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Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico

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Synopsis

Length at age and growth rates for 59 bull sharks, *Carcharhinus leucas,* collected from the northern Gulf of Mexico were estimated from the band patterns formed seasonally in the vertebral centra. The combined age at length data for both sexes were applied to a von Bertalanffy growth model producing parameter estimates of L_∞ = 285 cm TL, K = .076, $t_0 = -3.0$ yr. Lengths at age for males and females were similar except that males did not attain as great a length as females. Growth was apparently slow and varied among individuals, but in general, was estimated to be 15–20 cm yr^{-1} for the first five years, 10 cm yr^{-1} for years 6–10, 5–7 cm yr^{-1} for years 11–16, and less than 4–5 cm yr^{-1} thereafter. Males mature at 210–220 cm TL or 14–15 yr of age; females mature at >225 cm TL or 18+ yr of age. The largest male (245 cm TL) was 21.3 yr old; the largest female (268 cm TL) was 24.2 yr old.

Introduction

The bull shark, *Carcharhinus leucas,* is cosmopolitan in warm-temperate and tropical coastal marine waters (Garrick 1982). It is often associated with freshwater influenced areas, and penetrates freshwater systems (Thorson 1972, Bass et al. 1973, Montoya & Thorson 1977, Thomerson & Thorson 1977). The abundance of this cosmopolitan species in coastal waters has led to good documentation of the general life history of populations off South Africa (D'Aubrey 1971, Bass et al. 1973), off Brazil (Sadowsky 1967, 1971), in the Rio San Juan-Lake Nicaragua system (Thorson et al. 1966, Jensen 1976, Tuma 1976), along the east coast of Florida (Dodrill 1977, Snelson et al. 1984), and in the Gulf of Mexico (Springer 1940, Clark & von Schmidt 1965, Branstetter 1981).

The bull shark is a common coastal shark in the northern Gulf of Mexico, especially near the mouth of the Mississippi River (Springer 1938, 1940, Branstetter 1981). Its size and abundance makes it a frequent target of recreational fishermen, and a substantial part of a developing commercial fishery (Branstetter 1986). Although signifcant information exists on the reproductive biology of this species, age and growth data are only available for the Lake Nicaragua-Rio San Juan population (Thorson & Lacy 1982). This freshwater population has some unusual life history characteristics, therefore data from that population are not generally applicable to other populations. Here we report the age/length relationship and growth rate of the bull shark in the northern Gulf of Mexico.

Methods and materials

Specimens were examined from recreational catches (especially tournament entries), research longline and rod and reel efforts, and commercial fishery catches. In all, 96 bull sharks were collected in coastal and shelf waters from off Panama City, Florida to off Brownsville, Texas from 1979 through 1985.

All measurements were taken as the straight line distance between perpendiculars with caudal fins placed in a natural position (Branstetter 1980, 1986). Using data from 29 specimens in a formula (Dodrill 1977) which places the angle vertex at the pre-caudal notch, the mean upper caudal lobe angle was calculated to be 25°. This was similar to carcharhinid tail angle values derived by Thompson & Simanek (1977). Total lengths (TL) are used throughout this report, and for comparison with literature which reported in fork length (FL) or pre-caudal length (PCL), a TL was calculated from our proportional data base with the following formulae:

$$(TL) = 1.15\ (FL) + 7.32\ (n = 81;\ r = 0.994)$$
$$(TL) = 1.23\ (PCL) + 13.50\ (n = 81;\ r = 0.994)$$

Sadowsky's (1968) method of measuring TL as the straight line PCL length added to the upper caudal lobe length produced a TL 1.025 times greater than if measured on a straight line with the caudal fin in a natural position, and his length records were adjusted accordingly.

Most tournament entries were weighed with balance beam scales, but specimens taken on research or commercial longlines were weighed with a spring scale. Weights taken at sea were subject to variation caused by the motion of the boat, therefore minimum and maximum readings were averaged. Scale accuracies were tested before each sampling trip. Additional weight/length records were acquired from Galveston, Texas recreational tournament winners from 1976–1981.

Reproductive development and maturity determinations follow guidelines set forth in Springer (1960), Clark & von Schmidt (1965), and Branstetter (1981). Males were considered mature when the clasper and siphon sacs were fully developed; the presence of sperm does not constitute a maturity criterion (Clark & von Schmidt 1965). Virginity in females, determined by the presence or absence of a hymen covering the distal end of the oviducts, is not a maturity criterion. Females were considered mature based on uterine development, the presence of developing or ripe ovarian eggs, or the presence of uterine eggs or embryos.

For age and growth analysis, vertebrae were removed from 27 males (84–245 cm) and 32 females (134–268 cm). Centra were sampled from under the first dorsal fin origin, or when sampling commercial operations from the cervical region dorsal to the branchial chamber. Preliminary analyses showed no variation in centrum band numbers between these two adjacent regions. Early in the study, samples were preserved and stored in either formalin or alcohol, however, such storage made our analytical techniques more difficult. Samples collected later in the study were frozen.

Centra were prepared and analyzed by two methods. One author (SB) followed methods detailed in Branstetter & McEachran (1986) in which a sagittal section was cut from the center of a cleaned centrum, and polished on wet 400 grit sandpaper to a thickness of 0.5 mm. The section was viewed with transmitted sub-stage light using a binocular dissecting microscope equipped with an ocular micrometer. Incidental light was blocked by placing an opaque tube over the section between the microscope stage and the objective. The other author (B) bisected raw centra either frontally or sagittally, soaked the half-centrum in bleach, sanded the inner face smooth, and transmitted light through the half-centrum from a lateral light source for viewing.

Distinct marks (annuli) traversed the intermedialia of the centra (Fig. 1a). These annuli corresponded to the outer edges of the translucent bands on the face of the centrum and to translucent areas in the corpus calcareum of the section. The annuli bordered a band pair (one opaque and one translucent band). Additional annuli were noted for some specimens that corresponded to the edge of the calcified opaque band on the centrum face, and to opaque areas in the corpus calcareum. Because of

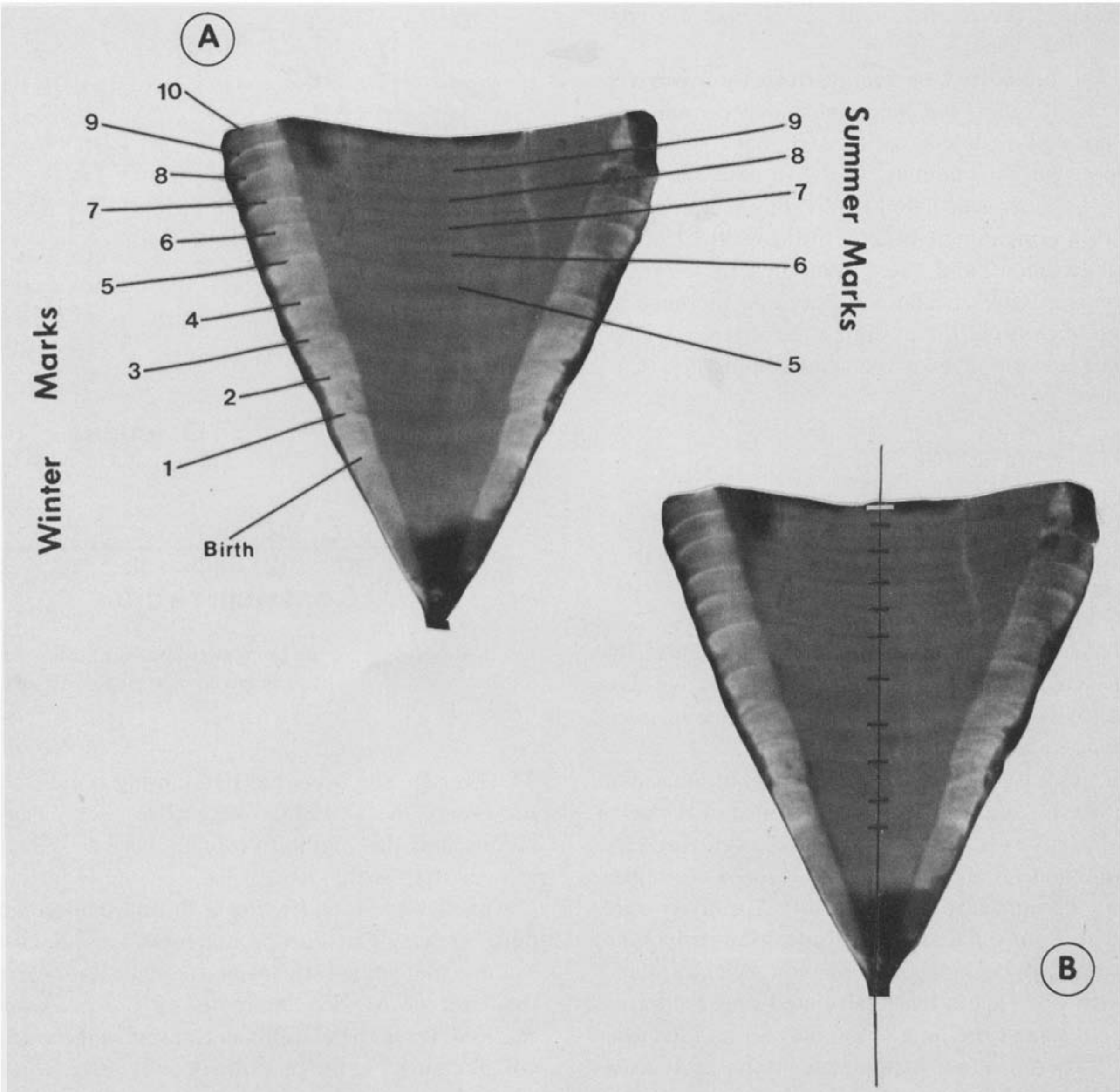

Fig. 1. A) One half of a sagittal section of a centrum from a 171 cm 9.8 yr old *Carcharhinus leucas* showing the marks used to estimate ages. Pre-birth marks discussed in the text were not distinct in this specimen, and did not reproduce in the photograph. Winter annuli corresponded to less calcified bands, summer annuli to calcified bands on the centrum face. The shark was captured in February, and the 10th winter annulus was just off the centrum edge. B) Method of measuring distances from the centrum focus to each annulus. Each measurement is the straight line distance through the center of the intermedialia.

this double marking, annuli were counted twice for each specimen. If agreement was not reached between the two counts, a third count was made. The third count always matched one of the other two reads, and this was the value accepted. Annulus counts were made without knowledge of the length of the specimen. The senior author examined all 59 specimens, the junior author 37, and these counts were compared to test for reader variation. Distances from the focus to the outer edge of each annulus, dorsal radius, and marginal increment were measured on a line from the focus through the center of the intermedialia to the centrum edge (Fig. 1b).

The periodicity of annulus formation was verified with marginal increment analysis, and corroborated with comparisons to back calculated lengths at each annulus. Relative marginal increment widths, calculated by dividing the measured marginal increment distance by the width of the last fully formed band, were compared by month of capture. Back calculations, based on the relationship of centrum radius dimensions to total length, were performed using the Dahl-Lea method (Carlander 1969):

$$TL_i = M_i(TL)/CR$$

where TL_i = total length at mark $i(M_i)$, TL = observed length at capture, and CR = centrum radius. The observed numbers of annuli in sharks of varying lengths were compared to back calculated lengths at annulus formation. Additionally, back calculated lengths were analyzed by age class and by cohort to test for the occurrence of Lee's phenomenon.

Ages are based on annulus counts of the senior author on centrum sections. Because of the relatively small sample size, sexes were combined for mathematical analyses, but both sexes are represented graphically for comparison. Birthdays were set at 1 June based on the late May-early June parturition period (Clark & von Schmidt 1965, Dodrill 1977), but back calculated ages are based on the age at the time of annulus formation (winter). Therefore, for summer caught sharks, there is a difference between the actual age and age at annulus formation (i.e. a shark taken in June aged at 6.0 yr would be 5+ yr old in back calculations). Growth rates were estimated by applying observed data to a computerized von Bertalanffy growth model (Fabens 1965).

Results

Centrum analysis

Centrum radii had an isometric relationship with TL (Fig. 2). The isometric relationship supported the use of the Dahl-Lea method of back calculations, but this method probably best described growth after birth.

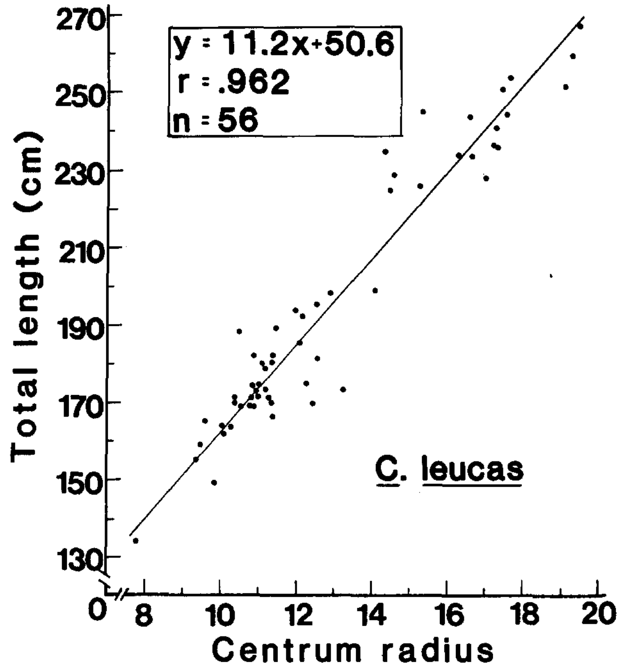

Fig. 2. Relationship of the centrum radii to total length for *Carcharhinus leucas*. Horizontal axis in ocular micrometer units (OMU). 1.0 OMU = 1.2 mm.

Annuli were found to form during embryonic development. The most prominent of these annuli was one that apparently formed at placentation. In the Gulf of Mexico, embryos of *Carcharhinus* sharks develop the placenta in October while some yolk remains, but the placenta does not attach and become functional until November (Branstetter 1981). Back calculated lengths at the formation of this annulus corresponded closely to lengths of embryos at the time of placentation (35–40 cm: Dodrill 1977). In a few centra, a second embryonic mark was discernable, and back calculations agreed in both time and embryo length to this mark being a winter mark homologous to those formed after birth; however this mark was only noted for a few sections, and may therefore be more closely related to maternal than environmental stimuli.

Neonatal sharks possessed only embryonic marks, and an additional annulus which formed at birth. Back calculated lengths at the formation of this annulus corresponded closely with known size at birth, 60–75 cm (Clark & von Schmidt 1965, Dodrill 1977).

Marginal increment analysis (Fig. 3) showed a trend for increasing marginal increment width through the summer months. The annuli appeared to form in late fall or early winter (October-December), becoming visible on the edge of the centrum by January. Therefore, the first growth band, bordered by the birth and first winter annulus, represented approximately six months growth; subsequent bands represented annual growth increments.

Annuli associated with opaque zones of the centrum face were considered to be summer annuli (see Fig. 1A). For the few specimens possessing such marks, it was necessary to properly document each mark as either a winter or summer mark.

Annulus counts by each author were consistent; counts between authors varied. In all but one case, the counts by the senior author were higher. Greater than 50% of the 37 comparative counts matched, or differed by only one annulus. Thirty-one of the 37 differed by three annuli or less. The six remaining counts varied by 4–6 annuli, and these were from very large, old specimens.

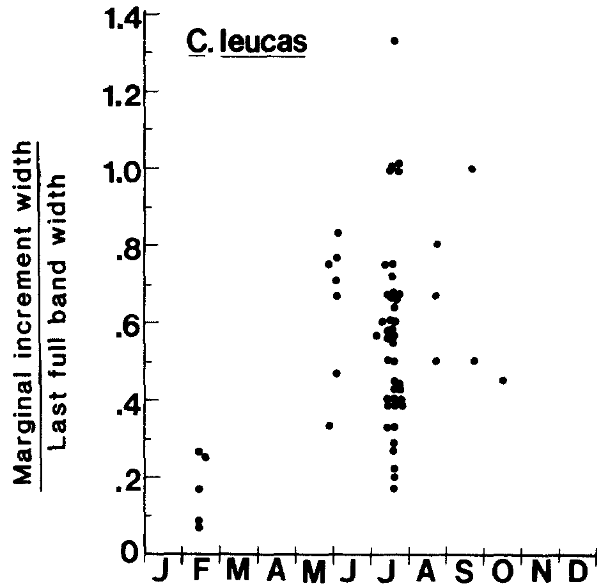

Fig. 3. Relative marginal increment widths compared by month for *Carcharhinus leucas*.

Age and growth estimates

Age at length for individual specimens of *Carcharhinus leucas* varied considerably, and was not sex dependent. Sharks of both sexes of nearly identical lengths varied widely in age. For example, a 168 cm male was 10.1 yr of age, a 169 cm male was 8.8 yr of age, another male at 169 cm was 12.2 yr old, two females at 170 cm were 8.0 yr old, and another at 170 cm was 11.0 yr old. This variation in age at a given length was also apparent in back calculations (Table 1). Back calculated lengths at age were similar for sharks of similar length within an age class. However, back calculated length ranges at age sometimes varied >20 cm.

The lack of small juveniles in the data set required using back calculations to estimate length at age for early age groups. Back calculated data produced much lower length at age estimates than the ages estimated for our few juveniles (Table 1). An 84 cm male (0.2 yr) and a 134 cm female (3.3 yr) were much younger than predicted by back calculations. The underestimate of growth from back calculations was explained by analysis of back calculated lengths by age class (Table 2) which indicated Lee's phenomenon.

Specimens were collected from 1979 through 1985, therefore back calculations were analyzed by cohort to see if the variations were cohort dependent. As with the other analyses, large variations in lengths at age were apparent in each cohort, and were not sex dependent. For example, four females in the 1956 cohort at 23 yr of age varied from 241 to 260 cm.

Because of the small data base and the variable length at age data for both sexes, sexes were combined to derive a von Bertalanffy curve. The observed age/length data were fit to a von Bertalanffy growth model with varying success. A curve derived from all actual data points produced unrealistic parameter estimates (L_∞ = 374 cm; K = 0.040; t_0 = −5.6 yr), similar to estimates presented in Figure 4 for back calculated data. The more realistic values presented in Figure 4 for observed age/

length data were derived by using mean values of a curve hand fit through the upper data points. Even so, the lack of small individuals in the data set resulted in an underestimate of the early growth rate, as with the back calculated data.

Back calculations and the von Bertalanffy curve suggested that growth was approximately 10–15 cm yr^{-1} for the first five years, however the number of annuli present in our juvenile specimens suggested that the growth rate was probably nearer 15–20 cm yr^{-1} for this time period. Growth then gradually decreased to 10 cm yr^{-1}, from 10 to 5 cm yr^{-1} for ages 5–16, and was less than 4–5 cm yr^{-1} thereafter.

The slow growth rate indicated that the bull shark reached maturity at a relatively advanced age. The largest immature male was 212 cm, the smallest mature male was 217 cm. The largest immature male aged (199 cm) was 13.2 yr of age, and the smallest mature male aged (229 cm) was 16.2 yr of age. For females, the largest immature specimens collected (195, 198 cm) were aged at 12.2 yr and 13.2 yr, and the smallest mature females collected (226 cm, 228 cm) were both 18.2 yr of age. All but two females larger than this were mature; these two specimens (241 cm – 23.1 yr of age; 242 cm – not aged) had not carried young, but did have mature ovaries (Branstetter 1981). The largest male (245 cm) was 21.3 yr of age, the largest female (268 cm) was 24.2 yr old.

There were no specimens or weight data for sharks between lengths of 210 and 225 cm; approximately the size at maturity for both sexes (Fig. 5). The two closest specimens by weight were a 194 cm (69 kg) female and a 234 cm (83 kg) individual. The next two closest specimens by weight (195 cm, 229 cm) differed by 31 kg.

Table 1. Length at age for observed and back calculated data for *Carcharhinus leucas*. Lengths are to the nearest cm TL. Values indicate low-mean-high (n) for each age class.

Winter mark	0	I	II	III	IV
Age	0	0+	1+	2+	3+
observed data	84 (1)	NA (0)	NA (0)	134 (1)	NA (0)
back calculated data	54-64-74 (59)	67-78-90 (58)	79-92-107 (58)	94-103-124 (58)	101-115-131 (57)
V	VI	VII	VIII	IX	X
4+	5+	6+	7+	8+	9+
NA (0)	NA (0)	155-159-163 (3)	148-164-171 (6)	163-171-182 (7)	168-174-183 (9)
111-125-134 (57)	121-136-153 (57)	129-144-158 (57)	137-153-167 (54)	143-160-181 (48)	153-167-184 (41)
XI	XII	XIII	XIV	XV	XVI
10+	11+	12+	13+	14+	15+
170-183-194 (6)	169-182-195 (6)	198-199-199 (2)	NA (0)	NA (0)	225-227-229 (2)
162-174-187 (32)	166-181-192 (26)	176-190-199 (20)	191-198-207 (18)	193-206-214 (18)	200-213-224 (18)
XVII	XVIII	XIX	XX	XXI	XXII
16+	17+	18+	19+	20+	21+
NA (0)	226-227-228 (2)	NA (0)	234-235-235 (2)	234-241-245 (3)	236-241-245 (2)
207-219-232 (16)	214-225-239 (16)	217-230-244 (14)	221-235-249 (14)	226-241-256 (12)	230-245-260 (9)
XXIII	XXIV				
22+	23+				
241-253-260 (6)	268 (1)				
238-251-262 (7)	265 (1)				

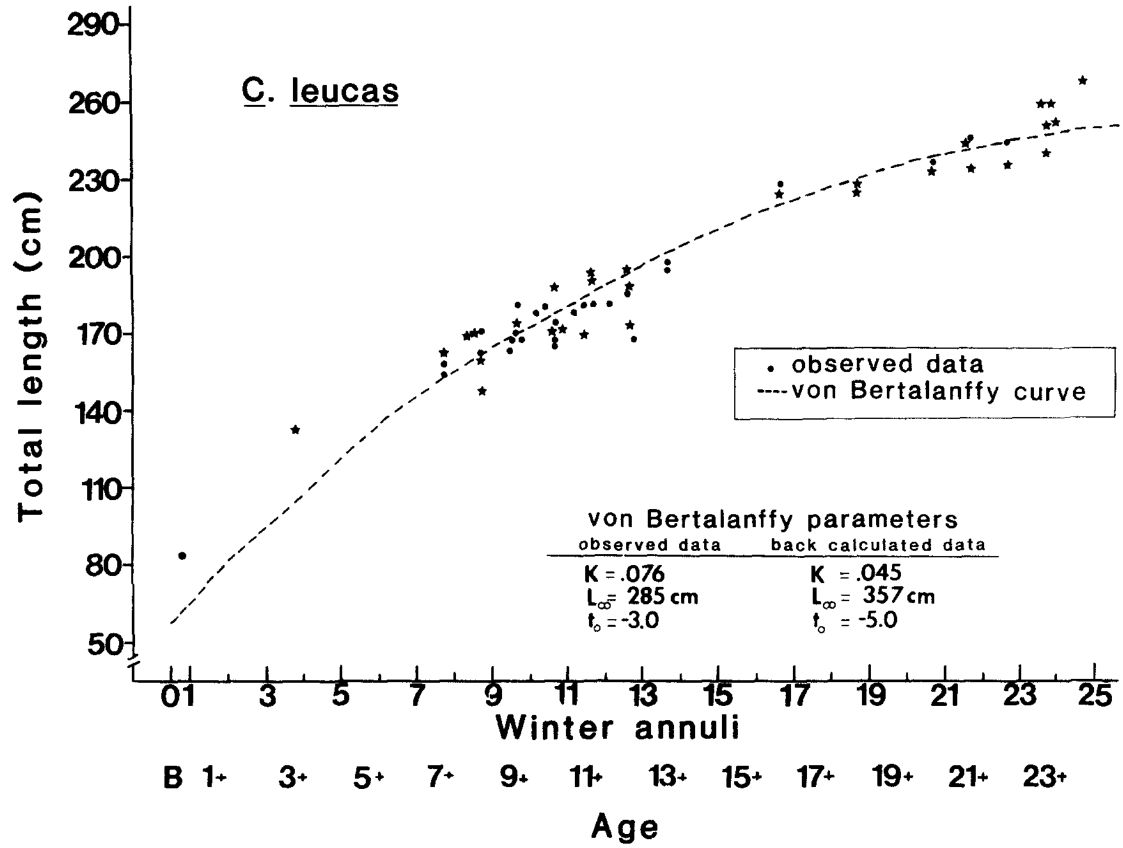

Fig. 4. A von Bertalanffy growth curve calculated from observed age estimates for 59 *Carcharhinus leucas*. Individuals are plotted by the time elapsed since the formation of last winter annulus. B = birth mark. Stars represent females, dots males. Ages in years.

Discussion

Centrum analysis

Because of the slow and variable growth rate exhibited in our data, the differences in annulus counts between readers did not have a great overall effect on the final results. The observed variations in age at length found by a single reader were of similar magnitude as our between reader variations. Between reader differences were attributed to the different examination methods. Cailliet et al. (1983b) also noted difficulties in attaining count agreements between readers and between methods for age analysis on several shark species.

The isometric relationship between centrum growth and length has been noted for lamnids (Pratt & Casey 1983, Cailliet et al. 1985), alopiids (Cailliet & Bedford 1983), carcharhinids (Cailliet et al. 1983a, Gruber & Stout 1983, Branstetter & McEachran 1986), and one sphyrnid (Schwartz 1983a, Branstetter 1987a). The regression (Fig. 2) did not pass through the origin, suggesting the need for a correction factor (Fraser-Lee method), however such a correction factor does not adequately describe the rapid embryonic growth of carcharhinids (Casey et al. 1985, Branstetter 1987c).

Pre-birth marks have been found in centra of other placental species. Casey et al. (1985) noted that these marks formed during embryonic growth of *Carcharhinus plumbeus*. They found that the back calculated length at the time of mark formation corresponded closely with the observed embryo lengths and time of placenta formation and attachment. Branstetter (1987c) presented similar evidence for the formation of pre-birth marks in

Table 2. Back calculated lengths for *Carcharhinus leucas* age classes based on the age at the formation of the winter mark. Lengths expressed to the nearest cm TL.

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+	16+	17+	18+	19+	20+	21+	22+	23+
0–2	0	–	–	–																						
3	1	73	89	108	126																					
4–6	0	–	–	–	–	–	–	–																		
7	3	66	86	100	112	122	133	146	155																	
8	6	67	83	96	110	121	131	141	149	160																
9	7	65	78	90	106	120	131	140	149	160	169															
10	9	66	80	93	106	118	129	140	148	157	165	172														
11	4	63	78	88	99	109	120	131	141	152	159	169	176													
12	6	63	76	92	103	113	123	133	143	151	159	166	173	179												
13	2	63	75	89	101	112	125	135	145	156	167	175	183	190	196											
14–15	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–									
16	2	70	79	90	106	115	123	131	136	145	155	165	171	181	191	200	210	218								
17	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–							
18	2	59	71	85	97	105	116	128	137	145	156	165	177	183	193	200	208	214	220	225						
19–20	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–				
21	3	62	72	88	101	111	121	130	138	149	156	163	171	180	188	200	206	215	221	228	232	236	239			
22	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
23	6	65	80	91	101	111	120	128	138	146	156	164	173	182	190	197	204	212	218	224	230	237	241	245	250	
24	1	58	73	87	97	108	124	142	155	166	169	177	185	191	199	207	214	224	233	239	245	247	256	259	263	266

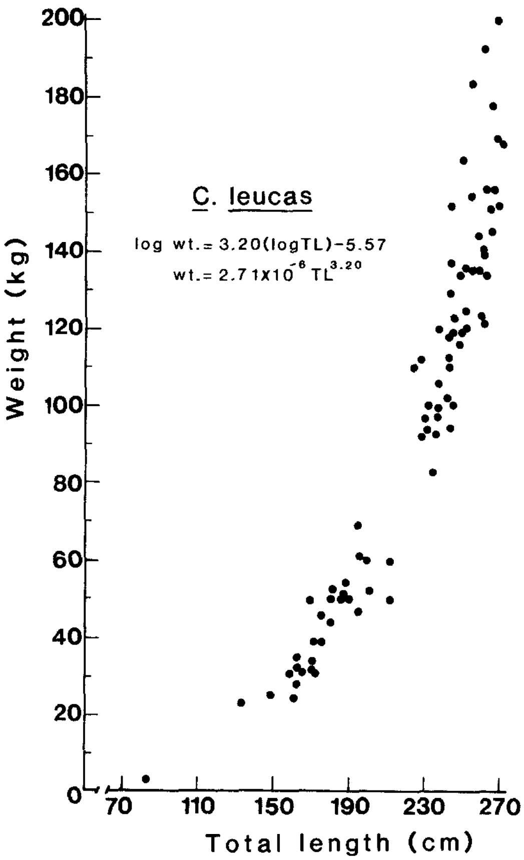

Fig. 5. Weight/length relationship for 80 *Carcharhinus leucas*, sexes combined. Some data points are from recreational tournament winners from 1976–1981, and were not examined by the authors.

C. limbatus and *C. brevipinna*. Correspondingly, Radtke & Cailliet (1984: Fig. 1) noted a slight decrease followed by a sharp increase in calcium and phosphorus levels in *C. amblyrhynchos* centra at approximately mid-term in development, again about the time of placenta formation and attachment. No embryonic marks were noted for the aplacental *Galeocerdo cuvieri* (Branstetter et al. 1987), and Cailliet et al. (1986: Figs. 4–6) did not show a definite rise in calcium or phosphorus concentrations in developing embryonic centra of the aplacental *Alopias vulpinus*. Based on our back calculations we suggested that occasional additional pre-birth marks in *C. leucas* centra might be true winter annuli. Casey et al. (1985) noted the occasional presence of several pre-birth marks in *C. plumbeus* centra, therefore further analysis is needed to better document the stimuli which produce these marks.

Several shark species apparently produce annual post-natal annuli or bands. Several studies have shown that the bands on the centrum face form seasonally: the calcified band in summer and the less calcified band in winter [see Cailliet et al. (1983b) and Cailliet et al. (1986) for a review]. The annuli used in our analyses corresponded to the outer edge of the less calcified band of the centrum face, and marginal increment analysis indicated the annuli formed in winter. A winter formation for post-natal annuli has been verified for several species of *Carcharhinus* (Casey et al. 1985, Branstetter 1987a, 1987c). Annual periodicity of bands and/or annuli has been validated using tetracycline injected *Negaprion brevirostris* (Gruber & Stout 1983) and *Triakis semifasciatus* (Smith 1984) released in the wild, and *Rhizoprionodon terraenovae* and *C. plumbeus* reared in laboratory aquaria (Branstetter 1987b).

Age and growth

Our growth estimates for juvenile *Carcharhinus leucas* was complicated because there is a lack of definitive information on the length at birth. Bigelow & Schroeder (1948) and Dodrill (1977) suggested that most pups were born at 60–75 cm, but Clark & von Schmidt (1965) considered this an underestimate, and agreed with Springer (1960) that pups were born at 75 cm or greater. This latter idea has been corroborated by the summer (June-August) collections of juveniles at this size or greater. Clark & von Schmidt took what they considered to be a neonate (88 cm) in May. Caillouet et al. (1969) gill-netted 38 immature bull sharks from June through August ($\bar{x}$ = 82 cm) and considered them to be neonates. Dodrill (1977) took two juveniles (79, 81 cm) with umbilical scars in July, and a 73.5 cm juvenile in August. Branstetter (1981) collected an 84 cm neonate with an umbilical scar in August. Snelson et al. (1984) took 14 juveniles (73.5–85.8 cm) in June through August and noted most had fresh umbilical scars.

Contradictory to these large free swimming neo-

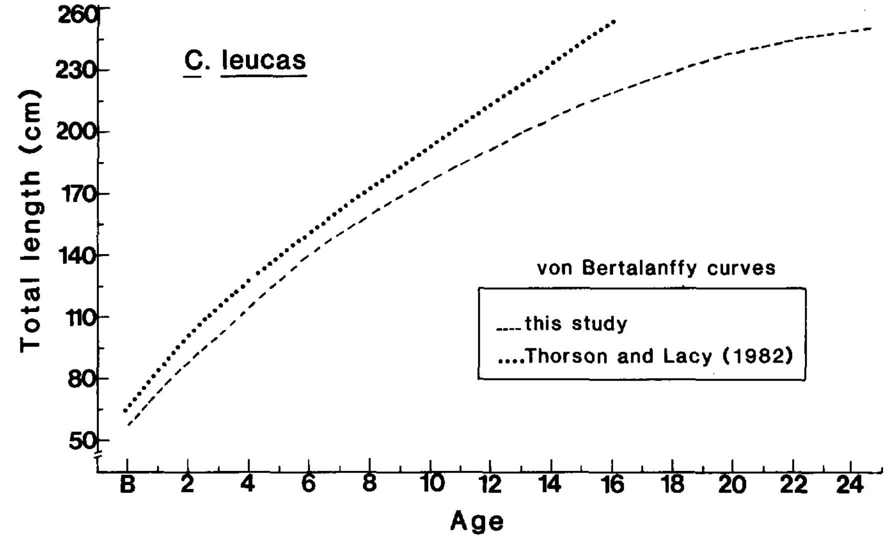

Fig. 6. A comparison of the von Bertalanffy growth curve of this study with a curve derived from data of Thorson & Lacy (1982). B = birth mark. Ages in years.

nates, full-term embryos near parturition are often much smaller. Clark & von Schmidt (1965) examined two full term litters (66–69 cm, 67–74 cm) in May, and Snelson et al. (1984) examined a full term litter (60.8–70.6 cm) in May. The variation in lengths of full term embryos in a single litter prompted Dodrill (1977) to propose that certain pups in a uterus may develop to extraordinary size at the expense of other litter mates. His three smallest full term pups (59.0–63.5 cm) were in the same uterus as the largest embryo (74 cm) in a litter of 10, and his next smallest full term embryo (66 cm) was in the same uterus as the largest embryo he examined (80 cm). If there is a variation in size at birth, standard collecting gear may select for extraordinarily large neonates. More likely, with the variable growth rate, some of the 'neonates' listed above may have been older, more slowly growing specimens. The 88 cm specimen taken by Clark & von Schmidt (1965) in May, the pupping period for bull sharks, would have been extremely large for a newborn, and was probably a slow growing one year old. Several of the specimens examined by Caillouet et al. (1969) may have also been yearlings. The effect of Lee's phenomenon on our data precluded a good estimate of size at birth from our back calculated data, however the broad range of our data supported Dodrill's hypothesis that certain pups develop to an extraordinary size (>75 cm) with others born at 60–75 cm.

Analysis of centra indicated that *Carcharhinus leucas* grows much more slowly than had been predicted by length frequency analyses (Clark & von Schmidt 1965, Caillouet et al. 1969, Sadowsky 1971, Dodrill 1977). The growth rate for juvenile sharks as indicated by centrum analysis in our study and that of Thorson & Lacy (1982) was estimated to be 15–20 cm for the first five years (Table 1). Accordingly, Sadowsky (1971) was probably correct in estimating that 96–109 cm individuals were one year old, and 121–125 cm individuals were two years of age. Dodrill (1977) was also accurate in assessing that 92 and 98 cm specimens taken in April were 11–12 months of age, but he overestimated later growth in that he predicted 132–163 cm sharks were 1.5 yr old, 172–187 cm sharks were 2 yr old, and 197–200 cm sharks were 3 yr old.

Tagging studies of Bass (1977) and Thorson & Lacy (1982) corroborate our growth rate estimates. Bass reported a 93 cm PCL (126.5 cm TL) female grew to 102 cm PCL (137.9 cm TL) in 1.5 yr, and a 169 cm PCL male (222.5 cm TL) grew to only 180 cm PCL (236.4 cm TL) in 7.7 yr. Thorson & Lacy (1982), who used centra analyses coupled with tag returns, presented a growth rate very similar to our data for the Gulf of Mexico population

(Fig. 6). Ages estimated for our two juveniles fit more closely with their age/length data, further corroborating that our back calculations and von Bertalanffy curve underestimated juvenile growth. Their largest specimens were near 200 cm, and 10 yr old or less. They could only extrapolate the last known growth rate (ca. 10 cm yr^{-1}) to the largest known size for their population (260 cm). Our data (Fig. 4, Table 1), indicated that at this age, growth was slowing from 10 cm to 5–7 cm yr^{-1}, therefore Thorson & Lacy's extrapolation probably represented too rapid a growth rate for larger individuals. In addition, their large individuals were all males; slight differences in growth rates for adult males and females in older age classes could account for some of the variation.

Parameter estimates for the von Bertalanffy curve reflected the slow growth rate. The t_0 value (−3.0 yr) overestimated the 11–12 month gestation period (Clark & von Schmidt 1965, Dodrill 1977). This overestimate has been noted for several carcharhinid sharks (Casey et al. 1985, Parsons 1985, Branstetter & McEachran 1986). The K value (0.076) was similar to values derived for *Carcharhinus plumbeus* (Casey et al. 1985) and *Sphyrna lewini* (Branstetter 1987a), but was much lower than values estimated for the more rapidly growing *C. acronotus* (Schwartz 1983b), *C. falciformis* (Branstetter 1987a), *C. limbatus*, and *C. brevipinna* (Branstetter 1987c). Although Compagno (1984) listed the maximum length of *C. leucas* to be near 340 cm, only one specimen (316 cm: Sadowsky 1967) has been reported to exceed 300 cm (see Garrick 1982 for review). In the northwestern Atlantic the largest specimens have been 250–285 cm (Springer 1960, Clark & von Schmidt 1965, Dodrill 1977, this study); in accord with the L_∞ of the von Bertalanffy curve.

There is a general lack of data on specimens corresponding to the approximate length at maturity. Except for a 217 cm male (no weight taken) no sharks were collected between 212 and 226 cm; a similar gap in length (210–225 cm) occurred in the records of other studies on populations with similar life history characteristics. Clark & von Schmidt (1965) collected immature males 166–210 cm, mature males 219–249 cm, immature females 164–200 cm, and mature females 221–264 cm along the Gulf coast of Florida. Bass et al. (1973) took only eight specimens 211–226 cm in over 400 bull sharks examined off the southeast coast of South Africa.

This gap in data in the weight/length relationship could not be defined by time. Most of our specimens were collected in summer, and it was possible that such a length and weight increase occurred during the winter as the specimens matured. However, there was no indication in back calculations that this length increase occurred in one year. According to the age/length data, sharks at this length were growing at 5–7 cm yr^{-1}, therefore, this 10–15 cm increase should have taken at least two years. The gap needs better definition by time.

Conclusions

We encountered several problems because we lacked certain age groups and analysis of vertebrae produced variations in age at length. Additional studies on this species would be beneficial. The availability and abundance of *C. leucas* in coastal and estuarine waters make it an excellent candidate for long-term tag-recapture tetracycline studies similar to those of Gruber & Stout (1983), Smith (1984), and Branstetter (1987b). However, our results for Gulf of Mexico *C. leucas* corresponded with that of Thorson & Lacy (1982) for the Lake Nicaragua-Rio San Juan population, and indicated the growth rate of the bull shark is slow and individually varied. As with many other elasmobranchs, this combination of K-selected characteristics may result in an over-exploitation of this species under increased recreational and commercial fishing pressure (Branstetter et al. 1987).

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