

Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico

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Synopsis

The silky shark, *Carcharhinus falciformis*, and scalloped hammerhead, *Sphyrna lewini*, represent >80% of the shark by-catch of the winter swordfish/tuna longline fishery of the northwestern Gulf of Mexico. This catch represents a potential supplemental fishery, yet little is known of the life histories of the two species. This report relates reproductive biology data to age and growth estimates for 135 *C. falciformis* and 78 *S. lewini*. Unlike other regional populations, *C. falciformis* in the Gulf of Mexico may have a seasonal 12 month gestation period. Males mature at 210–220 cm TL (6–7 yr); females at >225 cm TL (7–9 yr). Application of age at length data for combined sexes produced von Bertalanffy growth model parameter estimates of $L_{\infty} = 291$ cm TL, $K = 0.153$, $t_0 = -2.2$ yr. Adult male *S. lewini* outnumbered adult females in catches because of differences in the distributions of the sexually segregated population. Males mature at 180 cm TL (10 yr); females at 250 cm TL (15 yr). von Bertalanffy parameter estimates for combined sexes of this species were $L_{\infty} = 329$ cm TL, $K = 0.073$, $t_0 = -2.2$ yr.

Introduction

Sharks represent a substantial by-catch of pelagic longline operations (Wathne 1959, Anderson 1985, Witzell 1985). According to Anderson (1985), the combined commercial and recreational catch in the Gulf of Mexico exceeds the estimated maximum-sustainable-yield (MSY) of 9400 tons (Gulf of Mexico Fisheries Management Council 1980). Because of their generally low reproductive rate and direct relationship between stock and recruitment, sharks are extremely susceptible to overfishing (Holden 1974, 1977). A continued increase in shark catches may necessitate the implementation of a management plan for the sustained use of the resource.

At present, development of a management plan is difficult because of a lack of adequate biological

data, especially accurate age and growth information, on the commonly caught sharks. Therefore, in 1981, a study was initiated to better define the biological characteristics of the sharks taken in the recreational and commercial fisheries of the northwestern Gulf of Mexico.

Two cosmopolitan species dominate the shark by-catch of the winter swordfishery in the western Gulf of Mexico – the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*. Despite their common worldwide occurrence little is known of their life histories. Compagno (1984) summarized the available information on the reproductive life history on both species, and when this survey originated, growth information was only available for tag-recaptured neonatal *S. lewini* in Hawaii (Clarke 1971). Re-

cently, juvenile and adolescent growth rates have been estimated for *S. lewini* off North Carolina (Schwartz 1983) and *C. falciformis* from the western Pacific (Yoshimura & Kawasaki 1985).

This survey examined neonates to large adults of both species for reproductive life history and age and growth rates. Integration of these data better indicates the potential of these two species to be a viable fishery resource under the presently increasing fishing pressure.

Methods and materials

Sharks were examined aboard commercial vessels targeting swordfish or tuna along the edge of the continental shelf from the mouth of the Mississippi River to Brownsville, Texas in 1982–1985. In all, 135 *Carcharhinus falciformis* and 44 *Sphyrna lewini* were examined or tagged. An additional 34 specimens of *S. lewini* collected from 1978–1981 in the north central Gulf of Mexico (Branstetter 1981) were used for morphometric analyses, weight relationships, and reproductive information.

Measurements were taken on a straight line between perpendiculars with the caudal fin in a natural position (Branstetter 1986). Total lengths (TL) are used throughout this report. For comparisons with published studies that reported lengths as fork length (FL), a TL was calculated for *C. falciformis* as $TL = 1.20(FL) - 1.16$ ($n = 108$, $r = 0.997$), and for *S. lewini* as $TL = 1.31(FL) - 0.64$ ($n = 55$, $r = 0.997$).

Weights were taken with spring scales and scale accuracies were tested before each sampling trip. If motion of the boat caused reading variations, the minimum and maximum readings were averaged.

Reproductive development and maturity determinations follow definitions of Springer (1960), Clark & von Schmidt (1965), and Branstetter (1981). Males were considered mature only if the claspers and siphon sacs were fully developed; sperm is produced before the claspers are fully calcified. Females were classified as virgin if the hymen covering the distal end of the uteri was intact. Virginity, or lack of it, is not a criterion for maturity. Maturity in females is indicated by de-

veloping or ripe eggs in the ovary, eggs or embryos in the uterus, or expanded uteri that have carried young before.

For age and growth analyses vertebrae were removed from 100 *Carcharhinus falciformis* and 25 *Sphyrna lewini*. Centra were sampled from the cervical region dorsal to the branchial chamber, and stored frozen. Opaque (calcified) and translucent (less calcified) bands (Radtke & Cailliet 1984) are found on the centra faces, however, more accurate counts of these bands can be achieved by examining sections cut from the centra (Branstetter & McEachran 1986). Following techniques detailed in Branstetter & McEachran (1986) and Branstetter (1986), sagittal sections were cut from the center of representative centra, 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.

Within a section, distinct marks (annuli), as illustrated in Casey et al. (1985: fig. 1) and Branstetter (1986: fig. 3), were found to traverse the intermedialia of a centrum. These annuli corresponded to translucent areas in the corpus calcareum and to the outer edges of the translucent bands on the centrum face. Annulus counts were performed twice; if they differed, a third count was made. The distance from the centrum focus to the outer edge of each annulus, marginal increment, and dorsal radius were measured on a line through the center of the intermedialia. To verify the periodicity of annulus formation, absolute marginal increment distance was compared by month for each species. Growth rates based on observed number of annuli in sharks of different lengths were compared to back calculated lengths at previous ages. Back calculations were performed using simple ratios (Dahl-Lea method):

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

where TL_i = total length at mark i (M_i), TL = length at capture, and CR = centrum radius.

Many Gulf of Mexico carcharhinids and sphyrnids have a two to three week parturition period in late spring (May–June) (Branstetter 1981, Parsons

1983), so for simplicity, a 1 June birthday was used for calculating actual ages. Ages for back calculated data are based on the age at the formation of what was shown to be winter formed annuli, therefore for summer caught sharks the back calculated age and the observed age are different (i.e. a shark taken in June that was estimated to be 6.0 yr of age would only have been 5+ yr of age in back calculations). Back calculations were compared by age class to test for the occurrence of Lee's Phenomenon. Growth rates were estimated with a computerized von Bertalanffy growth model (Fabens 1965) using observed age/length data.

Results

Carcharhinus falciformis

The silky shark was very abundant in the continental shelf edge waters of northwestern Gulf of Mexico from the 140–225 m contours, and comprised 63% of the shark by-catch on swordfish longlines (Branstetter 1986). This gear was not designed to retain sharks, and many larger individuals probably escaped. The majority boarded were immature sharks. Overall, 55 males, 64 females, and 16 of undetermined sex were examined.

The six adult sharks collected provided insights into the poorly described reproductive cycle of this species. Two males (256, 257 cm) collected in March were ripening with small amounts of sperm in the seminal vesicles, and the third male (267 cm) taken in late April was ripe. A 232 cm female collected in March contained one male (46.6 cm) and three female (54.2–57.0 cm) embryos in one uterus; the pups in the other uterus apparently had aborted while the shark was on the longline. Two litters of 13 pups were examined in April: a 233 cm female carried 10 male (53.3–64.3 cm) and three female (59.0–63.3 cm) embryos, and a 267 cm female carried five male (56.4–59.4 cm) and eight female (56.6–60.3 cm) embryos. In May 1981, prior to this study, several full term litters (~70 cm) were noted in catches of silky sharks (J. McEachran, personal communication). The three near-term pregnant females did not have developing ovarian eggs.

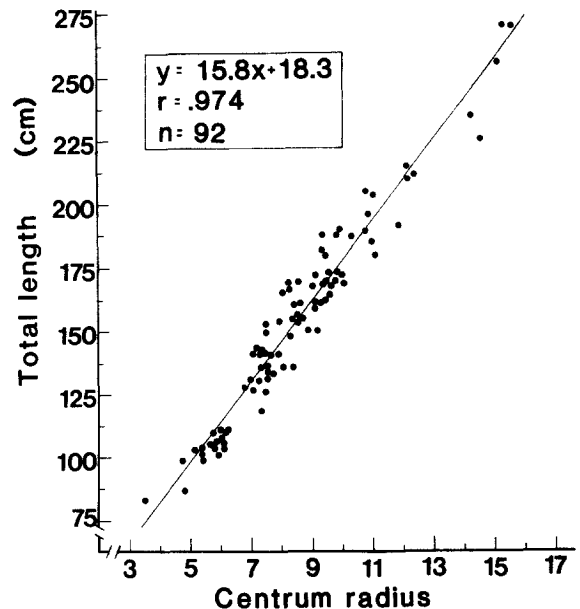


Fig. 1. Relationship of centrum radii to total length for *Carcharhinus falciformis*. Centrum radii measurements in ocular micrometer units (OMU). 1.0 OMU = 1.2 mm.

Centrum sections were examined from neonates to large adults (82–267 cm). Annulus counts between the two reads agreed for almost all specimens. The few counts that did not agree differed \pm one annulus. A third count for these individuals matched one of the first two, and this was the count accepted.

Centrum radii had an isometric relationship with lengths of the sharks (Fig. 1). Although the regression did not pass through the origin, the use of a correction factor (Fraser-Lee method) did not adequately describe the rapid embryonic growth (Casey et al. 1985, Branstetter 1986). Therefore, the Dahl-Lea method of back calculation best described growth after birth.

Marginal increment widths compared by month for all specimens except first summer neonates (Fig. 2) indicated the annuli formed late in the calendar year (October–December), became visible on the centrum edge by January, and were farthest from the centrum edge in summer. The relatively broad scatter for any given month was caused by younger, more rapidly growing sharks having wider marginal increments than older, more slowly growing sharks.

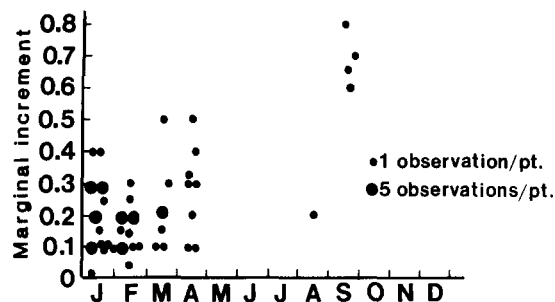


Fig. 2. Absolute marginal increments of 100 *Carcharhinus falciformis* compared by month. Vertical axis is in ocular micrometer units (OMU). 1.0 OMU = 1.2 mm.

The first annulus formed at or near birth. Embryonic sharks had no annuli, and neonatal sharks had only one annulus. Back calculated lengths at this first annulus for all specimens corresponded closely with the known length at birth. Therefore, based on a late spring parturition period, the band bordered by the birth and the first winter annulus

represented approximately six months growth; remaining bands represented annual growth rates.

Observed numbers of annuli for sharks of various lengths and back calculated lengths at annuli were similar between males and females. Back calculations by age class did not reveal the occurrence of Lee's phenomenon, therefore all specimens of both sexes were combined for growth analysis. All but seven specimens were collected from January through April, and observed mean lengths for each age class corresponded closely with back calculated mean lengths at the winter annuli (Table 1), except for the two neonates (82, 84 cm) taken in late summer. Growth through the first winter was approximately 30 cm, but reduced to approximately 20 cm yr⁻¹ between the formation of annuli II-IV, decreased from 15 to 10 cm yr⁻¹ for annuli V-X, and 10-5 cm yr⁻¹ after maturity.

Age classes and growth rates estimated by centrum analysis were supported by a length frequency

Table 1. Length at age for observed and back calculated data for *Carcharhinus falciformis* and *Sphyrna lewini*. Lengths given are the low-mean-high values for each age class to the nearest cm TL. Number of specimens in parentheses.

Winter annulus age	0 0	I 0+	II 1+	III 2+	IV 3+	
<i>Carcharhinus faliformis</i>						
observed data	82-83-84 (2)	86-104-111 (19)	110-133-141 (15)	130-150-167 (18)	155-168-187 (20)	
back calculated data	55-73-85 (100)	81-101-118 (98)	108-127-140 (79)	122-147-166 (64)	147-165-181 (46)	
<i>Sphyrna lewini</i>						
observed data	48-49-49 (2)	NA (0)	NA (0)	107-110-115 (3)	NA (0)	
back calculated data	46-50-60 (24)	61-72-83 (22)	84-93-105 (22)	103-110-116 (22)	114-123-133 (19)	
V 4+	VI 5+	VII 6+	VIII 7+	IX 8+	X 9+	
167-185-195 (9)	190-198-211 (8)	214 (1)	NA (0)	NA (0)	225-230-233 (3)	
163-181-197 (26)	184-194-205 (26)	180-207-221 (9)	195-218-231 (7)	205-228-240 (7)	217-235-247 (7)	
124-127-130 (3)	140-144-147 (2)	155 (1)	161-166-170 (3)	NA (0)	181-187-195 (3)	
122-133-142 (19)	138-145-154 (16)	147-155-164 (14)	156-163-174 (13)	170-174-186 (10)	176-184-195 (10)	
XI 10+	XII 11+	XIII 12+	XIV 13+	XV 14+	XVI 15+	XVII 16+
256-257-257 (2)	NA (0)	267 (1)	267 (1)			
250-252-254 (4)	257-258-260 (2)	263-264-265 (2)	265 (1)			
185 (1)	202-208-213 (2)	221 (1)	240 (1)	236 (1)	NA (0)	249 (1)
183-193-202 (7)	200-206-214 (6)	212-219-231 (4)	223-230-237 (3)	234-235-235 (2)	244 (1)	248 (1)

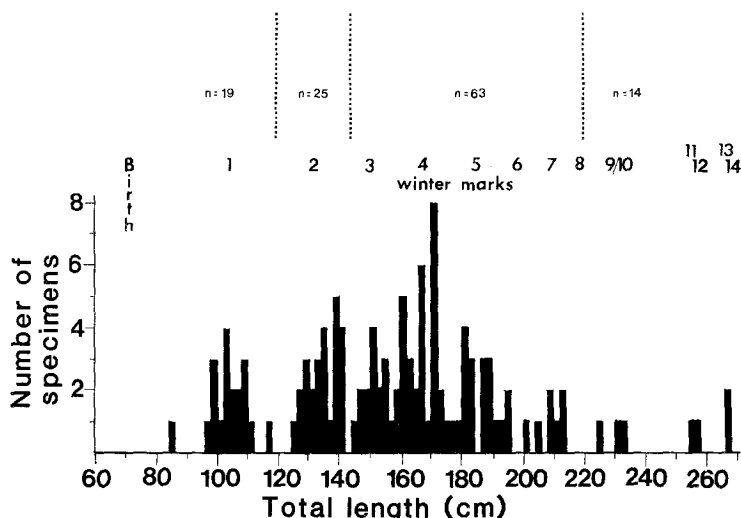


Fig. 3. Length frequency distribution of *Carcharhinus falciformis* taken on pelagic swordfish/tuna longlines in the northwestern Gulf of Mexico. Length frequency corresponded with back calculated lengths at the formation of winter annuli in centra for early age classes, but became less distinct for older, more slowly growing age classes.

distribution of the catch (Fig. 3). Although the catch probably did not accurately reflect the population structure because of the gear bias, peaks in the length frequency distribution matched closely with lengths at age estimated from centra.

Based on the comparative widths of the centrum bands formed in 1980 and 1981 slow growth occurred in 1980 for 10 individuals. Assuming that growth slows with age, the band width for 1980 should have been greater than that for 1981; however, the 1980 band in these individuals was distinctly smaller than the 1981 band. According to back calculated lengths at the time of annulus formation these individuals grew less in 1980 and were smaller than the mean length of their respective age classes. Additionally, back calculations indicated that five of the ten sharks examined from the 1980 cohort were born at <70 cm. This is less than the normal size at birth, and was a greater percentage of small newborns than for other cohorts.

Males mature at 210–220 cm which corresponded to an estimated age of six or seven years. The largest immature male (211 cm) was 5.8 yr of age. No small mature males were collected. The smallest mature male (256 cm) was 10.9 yr of age, and the largest mature male (267 cm) was 12.8 yr old.

Females mature at >225 cm, corresponding to

approximately nine years of age. Two 214 cm virgin females (6.6, 6.6 yr) collected in February had small developing (7–10 mm) ovarian eggs. The largest immature female (225 cm) and smallest gravid female (232 cm) were both 9.8 yr of age. The largest female (267 cm) was 13.8 yr old.

Because growth rates between the sexes appeared to be similar, length at age data for the two sexes were combined to derive the von Bertalanffy curve (Fig. 4). The curve fits known life history characteristics, except that the t_0 value was much greater than the estimated 12 gestation period. Length at birth estimated by the curve was 72 cm. No specimens were examined that were as large as the estimated L_∞ , but the L_∞ was intermediate between the largest reported male (272 cm) and female (305 cm) collected in the northwestern Atlantic (Springer 1960).

The distinct weight/length relationship (Fig. 5) for this species was inversely related to linear growth. Weights did not substantially increase until the linear growth rates declined.

Of 114 stomachs examined, 110 were empty or contained only unidentified squid beaks. Stomachs of three specimens contained tuna (*Thunnus* or *Euthynnus*), mackerel (*Scomber*), mullet (*Mugil*), and unidentified fish and squid; the

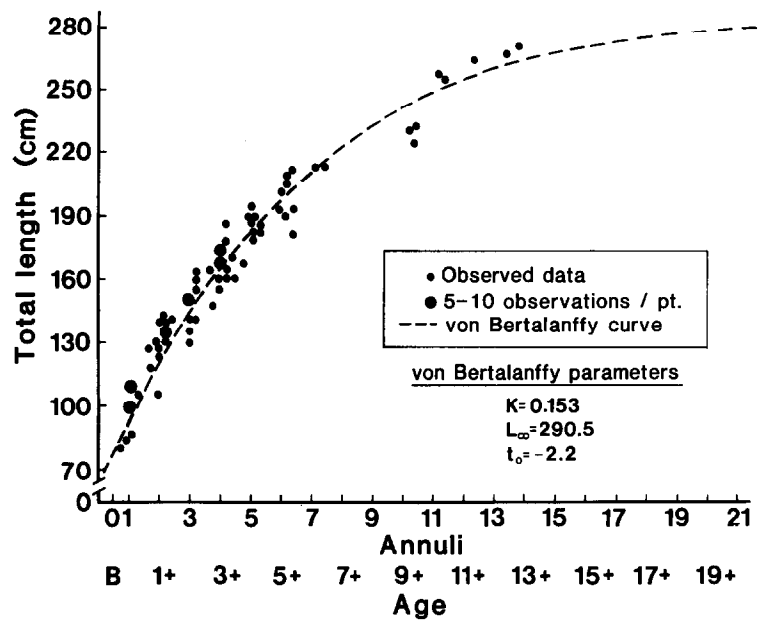


Fig. 4. A von Bertalanffy growth curve for *Carcharhinus falciformis*; sexes combined. Individuals are plotted by their estimated actual age (time elapsed since the formation of the outer-most winter annulus).

fourth specimen, taken on a demersal snapper longline, contained an unidentified ophichthid eel.

Sphyrna lewini

The scalloped hammerhead frequents both coastal and pelagic waters of the Gulf of Mexico (Branstet-

ter 1981). It was the second most common shark taken on swordfish longlines, and comprised 18% of the shark by-catch. Females outnumbered males 27 to 16, but only one mature (non-gravid) female was caught versus 11 mature males.

Centra were examined from neonates to adults (48–249 cm), but no exceptionally large individuals

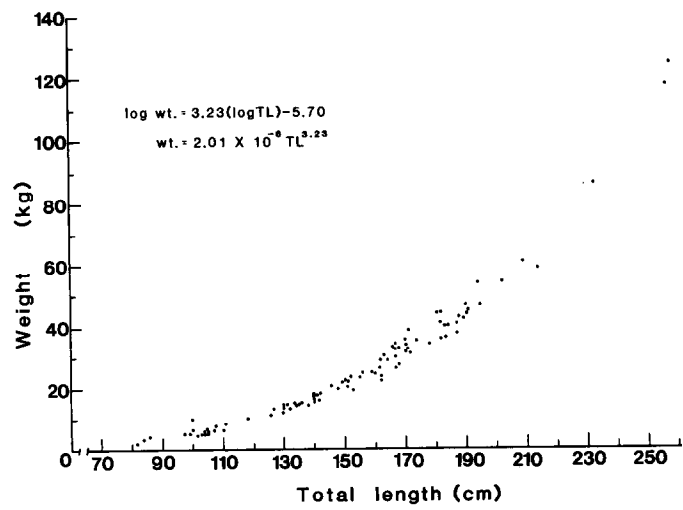


Fig. 5. Weight-length relationship for *Carcharhinus falciformis*; sexes combined.

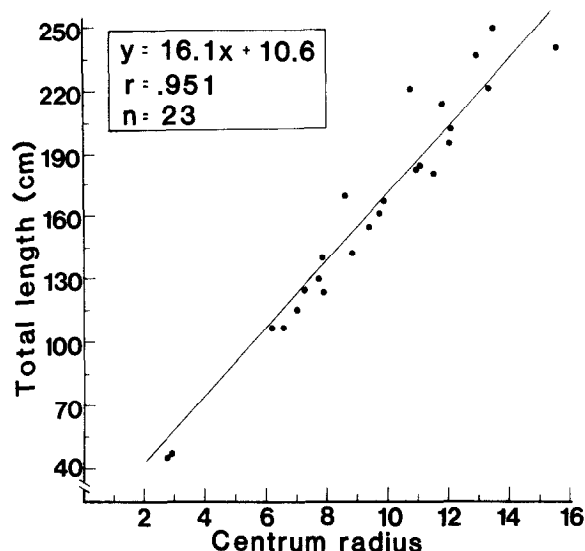


Fig. 6. Relationship of centrum radii to total length for *Sphyrna lewini*. Centrum radii measurements in ocular micrometer units (OMU). 1.0 OMU = 1.2 mm.

were collected. Annulus counts between the two reads agreed for all specimens. Back calculations were based on the isometric relationship between centrum radii and lengths of the sharks (Fig. 6). As with the silky shark, the regression did not pass through the origin, but a correction factor did not adequately describe the rapid embryonic growth.

Annulus periodicity was the same as for the silky shark. The two neonatal scalloped hammerheads had only one annulus, and back calculations of lengths at this annulus for all specimens indicated it formed at or near birth. All but two specimens were collected from January through March, which hindered marginal increment analysis (Fig. 7). All specimens collected in winter had the less calcified translucent band on or near the centrum edge, and the two specimens collected in July and August had the calcified opaque band forming along the centrum edge. Although indistinct, the trend for increasing marginal increment width through the summer suggested an annual formation of annuli.

Only four males were aged, and all four had similar numbers of annuli compared to similarly sized females. Additionally, back calculated lengths at previous ages for both sexes were similar, and analysis by age class did not indicate Lee's phenomenon. Therefore, because of the small

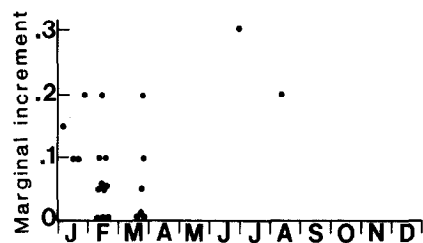


Fig. 7. Absolute marginal increments of 22 *Sphyrna lewini* compared by month. Vertical axis is in ocular micrometer units (OMU). 1.0 OMU = 1.2 mm.

sample size, all specimens were combined for analysis. Observed numbers of annuli at length compared closely with back calculations (Table 1). Growth from birth through the first winter was approximately 15 cm, and became 15–20 cm yr⁻¹ for the next two years. Growth rates then reduced from 15 to 10 cm yr⁻¹ for winter annuli III–V, and continued to decline from 10–12 cm yr⁻¹ to 5–7 cm yr⁻¹ for annuli VI–XVII.

My data indicated that females mature at approximately 250 cm or about 15 yr of age, males at approximately 180 cm or 9–10 yr of age. Two immature females (236, 240 cm) were 14.8 and 13.6 yr old. A 248 cm immature female was not aged, but a non-gravid 249 cm female (16.8 yr) had carried young before. No large immature males were aged, but the largest collected was 173 cm. The smallest mature male (195 cm) was 9.8 yr old, and the largest (213 cm) was 11.6 yr old.

The von Bertalanffy curve using data for both sexes combined (Fig. 8) fit known life history characteristics. As with the silky shark, the gestation period of the scalloped hammerhead is poorly known, but is assumed to be approximately 12 months. Therefore the t_0 value probably underestimated the rapid embryonic development. Size at birth estimated by the curve was 49 cm. The L_∞ is slightly larger than the largest reported specimen of 309 cm (Clarke 1971).

The weight-length relationship for immature individuals was distinct, but the relationship for mature individuals, especially males, varied considerably (Fig. 9). As with the silky shark, linear growth rate was inversely related to weight gain.

Stomachs of 49 specimens were empty; 10 con-

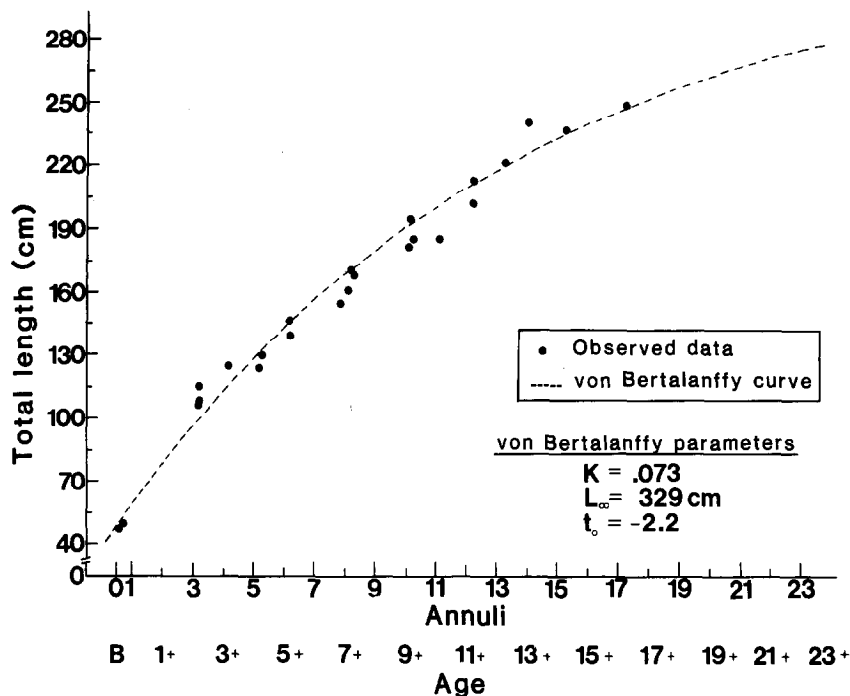


Fig. 8. A von Bertalanffy growth curve for *Sphyrna lewini*; sexes combined. Individuals are plotted by their estimated actual age (time elapsed since the formation of the outer-most winter annulus).

tained a variety of pelagic and demersal fishes (*Selar*, *Mugil*, *Cynoscion*, *Calamus*, unidentifiable ophichthid eels) and squid (*Loligo pealii*, and unidentified squid beaks).

Discussion

Annulus periodicity

The annual periodicity of centrum annulus formation was hindered by the winter collection of most specimens. However, all specimens collected in winter had the less calcified translucent zone on the centrum edge, and the few summer collections had the calcified opaque zone on the centrum edge. Radtke & Cailliet (1984) found similar periodic calcium and phosphorus fluctuations in *Carcharhinus amblyrhynchos*. Through use of marginal increment analysis and back calculations an annual periodicity to annuli has been verified for several carcharhinid species (Casey et al. 1985, Branstetter & McEachran 1986, Cailliet et al. 1986, Branstetter 1987a). Annual periodicity has additionally been validated using tetracycline injected *Rhizoprionodon terraenovae* and *Carcharhinus plumbeus* held in laboratory aquaria (Branstetter 1987b), and *Negaprion brevirostris* (Gruber & Stout 1983) and *Triakis semifasciatus* (Smith 1984) released in the wild.

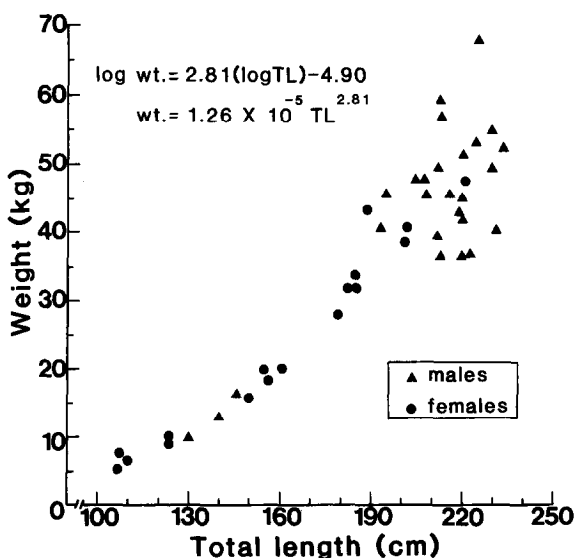


Fig. 9. Weight-length relationship for *Sphyrna lewini*; sexes combined.

Back calculations do not truly verify periodicity (Smith 1983), but can verify growth rates estimated from observed numbers of annuli in sharks of various lengths. In the case of these two species, the two methods matched closely. Similar results were attained in studies on lamnids (Pratt & Casey 1983, Cailliet et al. 1985), carcharhinids (Casey et al. 1985, Branstetter 1987a), and sphyrnids (Schwartz 1983).

Carcharhinus falciformis

Carcharhinus falciformis populations in different oceans have similar life history characteristics with females maturing at slightly larger lengths than males. For the western North Atlantic, Springer (1960) listed 12 mature males 218–272 cm, and 34 mature females 235–305 cm. In the eastern Atlantic, Cadenat & Blache (1981) noted males <215 cm were immature, all males >220 cm were mature, and their mature females were all >250 cm. At Aldabra Atoll, north of Madagascar, Stevens (1984a) listed males >214 cm as mature, a virgin 202 cm female as mature, and two at 208 cm as gravid. Off New South Wales, Australia, Stevens (1984b) examined a 208 cm immature male, a 216 cm mature virgin female, and two 220 cm mature females. In the western central Pacific, Strasburg (1958) collected immature females 186–218 cm, and gravid females at 213–232 cm. My data suggested that in the Gulf of Mexico males mature at 215–220 cm similar to other populations, but this record and that of Springer (1960), suggests females in the northwestern Atlantic mature at slightly larger lengths than other populations (>225 versus 210–220 cm).

In contrast to the reports that the silky shark does not have a seasonal gestation period (Strasburg 1958, Bane 1966, Bass et al. 1973), the population in the Gulf of Mexico may have a definable 12 month gestation period. Three litters examined in March and April were near-term, and several full term litters have been observed in May suggesting a parturition period in late spring (May–June). The ripening males taken in March and near ripe male taken in April suggest the occurrence of a late spring (May–June) mating period. The lack of de-

veloping ova in the near-term females suggests a non-gravid year in reproductive cycle, typical of many carcharhinids (Branstetter 1981). The entire cycle is probably two years.

More refined data are needed to adequately define the reproductive cycle of this common pelagic shark. As with most adult carcharhinids, the silky shark segregates by sex (Strasburg 1958), therefore mating may only occur during a short period when the two sexes come together. For populations which apparently have no seasonal gestation period the females must either store sperm for some period of time following a contracted mating season (Pratt 1980), or different portions of the male population ripen throughout the year and are in close association with the females.

The pups are born at approximately 75 cm (Springer 1960). This agreed with the length at birth estimated by the von Bertalanffy curve (72 cm), and back calculations ($\bar{x} = 73$ cm), although back calculated length at birth varied considerably (55–85 cm). Centrum analysis supported the assumption that birth occurred well in advance of the first winter annulus formation. For most specimens the distance between the birth and first winter annulus represented a mean length increase of 28 cm. This was supported by the catch of 16 neonates (98–111 cm) in January that still had faintly discernable umbilical scars. However, back calculations for 12 specimens indicated growth from birth to the first annulus formation was <20 cm, which suggested either these sharks had slow post-natal growth or were born later in the summer. This would help explain the wide variation in length ranges for early age classes. If there is a protracted parturition period, the arbitrary birth date of 1 June used to estimate ages is not particularly accurate.

The small size at birth for *Carcharhinus falciformis* makes the pups vulnerable to predation from the large pelagic sharks of the continental shelf edge. Their rapid increase in length would increase swimming efficiency and speed (Thompson & Simanek 1977) thus improving survival chances. The neonates may spend the first few months of life associated with snapper reef areas on the outer continental shelf (Springer 1967), but they move to

a pelagic existence by the first winter. This was indicated by the capture of several first winter juveniles on pelagic longlines during this study and a study by Branstetter (1981). Similar rapid neonatal growth occurs in two coastal species, *C. limbatus*, and *C. brevipinna* (Branstetter 1987a), that use the shallow beach areas as nursery grounds, thus exposing the young to predation from the abundant coastal sharks. The young of two slow growing coastal sharks, *C. plumbeus* (Casey et al. 1985) and *C. leucas* (Thorson & Lacy 1982, Branstetter 1986) remain in relatively protected estuarine nursery areas until they are near 100 cm in length. A third slow growing species, *C. obscurus* (Schwartz 1983) occupies a similar range ecologically with *C. falciformis*, but its young are born at relatively large sizes (75–90 cm).

Small numbers of juvenile *C. falciformis* have been aged off North Carolina (Schwartz 1983) and in the western Pacific Ocean (Yoshimura & Kawasaki 1985). Both of these studies used the same criteria as I did to define annual zones on the centrum faces, but they did not use sections for analysis. Schwartz (1983) listed a 125 cm male and female each with five annual bands, a much slower growth rate than estimated by my data. According to Yoshimura & Kawasaki (1985) juvenile silky sharks associated with flotsam in the southwestern Pacific grow at only a slightly slower growth rate than my estimates through the formation of the first four bands. The differences in their data and mine may be caused, in part, by the lack of a seasonal gestation period for the silky shark in the Pacific Ocean (Strasburg 1958, Stevens 1984b). However, their two sharks with VI bands (~120, ~140 cm) were smaller than sharks with only IV bands, and were much smaller than the smallest shark I examined with VI winter annuli (190 cm). These two sharks may have been more slowly growing individuals that were schooling with sharks of like size.

In the northwestern Atlantic males reach a maximum length near 275 cm (Springer 1960). The largest male aged in this study (267 cm) was 12.8 yr old. The growth rate at this size was approximately 5 cm yr⁻¹, therefore, this shark may have been within one to two years of reaching its maximum

size. Males apparently reach maturity at approximately 75% of their maximum length.

No extremely large females were examined, but they are thought to reach lengths in excess of 325 cm (Garrick et al. 1964). Although the L_{∞} from the von Bertalanffy curve (Fig. 4) is a good compromise between the largest male (272 cm) and female (305 cm) reported from the northwestern Atlantic (Springer 1960), it is too low for females. Substitution of an L_{∞} of 325 cm into the formula produced a lower K value (0.11), but changed the growth rate estimated here very little. Based on a maximum length range of 305–325 cm, females mature at 70–75% of their maximum length.

An extrapolation of annual growth rates for large adults of either sex to estimate longevity may not be valid. As the sharks near their maximum length or weight, centrum development, and the corresponding band structure, may not accurately represent time. Further examination of extraordinarily large specimens is needed to verify longevity.

Sphyrna lewini

Males have outnumbered females in published catch records (Clark & von Schmidt 1965, Clarke 1971, Wallett 1973, Bass et al. 1975, Dodrill 1977, Branstetter 1981) therefore reproductive life history information for the scalloped hammerhead is sketchy. Although Bass et al. (1975) captured mature males at 145–165 cm off South Africa, most published records suggest that males mature at approximately 180 cm (Clark & von Schmidt 1965, Dodrill 1977, Cadenat & Blache 1981, this study).

Accurate information on size at maturity for females is lacking; specimens collected were either nearing maturity or were extremely large (~300 cm). Dodrill (1977) listed a 182 cm female as immature and a 221 cm female as probably mature, but the specimen was not examined internally. A 204 cm female (Branstetter 1981) and a 212 cm female (Bass et al. 1975) were both virgins with mature reproductive tracts. This latter record was probably the basis for Compagno's (1984) listing of 212 cm as the length at maturity. However, the smallest fully mature female on record has been 250 cm (Stevens 1984a).

Data I collected agreed more closely with that of Stevens (1984a), suggesting that females must mature near 250 cm, much larger than the males. A non-virgin 236 cm female and a virgin 248 cm female were immature, but a 249 cm mature female had carried young previously.

The lack of data on females may be because they are associated more with oceanic waters than shelf waters where most surveys have occurred. Clarke (1971) thought females only moved into coastal waters of Hawaii to pup and breed, moving offshore again quickly. Offshore aggregations of *S. lewini* around sea mounts in the Gulf of California are dominated by females (Klimley 1981). Collections I made were near the continental shelf edge and females outnumbered males 27 to 16. However, all but one female were immature which suggests adult females may inhabit regions farther offshore.

Back calculated size at birth (45–60 cm; \bar{x} = 50.3 cm), and the size at birth estimated by the von Bertalanffy curve (49 cm) agreed with previous reports of full term embryos and free swimming young. The smallest free swimming young are 38.2 cm from the northwestern Atlantic (Dodrill 1977), 43.2 cm from the southwestern Atlantic (Sadovsky 1965), 39.5 cm from Hawaii (Clarke 1971), and 45 cm from South Africa (Bass et al. 1975). These small free swimming young may have been runts; most full term litters are 40–50 cm, and the average size of neonates is >50 cm (Sadovsky 1965, Clarke 1971, Dodrill 1977). Scalloped hammerheads have large litters (>30 pups), therefore a variation in size at birth may occur if some develop at the expense of other litter mates.

My growth data corresponded closely with two other age and growth reports for the scalloped hammerhead. Clarke (1971) reported that tagged neonates released in the wild grew 1.1 cm in 33 days, 3.7 cm in 56 days, 6.0 cm in 78 days, and that 10 pond reared specimens grew 5.9–17.7 cm (\bar{x} = 10.9) in 92–100 days. Schwartz (1983), who counted bands on the centrum faces from 21 male and 14 female juveniles and subadults (one 204 cm male was mature), estimated that the sharks grew 10–15 cm yr⁻¹ for the first five years. My analyses indicated that growth through the first winter was

approximately 15 cm, and an annual growth rate of 10–15 cm continued for the next few years. Schwartz (1983) estimated that growth from the fifth through the eighth year (his oldest specimen) gradually decreased from 10 to 5 cm yr⁻¹. His largest female, 144 cm, was five yr old, and I aged two specimens at this size (140, 147 cm) to be 5.8 yr old. However, his largest male (204 cm) was aged at 8 yr, whereas a 202 cm female and a 213 cm male from my study were 11.8 yr old. Growth rates at this length (see Table 1) are approximately 10 cm yr⁻¹ corresponding to <1 mm growth in the centrum radius, and without looking at centrum sections, Schwartz may have missed some of the narrow outer bands.

Although a mean length at age could be estimated for the species, individual variations in growth resulted in sharks of similar length being different ages. Back calculations suggested that the smallest mature male (195 cm, 9.8 yr) had grown rapidly compared to other specimens, especially during its fifth and six years. The mean growth rate for age V and VI was approximately 10 cm yr⁻¹ (Table 1), but back calculations showed that this shark increased from 136 to 150 cm between annuli V (4+ yr) and VI (5+ yr), and from 150 to 164 cm between annuli VI and VII (6+ yr). A 236 cm female had grown more slowly and was a year older than a 240 cm female.

The L_{∞} estimated by the von Bertalanffy curve (329 cm) is only slightly greater than the largest reported specimens in three populations: 272 cm male, 309 cm female in Hawaii (Clarke 1971); 295 cm male, 307 cm female off South Africa (Bass et al. 1975); 300 cm male and female in the Gulf of Mexico (Branstetter 1981).

No specimens nearing the maximum size for this species have been aged, however, according to the von Bertalanffy formula (Fig. 8), the largest males noted above, 272–300 cm, would be 22–30 yr of age, therefore they mature (10 yr) at 33–50% of such an estimated maximum life span. The largest females noted above, 305–310 cm, would be approximately 35 yr old. Females mature at approximately 15 yr of age, therefore they may be maturing at about 40–50% of their maximum life span. As noted earlier, such extrapolation may be invalid, and large (old) specimens need to be examined to verify these estimates.

Sphyrna lewini produces large litters (>30) of relatively small pups, and predation on the young is probably heavy. In Hawaii, the young move from protected bays to coastal reefs in the first few months of life, and subadult and adult male *S. lewini* prey heavily on the young (Clarke 1971). In the Gulf of Mexico neonatal *S. lewini* are commonly taken in shrimp trawls in shallow waters, and their occurrence in coastal waters makes them vulnerable to predation by the common coastal sharks. With the slow growth, late maturation, and possible heavy predation on immature individuals, the population may be dependent on the production of large cohorts to sustain the adult population.

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