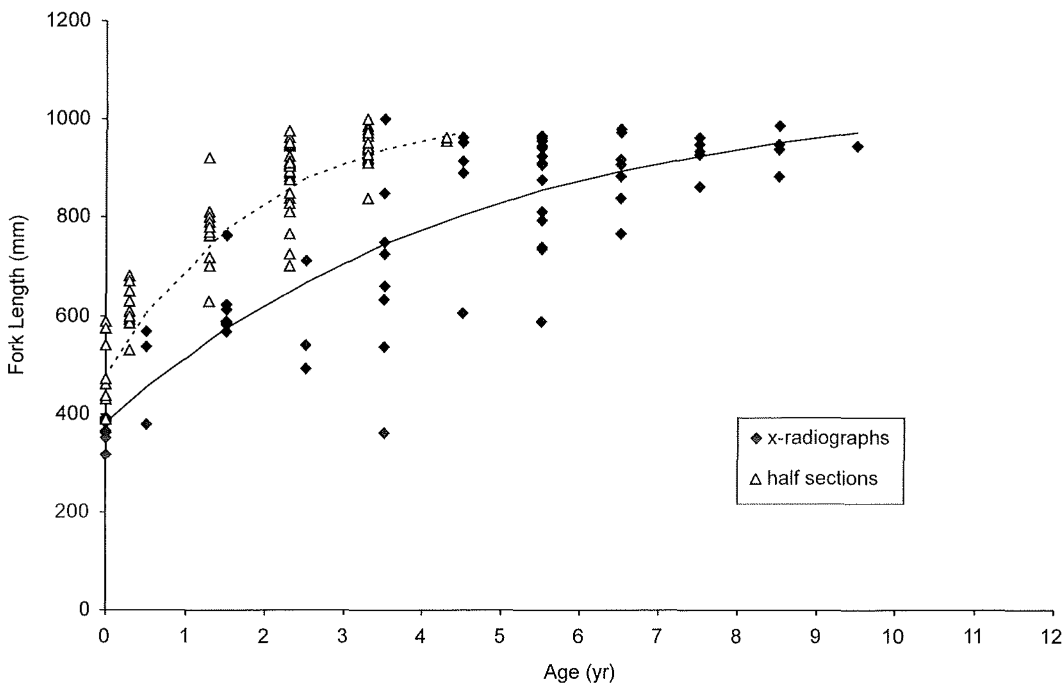

Fig. 2. The traditional von Bertalanffy growth model fitted to observed size-at-age data for male blacknose sharks from the original age estimates of Carlson et al. (1999) and revised estimates from x-radiographs. Symbols are slightly offset for clarity.

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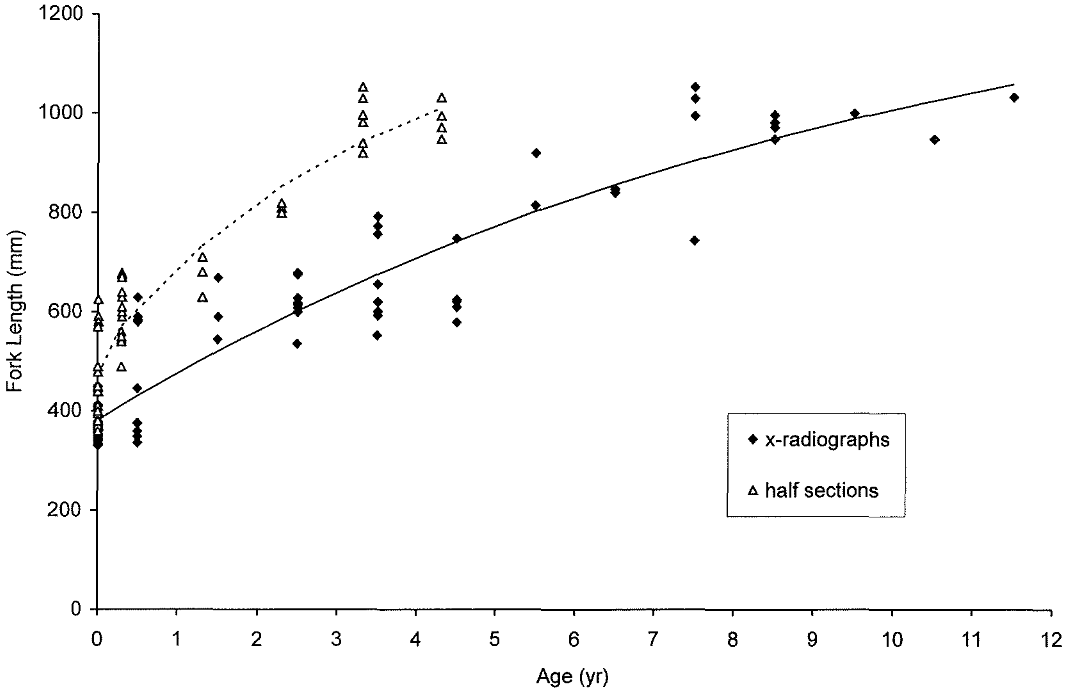

Fig. 3. The traditional von Bertalanffy growth model fitted to observed size-at-age data for female blacknose sharks from the original age estimates of Carlson et al. (1999) and revised estimates from x-radiographs. Symbols are slightly offset for clarity.

instead of t_0 (Cailliet and Goldman, 2004; Cailliet et al. 2006). These authors suggest that L_0 be used in lieu of t_0 whenever possible, as the traditional von Bertalanffy growth model may be an unsuitable descriptor of growth for species that do not draw out toward an asymptote with increasing age and because L_0 is more biologically meaningful than t_0.

All age estimates from growth band counts were based on the hypothesis of annual growth band deposition on the basis of validation of two blacknose sharks in two age classes. As discussed in Beamish and McFarlane (1983), validation of absolute age is only complete when it has been done for all ages, especially the first growth band. However, Cailliet and Goldman (2004) noted that only about 15 of 159 reviewed studies on elasmobranchs had some form of validation. Only studies by Parsons (1993) on bonnethead, *Sphyrna tiburo*, have successfully validated multiple ages. Nevertheless, recent OTC marking methods reporting yearly band formation in sharks are increasing (e.g., Skomal and Natanson, 2003; Goldman et al., 2006). Other methods such as bomb radiocarbon (Campana et al., 2002) have also been used to determine yearly band formation in sharks (Cailliet et al., 2006).

Using the original age estimates of Carlson et al. (1999), Driggers et al. (2004) reported that blacknose sharks in the U.S. South Atlantic Ocean have significantly lower growth rates (K) than conspecifics in the Gulf of Mexico. We did not have access to the original samples of Driggers et al. (2004), so a direct comparison using multiple models was not possible. However, the new von Bertalanffy growth estimates on the basis of x-radiographs in this study suggest that growth rates are not as dissimilar as originally reported. Detecting real differences in growth estimates can be difficult, especially when differences exist in vertebral preparation (i.e., sections vs x-rays) and sample size (Cailliet and Goldman, 2004). To fully evaluate the extent of any growth differences between blacknose sharks, a new synoptic study utilizing similar techniques would be required to fully resolve the question of separate stocks.

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