Age and Growth of the Blacknose Shark, *Carcharhinus acronotus*, in the Eastern Gulf of Mexico

JOHN K. CARLSON, ENRIC CORTÉS, AND ALLYN G. JOHNSON

Age and growth of the blacknose shark, *Carcharhinus acronotus*, from the eastern Gulf of Mexico was estimated by counting bands on the vertebral centra from 123 individuals. Back-calculated von Bertalanffy growth functions were constructed for populations in northwest Florida and Tampa Bay, Florida. Von Bertalanffy growth function parameters for males in northwest Florida (L_∞ = 963.1 mm FL, K = 0.59, t_0 = −0.754 yr) were significantly different from those in Tampa Bay (L_∞ = 801.0 mm FL, K = 0.771, t_0 = −0.797 yr), as were those for females (L_∞ = 1136.5 mm FL, K = 0.352, t_0 = −1.212 yr in northwest Florida; L_∞ = 1241.3 mm FL, K = 0.237, t_0 = −1.536 yr in Tampa Bay). Theoretical longevity, estimated as the age at which 95% of L_∞ is reached, varied from age 10–16 yr for females and 4.5–9.0 yr for males, depending on geographic area. The oldest sharks aged were 4.5+ yr. Centrum edge and marginal increment analyses lent support to the hypothesis that narrow dark bands are formed during winter months. Length-frequency analysis verified back-calculated size at ages 0, 1, and 2. The growth dynamics of blacknose sharks are similar to those of other relatively small, fast-growing, short-lived species of sharks.

T HE blacknose shark, *Carcharhinus acronotus*, occurs in the northwestern Atlantic Ocean from North Carolina to Florida, and throughout the Caribbean Sea, and the Gulf of Mexico (Garrick, 1982; Bonfil, 1997). Along the U.S. Atlantic and Gulf of Mexico coasts, it is managed under the small coastal shark complex that includes relatively small, fast-growing, and short-lived sharks (National Marine Fisheries Service, 1993). Although this species makes up a significant portion of a small drift net fishery (Trent et al., 1997) and is a minor component of the longline fishery (Branstetter and Burgess, 1997), it is not currently considered to be overfished.

Life-history information on the blacknose shark in the Gulf of Mexico is largely anecdotal. Blacknose sharks attain a maximum total length (TL) of 1370 mm (Garrick, 1982), mate in spring (Clark and von Schmidt, 1965), and give birth in June to pups 45–50 cm TL (Branstetter, 1981). Maturity is reached at 103 cm TL for males and 110 cm TL for females (Clark and von Schmidt, 1965; Branstetter, 1981).

There is little information on age and growth of the blacknose shark. Schwartz (1984) estimated age and growth parameters off North Carolina using silver nitrate staining of vertebral centra. Because variation in age and growth has been reported among conspecific shark populations (Saunders and McFarlane, 1993; Wintner and Cliff, 1995; Carlson and Parsons, 1997), accurate information on each population is important for appropriate management. The pur-

pose of this study was to estimate age and growth of the blacknose shark from the eastern Gulf of Mexico.

MATERIALS AND METHODS

Blacknose sharks (n = 74 males, 390–1001 mm FL; n = 49 females, 360–1053 mm FL) were collected off the west coast of Florida from St. Andrew Bay to Apalachicola Bay and from Tampa Bay during March–October from 1992–1997 using gill nets (multiple panels of 8.9 to 20.3 cm stretched mesh sizes) and longlines. Sharks were measured to the nearest millimeter for body lengths (PC = precaudal, FL = fork length, and TL = total length), sex and life-history stage (neonate, juvenile, adult) were recorded, and vertebrae were collected for age determination. Vertebrae were always removed from the column between the origin and termination of 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 with a scalpel and soaked in a 5% sodium hypochlorite solution for 5–30 min to remove remaining tissue. After cleaning, the vertebrae were soaked in distilled water for 30 min and stored in 95% isopropanol alcohol. Prior to examination, vertebrae were removed from alcohol and dried for 24 hr and measured (length and width in millimeters).

Two methods were tested to enhance visibility of growth bands. The first method used "half

section" vertebrae, in which the vertebra was cut in half sagittally and stained to enhance the growth bands (annuli) with 0.01% crystal violet (one-half vertebra) and 1% silver nitrate (one-half vertebra), following the methods of Johnson (1979) and Schwartz (1983, 1984). Stained vertebral halves were examined using a dissecting microscope under reflected light. The second "bow tie" method was applied to a random subsample (n = 30) of vertebral samples (Branstetter and McEachran, 1986). Sagittal sections were cut from the centrum at three thicknesses: 0.35 mm, 0.50 mm, and 0.70 mm. Sections were stained with 0.01% crystal violet following Schwartz (1983), and alizarin red following Gruber and Stout (1983). Sections were also left unstained. Each section was mounted on a glass microscope slide with clear resin and examined using a dissecting microscope under transmitted light.

Preparations of thin sections (i.e., bow tie method) using alizarin red and unstained vertebrae produced poor visibility and enhancement of growth bands. The technique using crystal violet resulted in better visibility but allowed us to sufficiently distinguish growth bands in only 10 vertebral sections. In contrast, growth bands were clearly visible on the half sections as was indicated and described by Schwartz (1984).

We found no differences in growth band counts between the 10 sections prepared using the bow tie and half section methods using crystal violet (paired t-test; df = 9, $P \geq 0.05$). In addition, no difference was found in growth band counts or measurements (paired t-test; df = 122, $P \geq 0.05$) between the two stains (crystal violet and silver nitrate) on vertebrae prepared with the half section method. Because the growth bands were generally more apparent using the crystal violet stain on half section vertebrae, we developed our growth models based on this technique.

The distances from the centrum origin to the distal edge of each growth band and from the centrum origin to the centrum edge (R) on the vertebral face were measured using an ocular micrometer following the description of winter marks by Branstetter and Stiles (1987). All three authors examined the same centrum halves for age determination. Two sets of independent age readings were made, the second set after consultation among the authors. The index of average percent error (APE; Beamish and Fournier, 1981) and the percentage of disagreements by ± i-rings among authors was computed for the first set of age readings.

Body length and vertebral radius had strong positive correlations. However, the variance of the radius increased with increasing size most notably in sharks greater than 800 mm FL (e.g., if FL = 899–952 mm, then the radius ranged from 5.5–9.4 mm, mean = 7.5 mm, n = 22). This divergence of measurements made back-calculation of body length at growth band completion (distal edge completion of growth band) using regression methods impractical; thus we used the direct proportional method of Dahl-Lea (Lea, 1910). To develop back-calculated FL at growth band completion and resulting theoretical growth curves, we assumed that (1) growth bands are formed once a year, (2) the narrow dark bands are deposited during October–January (late fall to early winter), and (3) the birth mark is the band associated with a pronounced change in angle and is formed during April–June, with conception occurring in the previous spring–summer.

Separate growth curves were constructed using back-calculated size at age for males and females for each area. Theoretical growth parameters were derived using the SAS PROC NLIN, which is a nonlinear curve fitting program, using back-calculated lengths at the last mark formed before capture following the recommendations of Vaughan and Burton (1994).

Length frequency distributions from northwest Florida were developed as a verification of the growth model. Ages were assigned by visual examination of the breakpoint where the modal groups were the lowest. Growth models were compared statistically using a method proposed by Kappenman (1981). Theoretical longevity was estimated as the age at which 95% of L_∞ is reached [5(ln2)/K; Fabens, 1965; Cailliet et al., 1992]. Age at maturity was estimated by transforming size at maturity information into ages through the theoretical growth curves.

Verification of the period of band formation was made by characterizing the centrum edge. Using a dissecting microscope under reflected light, it appeared alternatively as (1) a narrow dark band, (2) a narrow light band, or (3) a broad light band. Relative marginal increment analysis was used to examine trends in band formation following the procedure described in Natanson et al. (1995).

RESULTS

The first set of age determination readings resulted in two or three of three age estimates agreeing in 89.1% of the cases, with an APE of 7.6%. The second set of age estimations (after consultation among the authors) found agree-

ment for 123 of the 124 sharks. The only shark with disagreement was discarded.

Fork length and radius were positively correlated and not significantly different between sexes (ANCOVA: $F = 0.005$, df $= 1$, $P \geq 0.05$). Sexes were combined to produce an overall linear relationship: FL $= 93.46(R) + 223.43$ (n $= 123$, $r^2 = 0.83$), where FL $=$ fork length of the shark (mm) and R $=$ vertebral radius (mm).

For construction of growth models, we propose that the birth mark is age 0 yr, the next mark (formed during October–January) represents about 0.5 yr and additional narrow dark bands are one year apart. Observed sizes at age were generally larger than back-calculated sizes

at age (Table 1). However, Lee's phenomenon was not apparent in back-calculated lengths of older fish. Comparison of the results of back-calculating FL at age for the northwest Florida and Tampa Bay areas indicated that northwest Florida males were significantly larger at age after 0.5 yr than Tampa Bay males (t-test, $P < 0.05$), but females from both areas were not different (t-test, $P \geq 0.05$; Table 2). A comparison with the von Bertalanffy growth model from sharks captured in North Carolina (Schwartz, 1984) revealed that female blacknose sharks from North Carolina were larger throughout most ages than those from the eastern Gulf of Mexico (Fig. 1). Back-calculated weighted mean

TABLE 1. MEAN BACK-CALCULATED FORK LENGTH (mm) AT NARROW DARK BAND COMPLETION (AGE) FOR BLACK-NOSE SHARKS FROM THE GULF OF MEXICO. Area 1 is northwest Florida, and area 2 is Tampa Bay. BM is the birth mark.

| Band group | Area | Sex | Observed fork length at capture | | | Narrow band (age in years) | | | | | | Band Age |
			N	Range	Mean ± SD	1 (BM) 0	2 0.5	3 1.5	4 2.5	5 3.5	6 4.5	
1	1	F	8	372–625	485.0 ± 100.2	391.2						
		M	4	430–589	533.5 ± 72.0	353.6						
	2	F	9	360–570	433.3 ± 64.4	369.2						
		M	6	390–470	429.2 ± 33.8	346.2						
2	1	F	5	545–679	631.8 ± 60.9	358.7	534.4					
		M	2	585–590	587.5 ± 3.5	370.0	460.7					
	2	F	10	490–670	589.0 ± 53.8	358.3	490.2					
		M	9	530–680	625.6 ± 45.3	375.7	538.9					
3	1	F	1	629	629.0 —	349.4	442.6	535.8				
		M	3	764–920	831.3 ± 80.2	364.6	525.5	756.7				
	2	F	3	630–710	673.3 ± 40.4	368.6	515.6	604.3				
		M	8	630–800	736.3 ± 58.8	380.0	539.6	640.2				
4	1	F	0									
		M	19	725–978	904.0 ± 57.1	351.2	557.1	702.1	814.4			
	2	F	3	800–820	810.0 ± 10.0	378.7	541.3	666.7	765.2			
		M	4	700–850	797.5 ± 67.0	368.0	498.9	615.9	709.6			
5	1	F	5	920–1053	996.4 ± 50.9	372.7	610.6	761.8	870.1	962.4		
		M	13	919–1001	954.0 ± 25.7	367.6	567.8	732.7	814.5	889.3		
	2	F	1	940	940.0 —	340.0	580.0	780.0	840.0	880.0		
		M	3	840–930	893.3 ± 47.3	379.0	514.6	628.6	700.1	821.6		
6	1	F	4	948–1033	987.0 ± 36.2	330.4	564.4	715.6	827.1	899.6	925.9	
		M	3	955–963	960.0 ± 4.4	359.7	589.0	700.6	805.6	864.9	919.0	
	2	F	0									
		M	0									
Weighted mean												
	1	F	23			367.7	561.7	720.7	851.0	934.5	952.9	
		M	44			358.6	555.8	713.7	813.7	884.7	919.0	
	2	F	26			364.9	509.0	656.2	783.9	880.0		
		M	30			370.3	529.4	631.4	705.5	821.6		
Growth increment												
	1	F				367.7	194.0	159.0	130.3	83.5	18.4	
		M				358.6	197.2	157.9	100.0	71.0	34.3	
	2	F				364.9	144.1	147.2	127.7	96.1		
		M				370.3	159.1	102.0	74.1	116.1		

TABLE 2. VON BERTALANFFY GROWTH PARAMETERS OF BLACKNOSE SHARKS FROM THE EASTERN GULF OF MEXICO CALCULATED USING BACK-CALCULATED SIZES AT AGE. Von Bertalanffy growth parameters of blacknose sharks off North Carolina (Schwartz, 1984) are included for comparison.

| Sex | Von Bertalanffy growth parameters | | | | | | n | Area |
	L_∞ (FL)	K	t_0	SE of L_∞	SE of K	SE of t_0		
Female	1136.5	0.352	−1.212	166.8	0.157	0.392	23	NW Florida
Male	963.1	0.590	−0.754	35.7	0.09	0.127	44	
Female	1241.3	0.237	−1.536	405.1	0.152	0.443	26	Tampa Bay
Male	801.0	0.771	−0.797	52.6	0.229	0.229	30	
Female	1650	0.138	−2.680	—	—	—	42	North Carolina
Male	1887	0.117	−2.010	—	—	—	30	

FL at birth mark completion and mean FL at birth mark completion predicted by the von Bertalanffy growth function were similar in northwest Florida (359 mm vs 345 mm for males, 368 mm vs 392 mm for females, respectively) and Tampa Bay (370.0 mm vs 367 mm for males and 365 vs 369 mm for females, respectively). Results of Kappenman's test indicated that growth parameters of males and females calculated using back-calculated size at age differed within and between areas (northwest Florida and Tampa Bay).

Theoretical longevity estimates were 10 and 15 yr for females and 6 and 4.5 yr for males in northwest Florida and Tampa Bay, respectively. Preliminary reproductive data (JKC, unpubl. data) suggest that blacknose sharks off northwest Florida mature at about 800 mm FL (approximately 2.5 yr) and 875 mm FL (approximately 3.0 yr) for males and females, respectively.

We found monthly variation in categorization of the centrum edge. Narrow light bands were found in all months except October, with the highest frequency during the early summer months (Fig. 2). Broad light bands were found predominantly in later summer months. A mode for narrow dark bands was found in October and was regarded as the beginning of the formation of a winter band.

Although not statistically different (single factor ANOVA; df = 7, $P \geq 0.05$), marginal increment analysis showed a general trend of increas-
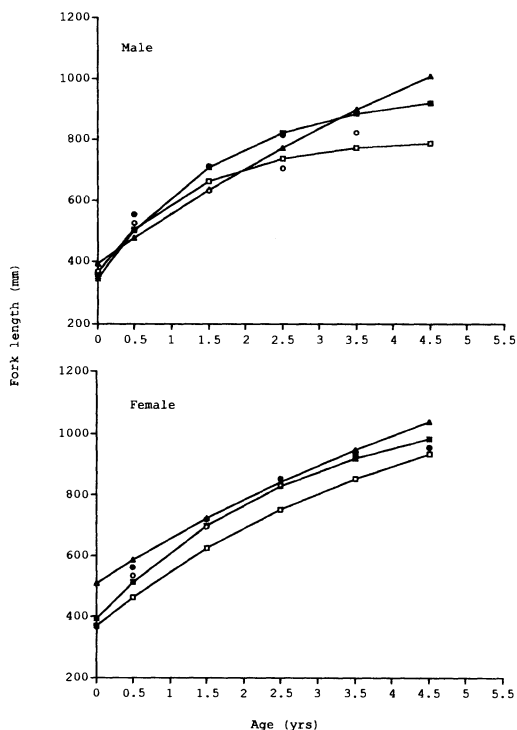

Fig. 1. Von Bertalanffy growth functions from back-calculated size at age for male and female blacknose sharks from northwest Florida (*) and Tampa Bay (□) in the eastern Gulf of Mexico and North Carolina (△) by Schwartz (1984). Back-calculated mean sizes at age are also indicated from northwest Florida (●) and Tampa Bay (○).
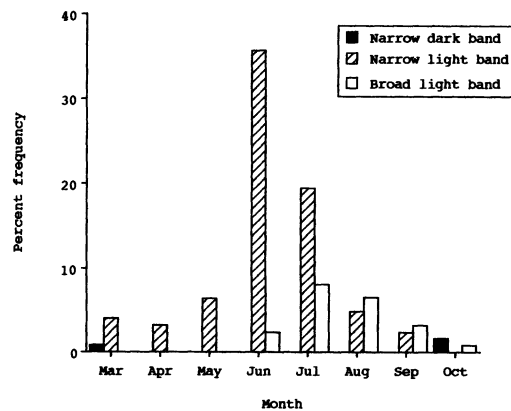

Fig. 2. Categorization of the centrum edge by month for the blacknose shark. Sexes and areas are combined.
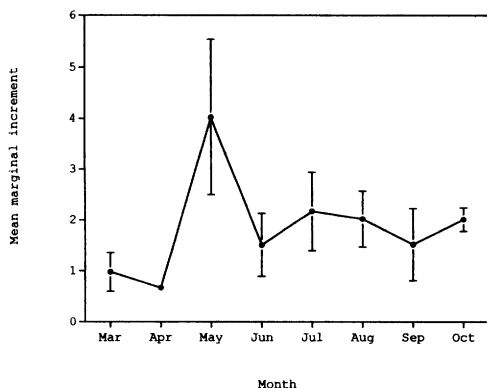
Fig. 3. Mean marginal increment analysis by month for combined sexes and areas for the black-nose shark. Vertical bars are ± 1 SD.

ing increment growth from March to October, with a peak in May (Fig. 3). Although this trend is indicative of winter band formation, this could not be confirmed due to a lack of winter samples.

Visual inspection of modal groups in length frequency histograms revealed similarities with back-calculated sizes from the von Bertalanffy growth function (Fig. 4). For males in northwest Florida, mean length at age 0+ was 359 (back-calculated) versus 434 (observed) mm FL, 635 versus 686 mm FL at age 1+, and 764 versus 873 mm FL at age 2+. For females in northwest Florida, mean length at age 0+ was 368 versus 437 mm FL, 641 versus 683 mm FL at age 1+, and 786 versus 870 mm FL at age 2+. Back-calculated sizes at age were smaller than those observed in length frequency analysis probably because the former corresponded to the time of winter band formation (Oct.–March) after each birthday (June), whereas the latter include specimens collected from March through October (before and after each birthday).

DISCUSSION

Growth parameters derived for blacknose sharks from the eastern Gulf of Mexico show that they attain a smaller theoretical maximum size (L_∞) and that they reach L_∞ at a faster rate (K) than their counterparts off North Carolina, although these differences could not be tested statistically because we did not have access to the original data from Schwartz (1984; Table 2). However, these discrepancies in parameter estimates between blacknose sharks from the Gulf of Mexico and northwest Atlantic may be due to differences in sample size and interpretation of growth bands. Schwartz (1984) pointed out
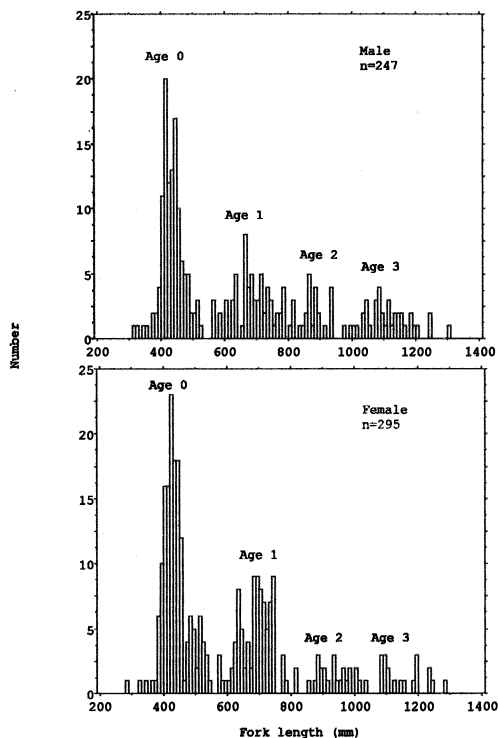

Fig. 4. Length frequency distributions of blacknose sharks caught in northwest Florida from March to October 1992–1997. Ages were assigned by visual examination of the breakpoint where the modal groups were the lowest.

that his small sample size for age-0 and age-1 sharks (n = 6), combined with his assumption that the first band observed was a false band, might explain his larger back-calculated lengths at birth (665 mm FL for females and 563 mm FL for males). We attempted to minimize the sources of bias that might hinder comparison with Schwartz's (1984) study by using the same stains (crystal violet and silver nitrate) to reveal growth bands in vertebral centra. In addition, age-0 and age-1 blacknose sharks were well represented in our samples. We thus contend that the discrepancies in von Bertalanffy growth function parameter estimates between the two studies are, at least in part, the result of differences in sample sizes and assumptions between this and Schwartz's (1984) study.

The variability in vertebral measurements for a given body length in larger sharks might be interpreted as an indication that vertebral samples were removed from different parts of the vertebral column. However, this was not the case in this study. Increasing variability of the radius of the aging structure with increasing body size is not an unusual phenomenon, and

in fact it is a prediction of all proportional back-calculation hypotheses (Francis, 1990).

Observed longevity estimates in the present study were similar to those of Schwartz (1984). The oldest animals aged by Schwartz (1984) were age-6 males and age-5 females, compared to our estimates of 4.5+ yr for both males and females in the present study. These ages appear low when compared with findings for other small coastal species of sharks in the Gulf of Mexico that attain even smaller maximum sizes than the blacknose shark. For example, maximum ages observed for the bonnethead shark, *Sphyrna tiburo*, were age 6+ (Parsons, 1993a; Carlson and Parsons, 1997) and age 7+ for the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Parsons, 1985; Branstetter, 1987a). The relatively lower maximum ages observed for blacknose sharks in the present study may be due to aging methodology. However, the use of thin sections with transmitted light did not improve elucidation of growth bands in this study. Moreover, growth band counts between "half" and "thin" sections were not different suggesting both methods would result in similar estimates of longevity. It is possible than an alternate method such as X-ray radiography or histology may be required for this species. Future work should investigate this possibility.

Theoretical maximum ages for blacknose sharks were in agreement with those in other studies on small coastal species of sharks. By applying methods outlined in Cailliet et al. (1992) to information from studies by Parsons (1985, 1993a) and Carlson and Parsons (1997), Atlantic sharpnose and bonnethead sharks were calculated to have theoretical maximum ages between 5 and 9 yr for males and between 9 and 12 yr for females. Thus, the characteristic of lower maximum age for small coastal compared to large coastal species of sharks is further supported in the present study.

Real differences in growth dynamics may also exist between blacknose sharks from the Gulf of Mexico and northwestern Atlantic. The largest blacknose sharks in Schwartz's (1984) study off North Carolina were considerably larger (1400 mm FL for males and 1350 mm FL for females) than those in the present study (1001 mm FL for males and 1053 mm FL for females). Schwartz (1984) proposed that two breeding and pupping populations of blacknose sharks exist off North Carolina and in the Gulf of Mexico and further hypothesized that there is constant exchange between these two populations. In fact, differences in life-history traits between geographically separated populations of sharks are not unusual, as would be expected from phenotypic plasticity. Studies on spiny dogfish, *Squalus acanthias*, from the northwest Atlantic (Nammack et al., 1985) and the north Pacific (Saunders and McFarlane, 1993) have shown marked differences in age and growth dynamics. Wintner and Cliff (1995) found differences in size at maturity and maximum size between blacktip, *Carcharhinus limbatus*, sharks from South Africa and the Gulf of Mexico. Parsons (1993a, 1993b) and Carlson and Parsons (1997) found clinal variation in life-history traits of populations of bonnethead sharks from the eastern Gulf of Mexico.

Results of the marginal increment and centrum edge analyses were inconclusive. Both analyses were indicative of narrow dark band deposition during October–March, but the lack of samples from November–February prevented us from confirming this contention. Although peaks were not statistically different, marginal increment analysis of the vertebrae in our collection showed a similar pattern to that reported for the dusky shark, *Carcharhinus obscurus*, by Natanson et al. (1995), who suggested annual winter mark formation between September and April. Characterization of narrow bands on the centrum edge has been used for verification of winter deposition for bull, *C. leucas* (Branstetter and Stiles, 1987), blacktip, spinner, *C. brevipinna*, (Branstetter, 1987b) silky, *C. falciformis*, and scalloped hammerhead, *Sphyrna lewini*, (Branstetter, 1987c) sharks from the Gulf of Mexico.

Length frequency analysis supported our back-calculated sizes at age. Despite inherent difficulties associated with this method and its applicability to younger age classes only (Cailliet, 1990), predictions from the von Bertalanffy growth function matched well the observed modes in histograms of age 0, 1, and 2 male and female blacknose sharks. Only validation studies through chemical marking will ascertain that vertebral bands are indeed deposited annually in blacknose sharks. In the Gulf of Mexico, only three studies have investigated the frequency of band deposition through oxytetracycline marking. In captive neonate Atlantic sharpnose and sandbar shark, *C. plumbeus*, Branstetter (1987a) found annual deposition, with band formation between October and December. Parsons (1993a) also reported yearly band deposition in captive and wild bonnethead sharks throughout all observed ages.

In all, growth parameters estimated for the blacknose shark are within the range of those derived for other species of small coastal sharks in the Gulf of Mexico. Parsons (1993a) and Carlson and Parsons (1997) reported K-values of 0.28–0.69 for female and male bonnethead

sharks from Tampa Bay and northwest Florida. Atlantic sharpnose sharks have K-values of 0.36–0.53 (Parsons, 1985; Branstetter, 1987a).

Results of this study support the generalization that sharks in the small coastal complex are faster growing, and exhibit early maturation and shorter longevity. However, accurate management of blacknose sharks requires further information on fisheries interactions as well as more precise estimates of additional life-history characteristics.

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NOAA, NATIONAL MARINE FISHERIES SERVICE, SOUTHEAST FISHERIES SCIENCE CENTER, 3500 DELWOOD BEACH ROAD, PANAMA CITY, FLORIDA 32408. E-mail: (JKC) carlson@bio.fsu.edu; (EC) cortes@bio.fsu.edu; and (AGJ) ajohnson@nmfs.ssp.pc.gov. Send reprint requests to JKC.