

1987

A Comparison Of The Age And Growth Of The Tiger Shark, *Galeocerdo-Cuvieri*, From Off Virginia And From The Northwestern Gulf-Of-Mexico

Steve Branstetter

Virginia Institute of Marine Science

John A. Musick

Virginia Institute of Marine Science

James A. Colvocoresses

Virginia Institute of Marine Science

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Aquaculture and Fisheries Commons](#)

Recommended Citation

Branstetter, Steve; Musick, John A.; and Colvocoresses, James A., "A Comparison Of The Age And Growth Of The Tiger Shark, *Galeocerdo-Cuvieri*, From Off Virginia And From The Northwestern Gulf-Of-Mexico" (1987). *VIMS Articles*. 621.
<https://scholarworks.wm.edu/vimsarticles/621>

This Article is brought to you for free and open access by W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

A COMPARISON OF THE AGE AND GROWTH OF THE TIGER SHARK, *GALEOCERDO CUVIERI*, FROM OFF VIRGINIA AND FROM THE NORTHWESTERN GULF OF MEXICO¹

STEVEN BRANSTETTER,² J. A. MUSICK,³ AND J. A. COLVOCORESSES³

ABSTRACT

Lengths at age and growth rates for the tiger shark, *Galeocerdo cuvieri*, in the northwestern Atlantic and Gulf of Mexico were estimated from bands formed seasonally in the vertebral centra. The tiger shark grows rapidly compared with many other shark species. Growth rates for Gulf of Mexico juveniles were faster than for Atlantic juveniles. This produced significantly different ($P < 0.01$) estimates of the parameters of von Bertalanffy curves for the two regional samples. With sexes combined, parameter estimates for the Gulf of Mexico sample were $L_{\infty} = 388$ cm TL, $K = 0.184$, $t_0 = -1.13$ years; for the Atlantic sample they were $L_{\infty} = 440$ cm TL, $K = 0.107$, $t_0 = -2.35$ years. Males mature at approximately 310 cm TL, females at 315-320 cm TL, but the regional differences in juvenile growth rates result in different ages at maturity. In the Gulf of Mexico, males mature in 7 years, females in 8 years; in the Atlantic, males and females both mature in approximately 10 years. The largest male and female examined (381 cm TL) were 15 and 16 years of age.

The tiger shark, *Galeocerdo cuvieri*, is cosmopolitan in warm-temperate and tropical coastal and oceanic waters of the western North Atlantic (Castro 1983). It is usually found alone or in small groups of three to six individuals distributed rather homogeneously over most bottom types (Springer 1963). Because of its large size, it is one of the most frequent entries in recreational fishing tournaments, and it occurs regularly, but in low numbers, in longline catches (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981, 1986). Along the U.S. Atlantic coast, the tiger shark occurs year-round off Florida, migrates as far north as Cape Cod in summer (Casey 1964), and returns to more southerly latitudes in fall (Musick et al. 1985). In the Gulf of Mexico, the species occurs in coastal waters from spring through fall, and in deeper continental shelf and offshore regions year-round (Branstetter 1981, 1986).

The low catch rates and semisolitary nature of the tiger shark have hindered a comprehensive study of its biology. The tiger shark is both a scavenger (Gudger 1949; Clark and von Schmidt 1965) and euryphagous predator (Bass et al. 1975; Dodrill and Gilmore 1978). Information on the reproductive biology of the tiger shark must be gleaned from scat-

tered observations on pregnant females taken in the Indo-West Pacific and Indian Ocean (Kauffman 1950; Bass et al. 1975) and in the northwestern Atlantic (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981). Age and growth rates for the tiger shark have not been reported.

Alternating opaque (calcified) and translucent (less calcified) bands form in the vertebral centra of many elasmobranchs during growth (Radtke and Cailliet 1984), and if a regular periodicity can be demonstrated for the formation of these bands throughout the life of the animal (Beamish and McFarlane 1983), they can be used to assess ages for individuals in the sample and to estimate growth rates for the population. Using these bands, age and growth data for collections of tiger sharks from Virginia and the northwestern Gulf of Mexico were developed, compared, and integrated with known life history characteristics.

METHODS AND MATERIALS

Tiger sharks were examined from research and commercial longline catches and from recreational fishing tournaments. The Atlantic sample consisted of 27 specimens taken during 1983 and 1984 summer tournaments, and 42 specimens collected in May through October on longlines fished in continental shelf waters (primarily <40 m) within a 50 km radius of the mouth of Chesapeake Bay from 1977 to 1983. The Gulf of Mexico sample consisted

¹Contribution No. 1365 of the Virginia Institute of Marine Sciences.

²Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843.

³Virginia Institute of Marine Sciences, Gloucester Point, VA 23062.

of 21 specimens taken on longlines fished in continental shelf waters of the northwestern Gulf in summer and along the shelf edge in winter from 1981 to 1985. Nine more tiger sharks were examined during a summer tournament in Texas. Between 1978 and 1985, an additional 41 specimens were tagged and released between Panama City, FL and Brownsville, TX. Data on morphometrics, lengths at maturity, and weight/length relationships were supplemented by specimens collected in the north central Gulf of Mexico (Branstetter 1981) and by 23 weight/length records from specimens taken from 1976-81 Galveston, TX shark tournaments.

Measurements were taken as the straight line distance between perpendiculars with caudal fins placed in a natural position (Dodrill 1977; Branstetter 1981, 1986). The upper caudal lobe angle was calculated to be approximately 21-22°, based on a formula by Dodrill (1977) which places the vertex of the angle at the upper caudal notch. This is slightly less than the values calculated by Thompson and Simanek (1977), who measured the angle through the center of the caudal peduncle, not the upper caudal notch. Total lengths (TL) are used throughout this report, but because measurements were taken by different people, there could have been variation in placement of the long flexible upper caudal lobe into a natural angle. Therefore, for each regional sample, regressions were calculated to compare total length to the more precisely measurable fork length (FL) or precaudal length (PCL).

Weights of tiger sharks from tournaments and Virginia specimens were made with balance beam scales, and Gulf of Mexico specimens taken on longlines were weighed with spring scales. Scales were tested for accuracy between sampling periods.

Reproductive development and maturity determinations follow Springer (1960), Clark and von Schmidt (1965), and Branstetter (1981). Males were considered mature only if the claspers were fully calcified and siphon sacs were fully developed. Sperm is produced before the claspers calcify and cannot be used as a criterion of maturity. Virginity in females, indicated by the presence or absence of a hymen covering the distal end of the oviducts, is not a criterion for maturity. Females were considered mature when developing or ripe eggs were in the ovary, eggs or embryos were present in the uteri, or by uterine expansion of nongravid females.

For age and growth analysis vertebrae were removed from 25 females (125-381 cm) and 19 males (156-381 cm) from off Virginia, and from 10 females

(91-355 cm) and 7 males (140-340 cm) from the Gulf of Mexico. An additional eight Gulf of Mexico specimens (100-285 cm) had been processed for sale, and sex could not be determined. A section of the vertebral column was removed from under the origin of the first dorsal fin or, when sampling commercial operations, from the cervical region dorsal to the branchial chamber. Samples were frozen or preserved in 10% formalin and stored in ethyl or isopropyl alcohol. Following methods detailed in Branstetter and McEachran (1986), individual centra were cleaned and a sagittal section cut from the center. Sections were polished on wet 400 grit sandpaper and observed with a binocular dissecting microscope using transmitted light. To block incidental light, an opaque tube was placed over the section between the microscope stage and objective.

Distinct marks (annuli), as illustrated in Casey et al. (1985: fig. 1) and Branstetter and Stiles (in press: fig. 1), were visible in the intermedialia of centrum sections. These annuli corresponded to translucent areas in the corpus calcareum and to the outer edge of translucent bands on the centrum face. The annuli formed distinct borders for the growth bands. Bands were counted without knowledge of the length of the specimen. All band counts were made by the senior author. Counts for each specimen were performed twice, and if agreement was not reached, a third count was made for comparative purposes. The distance from the section focus to each annulus, centrum dorsal radius, and marginal increment was measured on a line from the focus through the center of the intermedialia.

The periodicity of annulus formation was verified through marginal increment analysis and corroborated with comparisons to back-calculated lengths at each mark. Relative marginal increments were calculated by dividing absolute marginal increment widths by the width of the last fully formed band, and relative marginal increments were compared by month of capture. Back calculations were performed using the Dahl-Lea method (Carlander 1969) where

$$TL_i = M_i(TL)CR$$

and TL_i = total length at mark i (M_i), TL = observed length at capture, and CR = centrum radius. Back calculations were analyzed for each sample as a whole and by age class.

Tiger sharks are born in the Gulf of Mexico and along the southeastern U.S. Atlantic coast in early

summer (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981). Therefore, for simplicity, a 1 June birthday was used to estimate actual ages. For back calculations, ages were based on the age at the formation of winter annuli; therefore, for summer caught tiger sharks, there is a difference between the actual age and the age at annulus formation (i.e., a tiger shark taken in June that was aged at 6.0 years would be 5+ years of age in back calculations). To estimate growth rates, observed age/length data were applied to a computerized von Bertalanffy growth model (Fabens 1965). Males and females were taken in similar numbers, and both sexes for both samples are represented graphically; however, because of the small data base, sexes were combined for all mathematical analyses.

Apparent differences in mean lengths at age between the two samples were tested for significance using *t*-tests (Snedacor and Cochran 1980), and independent von Bertalanffy curves for the two regional samples were tested for differences following methods of Bernard (1981) using computer analysis (SAS Institute 1985).

RESULTS

A FL/TL plot of data from both samples (Fig. 1) can be used for general conversions of lengths reported in this paper. However, analyzed separately, the two regional samples had nonsignificantly different regression formulas for the relationships of FL or PCL to TL:

Gulf

$$FL = 0.871(TL) - 13.5 \quad (n = 33, r = 0.998)$$

$$PCL = 0.788(TL) - 12.1 \quad (n = 34, r = 0.977)$$

Atlantic

$$FL = 0.853(TL) - 10.1 \quad (n = 66, r = 0.994)$$

$$PCL = 0.797(TL) - 14.2 \quad (n = 68, r = 0.992)$$

Combining data for both samples, the relationship of centrum radii (CR) to length (TL) (Fig. 2) could be described by linear regression:

$$TL = 14.72 CR + 51.15 \quad (n = 64, r = 0.972)$$

Although the regression did not pass through the origin, no correction factor, such as the Fraser-Lee method (Carlander 1969), was applied because this factor did not adequately describe the rapid embryonic growth (Casey et al. 1985; Branstetter 1986). For simplicity, this isometric relationship was used for back-calculating lengths at previous ages and did not produce Lee's phenomenon (Table 1). However, the relationship was slightly curvilinear and was more accurately described by separating the data into immature vs. mature specimens (< or > 310 cm):

$$\text{Immature - TL} = 17.7 CR + 20.18 \\ (n = 44, r = 0.972)$$

$$\text{Mature - TL} = 7.6 CR + 190.21 \\ (n = 20, r = 0.796).$$

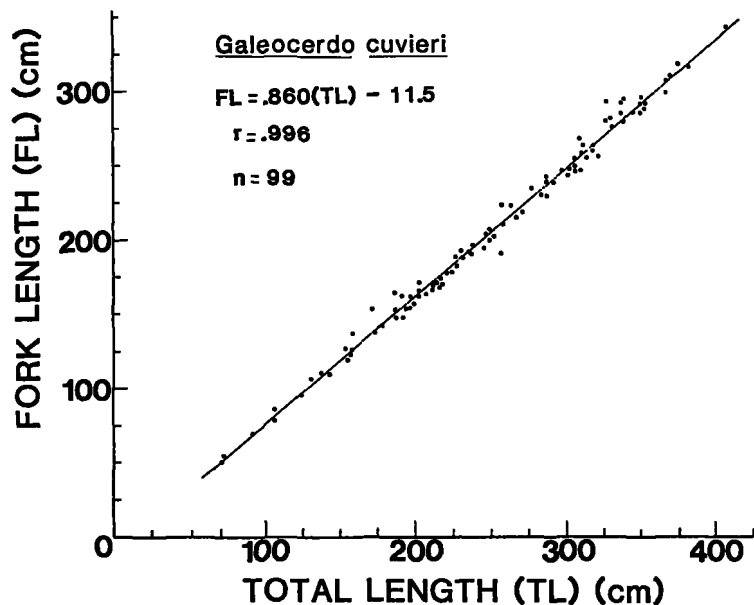


FIGURE 1.—Relationship between fork length and total length for *Galeocerdo cuvieri* taken in the Gulf of Mexico and off the Virginia coast.

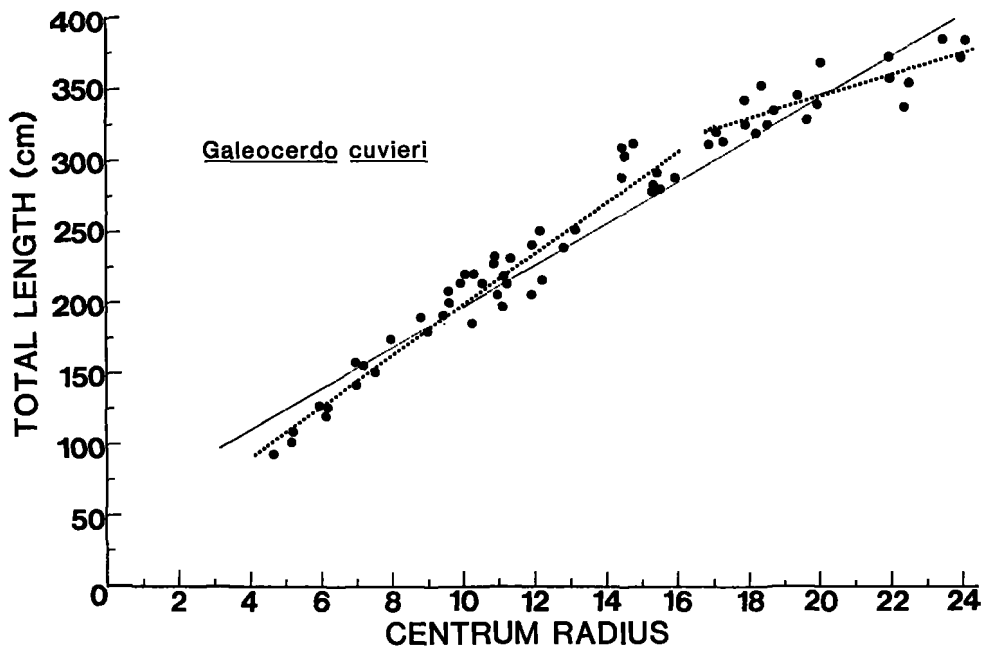


FIGURE 2.—Relationship of centrum dorsal radii to total length for *Galeocerdo cuvieri* taken in the Gulf of Mexico and off the Virginia coast. Centrum radii measurements are in ocular micrometer units (omu). 1 omu = 1.2 mm. See text for discussion of the different regressions.

Neonatal tiger sharks had only one annulus. Back calculations of length at the formation of this annulus indicated that it was formed at birth. Prebirth marks, which formed at placentation (Radtke and Cailliet 1984; Casey et al. 1985; Branstetter 1987c; Branstetter and Stiles in press), were not found in this aplacentally developing species; a condition also noted for the aplacental *Alopias vulpinus* (Cailliet et al. 1986).

Marginal increment analysis on all but neonatal tiger sharks (Fig. 3) indicated that the annuli formed in late fall or early winter (October-December) became visible off the centrum edge by January and were farthest from the centrum edge in summer. This "winter" annulus was consistent throughout the size range of the sample (Beamish and McFarlane 1983). Therefore, the first band bordered by the birth mark and the first winter annulus represented approximately 6 months growth; remaining bands formed annually.

Annuli along the periphery of centra in large (old) tiger sharks were closely spaced, making counts for these individuals more difficult. Annulus counts between the two readings were identical except for some of the larger individuals. In these cases, results of a third count matched one of the two previous counts, and this was the value accepted.

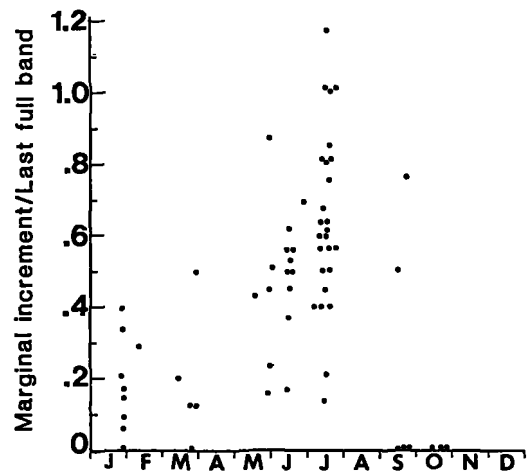


FIGURE 3.—Marginal increment widths as a ratio of the width of the last fully formed band in vertebral centra of *Galeocerdo cuvieri* compared by month. Specimens from the two regional samples are combined.

The two regional samples of tiger sharks exhibited similar growth rates. By combining observed length at age data from both samples a single von Bertalanffy curve could be fitted by using Fabens (1965)

TABLE 1.—Back calculations by age class for the Virginia and Gulf of Mexico samples of tiger sharks, *Galeocerdo cuvieri*. Ages are based on age at the formation of the winter mark. Lengths to nearest cm TL. Significantly different mean lengths at age between samples indicated by asterisks (** $P < 0.001$; * $P < 0.01$).

Winter mark	n	Age at the formation of the winter mark																
		B	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+
0	0	—																
1	2	76	126															
2	2	74	130	156														
3	6	73	125	159	185													
4	9	73	122	161	189	209												
5	1	84	126	160	192	219	237											
6	2	78	135	178	205	223	244	262										
7	2	75	120	151	186	218	243	259	274									
8	2	82	118	163	198	224	242	261	278	294								
9	1	73	122	148	165	196	224	249	271	290	309							
10	5	72	116	154	186	211	229	250	270	290	305	314						
11	6	72	121	159	184	211	239	262	280	300	316	326	336					
12	1	78	118	144	176	211	230	245	270	284	296	311	322	330				
13	1	73	128	183	219	238	256	284	302	317	326	335	348	356	366			
14	1	62	107	153	187	207	253	270	281	299	314	324	337	345	351	362		
15	2	77	123	158	189	214	236	261	287	301	313	325	334	346	355	364	372	
16	1	72	111	150	180	198	214	244	260	274	285	304	318	331	346	359	364	378
\bar{X}		74	122	159**	188**	213**	237**	258**	277**	295*	310*	321	334	342	355	362	369	378
cm/yr		¹ (48)	37	29	25	24	21	19	18	15	11	13	8	13	7	7	9	
cm/yr		¹ (49)	51	35	29	24	18	18	17	16	13	9						
\bar{X}		73	122	173**	208**	237**	261**	279**	297**	314*	330*	343	352					
0	1	77																
1	4	70	114															
2	3	74	129	169														
3	5	74	125	180	212													
4	2	80	124	170	214	241												
5	2	77	125	169	208	235	267											
6	1	68	115	166	198	227	256	281										
7	2	74	130	172	197	233	249	274	288									
8	1	61	105	179	202	229	250	275	300	307								
9	2	74	126	178	209	237	263	280	301	317	329							
10	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	1	68	113	166	215	254	283	290	306	316	333	343	352					

¹Six months growth.

procedure (Fig. 4) to adequately describe the growth rate. However, young age classes in the Gulf of Mexico (hereafter referred as Gulf) sample were slightly larger at age than their Atlantic counterpart. Independent von Bertalanffy curves for each data set had different parameter estimates. Regressions of the curves, linearized by log transformation, were analyzed for covariance (SAS Institute 1985) and were significantly different ($P < 0.0001$). Simultaneous nonlinear regression analysis of the two von Bertalanffy curves derived from back-calculated mean lengths at age produced parameter estimates with nonoverlapping simultaneous confidence intervals (Bernard 1981).

Back calculations by age class for each sample (Table 1) also showed the more rapid growth of the Gulf juveniles. Mean lengths at the formation of the winter annuli were significantly different ($P < 0.01$ or $P < 0.001$) for early age classes of the two samples. Neonates in both samples increased near-

ly 50 cm in length the first 6 months, and the Age I Gulf tiger sharks continued to grow at 50 cm/year, but Atlantic Age I individuals grew <40 cm/year. Gulf tiger sharks continued to grow approximately 4 cm/year faster than the Atlantic population until the fourth year. Growth rates then became similar; Gulf tiger sharks were simply larger at age.

Observed and back-calculated lengths at age (Table 2) corresponded within each sample. Comparisons of observed and back-calculated lengths did not indicate the occurrence of Lee's phenomenon. Differences in observed and back-calculated lengths at age were attributable to the fact that most specimens in both samples were taken in summer; therefore, observed lengths at age were larger than back-calculated lengths at age based on the winter formed annuli.

The growth rate estimated from centra was validated with one tag-recapture. A female, tagged 3 November 1978, was estimated to be 230 cm, and

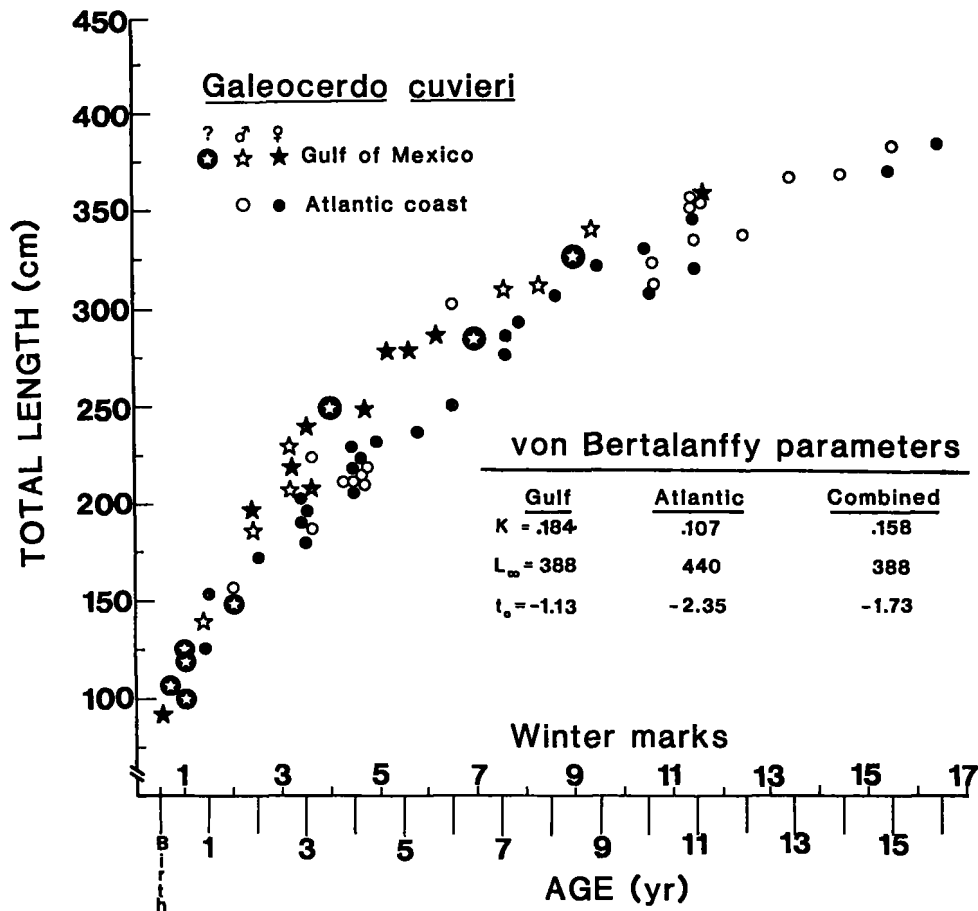


FIGURE 4.—Length at age for *Galeocerdo cuvieri* from the Gulf of Mexico and the Atlantic coast of Virginia. Individuals are plotted by their estimated actual ages (time elapsed since formation of the last winter mark). Birthdays set at 1 June.

at recapture, 7 April 1984, was estimated to be 320 cm from the weight/length relationship. The tiger shark grew 90 cm in 5.4 years. By using the age/length relationship estimated by the growth curve (Fig. 4), the shark would have been 3.4 years of age when tagged and 8.8 years of age at recapture.

Even with the relatively rapid growth rate exhibited by this species, a length-frequency analysis for both samples (Fig. 5) did not distinguish age classes. The size distribution did indicate that young juvenile tiger sharks occur only rarely in the Virginia region.

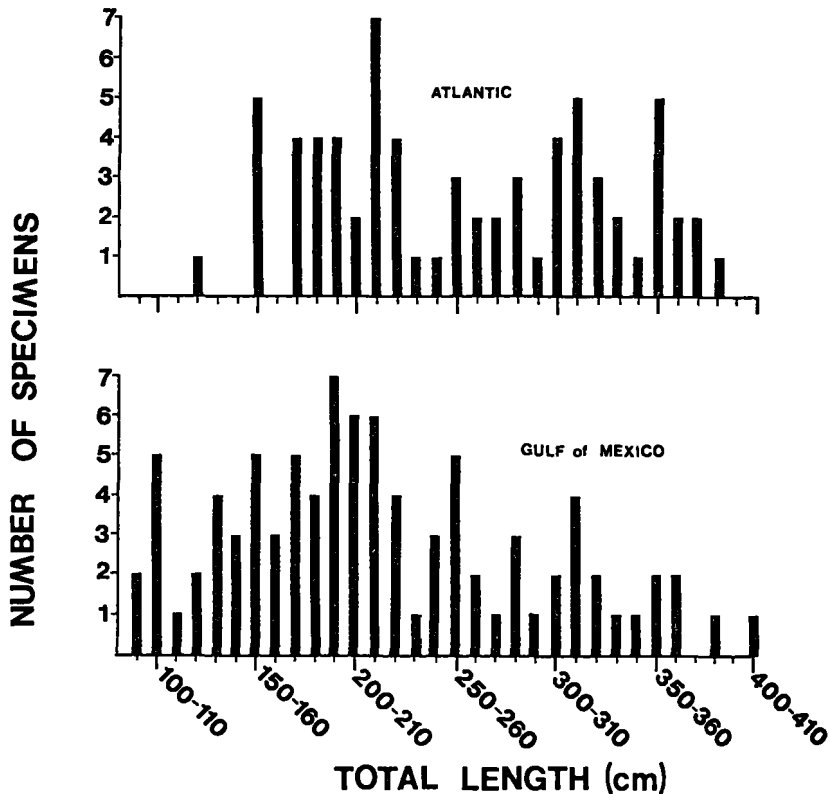
Males matured at approximately 310 cm, females at 315-320 cm, and the differences in growth rates between the two samples meant that they reached maturity at different ages. For the Gulf of Mexico, the smallest mature males (310, 311 cm) were 8.0 and 7.8 years old. The largest male aged (340 cm)

was only 8.8 years old. Back calculations indicated that this individual grew relatively rapidly compared with smaller individuals in the sample, and the only larger male collected (363 cm) was not aged. The smallest mature female (325 cm) was 8.8 years old, the largest (355 cm) was 11:2 years old. For the Atlantic sample, two immature males (310, 311 cm) were not aged, but a 312 cm mature male was 10.1 years old. The largest male (381 cm) was 15.1 years old. The largest immature female (307 cm) was 8.1 years of age, the smallest mature females (318, 319 cm) were 9.0 and 11.1 years of age, and the largest female (381 cm) was 16.1 years old.

The rapid linear growth early in life did not correspond to a great increase in the weight of the individuals (Fig. 6). Growth from the third through the seventh winter decreased from 30 to 20 cm/year, and weights increased during this period. As the

TABLE 2.—Comparison of length at age for observed and back-calculated data for Atlantic and Gulf populations of the tiger shark, *Galeocerdo cuvieri*. Lengths are to the nearest cm TL. Values indicate low-mean-high (n) for each age class.

Winter mark: Age:	0 0	I 0+	II 1+	III 2+	IV 3+	V 4+
Gulf						
observed	91-99-106 (2)	100-121-140 (4)	150-179-199 (3)	205-220-240 (5)	248-249-250 (2)	278-279-279 (2)
back calculation	50-73-85 (25)	96-122-137 (23)	149-173-184 (19)	192-208-228 (16)	225-237-254 (11)	239-261-283 (9)
Atlantic						
observed	NA (0)	125-140-155 (2)	156-165-173 (2)	180-192-225 (6)	205-216-229 (9)	237 (1)
back calculation	60-74-84 (44)	101-122-149 (44)	138-159-188 (42)	161-188-220 (40)	183-213-238 (34)	202-237-256 (25)
Winter mark: Age:	VI 5+	VII 6+	VIII 7+	IX 8+	X 9+	XI 10+
Gulf						
observed	288 (1)	285-298-310 (2)	311 (1)	325-333-340 (2)	NA (0)	355 (1)
back calculation	272-279-290 (7)	283-297-306 (6)	307-314-318 (4)	325-330-333 (3)	343 (1)	352 (1)
Atlantic						
observed	250-276-302 (2)	278-282-286 (2)	292-300-307 (2)	318 (1)	307-322-335 (5)	319-341-354 (6)
back calculation	221-258-284 (24)	245-277-302 (22)	270-295-317 (20)	292-310-327 (18)	304-321-341 (17)	315-334-349 (12)
Winter mark: Age:	XII 11+	XIII 12+	XIV 13+	XV 14+	XVI 15+	
Atlantic						
observed	338 (1)	368 (1)	368 (1)	370-376-381 (2)	381 (1)	
back calculation	340-343-356 (6)	346-355-366 (5)	359-362-369 (4)	364-369-378 (3)	378 (1)	

FIGURE 5.—Length frequency of *Galeocerdo cuvieri* collected off Virginia and in the Gulf of Mexico. Specimens are grouped into 10 cm size classes.

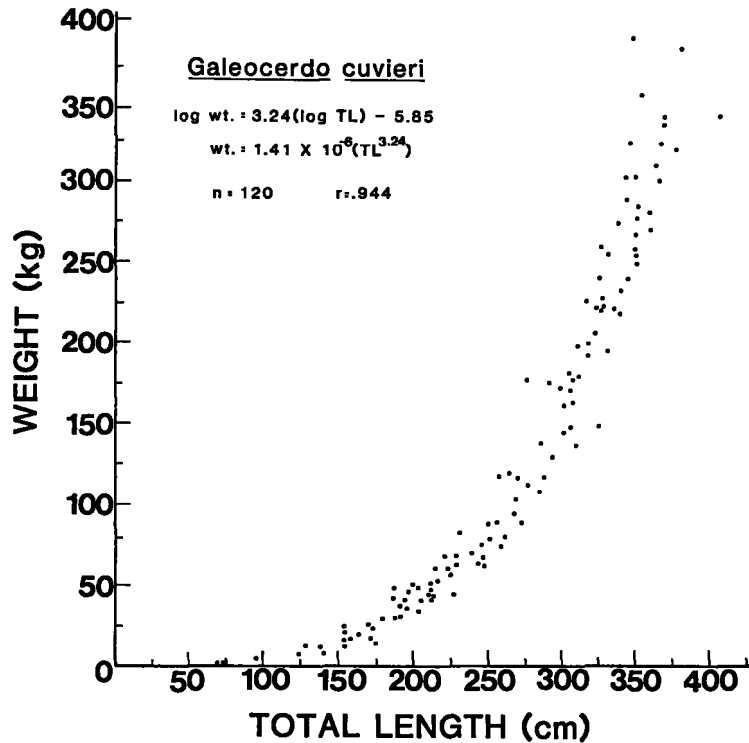


FIGURE 6.—Weight/length relationship for Atlantic and Gulf of Mexico *Galeocerdo cuvieri*, sexes combined.

animals matured at 310-320 cm, linear growth slowed from 15 cm/year to <10 cm/year, and weights increased dramatically.

DISCUSSION

An isometric relationship between centrum growth and length has been noted for many shark genera (Cailliet et al. 1983; Gruber and Stout 1983; Branstetter and McEachran 1986). The slight curvilinear relationship between centrum growth and length noted for *Galeocerdo cuvieri* suggested there were two distinct growth stanzas. A similar relationship was also noted for *Isurus oxyrinchus* (Pratt and Casey 1983). The point of inflection in the curve is generally at the length corresponding to the onset of maturity, a decreased linear growth rate and an increased weight gain rate. Apparently, centrum growth is correlated to the structural support necessary for length increases, but an increasing rate of weight gain does not require additional strengthening of the vertebral column.

Marginal increment analysis of annulus periodicity demonstrated that one growth band, consisting of

one calcified opaque zone and one less calcified translucent zone, formed annually. A similar periodicity for growth bands or annuli has been verified for several shark genera (Gruber and Stout 1983; Cailliet et al. 1986; Branstetter and McEachran 1986) and validated using tetracycline injected *Negaprion brevirostris* (Gruber and Stout 1983), *Triakis semifasciatus* (Smith 1984), *Rhizoprionodon terraenovae*, and *Carcharhinus plumbeus* (Branstetter 1987a). In contrast, Parker and Stott (1965) and Pratt and Casey (1983) provided evidence that lamnoids produce two band pairs per year, and Natanson (1984) could find no regular periodicity in centrum bands of *Squatina californica*.

Our estimates indicated the tiger shark doubles in length the first year of life. This is supported by growth of a full-term embryo (69 cm) placed in an aquarium by Clark and von Schmidt (1965) on 21 May, where it survived 12 weeks growing to 89 cm.

Rapid linear growth for juvenile tiger sharks may be necessary for adequate cohort survival. With a 13-16 mo gestation period (Clark and von Schmidt 1965) and a mating season which occurs before full-term females have pupped, the female reproductive

cycle is at least 2 years. Considering the litter size (40-70 pups) (Kauffman 1950; Bass et al. 1975; Branstetter 1981), natural mortality must be high for young age classes. Pups are born in coastal waters at a relatively large size (>70 cm) which reduces some predation, but the elongate, flexible body produces an inefficient anguilliform swimming motion. Additionally, early in life, the caudal fin is extremely flexible and has a low thrust angle (Thompson and Simanek 1977). The combination of these characteristics precludes rapid swimming speeds, thus making the pups vulnerable to predation by the abundant coastal sharks including their own species. Not only does rapid linear growth make them larger than most potential predators, it may help decrease predation by increasing swimming efficiency and speed through increased body rigidity (producing a more carangiform motion) and increased caudal fin thrust angle.

Linear growth continues at >20 cm/year until the tiger sharks are near maturity. Such rapid growth is similar to that noted for several lamnoids (Parker and Stott 1965; Gruber and Compagno 1981; Pratt and Casey 1983; Cailliet et al. 1985), but contrasts sharply to the slow growth rates estimated for several carcharhinids and sphyrynids (Thorson and Lacy 1982; Gruber and Stout 1983; Schwartz 1983a). Even the more rapidly growing carcharhinids do not have such large relative increases in length (Parsons 1985; Branstetter and McEachran 1986).

The mean lengths at age between the Gulf of Mexico and Atlantic tiger sharks were significantly different, and probably represent ecophenotypic differences between the two regions. However, the two regional groups are not isolated. Our one tag-recapture was tagged off Mobile Bay, AL and recaptured in the Florida Straits off Havana, Cuba, and there are similar tag returns of tiger sharks that moved between the Gulf of Mexico and the Atlantic (J. Casey pers. commun.*). However, long migrations between the two regions may be restricted to larger individuals with juveniles remaining in their respective regions.

If juvenile tiger sharks do remain in their respective regions early in life, growth rate differences between the two regions may be caused by differences in early life histories. In the Gulf of Mexico, the pups apparently only migrate short distances inshore-offshore seasonally. In the Atlantic, the pups

are born south of Cape Hatteras, probably in the Florida region (Dodrill 1977). These neonates may not migrate north during their first year, as small individuals, <150 cm, are rare in the Virginia region (Fig. 5). During this time, the growth rates for both groups are similar. The extensive northern migration for 1+ year old Atlantic juveniles, 150-200 cm, may be energetically costly, hindering growth. Therefore, the Gulf young that do not migrate great distances are able to attain greater lengths during this time period. The increased swimming efficiency attained with lengths >250 cm could possibly explain why growth rates become similar.

For juveniles of both regions, the energy requirements for the inefficient swimming motion and rapid linear growth apparently restrict any great increase in weight (Fig. 6). Only after the tiger sharks reach lengths >200 cm (3+ years of age) does weight increase substantially, and correspondingly linear growth begins declining. After reaching maturity (310-320 cm) linear growth is <10 cm/year while weight growth is substantial, corresponding to the change in centrum radius/length relationship (Fig. 3).

The von Bertalanffy parameter estimates for the two collections closely bracket known life history characteristics. With sexes combined, the L_{∞} for the Gulf of Mexico collection and for both samples combined (388 cm) is smaller than many reported large individuals, but is a reasonable compromise between the maximum reported lengths for males and females: 419 cm individual (McCormick et al. 1964); 370 cm male, 410 cm female (Bass et al. 1975); 410 cm female (Branstetter 1981); and a 381 cm male and female from this study. However, the tiger shark is thought to attain lengths in excess of 450 cm (Bigelow and Schroeder 1948; Castro 1983), more in agreement with the L_{∞} for the Atlantic sample (440 cm). The t_0 value for the Gulf sample (-1.13 years) is accurate, but the 13-16 mo gestation period is overestimated for the Atlantic sample (-2.35 years). The t_0 value for many shark species overestimates the gestation period (Casey et al. 1985; Branstetter 1986). The K values for each analysis reflect the rapid growth rate of this species and are similar to some of the more rapidly growing *Carcharhinus* species such as *C. limbatus*, *C. brevipinna* (Branstetter 1987c), *C. falciformis* (Branstetter 1987b), and *C. acronotus* (Schwartz 1983b).

At the estimated growth rate for the largest individuals (5-10 cm/year), exceptionally large specimens, 400-450 cm, would be 20-25 years of age. The

*J. Casey, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882, pers. commun. June 1986.

von Bertalanffy curve using observed lengths at age produced an estimated age at L_{∞} for the Gulf sample of 28 years, and 37 years for the Atlantic sample. This would mean that the species matures at 30-50% of its maximum age, and with a reproductive cycle of greater than 2 years, a female would reproduce less than 10 times. On the other hand, von Bertalanffy curves derived using back-calculated lengths at age for both samples produced estimated ages at L_{∞} of 45-50 years. Exceptionally high ages at L_{∞} may be due to the exponential function of the model, or it is also possible that as tiger sharks attain sizes near their maximum weight or length, centrum growth and band formation do not accurately represent age. Because no exceptionally large individuals were aged, we are unable to determine which is the case. Even so, the data indicate that the tiger shark is long-lived with a relatively low fecundity, and natural mortality for the young may be high. As with many other elasmobranchs, this combination of K -selected characteristics may result in an overexploitation of this species under increased recreational and commercial fishing pressure (Musick and Colvocoresses 1986).

ACKNOWLEDGMENTS

Appreciation is extended to commercial longline vessel owners and captains (Hollis Forrester, Bill Templeton, Lacy Smith, Arnold Davila, Olin Welborn, Buddy and Tinker Lindley, Joe Gayman, Henry Jones, and Floyd Condit), Mark's Sharks, Inc., the Biggs Pensacola Shark Rodeo, the Dauphin Island Deep Sea Rodeo, the Galveston Monster Fishermen Club Shark Tournament, and the Virginia Beach Sharks for allowing access to and examination of numerous tiger sharks. We thank Marine Advisory Service personnel Gary Graham and Tony Reisinger for their help during the course of this study. Debbie Branstetter provided continuous laboratory and field assistance in the Gulf of Mexico study, and John Gourley and Marta Nammack provided invaluable aid in the Virginia program. The senior author wishes to acknowledge the support and encouragement provided by John D. McEachran.

Different portions of this study were supported by the Gulf and South Atlantic Fishery Development Foundation, Inc., the Texas A&M Sea Grant College Program, the Virginia Sea Grant Program, the Graduate College and Association of Former Students of Texas A&M University, and the State of Texas.

LITERATURE CITED

- BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Carcharhinus* and *Mustelus*) and Sphyrnidae. Oceanogr. Res. Int. (Durban) Invest. Rep. 38, 100 p.
- BEAMISH, R. J., AND G. A. MCFARLANE.
1983. The forgotten requirements for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735-743.
- BERNARD, D. R.
1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat. Sci. 38:233-236.
- BIGLOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. In Fishes of the Western North Atlantic. Part I, No. 1, p. 59-546. Mem. Sears Found. Mar. Res., Yale University.
- BRANSTETTER, S.
1981. Biological notes on the sharks of the north central Gulf of Mexico. Contrib. Mar. Sci. 24:213-34.
1986. Biological parameters of the sharks of the northwestern Gulf of Mexico in relation to their potential as a commercial fishery resource. Unpubl. Ph.D. Thesis, Texas A&M University, 138 p.
1987a. Age and growth validation of new born sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 1987:293-300.
1987b. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Environ. Biol. Fishes 19:161-174.
1987c. Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. Copeia 1987.
- BRANSTETTER, S., AND J. D. MCEACHRAN.
1986. Age and growth of four carcharhinid sharks common to the Gulf of Mexico: a summary paper. In T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (editors), Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes, p. 361-371. Ichthol. Soc. Jpn., Tokyo.
- BRANSTETTER, S., AND R. STILES.
In press. Age and growth estimates for the bull shark, *Carcharhinus leucas*, in the northern Gulf of Mexico. Environ. Biol. Fishes.
- CAILLIET, G. M., L. K. MARTIN, J. T. HARVEY, D. KUSHER, AND B. A. WELDEN.
1983. Preliminary studies on the age and growth of the blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. In E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 179-188. U.S. Dep. Commer. NOAA Tech. Rep. NMFS 8.
- CAILLIET, G. M., L. J. NATANSON, B. A. WELDEN, AND D. EBERT.
1985. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. South. Calif. Acad. Sci. Mem. 9:49-60.
- CAILLIET, G. M., R. L. RADTKE, AND B. A. WELDEN.
1986. Elasmobranch age determination and verification: a review. In T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (editors), Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes, p. 345-360. Ichthol. Soc. Jpn., Tokyo.

- CARLANDER, K. D.
1969. Handbook of freshwater fishery biology. Volume 1. Iowa St. Univ. Press, Ames, 752 p.
- CASEY, J. G.
1964. Angler's guide to the sharks of the northeastern United States, Maine to Chesapeake Bay. U.S. Fish Wildl. Serv. Circ. 179, 32 p.
- CASEY, J. G., H. L. PRATT, JR., AND C. E. STILLWELL.
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42:963-975.
- CASTRO, J. I.
1983. The sharks of North American waters. Texas A&M Univ. Press, College Station, 180 p.
- CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15:13-83.
- DODRILL, J. W.
1977. A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. Unpubl. MS Thesis, Fla. Inst. Tech., 304 p.
- DODRILL, J. W., AND R. G. GILMORE.
1978. Land birds in the stomachs of tiger sharks, *Galeocerdo cuvieri* (Peron and Lesueur). Auk 95:585-586.
- FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.
- GRUBER, S. H., AND L. J. V. COMPAGNO.
1981. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*. Fish. Bull., U.S. 79:617-640.
- GRUBER, S. H., AND R. G. STOUT.
1983. Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). In E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 193-205. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.
- GUDGER, E. W.
1949. Natural history notes on tiger sharks, *Galeocerdo tigrinis*, caught at Key West, Florida, with emphasis on food and feeding habits. Copeia 1949:39-47.
- KAUFFMAN, D. E.
1950. Notes on the biology of the tiger shark (*Galeocerdo arcticus*) from Philippine waters. U.S. Fish Wildl. Serv. Res. Rep. 16, 10 p.
- MCCORMICK, H. W., T. ALLEN, AND W. YOUNG.
1963. Sharks on a line. In Shadows in the sea - the sharks, skates, and rays, Chap. 4, p. 89-114. Weathervane Books, N.Y.
- MUSICK, J. A., AND J. A. COLVOCORESSES.
In press. Seasonal recruitment of subtropical sharks in Chesapeake Bight USA. In A. Yanez-Anancibia and D. Pauly (editors), Proceedings of a workshop in tropical coastal demersal communities. Carman, Campeche, Mexico, 1986.
- MUSICK, J. A., J. A. COLVOCORESSES, E. F. LAWLER, AND W. G. RASCHI.
1985. Distribution of sharks in Chesapeake Bight. [Abstr.] Proceedings of the 65th Annual Meeting of the American Society of Ichthyologists and Herpetologists.
- NATANSON, L. J.
1984. Aspects of the age, growth, and reproduction of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. Unpubl. MA Thesis, San Jose St. Univ., San Jose, CA 71 p.
- PARKER, H. W., AND F. C. STOTT.
1965. Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). Zool. Meded. 40: 305-319.
- PARSONS, G. R.
1985. Growth and age estimation of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*: a comparison of techniques. Copeia 1985:80-85.
- PRATT, H. L., JR., AND J. G. CASEY.
1983. Age and growth of the shortfin mako, *Isurus paucus*, using four methods. Can. J. Fish. Aquat. Sci. 40:1944-1957.
- RADTKE, R. L., AND G. M. CAILLIET.
1984. Age estimation and growth of the gray reef shark, *Carcharhinus amblyrhynchos*, from the northwestern Hawaiian Islands. In Proceedings Second Symposium on Resource Investigations of the Northwestern Hawaiian Islands, p. 121-127. UNI-SEAGRANT-MR-84-01.
- SAS INSTITUTE, INC.
1985. SAS User's Guide: Basics, SAS User's Guide: Statistics, SAS/Graph Software Version 5. SAS Institute Inc., Cary, NC.
- SCHWARTZ, F. J.
1983a. Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks based on vertebral ring counts. In E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 167-174. U.S. Dep. Commer. NOAA Tech. Rep. NMFS 8.
1983b. Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus*, in North Carolina. Northeast Gulf Sci. 7:29-47.
- SMITH, S. E.
1984. Timing of vertebral-band deposition in tetracycline injected leopard sharks. Trans. Am. Fish. Soc. 113:308-313.
- SNEDACOR, G. W., AND W. G. COCHRAN.
1980. Statistical methods. Iowa State Univ. Press, Ames, 507 p.
- SPRINGER, S.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv. Fish. Bull. 61:1-38.
1963. Field observations on large sharks of the Florida-Caribbean region. In P. W. Gilbert (editor), Sharks and survival, Sect. II. Ch. 3, p. 95-113. Heath and Co., Boston.
- THOMPSON, K. S., AND D. E. SIMANEK.
1977. Body form and locomotion in sharks. Am. Zool. 17: 343-354.
- THORSON, T. B., AND E. J. LACY, JR.
1982. Age, growth rate and longevity of *Carcharhinus leucas* estimated from tagging and vertebral rings. Copeia 1982: 110-116.