Biological Parameters of Commercially Exploited Silky Sharks, *Carcharhinus falciformis*, from the Campeche Bank, Mexico.

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ABSTRACT

Age, growth, and reproductive parameters were estimated for silky sharks (*Carcharhinus falciformis*) off the Yucatan peninsula, Mexico, as a first and essential step towards the assessment and management of the species. Commercial catches were sampled from March 1985 to August 1989. Silky sharks off Yucatan are born in early summer after a 12 month gestation period at c. 76 cm TL. Males mature at 225 cm TL (≈10 y) and females at 232–245 cm TL (>12+ y). Maximum ages determined by analysis of alizarin-red-S-stained thin vertebral sections, were 22+ yr for females and 20+ yr for males. No differences in growth between the sexes were detected. Individual growth is quite variable in this species, but the von Bertalanffy model adequately described population growth. Parameters estimates of this model for combined sexes were: $k = 0.101$, $L_{inf} = 311$ cm TL and $t_0 = -2.718$. Age and growth determinations are supported by back-calculation and length frequency analysis. Present results are compared with those of previous studies for this species, and future work for Gulf of Mexico populations is proposed.

Introduction

The silky shark, *Carcharhinus falciformis* (Bibron), is a large, pantropical species attaining 330 cm TL (Garrick et al., 1964) that inhabits both coastal and oceanic waters. Fisheries for this species probably exist worldwide (Compagno, 1984). In southeast Mexico, the silky shark represents one of the more important species in the Yucatan shark fishery (Bonfil, 1987), and it is also exploited commercially along the rest of the Gulf of Mexico and on the Pacific coast of Mexico.

Worldwide there have been very few studies concerning silky shark biology. This has hindered studies of its potential for exploitation. Various discrete accounts of its biology are known thanks to its regular presence as bycatch on tuna, billfish, and other fisheries (Strasburg, 1958; Springer, 1960; Guitart-Manday, 1975). Apart from the studies of the uterus and placentation made by Gilbert and Schlernitzauer (1965, 1966), specific records of reproduction in this species are limited to the scattered field observations of, among others, Strasburg (1958), Springer (1960), Bane (1966), Bass et al. (1973), Stevens (1984, a and b), and Branstetter (1987), with the latter providing the most updated and comprehensive account. Schwartz (1983) reported limited data on its age and growth, and Branstetter and McEachran (1986) and Branstetter (1987) estimated the age and growth of populations in the Northwest Gulf of Mexico.

In Mexico, no specific studies on the biology of this species have been published. Only species accounts (Castro-Aguirre, 1967; Applegate et al., 1979) and its importance and structure in the commercial fisheries (Bonfil, 1987; Bonfil et al., 1988, 1990) have been reported. The present study analyzes the information gathered in almost five years of sampling commercial catches, and aims to estimate reproductive parameters and the age and growth of the silky shark, *Carcharhinus falciformis*, from the Campeche Bank, Mexico.

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Methods

All data were collected between March 1985 and August 1989, at the major commercial fishing ports of Yucatan, both onboard fishing vessels waiting to land their catches, and at nearby processing plants. Some limited sampling was also done during shark fishing research cruises made on I.N.P. (National Institute of Fisheries) RV *BIP III* and RV *BIP X*. All fishing operations took place on the Campeche Bank (Fig. 1). A total of 837 silky sharks were sexed and measured as recommended by Compagno (1984), i.e., with the shark lying on its belly and the upper caudal fin in line with the body axis; total lengths by other methods produce slightly shorter figures. Measurements, taken to the shortest centimetre were total length (TL), fork length (FL), precaudal length (PL), and the length from the tip of the snout to the beginning of the second dorsal fin (DL). Morphometric equations were derived (Table 1), and used to calculate total lengths when sharks were landed with their caudal fins removed.

Internal inspection of the specimens to determine maturity was seldom possible because of restrictions imposed by the handling and processing requirements of shark owners. We could only internally examine sharks when they were being processed. Only external characteristics were used for the determination of sexual maturity in males. Following Springer (1960) and Clark and von Schmidt (1965), males were considered fully mature when the claspers were completely calcified and the distal cartilages of the clasper could be spread open. Additionally, the presence of haematose spots in some male claspers, indicating recent copulation, served as confirmation of sexual maturity. Clasper lengths were

Table 1

Numerical relationships between different lengths of silky sharks from Yucatan (sexes combined). (TL= Total Length, FL= Fork Length, PL= Precaudal Length, DL= Length to beginning of 2nd dorsal fin, n= sample size; r = correlation coefficient.)

Equation	n	r
PL= 1.1505 + 1.1443 DL	196	0.999
FL= 2.8007 + 1.2305 DL	192	0.998
TL= 5.3314 + 1.5275 DL	145	0.997
FL= 1.3017 + 1.0758 PL	292	0.999
TL= 3.4378 + 1.3358 PL	283	0.997
TL= 1.8878 + 1.2412 FL	280	0.997

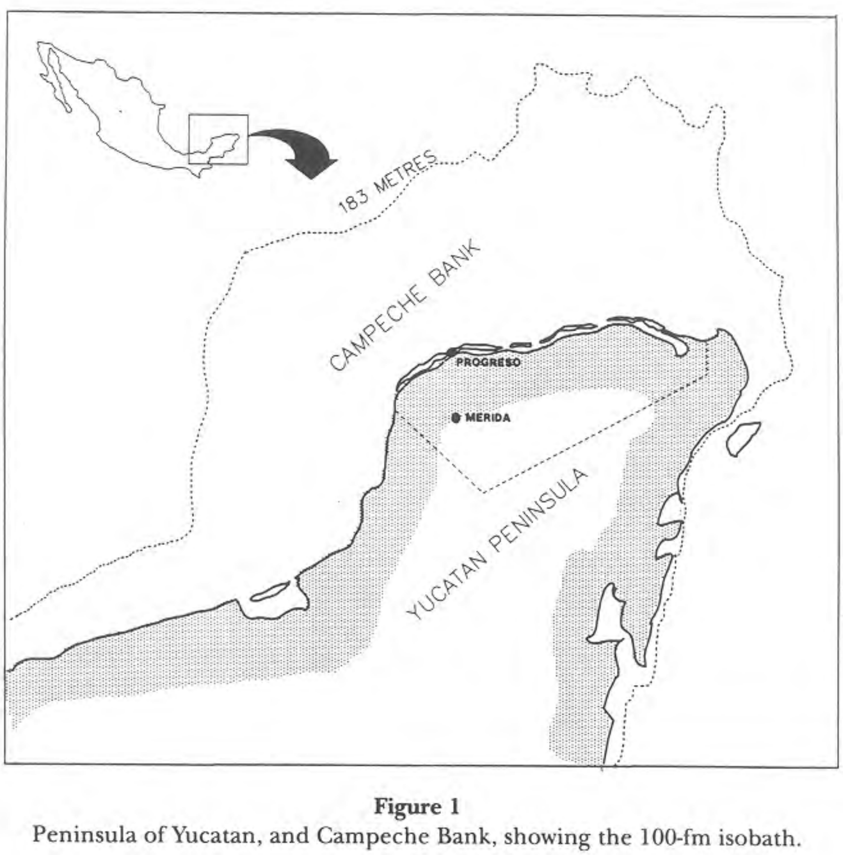

Figure 1
Peninsula of Yucatan, and Campeche Bank, showing the 100-fm isobath.

measured from the insertion of the inner corner of the pelvic fin to the distal tip of the clasper to the shortest millimetre. Given the distinct process of clasper development common to many shark species (Gilbert and Heath, 1972; Parsons, 1983; Natanson and Cailliet, 1986; Peres and Vooren, 1991), clasper length as a percentage of total length was plotted against total length in order to estimate the minimum size at which all males were mature. Pratt (1979) noted that external features can be misleading regarding sexual maturity for female sharks. Therefore, female maturity estimates were restricted to those fish examined at the processing plants. Females were considered mature if ripe ovarian eggs or embryos were present, or if distention of the uterus showed evidence of prior pregnancy. Whenever pregnant females were examined, all embryos in the litter were measured and sexed.

For age and growth studies, a sample of 4 or 5 vertebrae were removed from the region directly below the first dorsal fin for a total of 83 *Carcharhinus falciformis* of both sexes (43♂, 40♀), from newborn to adult sharks, found in the Campeche Bank. Each sample was fixed in 10% formalin for 24 hours, and stored in 70% isopropanol for up to 4 years. For the preparation of the thin sections, one vertebra from the sample was selected, and excessive connective tissue and vertebral processes were removed. Cleaned centra were placed in 50% bleach for periods varying from 5 minutes to several hours, depending on the size of the vertebrae; the larger ones required up to 6 hours and one or two changes of bleach solution. This treatment cleaned most of the unwanted connective tissue remaining on the face and around the centra (Cailliet et al., 1983). Care was taken not to leave samples in the bleach solution too long as this can soften and deform the whole centra. Afterwards, all centra were thoroughly rinsed in running tap water. Cleaned centra were cut in half across a frontal plane using an Isomet low speed saw. A thin (ca. 0.21 mm) slice was obtained from one of these halves by using the same cutting tool, thus a bow-tie shaped section was obtained for each centra.

Two staining techniques were tested on twin sets of 6 vertebrae of different sizes. First, an adaptation of the technique shown by Stevens (1975) was used. This consisted of immersion in a solution of silver nitrate (1%) coupled with exposure to UV light (direct sunlight) for 1–5 min, followed by removal of excess silver and by fixation with soaking in sodium thiosulphate (5%) for a couple of minutes. The second group of vertebrae were stained in an aqueous solution of alizarin red S and 0.1% NaOH in a ratio of 1:9 (Gruber and Stout, 1983) for periods varying between 20 minutes and 4 hours according to the centra sizes, larger ones taking more time. The samples were then rinsed for 15 minutes in running tap water and fixed in a solution of 3% hydrogen peroxide. All stained vertebrae were finally rinsed in tap water and stored back in isopropyl alcohol.

Throughout this paper, we follow the definitions of Wilson et al. (1983), according to which "an annulus is a concentric zone, band or mark, that is either a ridge or valley, or translucent or opaque. A unit passage time (i.e. 1 year) is not inherently implied." The terms band, ring, mark, or zone are regarded by the above mentioned authors as auxiliary descriptive terms. Following Cailliet et al. (1983), rings are treated here as the narrowest kind of concentric mark observed, and bands as wider concentric marks composed of groups of rings. Counts and measures of growth bands were performed on the thin sections viewed at 5× magnification under a binocular microscope equipped with an eyepiece micrometer. The centra faces were used only as an aid for identifying and counting poorly defined bands in the corpus calcareum and intermedialia. Both transmitted and reflected light were used to examine the samples depending on the quality of the definition of the growth marks. To increase contrast of the growth marks, transmitted light surrounding the sections was sometimes partially blocked by inserting suitable pieces of common writing paper between the container and the microscope platform.

Two separate counts were made by a single reader (senior author) for each sample, without knowledge of the total length or sex of the shark. When the two counts differed, a third reading produced a count that matched one of the first two. Agreeing counts were used in the calculation of the mean length at age for each age class.

The centrum radius was measured as a perpendicular line from the focus to the most distal edge of the vertebrae, which usually lay in the corpus calcareum. Distances to each growth mark were also measured as perpendicular lines from the focus to the most distal point of each growth mark along the corpus calcareum (Fig. 2). Marginal increments were measured perpendicularly from the last growth mark to the edge of the centrum. Birth marks were identified as a change in the angle of the inner margin of the corpus calcareum; this was sometimes coupled with a faint narrow annulus traversing the intermedialia. In most cases this annulus was proximal to the angle change.

Back-calculated lengths were derived from the vertebral radius-total length regression equation. The Dahl-Lea method (Casey et al., 1985; Branstetter, 1987) was also used, but discarded as it did not adequately describe early growth compared with the regression method. Care was taken to assign correct ages to the mean lengths-at-age as these can be different for direct vertebrae readings (length at time of capture) and back-calculated data (length at annuli formation).

With a maximum likelihood computer program (Genstat5), von Bertalanffy growth curves were fitted to the mean lengths at age obtained from the vertebral readings, as well as for those obtained via back calculation. Whenever necessary, comparisons between growth curves were performed using a computer-generated parallel curve analysis of covariance (Genstat5). Unless otherwise stated, all statistical analyses were performed using $\alpha = 0.05$.

Verification of the growth estimated from vertebrae was done using length-frequency data for 738 free-living silky sharks. These data were analyzed by Shepherd's method (Shepherd, 1987) with the LFDA (Length Frequency Data Analysis) package. Given the ability of this program to run alternatively with a single set of length-frequency data (LFD), or with a collection of time-related sets of data (Jones et al.[1]), runs were performed on monthly LFD sets available within each year (designated "partitioned" analyses), as well as on single yearly sets and on the pooled database (designated "summarized" analyses).

[1] Jones, C. G., M. Basson, and S. Holden. 1989. L.F.D.A. length frequeny data analysis. A prototype software package for the estimation of growth parameters from length-frequency distributions. Renewable Resources Assessment Group and Overseas Development Admin., unpubl. manuscr., 46 p.

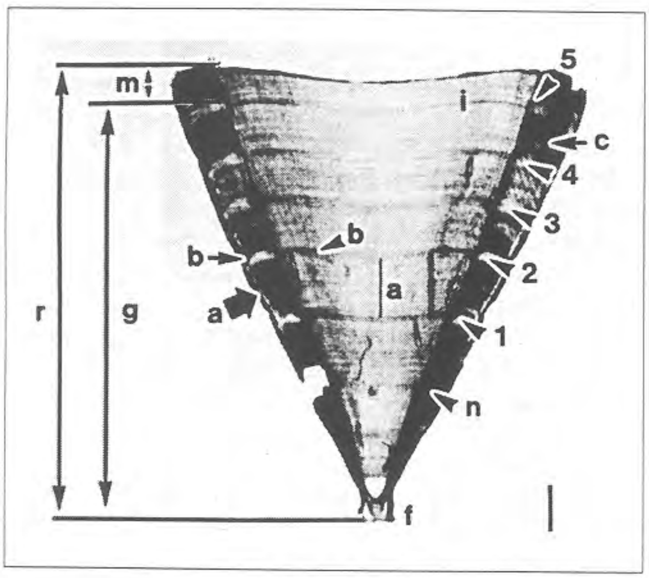

Figure 2
Bow-tie thin section of a 199-cm TL male *C. falciformis* alizarin-red-S stained vertebral centra with 5+ growth bands. The method used to measure the radius (r), marginal increment (m), and distance to a growth mark (g) is indicated, along with the broad "summer" annuli (a), the narrow "winter" annuli (b), the focus (f), birth mark (n), corpus calcareum (c) and intermedialia (i). Scale = 1 mm.

Results

A total of 738 freeliving silky sharks were analyzed (Fig. 3). The 352 males ranged from 69–314 cm TL, whereas females ranged from 65–308 cm TL. An additional 99 embryos ranging from 25 cm to 77 cm TL were examined.

Reproduction

Data on clasper length from 132 silky sharks showed mature males measure from 216 cm TL onwards, but some immature sharks were still found at 220+ cm TL. Fitting a Gompertz curve to the data (Fig. 4) indicated that 225 cm TL generally separated fully mature individuals from those with undeveloped or developing claspers. Taking 314 cm as the maximum total length observed for males in the Campeche Bank (present data), maturity is attained at 72% of the maximum length.

For female *Carcharhinus falciformis*, the limited data allowed only a rough reconstruction of a size range at first maturity. The smallest of 13 pregnant females examined were two specimens of 246 cm TL. Otherwise, mating bites which suggested maturity were observed on three females of 232 cm, 235 cm, and 241 cm TL. This range corresponds to 75–78% of the maximum total length observed in this study (308 cm).

Length-frequency distributions of late embryos and newborn sharks indicated a size at birth of c. 76 cm TL (Fig. 5). The smallest free-swimming shark was 65 cm TL, and the largest embryo was 77 cm TL.

Changes of mean total length of embryos in 13 litters indicated summer was the birth season and there was an approximate one-year gestation period (Fig. 6). A clear trend of embryonic development from September to July was found, and full-term embryos present from May through July. No embryos were recorded during August. For further calculations in this study, the month of July was set as the time of birth for silky sharks in the Campeche Bank. Assuming that mating takes place in late spring (Branstetter, 1987), an approximate 12-month gestation period can be derived from the present data.

Litter size varied between 2 and 12 embryos. Because of the fact that embryos are sometimes aborted by females trying to escape from the fishing gear, or may be expelled from the dead mother's belly during handling operations, this lower limit may be an underestimate. The sex ratio of 99 embryos was 1:1.17 (males:females). All free-living silky sharks (n=738) had a sex ratio of 1:1.10, while pre-adult and adult sharks (those larger than 200 cm TL; n=211) had a 1:1.37 sex ratio.

Age and Growth

The success of the two staining techniques was variable. Although silver nitrate staining yielded alternate brown-

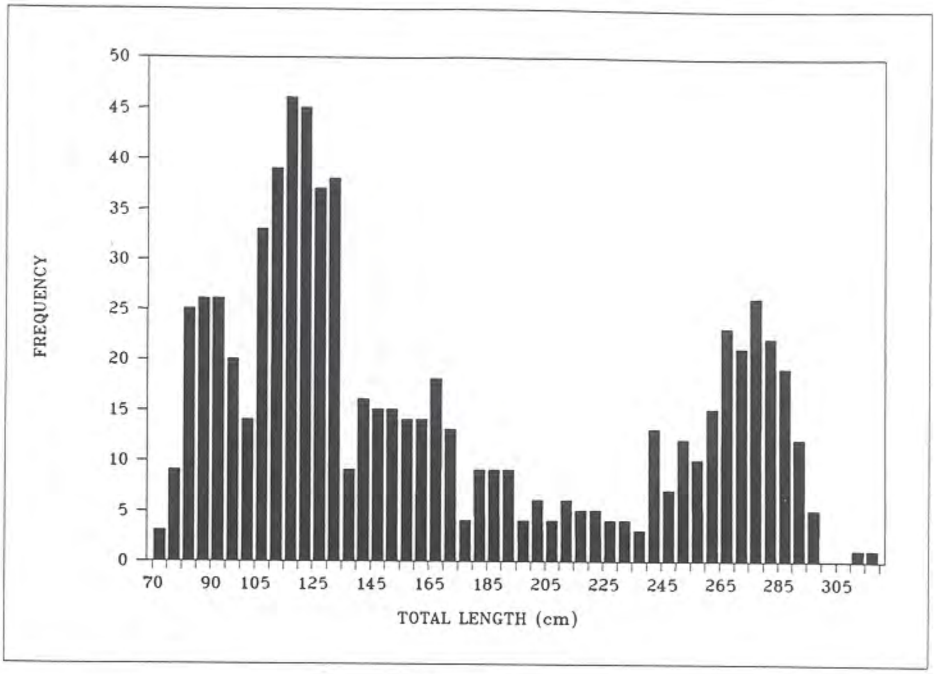

Figure 3
Length-frequency data set of the 738 freeliving sharks analyzed in the study, and used as one of the summarized data sets in the LFD analysis.

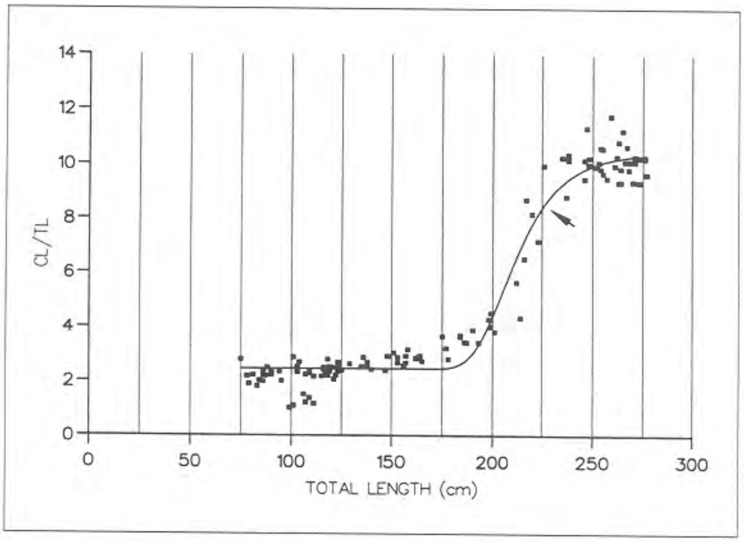

Figure 4
Estimation of size at first sexual maturity for male silky shark, based on the relative development of clasper length with total length. Squares are observations, arrow shows approximate size at which all sharks are mature.

ish and blackish bands on centra faces, poor differentiation was obtained on the exposed frontral-cut surfaces of the centra halves and the thin sections. In contrast, alizarin-red-S stained vertebrae provided a more consistent differentiation of the banding pattern throughout the centrum faces, frontal-cut surfaces, and thin sections. For this reason, and because of the ease of the alizarin-red-S method, this method was adopted for all samples.

In the corpus calcareum of a typical centrum section there was a clear pattern of annuli pairs composed of a broad dark purple band followed by a narrower light

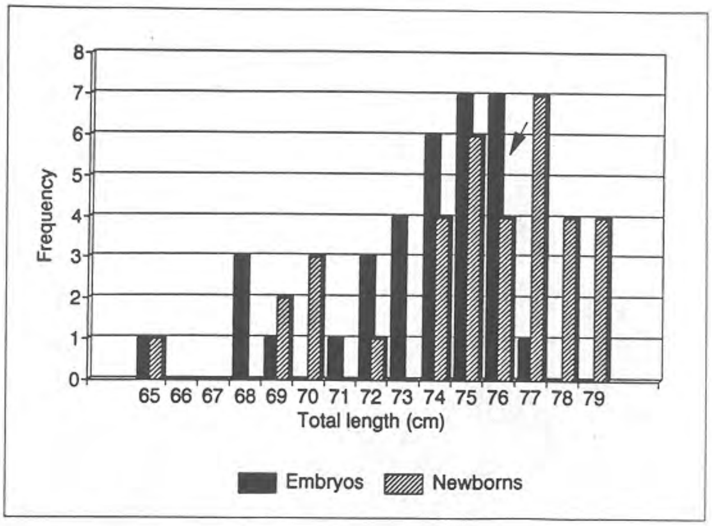

Figure 5
Estimation of size at birth (pointed by an arrow) for *Carcharhinus falciformis* from length frequencies of full term embryos and newborn sharks.

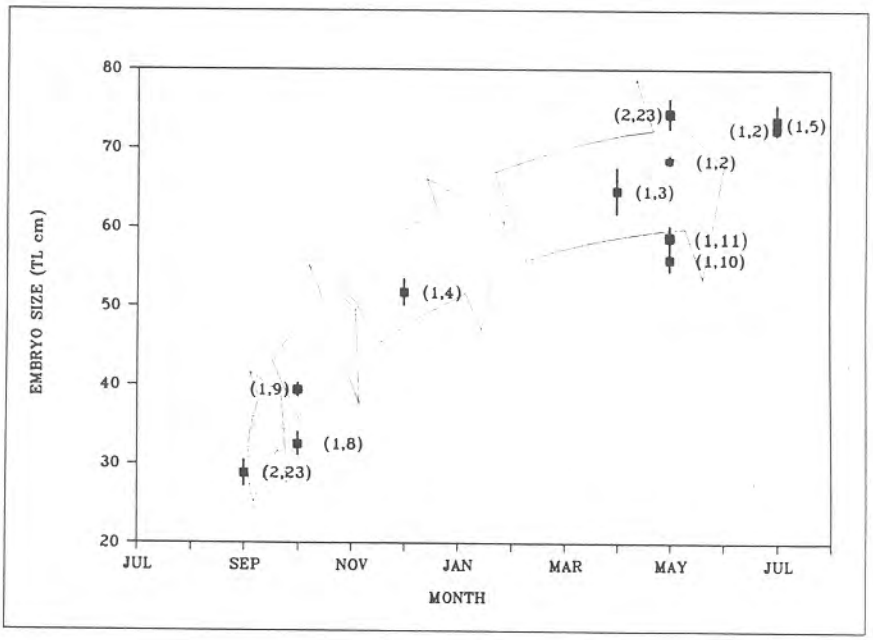

Figure 6
Development of silky shark embryos through time. Numbers in parentheses represent number of litters and total number of embryos. Squares are mean values; vertical lines are one standard deviation.

purple or white band. The broad annuli of the corpus calcareum corresponded to broad bands of narrowly spaced rings in the intermedialia, and the narrow translucent band corresponded to still narrower very dark rings (Fig. 2). The first 5–10 pairs of annuli were generally very broad in a section but consistently changed into very narrow pairs afterwards. Annulus counts after two separate readings agreed 45% of the time, 31% of the readings differed by one annulus, and 24% by more than one.

A significant linear relationship (α=0.0005) was found between the vertebral radius and total lengths of silky sharks (Fig. 7). Marginal increments increased during the calendar year with a maximum in December and a

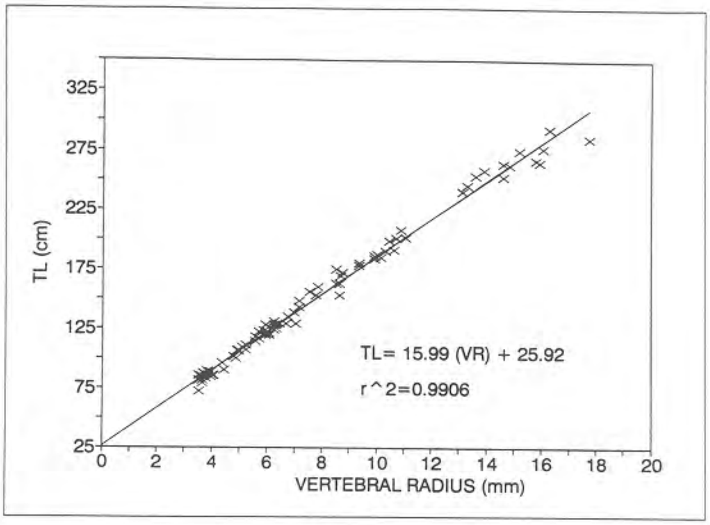

Figure 7
Linear relationship between vertebral radius and total length for silky sharks of the Campeche Bank.

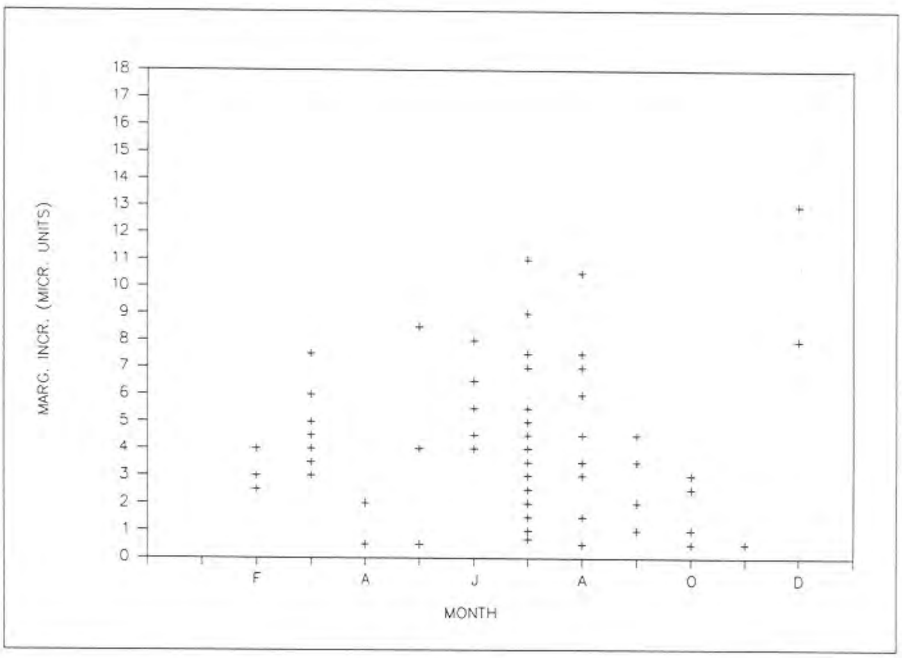

Figure 8
Estimation of time of annulus formation in centra of silky sharks based on the analysis of marginal increments for each month (neonates without winter mark excluded).

minimum in February (Fig. 8). Accordingly annulus formation occurred sometime between August and December. For growth calculations, December 30 was taken as the date of annulus formation.

With a July birth for silky sharks on the Campeche Bank and a December annulus formation, the first winter annulus represents only 6 months of growth; subsequent annuli formed annually. This was supported by the fact that mean growth represented by this first band was 13 cm, about half the average growth observed from the first to the second winter annulus (20 cm).

Fits of the von Bertalanffy Growth Model (VBGM) to the observed data for each sex provided values of k = 0.091, L_{inf} = 314.9 cm TL, and t_0 = −3.18 yr for females, and k = 0.098, L_{inf} =301 cm TL, and t_0 = −3.05 yr for males. Comparison of the two curves showed no significant differences in growth for males and females of *Carcharhinus falciformis.* Therefore, data for both sexes were combined and used to fit the VBGM to them (Fig. 9). Growth parameters for combined data were k = 0.089, L_{inf} = 313.1 cm TL, and t_0 = −3.3 yr.

The back calculations supported direct readings (Table 2). For these comparisons it must be noted that observed data should be greater than back calculations, as the former are based upon lengths at capture, whereas back calculations are based on lengths at band formation. The von Bertalanffy growth curve fitted to back-calculated mean lengths at age was not significantly different from that obtained for the direct readings (Fig. 9). Given the greater number of data taken into account for the back-calculated curve, parameters derived from this analysis were adopted as the ones best describing growth for silky sharks in the Campeche Bank. These values were k = 0.101 ,L_{inf}=311 cm TL, and t_0 = −2.718 yr. Analysis of the back-calculated mean lengths at age showed that strong variations in growth occurred between year classes in *Carcharhinus falciformis,* but overall, no Rosa-Lee phenomenon was detected (Fig. 10).

Back calculations illustrated that, on average, silky sharks in the Campeche Bank grew about 13 cm in their first 6 months of life, c. 19 cm/yr during the following 3 years, c. 15 cm/yr in the next 3 years, c. 11 cm/yr for the next 4 years, and finally c. 6 cm/yr or less for the rest of their life. According to the growth parameters adopted, and the lengths at maturity found for the species in the Campeche Bank, the age at maturity for males in the area is 10 yr, whereas for females it is 12+ years.

Analysis of length-frequency data with the LFDA program produced varying VBGM parameter estimates (Table 3). The growth parameter k varied between 0.085 and 0.13, L_{inf} from 298–365, and t_0 from 0.22–0.97. The overall range of results agreed well with those obtained by the vertebrae study especially for the growth parameter k. The averages of the VBGM parameters obtained from all successful runs of the program (k = 0.101, L_{inf} = 320 cm TL, and t_0 = 0.76 yr) provided good evidence for verification of the direct determination of growth in the silky sharks of the Campeche Bank.

Discussion

Reproduction

Few estimates of reproductive parameters are available for the silky shark; nevertheless, available data suggests a much smaller size at maturity for females in the Indian and Pacific Oceans compared with those in the Atlantic. In the western Indian Ocean, Bass et al. (1973) complemented observations on nine silky sharks with Fourmanoir's (1961) data, and found a larger size at birth (78–87 cm TL) and mature specimens of both sexes at larger total lengths (males at 240 cm TL, females at 248–260 cm TL) than those obtained by us. In approximately the same area (Aldabra Atoll), Stevens

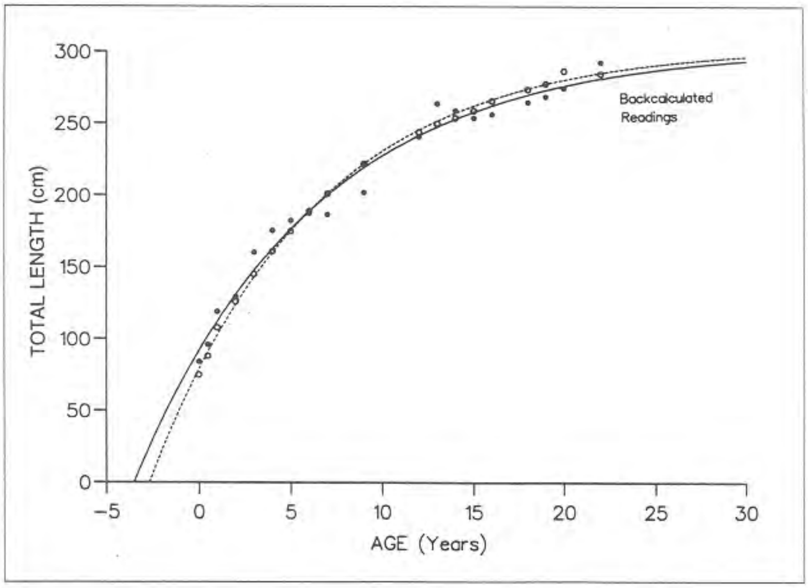

Figure 9

Von Bertalanffy growth curves fitted to mean lengths at age from direct vertebrae readings (dots), and back-calculation (circles) for *Carcharhinus falciformis.*

Table 2
Back calculated mean total lengths-at-age for silky sharks from the Campeche Bank (cm).

		Growth marks																							
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Age class	*n*	0	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+	19+	20+	21+	22+
Birth	15	76																							
1	6	74	88																						
2	16	74	87	109																					
3	11	74	85	100	118																				
4	5	75	92	108	128	149																			
5	4	77	94	114	135	149	162																		
6	4	75	85	107	124	141	156	172																	
7	5	76	87	107	119	134	146	159	174																
8	3	74	90	106	117	130	141	155	167	181															
10	1	67	80	108	133	143	156	164	172	181	189	195													
13	1	78	88	116	144	154	170	176	182	188	200	209	214	225	234										
14	1	80	96	118	142	168	191	202	212	220	229	234	241	244	253	258									
15	1	73	80	94	117	144	170	193	212	220	227	233	238	241	244	246	247								
16	1	75	84	99	111	130	144	151	161	170	187	205	216	220	226	230	236	241							
17	2	77	92	106	129	146	164	176	191	204	215	221	226	231	237	241	245	252	256						
19	2	76	87	108	124	145	168	191	210	225	233	242	247	251	255	258	261	264	266	268	270				
20	2	76	89	102	121	145	164	179	202	217	226	236	242	246	249	252	255	257	259	261	263	265			
21	2	76	86	109	128	144	167	192	208	223	230	238	246	252	259	266	271	276	281	284	287	291	293		
23	1	73	96	131	140	153	162	172	178	184	197	211	222	236	244	251	265	268	273	277	279	281	282	284	285
Mean TL		75	88	108	127	145	161	176	189	201	213	222	233	239	245	250	254	260	267	272	275	279	288	284	285
SD		3	4	8	10	10	13	16	19	21	18	17	13	12	11	11	12	13	10	10	11	13	8		
Observed (direct readings)																									
Mean TL		84	96	119	129	160	176	183	188	187		202			241	264	259	254	257		265	269	275		293
SD		5	9	10	8	6	16	15	11	2									11		12	6	10		
n		15	6	16	11	5	4	4	5	3		1			11	1	1	1	2		2	2	2		1

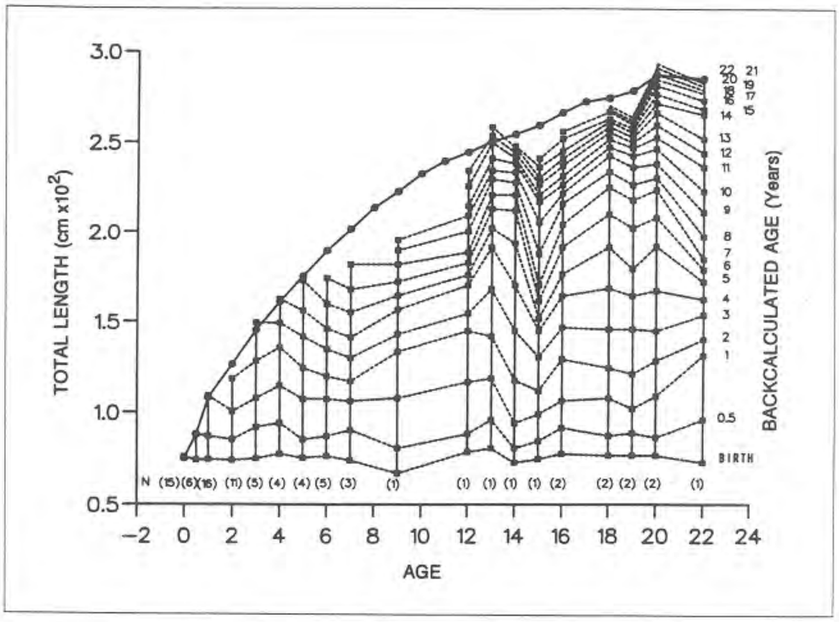

Figure 10
Variability of back-calculated mean lengths at age for silky shark. Circles are overall mean values. Boxes are back-calculated mean lengths at age obtained within cohorts, with numbers in parentheses indicating sample size (N) of each age class (solid lines). Broken lines interconnect the different values of length at age (corresponding age indicated in the right side of the graph) across cohorts. Some boxes on the upper right part of the graph are omitted for clarity.

Table 3
Von Bertalanffy Growth parameters for silky sharks from Yucatan obtained using the LFDA (Length Frequency Data Analysis) package. A partitioned analysis is based on multiple monthly LFD sets within a year. A summarized analysis is based on a single LFD set constructed by adding up monthly sets over time.

Type of analysis	Year	k	L_{inf} (cm TL)	t_0
Partitioned	1985	0.13	345	0.95
Partitioned	1986	0.115	325	0.97
Partitioned	1987	0.105	298	0.63
Partitioned	1988	0.085	313	0.22
Partitioned	1989	0.09	313	0.70
Summarized	1985	0.09	305	0.96
Summarized	1986	0.09	320	0.84
Summarized	1989	0.095	303	0.75
Summarized	All	0.115	365	0.86
Average		0.1016	320	0.76

(1984a) found *Carcharhinus falciformis* males 239 cm TL to be mature; contrastingly he noted mature females of only 216 cm TL. Additionally, Strasburg (1958) recorded gravid females of 213–236 cm TL in the Central Pacific, and Stevens (1984b) listed mature males at 214 cm TL and mature females at 202 and 208 cm TL for the southern Pacific (Tasman Sea).

Studies in the Atlantic more closely approximate our findings. For the eastern Atlantic, Bane (1966) and Cadenat and Blache (1981) provided lengths of 238–250 cm TL for mature females and 220 cm TL for mature males, roughly within the range of the present results. In the western North Atlantic, Springer (1960) reported a range of 68–84 cm TL for full-term embryos together with mature males from 221 cm and mature females from 233 cm. For the Gulf of Mexico, Branstetter (1987), with only six adult sharks, reported 215–220 cm as the range for male maturity and that females of 232–233 cm TL were mature. Size at birth and length for first maturity of females are roughly in accordance with our findings from the Campeche Bank. However, results from Springer (1960) and Branstetter (1987) suggest slightly smaller sizes at first maturity for males than those of ours. A possible explanation for these variations could be the different methods used for measuring length between their studies and ours.

More comprehensive research in the Gulf of Mexico may show females to have a size at maturity closer to that of the Indo-Pacific populations. On the other hand, it is possible for separate populations to have different characteristics.

Pratt (1979) found that the growth of claspers, testes, and epididymis of blue sharks is gradual and does not provide any clue to the approach of sexual maturity. Further, he determined that many male blue sharks, apparently fully mature when externally examined, lacked spermatophores and had small ductus defferentia and were thus not completely mature. Contrary to these findings, male silky sharks do have a well defined adolescence that extends approximately from 200 to 225 cm TL. The lack of internal examination of sharks in our study prevents verification of maturity derived from external features only. Further work will be needed to fully understand the onset of sexual maturity in male silky sharks.

The gestation time and birth season found here support Branstetter's (1987) suggestion of a 12-month late-spring-based cycle for development of *Carcharhinus falciformis* embryos in the Gulf of Mexico. Our findings are in contrast with Strasburg (1958), Fourmanoir (1961), Stevens (1984b),and Stevens and McLoughlin (1991), who noted an absence of a defined seasonality for reproduction in the Indian and Pacific Ocean populations. Although Strasburg (1958) does not present raw data, his analysis of 12 litters points towards a true difference in seasonality of reproduction between Gulf of Mexico and central Pacific populations. Based on these observations, Branstetter (1990) suggested silky shark populations might lack seasonal gestation periods in tropical areas; however, the Campeche Bank population has a seasonal gestation period and occupies in a tropical area. Furthermore, the populations studied by Bass et al. (1973) and Stevens (1984, a and b), and Stevens and McLoughlin (1991) all share roughly the same temperature ranges of the Gulf of Mexico but do not show a seasonal gestation period. Although available data are limited, there may be true differences among geographic populations. Estimation of the span of the total reproductive cycle in the females (i.e., if they give birth every year, or every other year) is also poorly known and should also be considered for future work. Branstetter (1987) gives the only available observations suggesting the entire cycle may take two years.

Age and Growth

Annuli, and growth bands, were readily discernible in silky shark vertebral centra. The poor resolution of bands on thin sections of vertebrae stained with silver nitrate was explained by Brown and Gruber (1988), who found that silver nitrate crystals formed in the sections and obscured the resolution needed for detailed studies.

The choice of December 30 for the date of annulus formation is only a preliminary estimate, as marginal increments appeared to decrease from August to November, and small sample sizes during this period prevented conclusive evidence. Branstetter (1987) reached the same conclusion for an early winter annulus formation for silkies in a nearby area but also suffered from few autumn data. More samples from the months of September to January are needed to document more accurately the date of annulus formation for Gulf of Mexico silky sharks.

Back calculations of size at birth (75 cm TL) matched the reproductive data on size at birth (76 cm TL). The present value of L_{inf} = 311 cm TL is in agreement with the maximum lengths of silky sharks collected in the Campeche Bank, which are 308 cm and 314 cm TL for females and males respectively. Longevity of the species is expected to be more than the 22+ years found for the largest specimen aged in this study (a 293 cm TL female). Several vertebral samples of sharks >300 cm TL in our possession are still waiting to be processed.

Our results differ somewhat with those found by Branstetter (1987) in the Northwest Gulf of Mexico. His fit of the von Bertalanffy model produced parameter estimates with a larger k (0.153), and a lower asymptotic length (290.5 cm TL) than those of the Campeche Bank ($k = 0.101$; $L_{inf} = 311$ cm TL). Furthermore, mean lengths-at-age between studies do not match for most of the sample range; Branstetter's values are consistently larger than the ones reported here.

Various explanations could be given for the disagreements found in growth parameters (sample bias, method of fitting the VBGM, combination of both); still, the differences in lengths-at-age remain unexplained. The sample size of both studies were rather similar, but the size ranges differed. Most vertebrae used in Branstetter's study came from sharks between 100 and 210 cm TL, but in our case two major groups at 80–205 cm and 240–295 cm TL constituted most of the samples. This difference may have a considerable effect on the shape of the VBGC and thus on the parameters. One of the reasons for Branstetter's low L_{inf} value is the absence of really large sharks in his samples. His largest specimen (267 cm TL) at age 13 was younger than the four sharks 275–293 cm TL aged in our study. The inclusion of larger, older specimens in our vertebrae samples is translated into a higher value of L_{inf} and a corresponding lower k value. In fact Branstetter (p.170) noted that the substitution of a L_{inf} value of 325 cm TL (which is closer to that presented here) produced a k value of 0.11 for his data, more in agreement with our findings. Accordingly, this could be the reason behind our different VBGM parameters.

Several hypotheses can be drawn to explain the different lengths-at-age of silky sharks from the Campeche Bank and the Northwestern Gulf of Mexico. Either true variations exist, or more likely, something is producing an artificial difference in growth analyses. An argument against the first possibility is the proximity of the sampling locations, making a single stock, or at least strongly intermixing stocks very likely. This in turn suggests the likelihood of similar growth rates. Furthermore, the fact that the faster growth was found in the northernmost site contradicts the theoretical relationship between latitude, temperature, metabolism, and a faster growing equatorial stock. Parsons (1987) found a similar situation of fast-growing northern bonnethead sharks, *Sphyrna tiburo* ,and slow-growing southern specimens in Florida. This suggests environmental factors other than mean temperature could be more determinant for shark growth.

The existence of two separate stocks with different growth parameters would explain the present situation, but this possibility needs to be studied through specific stock identification techniques, such as biochemical genetics, in order to be properly assessed. Defining the issue of single or multiple stocks for many shark species has direct and important implications on the management of these resources which are being increasingly exploited across the area. These populations are being quoted as a single stock without conclusive evidence (i.e., Branstetter, 1990; Hoff, 1990).

The assumption that there are no real differences in growth leads us to search for obscuring effects. Application of the same technique does not always assure the same results; variations in the interpretation of each individual reader can account for different results (Cailliet et al., 1990), and cross-reading samples has been shown to help locate and sometimes solve this problem (Tanaka et al., 1990). In both Gulf of Mexico studies, only one reader was used. Comparisons and cross reading of both samples might clarify this point. It is also possible that neither sample is sufficiently representative of the population. Branstetter's samples come mainly from offshore deep-water specimens fished as swordfish bycatch, while ours belong mainly to grouper and shark fisheries from the continental shelf. This implies that our samples for young sharks could be biased towards slow-growing specimens remaining inside the Campeche Bank, because the fast-growing individuals could move to a more pelagic existence in the edge of the continental shelf as suggested by Branstetter (1987; p.169–170). Meanwhile, the northwestern Gulf of Mexico samples would represent exactly the opposite picture with a bias towards fast-growing individuals which leave the grouper-grounds sooner than their slow-growing siblings from the same cohorts.

The variability in the parameter L_{inf} found from the results of the LFDA program is attributable to the sensitivity of this procedure to the differences in the various sets of data analyzed. Other direct studies of age and growth determination in sharks have used simple mode definition to support their findings (Pratt and Casey, 1983; Casey et al., 1985). However, those studies used results from vertebral aging to define the modes in the length-frequency distribution. Such analyses do not constitute independent evidence supporting the study of vertebrae. In contrast to this, the present use of methodologies such as that of Shepherd (1987) is independent of the direct determination of age and growth, thus it provides stronger verification.

Conclusions

The silky shark in the Campeche Bank has a 12-month gestation period, giving birth to 10–12 pups with average total length of 76 cm during late spring and early summer, possibly every two years. Sex ratios probably remain close to 1:1 during life. Both sexes attain late sexual maturity, males at 225 cm TL (=10 yr, ≈72% of max. length) and females between 232–246 cm TL (>12+ yr; ≈74–78% of max. length) or smaller. More research on maturation and reproduction needs to be done in this species.

Growth in the silky sharks of the Campeche Bank can be variable, but in general these fish are slow growing (k=0.101), reaching at least 22 years of age. For this species, the alizarin-red-S technique applied to thin sections of vertebrae is a better method for direct studies of age and growth than silver nitrate staining. Length-frequency data are a good way of providing additional estimates of growth to verify direct studies.

Some differences between results of age and growth studies of silky sharks in the northwestern Gulf of Mexico (k=0.15, L_{inf} = 291 cm TL) and the Campeche Bank (k=0.10, L_{inf} = 311 cm TL) have been identified here. This suggests that the two populations may be somewhat distinct. Genetic study of the species in the Gulf of Mexico is proposed as the way to clarify the status of these populations.

Management measures for *Carcharhinus falciformis* should first clarify the structure of Gulf of Mexico stock(s), and consider the life-history characteristics of slow growth, late maturation, and limited offspring, which point towards a very fragile resource. In all probability, local stocks of this species cannot support sustained heavy fishing pressure.

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