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## Age and Growth of the Sandbar Shark, *Carcharhinus plumbeus*, before and after Population Depletion

THOMAS R. SMINKEY AND JOHN A. MUSICK

Recent studies have shown that by 1991 the sandbar shark (*Carcharhinus plumbeus*) population along the Atlantic coast of the United States had declined in abundance to approximately 20% of its level in the late 1970s. This phenomenon allowed us to test the hypothesis that compensatory (density-dependent) growth occurred after severe population reduction. Age and growth of sandbar sharks were investigated by counting rings and back-calculating lengths at previous ages from vertebral samples collected in 1980–1981 and 1991–1992. The collections included 188 sharks from 1980–1981 and 412 sharks from 1990–1991 ranging in length from 51–172 cm precaudal length (PCL). All sharks were mature at lengths > 136 cm PCL. Minimum and maximum ring counts, which included a birth mark, were 1 and 25. Age at maturity was 15–16 years for both sample periods and both sexes. For sexes combined, the von Bertalanffy growth parameters were  $L_{\infty} = 199$  cm PCL,  $K = 0.057$ ,  $t_0 = -4.9$  years for the 1980–1981 sample and  $L_{\infty} = 164$  cm PCL,  $K = 0.089$ ,  $t_0 = -3.8$  years for the 1991–1992 sample. Statistical tests found significant differences between the two growth models. Significant differences in size at age and annual incremental growth of juveniles suggest a small increase in juvenile sandbar shark growth rate between the two sampling periods. However, age at maturity was unchanged between samples suggesting that any biological significance of a growth rate increase has not been realized.

THE sandbar shark, *Carcharhinus plumbeus*, is a large, predominantly coastal species which ranges from Cape Cod to Brazil in the western North Atlantic (Bigelow and Schroeder, 1948; Springer, 1960; Garrick, 1982). It is the most common large coastal shark in Virginia waters (Musick et al., 1993). The lower Chesapeake Bay and Eastern Shore, Virginia, lagoon system are important nursery grounds for neonate and juvenile sandbar sharks. Pregnant females seasonally enter these areas to pup from late May through late June (Musick and Colvocoresses, IOC/FAO, 1986, unpubl.). Mature male sandbar sharks are uncommon in Virginia waters.

The life history of the sandbar shark has been described in detail (Bigelow and Schroeder 1948; Springer 1960). Like most elasmobranchs, the reproductive strategy of the sandbar shark includes production of a few large offspring (average nine per litter), a relatively long gestation period (9–12 months) (Springer, 1960; Clark and Von Schmidt, 1965; Lawler, 1976), and first maturity at late age (Casey et al., 1985; Casey and Natanson, 1992). Such a species with a relatively low reproductive potential could easily be overexploited to dangerously low levels in a directed and unrestricted fishery (Nammack et al., 1985; Hoff, 1990; Pratt and Casey, 1990).

Historically, shark fisheries along the Atlantic Coast of the United States have been small and short-lived. During the 1940s and 1950s, sharks were caught for their vitamin A-rich livers and for their hides, with these fisheries concentrated in Florida (Springer, 1960; Casey et al., 1978). Small scale fishing effort for sharks continued during the 1960s, including a small commercial shark fishery near Great Machipongo Inlet on the eastern shore of Virginia (Hoese, 1962; Casey et al., 1983). Total U.S. commercial landings of pelagic, or large, sharks (all sharks except dogfish) from the western North Atlantic Ocean and Gulf of Mexico in the 1960s and 1970s ranged from 38 metric tons (t) (1971) to 608 t (1967) (Anderson, 1985; Anderson, 1990).

During the 1980s, interest in sharks for both food and recreation greatly increased. Shark meat became increasingly popular, and the demand for dried shark fins for export to Asia contributed to the proliferation of directed fisheries (Hoff and Musick, 1990; Fritchey, 1989). Total commercial landings in the Atlantic rose from 331 t in 1980 to 984 t in 1986, an increase of nearly 300% in only six years (Anderson, 1990). In the Gulf of Mexico, landings nearly tripled from 1979 (61 t) to 1980 (171 t) then continued to increase to 561 t in 1986 (Anderson, 1990). Combining the landings from the Atlantic and Gulf of Mexico, there was a sixfold

increase from the late 1970s to 1986, a span of only 10 years.

Because of its abundance throughout the region, the sandbar shark is an important component in these historical and current fishery efforts. The species comprises about 20% of the large-shark fauna and is second only to the blue shark in recreational catches along the east coast (Hoff, 1990). Additionally, although species composition is not well documented in the commercial fishery, the sandbar shark is one of the primary species caught by the directed fishery in the southeast United States because of its fin/carcass ratio (Anonymous, 1991). A decline in abundance by nearly two-thirds of adolescent and adult sandbar sharks in Virginia waters (Musick et al., 1993) is at least partially attributable to these intense fishing efforts.

Hoff and Musick (1990) reviewed the informational needs to effectively manage a shark fishery and, among others, identified the lack of accurate age estimates as contributing to the failure to develop a shark management plan. To properly manage a species, accurate growth information is essential.

Age and growth of the sandbar shark was previously investigated in the northwest Atlantic (Lawler, 1976; Casey et al., 1985; Casey and Natanson, 1992) and Hawaii (Wass, 1973), but several aspects of these studies warrant reexamination. The parameter  $L_{\infty}$  of the von Bertalanffy growth functions (VBGF) of Lawler (1976) and Casey et al. (1985) was large relative to the maximum reported size for the species, and sample sizes at older ages in both studies were small. As a result, the VBGFs may not have realistically described growth for this species. Further, these studies were done before the rapid expansion of both the commercial and recreational fisheries for sharks. The more recent study by Casey and Natanson (1992) developed the growth model based upon tag/length-increment data that may not be comparable to models derived from age-length data (Francis, 1988). In a study using captive animals (Wass, 1973), the calculated asymptotic size (139.4 cm precaudal length: PCL) and the age at maturity (approximately three years) of sandbar sharks from the Pacific Ocean were considerably lower than those determined by Lawler (1976), Casey et al. (1985), and Casey and Natanson (1992). These differences suggest sandbar shark growth may be faster in the Pacific than in the Atlantic, the growth of captive sharks does not accurately represent growth in the wild, or both.

If sandbar shark growth is affected by density-dependent factors, then lower intraspecific competition for food and other resources may

lead to faster growth, particularly among juvenile sandbar sharks. Three possible mechanisms for density-dependence in elasmobranch populations have been categorized as compensatory decreases in natural mortality, compensatory increases in fecundity when food is more available or through decreased uterine mortality, and compensatory increase in growth rate when food is more abundant resulting in earlier maturity and greater fecundity for each age-class (this assumes maturity and fecundity are size-related rather than age-related; Holden, 1973; Hoenig and Gruber, 1990).

Given the importance of accurate and timely growth models to fishery management and population modeling efforts, there were two objectives of this study. First, growth of sandbar sharks from the Chesapeake Bay and coastal Virginia waters were modeled using two collections of vertebrae to investigate the possibility of compensatory growth. One sample was collected during 1980 and 1981 and archived, and fresh material was collected in 1991–1992. The null hypothesis was that there is no difference in growth between the time periods. The second objective was to compare the resulting age/growth analyses to the growth models of Casey et al. (1985) (vertebral analysis) and Casey and Natanson (1992) (tag/length-increment analysis).

#### MATERIALS AND METHODS

Sandbar sharks were collected from sites in the Chesapeake Bay, Virginia, and adjacent coastal waters using longline fishing gear. Additional samples were obtained from off the west coast of Florida in Sept. 1991 and Feb. 1992. These sandbar sharks were mostly mature males, which are uncommon in Virginia waters. Results of genetic studies on sandbar sharks of the western North Atlantic, using animals collected from Virginia, the eastern Gulf of Mexico and the Yucatan area of Mexico, are consistent with a hypothesis of one population (Heist et al., 1995). Collections were made monthly from May to Oct. during 1991 and 1992. Archived samples were collected from the same sites and seasons in 1980 and 1981. After euthanizing a shark, a sample of several vertebrae was removed from below the origin of the first dorsal fin (vertebrae nos. 25–30). Vertebrae were trimmed, packed on ice, and frozen until processing, or fixed in formalin, rinsed, and preserved in isopropyl alcohol for later processing. Samples were collected from both sexes and all sizes available.

A total of 602 vertebral samples was pro-

cessed for analysis. The collection from 1980–1981 contained vertebrae from 38 males and 150 females ranging in length from 51–172 cm precaudal length (PCL; measured from the tip of the snout to the base of the caudal fin). In 1991–1992, 223 male and 191 female sandbar sharks were collected ranging in length from 43–161 cm. Total length (TL) can be converted to PCL using  $TL = 1.34 \cdot PCL - 0.64$  (both sexes;  $r^2 = 0.99$ ,  $n > 800$ ). Preparation of vertebrae followed the method of Branstetter and Stiles (1987). Vertebrae were thawed (if frozen), cleaned and air-dried. Sagittal sections were cut from the center of the centrum, polished with fine-grit wet sandpaper, and air-dried. Although stains have previously been used to enhance ring contrast (Stevens, 1975; Hoenig and Brown, 1988), satisfactory results were obtained without stains.

Initial aging of the prepared vertebrae sections was conducted using transmitted light on a binocular dissecting scope at 60× or 120× magnification. Banding patterns were readily discernible in sections, and a light and dark band pair were considered a growth increment with the narrow opaque ring counted as the annulus (Fig. 1). Vertebral radius and distance from focus to each annulus were measured using a dissecting microscope with transmitted light and a Biosonics video imaging and digitizing system. Additional blind readings were used to check precision of age determinations (all readings were by the senior author). The Index of Average Percentage Error (IAPE; Beamish and Fournier, 1981) was used to estimate error in counting annuli:

$$IAPE = 1/N \sum (1/R \sum (|X_{ij} - \bar{X}_j|)/X_j) \cdot 100,$$

where  $N$  is the number of fish aged,  $R$  is the number of readings,  $X_{ij}$  is the age of the  $j$ th fish at the  $i$ th reading, and  $\bar{X}_j$  is the mean age of the  $j$ th fish. Body length on vertebral radius regressions were computed to test for isometric growth.

To determine the time of ring formation in the vertebrae (considered to be Jan. by Casey et al., 1985), marginal increment analysis was performed on samples from juveniles that were more numerous and faster growing. The margin, or growth of a vertebra from the last annulus to the edge, was converted to the percent of the last full growth band and was averaged by month.

Body lengths at previous ages were back-calculated from vertebral measurements. Previous studies have most often used the Dahl-Lea direct proportion method, or the Fraser-Lee regression relationship. More recent studies

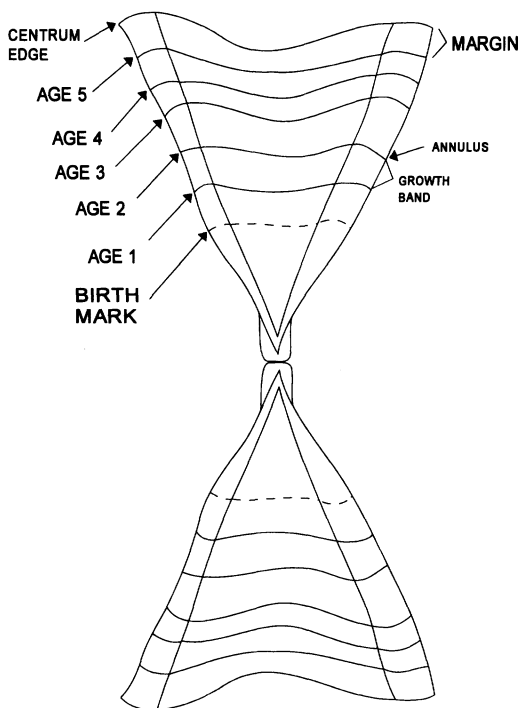


Fig. 1. Sagittal section through a 5+-year-old sandbar shark vertebra.

(Campana, 1990; Francis, 1990; Ricker, 1992) have shown that these estimators may not be totally appropriate.

Campana (1990) proposed the use of a biologically derived intercept, in a modified Fraser-Lee equation:

$$L_a = L_c + [(O_a - O_c) \cdot (L_c - L_0) / (O_c - O_0)]$$

where the biological intercept is at fish length =  $L_0$  and otolith radius =  $O_0$ , and  $L_a$  = length at age  $a$ ;  $L_c$  = length at capture,  $O_a$  = otolith distance from focus to annulus  $a$ ; and  $O_c$  = otolith radius at capture. He defined the biological intercept as the fish and otolith size at which proportionality of fish and otolith growth is initiated. (Any structure used for aging and proportional back-calculation may be substituted for his use of the otolith.) Using a cohort simulation model Campana (1990) showed that his equation produced more accurate back-calculated lengths than did the Fraser-Lee model.

In this study, the Campana (1990) equation was used with the size at birth as the biologically determined constant. Duncan's multiple range test (SAS Institute, Inc., 1979) was used to test differences between sexes and samples in the mean back-calculated lengths.

The mean back-calculated lengths at age for males and females, separately, were used to solve

the von Bertalanffy growth equation (von Bertalanffy, 1938), which is

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

where

$L_t$  = length at age  $t$

$L_\infty$  = asymptotic length

$K$  = growth coefficient

$t_0$  = age when length is theoretically zero.

Data were fitted to the equation using the NLIN procedure with MARQUARDT option of Statistical Analysis Systems (1979) computer software. Using Monte Carlo, simulations this iterative method was shown to produce the most accurate and precise estimates of known parameters and was easier to use than a traditional linear fitting technique (Vaughan and Kanciruk, 1982).

Growth models of sandbar sharks from the two sampling periods were compared statistically using various techniques. We directly compared incremental growth by age. By reparameterizing the von Bertalanffy growth model, Gallucci and Quinn (1979) proposed the use of a new parameter,  $\Omega = K \cdot L_\infty$ , which corresponds to the growth rate near  $t_0$ . Bernard (1981) proposed the use of Hotelling's  $T^2$  and subsequent modification of it to an F-statistic for testing of growth parameters when those parameters are correlated. The method of Kappenman (1981) for comparing growth curves based on the sum of squares of the differences between observed and predicted lengths (from an appropriate growth model) was also utilized. The 1991–1992 results also were compared to the reported analyses of Casey et al. (1985) and Casey and Natanson (1992).

## RESULTS

**Maturity.**—Size at maturity was based on 73 male sandbar sharks from the recent Florida sample and 281 females collected by the junior author from 1976–1992 which were measured and examined for reproductive stage. Eleven immature males were 122–136 cm PCL, two maturing males were 134 and 139 cm PCL, and the mature males were 129–156 cm PCL. The smallest mature female was 126 cm PCL, and the largest immature was 140 cm PCL. With the exception of the latter shark, all females > 134.5 cm PCL were mature and of those from 126–134 cm PCL approximately 25% (7/27) were mature. Springer (1960) reported the size of maturity was 71 inches TL (135 cm PCL) for

males and 72 inches TL (137 cm PCL) for females.

**Age / growth.**—Following the second reading of all vertebrae, a consensus age was determined for those samples that differed in age, and measurements were taken for back-calculation of size-at-age. Two vertebrae were discarded as unreconcilable after the second reading. Following the third reading, the percent agreement and the IAPE between the second and third readings were determined. The same age was determined in 59% of the samples, 89% agreed within one year, 98% agreed within two years, and 100% agreed within three years. The IAPE was 7.9. Vertebral radius vs length regression equations for single sex and sexes combined for both time periods were all significant ( $P < 0.001$ ): 1980–1981, female:  $PCL = 12.5 \cdot VR + 28.1$  ( $r^2 = 0.96$ ,  $n = 150$ ); 1980–1981, male:  $PCL = 13.0 \cdot VR + 25.4$  ( $r^2 = 0.95$ ,  $n = 38$ ); 1980–1981, both:  $PCL = 12.5 \cdot VR + 27.6$  ( $r^2 = 0.96$ ,  $n = 188$ ); 1991–1992, female:  $PCL = 13.8 \cdot VR + 13.6$  ( $r^2 = 0.98$ ,  $n = 183$ ); 1991–1992, male:  $PCL = 13.9 \cdot VR + 13.6$  ( $r^2 = 0.96$ ,  $n = 152$ ); 1991–1992, both:  $PCL = 13.8 \cdot VR + 13.8$  ( $r^2 = 0.97$ ,  $n = 335$ ).

Large average margins in May and June are followed by a smaller margin in July (Fig. 2). This pattern suggests annual rings form sometime in late June or early July or that the rings are not easily discernable until after summer growth has begun.

Back-calculated mean lengths-at-age from both sample periods in the present study were larger than those estimated by Casey et al. (1985) for ages 0–9 for male sandbar sharks and for ages 0–10 for females (Table 1). At older ages, the back-calculated lengths of Casey et al. (1985) were larger for both sexes. Results of the Duncan multiple range test indicated that, for the 1991–1992 period the mean back-calculated lengths of male and female sandbar sharks were the same at all ages tested (0–19;  $\alpha = 0.05$ ;  $n > 1$ ). For the 1980–1981 period, the mean back-calculated lengths of males and females were different only for ages 12, 13, 16, and 18 (Table 1). When sexes were combined and the comparison made between sample collection periods, the mean back-calculated lengths were different for ages 4–7 and 16–19 (Table 1).

Significant differences in mean annual growth increments of juveniles collected during the two periods were only present in the second, third, fifth, and sixth year of growth (Table 2). There were no significant differences between periods in increments at older ages.

Von Bertalanffy parameters which fit best for

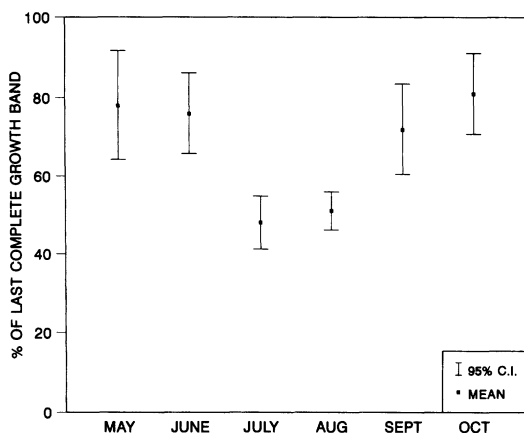


Fig. 2. Marginal vertebral growth of the sandbar shark.

the 1980–1981 period were females:  $L_{\infty} = 197$  cm PCL,  $K = 0.059$ ,  $t_0 = -4.8$  yr (Fig. 3A); males:  $L_{\infty} = 184$  cm PCL,  $K = 0.059$ ,  $t_0 = -5.4$  yr (Fig. 3B); sexes combined:  $L_{\infty} = 199$  cm PCL,  $K = 0.057$ ,  $t_0 = -4.9$  yr (Fig. 3C). The 1991–1992 period yielded best-fit parameters of females:  $L_{\infty} = 165$  cm PCL,  $K = 0.086$ ,  $t_0 = -3.9$  yr (Fig. 4A); males:  $L_{\infty} = 166$  cm PCL,  $K = 0.087$ ,  $t_0 = -3.8$  yr (Fig. 4B), sexes combined:  $L_{\infty} = 164$  cm PCL,  $K = 0.089$ ,  $t_0 = -3.8$  yr (Fig. 4C). The growth curves for the sexes combined for both time periods predict larger sizes at young ages (Fig. 5) than the models estimated by Casey et al. (1985) and Casey and Natanson (1992). The sizes at ages  $> 11$  predicted by the models of both time periods (Fig. 5) are smaller than those estimated by Casey et al. (1985) but are larger than those estimated by Casey and Natanson (1990).

Comparison of growth parameters using the methods of Bernard (1981), Gallucci and Quinn (1979), and Kappenman (1981) provided varying results. There was no significant difference in growth between male and female sandbar sharks collected in 1991–1992. For those collected in 1980–1981 the reparameterization technique of Bernard (1981), which used all three von Bertalanffy parameters, indicated there was a significant difference between growth of male and female sharks ( $T^2 > 3900$ ,  $P \ll 0.05$ ). However, the reparameterization technique of Gallucci and Quinn (1979), which uses only  $K$  and  $L_{\infty}$ , indicated no significant difference in growth between sexes ( $H = 1.97$ ,  $P > 0.10$ ). The Kappenman (1981) method also resulted in a significant difference in growth between sexes ( $P < 0.05$ ). When sexes were combined, all three tests found a significant dif-

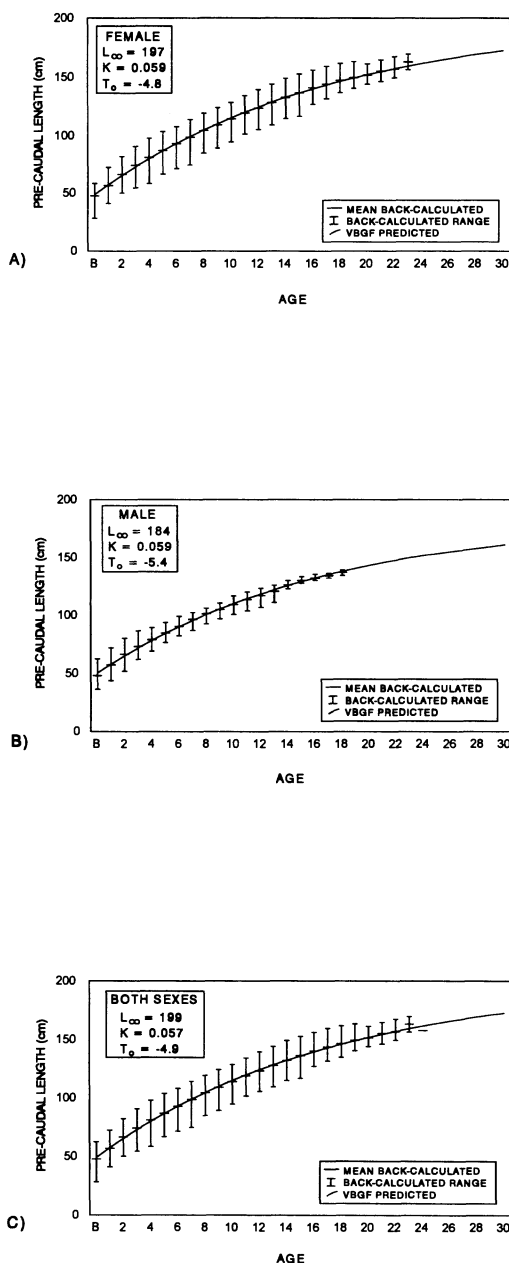


Fig. 3. Von Bertalanffy growth curves for the sandbar shark, *Carcharhinus plumbeus*, from 1980–1981 samples. (A) Female. (B) Male. (C) Sexes combined. Mean back-calculated lengths and ranges are included.

ference between growth of sandbar sharks from separate time periods.

## DISCUSSION

The linear regression of vertebral radius on length was statistically significant indicating a

TABLE 1. SANDBAR SHARK BACK-CALCULATED PRECAUDAL LENGTH (cm) AT AGE (B = BIRTH). Lengths from Casey et al. (1985) converted from fork length using:  $FL = 1.1 \cdot PCL + 1$ .

B	Mark (age in years)																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Female																									
1980-1981																									
n	150	143	133	123	110	100	93	87	80	79	75	67	64	59	54	50	43	32	25	22	14	11	6	2	1
Avg	48	57	67	75	81	87	93	99	105	109	114	119	124	128	133	137	141	144	147	150	152	155	157	163	158
SD	5	6	7	7	7	7	7	8	7	7	8	8	8	9	9	8	8	7	6	6	5	6	6	9	
1991-1992																									
n	191	165	136	100	78	72	62	56	54	53	46	38	34	29	23	20	16	14	11	5	3	2	1		
Avg	47	56	66	75	83	89	95	101	106	110	115	118	123	127	131	134	136	137	139	141	146	142	149		
SD	4	4	5	5	5	5	5	6	5	6	6	6	7	8	9	10	11	11	11	10	13	6.8			
Casey et al. (1985)																									
n	283	286	276	248	236	214	187	139	92	62	46	34	32	28	22	16	10	10	7	5	2	1	1		
Avg	39	46	58	67	75	81	87	94	100	106	115	124	130	136	140	145	147	153	156	163	183	180	185		
SD	3	4	5	4	5	5	6	7	8	9	10	9	10	10	8	6	8	10	13	15	8				
Male																									
1980-1981																									
n	38	33	30	22	17	14	11	10	9	9	9	7	7	6	5	5	4	2	2	1	1				
Avg	48	57	67	73	79	85	91	97	101	105	109	114	117	121	126	130	132	134	137	142	145				
SD	6	6	6	6	6	5	5	4	4	4	4	5	5	5	3	3	2	3	3						

TABLE 1. CONTINUED.

	Mark (age in years)																									
	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Male																										
1991-1992																										
n	221	189	153	114	96	86	83	81	80	78	77	77	76	72	61	39	31	17	9							
Avg	47	56	66	76	83	89	95	101	106	111	116	121	125	129	132	134	137	139	142							
SD	4	5	5	6	6	6	6	6	6	6	7	7	7	8	7	6	7	7	7							
Casey et al. (1985)																										
n	168	168	154	122	115	97	55	40	20	7	6	5	3	2	2	2	1									
Avg	40	45	56	65	73	79	85	90	96	111	117	119	128	132	137	141	139									
SD	3	3	4	4	5	5	6	7	10	11	12	9	5	7	9	9										
Sexes combined																										
1980-1981																										
n	188	176	163	145	127	114	104	97	89	88	84	74	71	65	59	55	47	34	27	13	15	11	6	2	1	
Avg	48	57	67	74	81	87	93	99	104	109	114	119	123	128	132	136	140	144	146	149	151	155	157	163	158	
SD	5	6	7	7	7	7	7	7	7	7	8	8	8	9	8	8	8	7	6	6	5	6	6	9		
1991-1992																										
n	412	354	289	214	174	158	145	137	134	131	123	115	110	101	84	59	47	31	20	5	3	2	1			
Avg	47	56	66	76	83	89	95	101	106	111	115	120	124	128	132	134	137	138	141	141	146	142	149			
SD	4	5	5	5	5	5	6	6	6	6	6	7	7	8	8	8	8	9	10	10	13	7				
Casey et al. (1985)																										
n	451	454	430	370	351	311	242	179	112	69	52	39	35	30	24	18	11	10	7	5	2	1	1			
Avg	39	46	57	66	74	81	86	93	99	107	115	123	130	136	140	145	147	153	156	163	183	180	185			
SD	3	4	5	5	5	6	7	8	9	9	9	9	10	10	8	6	8	10	13	15	8					



TABLE 2. JUVENILE SANDBAR SHARK ANNUAL GROWTH INCREMENTS (cm) BY SAMPLE PERIOD FOR SEXES COMBINED.

	Year											
	1	2	3	4	5	6	7	8	9	10	11	12
1980–1981	9.1	9.7	8.0	6.7	6.2	5.8	5.5	5.5	4.7	4.8	4.6	4.2
	NS	**	***	NS	*	**	NS	NS	NS	NS	NS	NS
1991–1992	9.2	10.5	9.2	7.1	6.6	6.5	5.7	5.4	4.8	4.5	4.6	4.3

\* Significant difference at  $\alpha = 0.10$ .\*\* Significant difference at  $\alpha = 0.05$ .

proportional relationship between the two variables. As vertebral radius increases (vertebral growth), the length increases (somatic growth) in a linear and predictable way. Further, recent evidence supports the assumption that the elasmobranch cartilaginous skeleton is a "closed system" with respect to calcium deposition, in that once incorporated into the tissue, calcium is not lost due to resorption or remodeling (Clement, 1992). It is likely that the observed density differences in centrum ring patterns are due to differences in mineralization during different growth phases (Cailliet et al., 1983). Therefore, the vertebra seems to be a suitable structure for back-calculating length at specific vertebral sizes, which can be converted to ages when a constant temporal periodicity of the rings can be ascertained.

The temporal nature of the marks in the vertebrae of the sandbar shark has not been fully resolved. Casey et al. (1985) considered the time of ring formation to be Jan. Our study, using juvenile sandbar sharks ages 0–8 (45–110 cm PCL), examined marginal growth of the vertebrae directly. The average marginal growth in May and June was similar to that in Oct. (78%, 76%, and 81% of previous annual increment, respectively), and marginal growth in July, Aug., and Sept. was 48%, 51%, and 72% (Fig. 2). It seems likely that annual growth is not continuous but, in fact, is composed of seasons—one of rapid growth and short duration (July–Oct.) and one of little or no somatic growth (Oct.–July). This trend is similar to that observed by Casey et al. (1985). Here, the growth period is from July–Sept. with nearly 75% of annual growth completed by the end of Sept. The period of rapid growth reported by Casey et al. (1985) was from June–Aug. and was from July–Sept. in the current study. This indicates that this growth phase is probably not regulated by the solar year but may be mitigated by water temperature or seasonal availability of food. The probable interpretation of these marginal analyses is that the ring is formed during the slow growth period of the winter months, but be-

cause it is compacted on the edge of the vertebral centra, it may not be distinguished as a valid mark until after the rapid growth of the summer months has added contrasting material to the outer edge of the vertebra. The alternative may be ring formation in June, just prior to the rapid-growth season. This second hypothesis would contradict the time of formation determined for many congeneric species (Branstetter and Stiles, 1987; Killam and Parsons, 1989; Bonfil et al., 1993). In any case, the error of incorrectly placing the time of ring formation by six months would only be a problem when analyzing observed length at age and placing those sharks collected in Jan.–June in the wrong age class. If age and growth modeling is based on back-calculated size at previous ages, this error is eliminated.

Campana (1990), Francis (1990), and Ricker (1992) discussed, at length, the importance of using the correct method of back-calculating lengths of fishes at previous ages from marks on hard parts used for aging. These authors' discussions centered on the error associated with the back-calculated length vs the actual length at a given age. The use of lengths calculated with the Campana (1990) equation for estimating von Bertalanffy parameters was based on the inclusion of an independently estimated size at a known age (length at birth). Campana (1990) contended the error associated with the estimated size at age approaches 0 as the ages approach the known age, in this case birth.

Casey et al. (1985) and Branstetter (1987) validated annual vertebral rings in sandbar sharks using tag-recapture and/or tetracycline injection information. Branstetter (1987) used two juvenile sharks that were 67 and 69 cm TL at injection. Casey et al. (1985) obtained vertebrae from six juvenile female sandbar sharks at liberty from 1–5 years and from one male sandbar shark, recaptured after eight years (152 cm FL). In each fish, the number of vertebral rings between tagging (from back-calculation) and recapture and the number of years at liberty agreed. The male shark in the Casey et al. (1985)

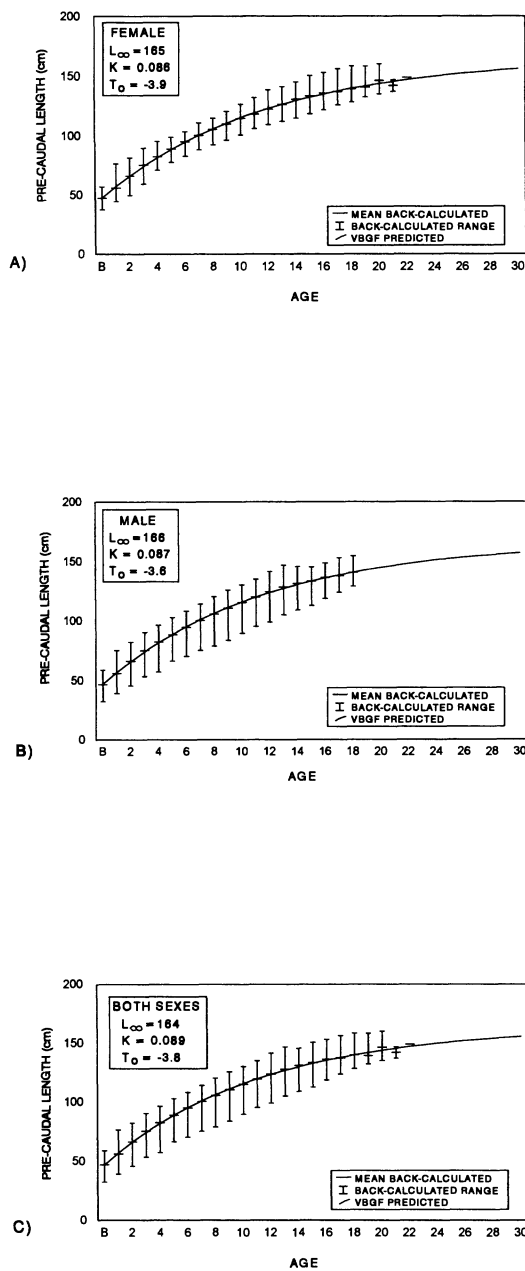


Fig. 4. Von Bertalanffy growth curves for the sandbar shark, *Carcharhinus plumbeus*, from 1991–1992 samples. (A) Female. (B) Male. (C) Sexes combined. Mean back-calculated lengths and ranges are included.

study was slightly larger than the minimum size at maturity (150 cm FL) reported by Springer (1960). Including the neonates studied by Branstetter (1987) and the juveniles and adult shark examined by Casey et al. (1985), annual periodicity has been validated in several age classes from birth to young adult. Although the re-

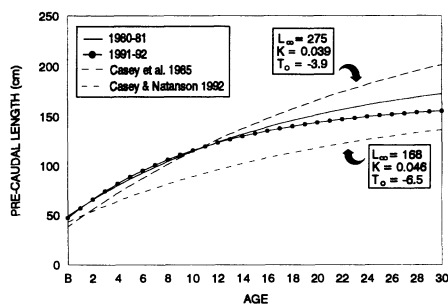


Fig. 5. Von Bertalanffy growth curves for sexes combined from 1980–1981 and 1991–1992 samples, and curves from Casey et al. (1985) and Casey and Natanson (1992). FL was converted to PCL using  $FL = 1.1 \cdot PCL + 1$ .

quirement of Beamish and McFarlane (1983) that ring periodicity must be proven in all age classes to be validated has not been completely satisfied, these studies (Casey et al., 1985; Branstetter, 1987) suggest rings are deposited annually from birth to maturity.

In a later paper, Casey and Natanson (1992) questioned the annual periodicity of vertebral rings, particularly at ages older than 5–6. A vertebral sample from one sandbar shark at liberty 3.3 years (127 cm FL at recapture) contained only two rings subsequent to tagging (from back-calculated vertebral radius at tagging). However, its growth increment of only 2.1 cm/yr was well below that expected for a sandbar shark of its size (approximately 7 cm/yr: Casey et al., 1985; and approximately 5 cm/yr: present study). If the vertebral radius:length relationship for such a slow-growing individual is even slightly different from the average ratio derived by the linear regression of Casey et al. (1985), then the calculated vertebral radius at tagging may be incorrect. Such an error could lead to inadvertent exclusion of one (or more) rings (Francis, 1990).

Although the annual periodicity of the vertebral rings has not been validated in all age classes, there is acceptable evidence suggesting that the periodicity is annual in juveniles through the age and size of first maturity in sandbar sharks (Branstetter, 1987; Casey et al., 1985). Contrary evidence (Casey and Natanson, 1992) is limited but does raise the possibility that the annual periodicity does not persist throughout the lifespan of this shark, particularly among females carrying pups. Given the data presented here, we have accepted the hypothesis of annual ring formation in the vertebrae and have based resultant VBGF models on back-calculated sizes at age using vertebral growth rings.

The  $L_{\infty}$  of the VBGF is a theoretical maxi-

imum size attained by the fish. In the case of a model derived from mean lengths-at-age, this parameter is also a mean (Francis, 1988). Here,  $L_{\infty}$  is a maximum mean length at a theoretical maximum age, and it need not be larger than the actual maximum reported size for an individual. Springer (1960) reported, that over a 20-year survey of commercial shark landings in Florida, he never saw a female sandbar shark longer than 234 cm TL (174 cm PCL) or a male sandbar shark longer than 226 cm TL (168 cm PCL). Only two female sandbar sharks exceeding 165 cm PCL (172, 174 cm) have been captured by the VIMS longline survey from 1974–1993. Consequently, the estimates of  $L_{\infty}$  from the 1991–1992 sample (females:  $L_{\infty} = 165$ , males:  $L_{\infty} = 166$ , sexes combined:  $L_{\infty} = 164$ ) seem reasonable as an estimate of maximum mean length. The estimates of  $L_{\infty}$  from the 1980–1981 period, by sex and sexes combined (females:  $L_{\infty} = 197$ , males:  $L_{\infty} = 184$ , sexes combined:  $L_{\infty} = 199$ ), are higher and may represent a theoretical maximum length rather than an actual attainable size for the species.

The VBGFs of sandbar sharks when sexes are combined are significantly different between sampling periods based on statistical tests specifically designed for the VBGF (Bernard, 1981; Gallucci and Quinn, 1979; Kappenman, 1981). Whether these differences reflect real growth differences and whether they are the result of some density-dependent factor is much harder to assess (Tanaka et al., 1990). Cailliet et al. (1990) and Tanaka et al. (1990) conducted comparative aging studies on two populations of *Mustelus manazo* and *Prionace glauca*, respectively, and concluded that differences in techniques of vertebrae preparation and growth band interpretation may bias the resultant growth models sufficient enough to occlude any real growth differences between populations. In the present study, all vertebrae were prepared and aged by the first author using predetermined objective criteria for band definition (S. Branstetter, pers. comm.) and multiple blind readings separated by 6–9 months. We believe this technique minimized any inherent bias introduced by multiple readers or vertebrae preparation methods.

Based on a long-term sampling survey of Virginia waters, the relative abundance of sandbar sharks declined by approximately two-thirds from 1974–1991 (Musick et al., 1993). If growth of sandbar sharks was density dependent, this decline in abundance could manifest itself in increased growth rates, particularly of juveniles. That the growth coefficient,  $K$ , increased between the 1980–1981 VBGF ( $K = 0.057$ ) and

the 1991–1992 VBGF ( $K = 0.089$ ) indicates an increase in growth rate; however, the  $L_{\infty}$  of the latter VBGF is considerably lower ( $L_{\infty} = 164$ ) than that of the former VBGF ( $L_{\infty} = 199$ ). Because  $L_{\infty}$  and  $K$  are inversely correlated in the VBGF, the higher  $K$  may merely indicate that growth more rapidly approaches a more realistic asymptote in the latter model. Conversely, the significantly larger mean lengths at ages 4–7 and the larger annual growth increments through the seventh year of life (from the 1991–1992 sample) support that early growth of sandbar sharks was actually faster. However, both models predict similar ages at maturity, 15–16 years, suggesting any increase in early growth has not been large enough or persisted long enough to decrease the age of first maturity.

Density-dependent growth of fish, primarily during the immature phase of the life history, has previously been documented for several teleosts. Chadwick (1987) reported a significant decline in fork length of Atlantic salmon, *Salmo salar*, with an increase in number of age 4+ smolts. Both an increase in growth rate and a decrease in age at first spawning have been associated with declines in catch/effort following intensive fisheries for two separate stocks of herring (Iles, 1967; Motoda and Hirano, 1963; as reported in Murphy, 1977). However, it may be difficult to demonstrate density effects on growth in some elasmobranchs due to long generation times and lifespans.

Musick et al. (1993) found that the relative abundance of juvenile sandbar sharks in the Chesapeake Bay was similar to and higher in 1990 and 1991 than in 1980 and 1981, respectively. This apparent increase in abundance was probably due to increased survival of young-of-year because of a decline in abundance of large coastal sharks (their principal predators; Musick et al., 1993). Such an increase in abundance of juveniles may preclude any actual increase in growth rate due to density-dependent factors in young-of-year and other early ages. However, abundance of older juveniles (> 4 yr) was much lower in 1990–1991 compared to 1980–1981 (Musick et al., 1993). It was primarily in these ages (4–7 yr old) that we find evidence of higher growth rates in the present study. Considering these factors, the statistical difference between growth models of the two sample periods, and the relatively short time elapsed (10–11 yr) between samples in this study compared to the lifespan of the species, it seems likely that the growth rate of juvenile sandbar sharks was slightly higher in 1991–1992 than in 1980–1981. But the age at first maturity was un-

changed, suggesting that any population-level consequences may not become apparent until several more years have passed.

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## Home Range of the Florida Red-Bellied Turtle (*Pseudemys nelsoni*) in a Florida Spring Run

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The home range of the Florida red-bellied turtle, *Pseudemys nelsoni*, in a Florida spring run is described using both maximum distance over water and Ford and Krumme's (1979) technique for producing a "composite" home range. Ford and Krumme's (1979) technique was also used to find the probabilities of capture/relocation within the composite home range. Spatial positions in the river were based on underwater captures/relocations and basking relocations. The results from both methods suggest that individuals at this study site use a small home range, on the order of 120 m in length, with no sex differences. These results are contrasted with those for *P. floridana* at the same site and with telemetry-generated data for *P. nelsoni* in a shallow lake in Paynes Prairie, Florida. Sympatric *P. floridana* appear to have larger home ranges, with a patchier distribution of nonzero capture/relocation probabilities. Estimates of the home-range areas of *P. nelsoni* in the lake are an order of magnitude larger than those in the run, perhaps due to more dispersed resources or the use of telemetry for relocating animals.

HOME range, "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943:351), is a standard ecological parameter. There are several methods for modeling home range which yield various shapes from which size may be calculated. These shapes include circles, ellipses, and various types of polygons (Anderson, 1982). Assessing use of the bounded area is also important (Jorgensen and Tanner, 1963), since use may reflect the distribution of resources within the home range. Home range use or utilization distribution can be calculated for an individual if it is relocated sufficiently often or, if the number of relocations per individual is small, averaged over many individuals using a mathematical technique (e.g., Ford and Krumme, 1979). The home-range size of semiaquatic turtles has often been estimated using the minimum convex polygon technique (Southwood, 1966) or Sexton's (1959:137–138)

definition, the "minimum direct distance over water between the two most distant points of capture." The latter is especially useful for turtles inhabiting rivers or streams.

Here I describe the home-range size and use of the Florida red-bellied turtle, *Pseudemys nelsoni*, in a small river, drawing on both Sexton's (1959) definition and the technique outlined in Ford and Krumme (1979). The latter technique possesses two distinct advantages for a data set with many individuals but few relocations per individual. First, a "composite" home range, using all the data from all the individuals, can be constructed. The composite home range can be considered as an alternative way of averaging relocation information from many individuals. Second, the probability of capture/relocation within the composite home range is found and can be interpreted as home-range use. This is the first report on home-range size for this species, and it is also the first time Ford and