Abstract.—Age and growth of the dusky shark, *Carcharhinus obscurus*, was estimated from bands in the vertebral centra of 122 individuals and from length-frequency data from 341 individuals. The von Bertalanffy growth function parameters from the vertebral analysis were considered more robust (L_∞=373, K=0.038, t_0=–6.28, male; L_∞=349, K=0.039, t_0=–7.04, female). Comparison of male and female growth curves generated from vertebral data indicate a statistically significant difference; however, these differences are due primarily to larger sizes attained by adult females. Estimates of age at maturity indicate that dusky sharks follow the typical carcharhinid pattern of slow growth and late age at maturity. The size at maturity is reported at 231 cm FL and 235 cm FL for males and females, respectively. These lengths correspond to approximately 19 years for males and 21 years for females. The oldest fish aged from vertebrae was a 33+ year-old female.

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Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean

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Sharks have become increasingly important in U.S. commercial fisheries in the western North Atlantic Ocean in recent years. U.S. landings of large coastal sharks, represented primarily by several species in the family Carcharhinidae, increased from 135 to 7,122 metric tons (t) from 1979 to 1989 (Anon., 1993). Musick et al. (1993) reported that annual recreational catches are estimated to be 35,000 U.S. tons and related annual mortality is over 10,000 U.S. tons (9,074 t). As a group, sharks tend to exhibit slow growth, late age at maturity, and low fecundity (Holden, 1973). As a consequence of these life history characteristics, recruitment in sharks is directly dependent on stock size (Holden, 1973). This direct relationship means that elasmobranchs may not be able to recover readily from overexploitation (Holden, 1973).

The dusky shark, *Carcharhinus obscurus*, is part of the species complex presently managed under the Secretarial Shark Fisheries Management Plan (FMP) for the Atlantic Ocean (Anon. 1993). Currently, dusky sharks are harvested in commercial fisheries off the southeastern United States and in the Gulf of Mexico. Recreational fishermen off the northeastern United States also catch dusky sharks (Casey and Hoey, 1985; Musick et al., 1993). The shark FMP (Anon. 1993) details the need for accurate life history information on individual species taken in the shark fishery. Proper management at the species level requires specific information on age and growth.

The dusky shark is a common coastal pelagic species with a worldwide distribution in temperate and tropical waters (Compagno, 1984). In the western North Atlantic, it ranges from as far as Banquereau Bank off Nova Scotia, Canada, to southern Brazil, including the Gulf of Mexico and Caribbean Sea (Hoey, 1983; Compagno, 1984). Tagging studies show dusky shark movements from southern New England to Yucatan, Mexico (Casey et al.[1]; Hoey, 1983).

Age and growth studies of large sharks are difficult because many species are highly migratory, making them available for only short seasonal periods, and different elements of the population segregate spatially by size and sex (Hoenig and Gruber, 1990). In addition, the large size attained by adults makes them difficult to sample. Recent literature has discussed the benefits of growth and longevity estimates attained from tag and recapture

[1] Casey, J. G., H. L. Pratt Jr., and C. E. Stillwell. 1980. The shark tagger summary. Newsletter of the Coop. Shark Tagging Program. U.S. Dep. Commer., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 28 Tarzwell Rd., Narragansett, RI, 02882-1199.

studies (Casey and Natanson, 1992). These data are not available for the dusky shark nor is validation of vertebral band periodicity. Previous attempts to age the dusky shark were based on limited data and were inconclusive (Lawler, 1976; Hoenig, 1979; Schwartz, 1983). We have attempted to strengthen age estimates of *C. obscurus* by using vertebral band counts together with marginal increment analysis and by using comparisons with length-frequency data. With the von Bertalanffy growth function thus derived, we estimate age at maturity and longevity for this species.

Materials and methods

Data and vertebral samples from dusky sharks were obtained between 1963 and 1993 from research cruises, sport fishing tournaments, and commercial shark fishermen from Cape Cod, Massachusetts, to off the east coast of Florida. Vertebral samples were taken in all months except January, March, and November.

Length measurements

Total and fork lengths were measured to the nearest centimeter (cm) for each specimen. Fork length (FL) was measured from the tip of the snout to the fork of the tail. Total length (TL) is defined as the distance from the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle (Kohler et al.[2]). All lengths used are fork lengths unless otherwise noted. FL can be converted to TL by using the regression equation:

$$FL = 0.8352\ (TL) - 2.2973.\ [r^2 = 0.99,\ n = 167]$$

Vertebral samples

Vertebral samples were taken from above the branchial chamber. Sections of vertebral columns were trimmed of excess tissue and then frozen or preserved in 70% ethanol (Casey et al., 1985).

Two vertebrae from each specimen were processed histologically following Casey et al. (1985), with the exception of the use of RDO (DuPage Kinetics) for decalcification. All vertebral sections were cut sagittally through the focus to a thickness of 80–100 microns, stained with Harris hematoxylin, and mounted in glycerin jelly (Humason, 1972).

Bands in the vertebra were counted from an image projected on a Summagraphics MM-1812 digitizing tablet (Skomal, 1990). Measurements from the focus to growth bands at points along the internal corpus calcareum were digitized directly into an IBM PC-XT computer. The radius of each centrum was measured from the focus to the distal margin of the intermedialia along the same diagonal as the band measurements. Annual growth marks were defined following Casey et al. (1985) for the sandbar shark, *Carcharhinus plumbeus*, where the annual mark is defined by a wide translucent zone that traverses the intermedialia and continues into the corpus calcareum as an opaque band.

Vertebral sections from 171 dusky sharks were prepared. Bands in the same centrum section were counted at least once by each of four investigators to verify that the band counts were repeatable. Sections were considered unreadable if bands could not be discerned in accordance with the above definition. If two readers considered the section unreadable, the sample was eliminated from the final analysis.

Counts were accepted if two or more readers agreed. The individual ring measurements for all readers in agreement were then averaged. If two readers agreed on one count and two on another for the same specimen, the higher count was accepted. Specimens where there was no initial agreement were recounted until two of the investigators reached a consensus or the sections were discarded.

The relationship between vertebral radius (VR) and FL was calculated to determine the most appropriate method for back calculation of the size-at-age data (Ricker, 1969). The FL to VR relationship was linear but did not pass through the origin. Therefore, the Lee method was considered more appropriate (Ricker, 1969):

$$l = a + (b \times s),$$

where l = the length of fish when the vertebra was obtained;
a = the intercept on the length axis;
b = the slope of the line; and
s = the total vertebral radius.

A von Bertalanffy growth function (VBGF) was fitted to the data by using the following equation (von Bertalanffy, 1938):

$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right),$$

where L_t = predicted length at time t;
L_∞ = mean asymptotic fork length (of the fish);
K = a growth rate constant (yr^{-1}); and
t_0 = the theoretical age at which the fish would have been zero length.

[2] Kohler, N. E., J. G. Casey, and P. A. Turner. Length-weight relationships for 13 Atlantic sharks. Unpubl. manuscr.

Growth in length data were analyzed by using FISHPARM, an IBM PC compatible program (Prager et al., 1987), which implements Marquardt's algorithm for nonlinear least squares parameter estimation (Marquardt, 1963).

Bernard's (1981) multivariate analysis for comparing growth curves was employed to test the hypothesis that male and female vertebral growth curves were the same. This method also determines which of the von Bertalanffy parameters are the most statistically significant cause of any differences in growth.

Marginal increment analysis

Validation, the confirmation of the temporal meaning of the growth increment (Brothers, 1983), is difficult to attain for large pelagic species and was attempted by using marginal increment analysis. The marginal increment ratio (MIR) (Skomal, 1990) was calculated by using the following equation:

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where VR = the vertebral radius;
R_n = the last complete band; and
R_{n-1} = the next to last complete band.

Mean MIR was plotted against month to locate periodic trends in band formation. The MIR relates the edge formation to the width of the previous completed band, which corrects for differences in band width between small and large fish.

Length frequency

Length-frequency distributions were analyzed by using Shepherd's (1987) model. The sample was separated by sex and calculations were made at 3-cm intervals. Initial values of L_∞ and K, based on biological parameters obtained from the literature (Springer, 1960; Compagno, 1984) were entered into the program which was then rerun until the highest score function was attained. The L_∞ and K associated with this score function were used to calculate t_0 by using the following equation:

$$t_0 = t + (1/K)\,(\ln[L_\infty - L_t]/L_\infty),$$

where t_0 = 0 (birth);
L_t = mean size at birth;
K = the von Bertalanffy growth constant; and
L_∞ = the mean asymptotic fork length.

Longevity

Estimates of longevity were obtained by using tag and recapture data. Data on eight recaptured dusky sharks at liberty for greater than 10 years were examined. Age at tagging was assigned from the size estimate provided at the time of release. This estimated age was based on growth curves derived from vertebrae. The number of years at liberty were then added to estimate age at recapture.

Results

Vertebral samples

Of the 171 processed vertebra, 36 (21.0%) were considered unreadable. Initial agreement by two or more readers was reached on 89 specimens. The remaining 50 sections were recounted by two of the investigators. A consensus was reached on 37 of those recounted and the rest were discarded as unreadable. Six were then eliminated for having no information on sex. The remaining 120 (70.2%) consisted of 53 male and 67 female specimens ranging in size from a 73 cm FL neonate to a 296 cm FL adult female. The FL-VR regression showed a linear relationship:

$$FL = 12.82(VR) + 24.99\ [n = 114;\ r^2 = 0.99].$$

The FL to VR relationship was significantly different between the sexes for all fish combined (ANCOVA, $P<0.05$). However, this was due to three large females whose removal from the analysis altered the curves and showed the males and females to be statistically indistinguishable ($P<0.05$) (Fig. 1). We chose to use the combined relationship without those three samples.

Back-calculated as compared with empirical length-at-age data show a smaller estimated size for fish of younger ages, when calculated from the vertebrae of the older fish, indicating the presence of a slight Lee's phenomenon for both sexes (Table 1). Lee's phenomenon was more pronounced in females and increased with age.

The MIR data showed a distinct, periodic trend of increasing increment growth from April through June (female) or July (male); after this peak there was a slight decrease and apparent leveling (Fig. 2). The decrease in incremental growth is not large enough to indicate a double band formation. The graph suggests that an annual winter band is formed between September and April. This band can be visible by February in males; no data were available for females. The time of annulus formation cannot

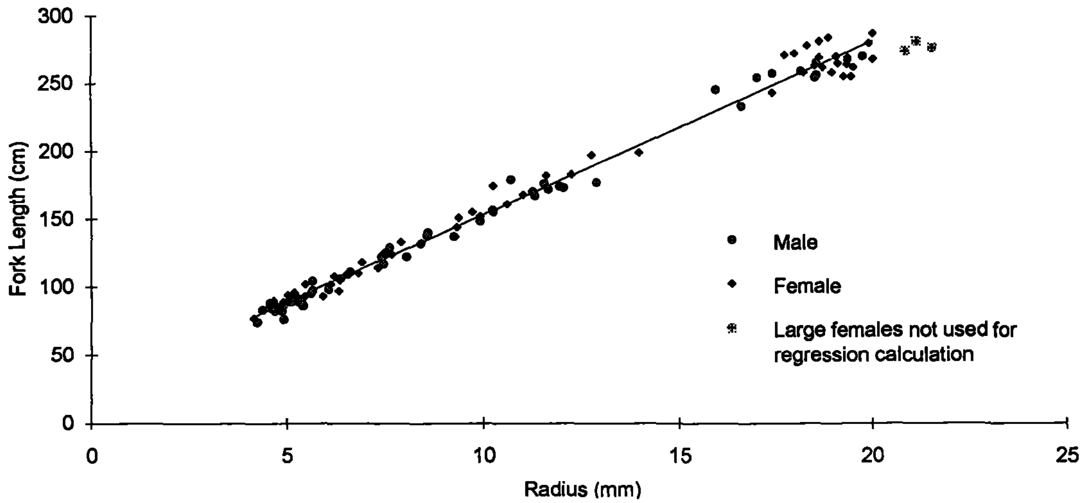

Figure 1

Relationship between vertebral radius (cm) and fork length (cm) for male and female dusky sharks, *Carcharhinus obscurus*.

be further established owing to a lack of winter samples. January was used as the month of band formation for the assignment of age classes (Casey et al., 1985).

Back-calculated length at first band (80.2 cm FL male; 85.8 cm FL female) corresponded closely to the known size at birth of 85–100 cm TL (Castro, 1983; Compagno, 1984). The first winter band would have formed after approximately six months growth (assuming January deposition and spring parturition), and the following bands represented annual growth (Branstetter, 1987). The oldest female in the sample was 33+ years and the oldest male, 25+ years.

The parameters of the VBGF determined from the back-calculated data were similar to known life history characteristics except that the predicted L_∞ for males was higher than that for females (Table 2). Those samples that were neonates with no visible birthmark were excluded from the VBGF analysis. Therefore, only 114 samples (47 male and 67 female) were included in the final calculations. The t_0 and K values appear similar between the sexes (Table 2). However, the male and female growth curves are significantly different ($P<0.05$) based on Bernard's (1981) multivariate analysis (Table 3). The results indicated that the differences were caused by the t_0 and L_∞ values (in order of significance).

The reported size at maturity for the dusky shark is 231 cm FL and 235 cm FL for males and females, respectively. These lengths correspond to 19 years for males and 21 years for females based on the vertebral growth curves (Table 4).

Length frequency

Length observations from a total of 208 female and 133 male dusky sharks were used to calculate von Bertalanffy parameters by using length-frequency analysis. Samples were obtained from 1961 to 1987 for the months May through November. Because of small yearly sample sizes, data for all years were combined by month.

A comparison of the VBGF parameters from the length-frequency analysis [LF] with those derived from vertebral analysis (Table 2) shows that the L_∞ and t_0 values from the vertebral analysis for females were lower than those derived from the length-frequency analysis, and that the K value for females was basically the same for both data sets. The length-frequency analysis for males results in a lower L_∞ than that from the vertebral analysis and in higher t_0 and K values. The VBGF differences in both sexes are not large and both curves indicate late age at maturity (males: 25 yr [LF], 19 yr [vertebral]; females: 16 yr [LF], 21 yr [vertebral]) and slow growth (males: K=0.049 [LF], 0.038 [vertebral]; females: K=0.040 [LF], 0.039 [vertebral]) (Fig. 3). The von Bertalanffy parameters for the sexes combined are shown for comparison (Table 2).

Longevity

Tagging records from NMFS Cooperative Shark Tagging Program show that 6,067 dusky sharks were tagged and 131 recaptured between 1962 and 1992.

Table 1

Back-calculated and observed size-at-age data for male and female dusky shark, *Carcharhinus obscurus*.

Male
Ring (age in years)

	Birth	6 months	0	1	2	3	4	5	6	7	8
Back-calculated											
$\bar{X}$	80.2	87.3	94.1	103	113.9	124.4	132	140.5	149.7	157.7	163.8
SD	5.6	5.5	6.2	7	9.2	10.6	10.7	11.7	12.7	12.6	10.5
n	47	34	30	28	25	21	20	20	19	17	
Observed											
$\bar{X}$	87.7	100.5	123.5	116.7	124.5	138		148	173.5	164	
SD	5.1	53.		2.1	5.5	4.9	0		0	0.7	7.9
n	13	4		2	3	4	1		1	2	3

Male
Ring (age in years)

	9	10	11	12	13	14	15	16	17	18	19
Back-calculated											
$\bar{X}$	161.7	179.2	188.6	196.1	202.4	209.8	216.1	220.5	226.5	232.3	237.9
SD	11.6	12.3	10.4	11.8	11.7	13.5	13	11.4	11.7	12.4	12.5
n	14	13	11	10	10	10	10	9	9	8	8
Observed											
$\bar{X}$	172	177.5	177				233		245		260.5
SD	0	2.1	0				0		0		9.2
n	1	2	1				1		1		2

Male
Ring (age in years)

	20	21	22	23	24	25	26	27	28	29	30
Back-calculated											
$\bar{X}$	246.4	252.6	254.9	256.6	252.6	255.2					
SD	14.5	13.2	15.1	16.1	0	0					
n	6	6	4	3	1	1					
Observed											
$\bar{X}$		256.5	256	263.5		265					
SD		3.5	0	9.2		0					
n		2	1	2	1						

Female
Ring (age in years)

	Birth	6 months	0	1	2	3	4	5	6	7	8
Back-calculated											
$\bar{X}$	85.8	92.3	99.3	107.4	118.8	128.6	136.2	143.7	150.5	157.8	164.8
SD	5.1	4.5	5	6.3	8.4	9.4	9.5	8.5	8.8	9.4	9.9
n	67	55	52	50	48	45	41	38	35	33	33
Observed											
$\bar{X}$	91.8	104.3	106.5	107	122.3	134.8	138.3	161	154.5		
SD	4.5	7.2	6.4	2.8	3.8	16.8	26	12.5	3.5		
n	12	3	2	2	3	4	3	3	2		

Table 1 (continued)

	Female Ring (age in years)										
	9	10	11	12	13	14	15	16	17	18	19
Back-calculated											
$\bar{X}$	171.5	178.8	186.3	192.9	199.8	206.2	212.4	216.7	222.6	228.4	233.4
SD	10.2	9.6	10.8	10.9	12.4	12.9	13.3	10.5	11.6	12.3	12.6
n	33	30	28	28	28	28	28	27	27	27	27
Observed											
$\bar{X}$	183	190					262				281
SD	15.5	9.9					0				0
n	3	2					1				1

	Female Ring (age in years)										
	20	21	22	23	24	25	26	27	28	29	30
Back-calculated											
$\bar{X}$	237.9	242.1	246	149.8	252.9	256.4	258.6	262.9	265.4	266.2	265.1
SD	12.3	12.1	12.5	12.2	12.6	13.5	11.9	13.3	11.8	15.2	12.7
n	26	24	23	22	20	16	15	13	9	5	4
Observed											
$\bar{X}$	253.4	263	284	156.5	161.5	274	266.5	272	270.8	281	262
SD	14.8	0	0	2.1	9	0	16.3	10.5	6.5	0	0
n	2	1	1	2	4	1	2	4	4	1	1

	Female Ring (age in years)										
	31	32	33	34	35	36	37	38	39	40	41
Back-calculated											
$\bar{X}$	267.9	277.1	291.4								
SD	15.2	16.6	0								
n	3	2	1								
Observed											
$\bar{X}$	269	269	276								
SD	0	0	0								
n	1	1	1								

Eight of these fish were at liberty from 10.1 to 15.8 years. Estimated ages at tagging were based on the vertebral growth curve and ranged from birth to 27 years. The best example of longevity came from a dusky shark that was tagged at an estimated 27 years (260 cm FL) and was recaptured 12 years later at an estimated age of 39 years (Table 5).

Discussion

In the present study, vertebral data and length-frequency data were independently analyzed to derive estimates of von Bertalanffy growth parameters for the dusky shark. Because of the differences between the methods and their sensitivity to the data used to calculate the VBGF parameters, each method produced slightly different growth curves and, therefore, different estimates of age at maturity and longevity (calculated based on maximum reported size). The length-frequency estimates obtained from the dusky shark data are probably somewhat biased owing to limitations of the data and properties of the length-frequency model (Majkowski et al., 1987; Shepherd et al., 1987; Natanson, 1990). As a slow-growing, long-lived species, the dusky shark may have overlapping lengths at age which may obscure length modes and bias the estimates of model parameters (Rosenberg and Beddington, 1987; Shepherd et al., 1987). The vertebral method is therefore considered the more robust method and the length-frequency parameters are used for comparison only.

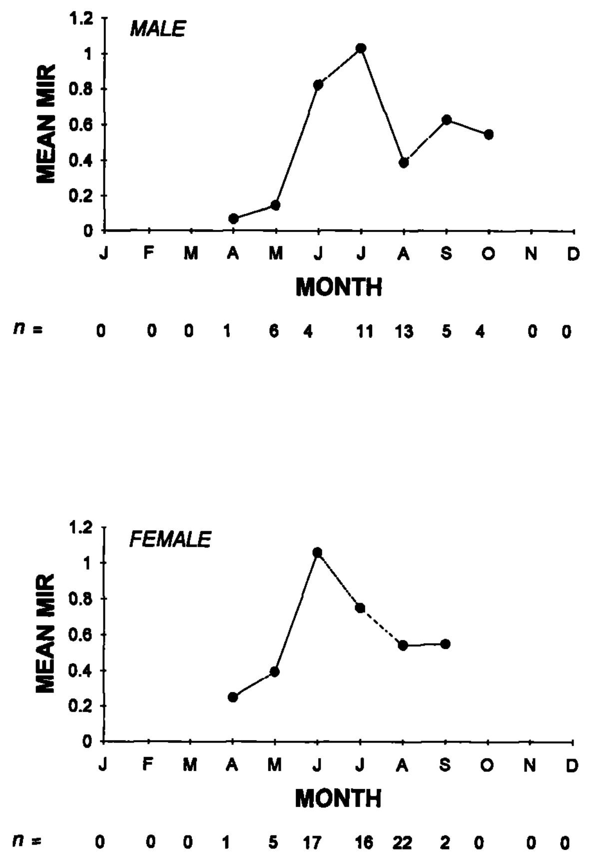

Figure 2
Mean vertebral marginal increment ratios (MIR) by month for each of four readers for the dusky shark, *Carcharhinus obscurus*. Number of samples used to calculate the means for each month are located below the figure.

Yoccoz (1991) has brought up questions as to the validity of judging biological significance based on statistical tests. He suggests that statistical significance is not necessarily indicative of biological significance; this appears to be the case with the dusky shark. The statistically significant differences shown between male and female dusky shark vertebral growth curves may not reflect biological differences. Examination of the length-at-age data suggests that biologically the differences between male and female vertebral curves are small. The age and size at maturity differ by only two years and five centimeters for males and females (Table 4). Females are presumed to grow ultimately to a larger size than males. This means that either growth slows in males after maturity or that males do not live as long as females.

The vertebral VBGF derived in this study is very similar to the curve attained by Hoenig (1979) for combined sexes for the ages under consideration (birth to 33 years) but is different from data presented by Lawler (1976) and Schwartz (1983). Hoenig's (1979) parameter values for the VBGF have a slightly higher L_∞ and t_0 and lower K than parameters derived from vertebral analysis in the present study (Table 2). Lawler (1976), using vertebral analysis to determine the age of female dusky sharks, obtained VBGF-parameter values markedly different from the present study (Table 2). The L_∞ in his study is more than twice as large as the L_∞ reported here and his K value suggests a much slower growth rate. These two factors combine to make Lawler's (1976) curve appear as a straight line from birth to 34 years.

Table 2
The von Bertalanffy parameters derived in this study compared to those derived in Hoenig's (1979) study of male and female dusky sharks and Lawler's (1976) study of female dusky sharks, *Carcharhinus obscurus*.

	Male				Female				Combined			
Parameters	L_∞	K	t_0	n	L_∞	K	t_0	n	L_∞	K	t_0	n
This study:												
Vertebrae	373	0.038	–6.28	47	349	0.039	–7.04	67	352	0.040	–6.43	120
Length-frequency	293	0.049	–5.99	133	392	0.040	–5.34	208	296	0.062	–4.68	350
Hoenig, 1979									385	0.034	–5.99	22
Lawler, 1976					732	0.014	–6.7	13				

Lawler's (1976) L_∞ is unrealistically high when compared with the maximum reported size from the literature (308 cm FL [Springer, 1960]) and with those derived in both Hoenig's (1979) study and the present one. Schwartz (1983) also used vertebral bands in an attempt to age the dusky shark. In general, his back-calculated size-at-age data (Schwartz, 1983; Table 4) are lower than those in the present study. His estimates of size at birth are much lower than reported sizes at birth, suggesting that prebirth bands may have been counted (Casey et al., 1985). Marginal increment data from the present study do not support Schwartz's (1983) hypothesis of a much faster growth rate with two bands per year based on his marginal increment data.

Tagging data combined with vertebral estimates indicate that the dusky shark can live for at least 40 years. The largest reported dusky shark in the literature was a 308 cm FL female (Springer, 1960) which corresponds to 51 years based on our vertebral VBGF. Tag and recapture data on the large dusky shark at liberty for 12 years add credence to the vertebral longevity estimate by verifying that these fish do live up to 40 years. Thus, the dusky shark appears to be a long-lived, late-maturing species, exhibiting a pattern typical of carcharhinids. The female bull shark, *C. leucas*, can live over 24 years and does not reach maturity until at least 18 years of age (Branstetter and Stiles, 1987). Tagging evidence has shown that the sandbar shark, *C. plumbeus*, can reach ages of at least 40 years and may not mature until 29 years of age (Casey and Natanson, 1992). The lemon shark, *Negaprion brevirostris*, which reaches at least 20 years of age and does not reproduce until 11 to 13 years, also follows this pattern (Brown and Gruber, 1988). Preliminary estimates on the age of the bronze whaler, *C. brachyurus*, indicate that males do not mature for 13 to 19 years and females for 19 to 20 years. Both may attain ages over 30 years (Walter and Ebert, 1991). The blue shark, *Prionace glauca*, appears to be atypical of most carcharhinids in having a relatively fast growth rate and a short life-span (13–16 years) (Skomal, 1990). A recent recapture from an Australian school shark, *Galeorhinus australis*, after 42 years at liberty indicates that the galeorhinids also follow this pattern.[3]

Casey and Natanson's (1992) study on the age of the sandbar shark (*C. plumbeus*) showed that in a

Table 3

Results of comparison of the vertebral von Bertalanffy growth equations for male and female dusky sharks, *Carcharhinus obscurus*, using Bernard's (1981) multivariate analysis. Shown is the estimated variance-covariance matrix (S).

	L_∞	K	t_0	
L_∞	131.9769	–0.02831	–3.16979	
K		0.0000065	0.00077	= S
t_0			0.115042	

[3] Olsen, A. H. Newton 5074, South Australia. Personal commun., Jan. 1994.

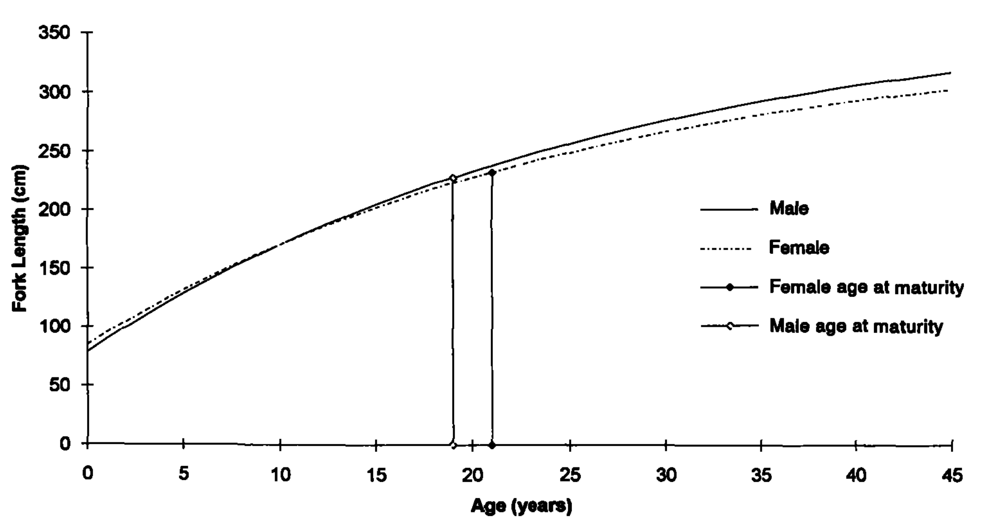

Figure 3

Von Bertalanffy growth curves generated from vertebral data for male and female dusky sharks, *Carcharhinus obscurus*.

species where good tag and recapture data are available (i.e. where specimens are measured at both tagging and recapture, properly identified, and there is sufficient sample size), a better estimate of longevity is produced than from hardpart analysis. They concluded that the initial growth curve based on vertebrae for the sandbar shark had severely underestimated the age at maturity and maximum age and had overestimated the growth rate (Casey et al., 1985). At the present time, the vertebral growth curve

Table 4

Size at age of the dusky shark, *Carcharhinus obscurus*, calculated from the von Bertalanffy growth equations. Size at age closest to maturity is in bold type.

Years	Length-frequency male	Length-frequency female	Length-frequency combined	Vertebral male	Vertebral female	Vertebral combined
Birth	75	75	75	78	84	81
1	95	100	100	89	95	92
2	104	111	112	100	105	102
3	113	122	123	110	114	112
4	122	133	134	119	123	121
5	130	143	143	129	132	131
6	138	153	153	138	140	139
7	145	162	161	146	148	148
8	152	171	169	155	156	156
9	159	180	177	163	163	164
10	166	188	184	170	171	171
11	172	196	191	178	177	178
12	177	204	197	185	184	185
13	183	211	203	192	190	192
14	188	218	209	199	197	198
15	193	225	214	205	202	204
16	198	**232**	219	211	208	210
17	203	238	223	217	214	216
18	207	244	228	223	219	221
19	211	250	**232**	**228**	224	226
20	215	255	**236**	234	229	**231**
21	219	261	239	239	**233**	236
22	222	266	243	244	238	241
23	226	271	246	249	242	245
24	229	276	249	253	246	250
25	**232**	280	252	258	250	254
26	235	294	254	262	254	257
27	238	289	257	266	258	261
28	240	293	259	270	261	265
29	243	297	262	274	264	268
30	245	300	264	277	268	272
31	247	304	266	281	271	275
32	250	307	267	284	274	278
33	252	311	269	287	277	281
34	254	314	271	291	280	284
35	256	317	272	294	282	286
36	257	320	274	297	285	289
37	259	323	275	299	287	292
38	261	325	276	302	290	294
39	262	328	277	305	292	296
40	264	331	279	307	294	298
41	265	333	280	310	296	301
42	266	335	281	312	298	303
43	268	338	282	314	300	305
44	269	340	282	316	302	307
45	270	342	283	318	304	308

Table 5

Tag and recapture data used to obtain longevity estimates for the dusky shark, *Carcharhinus obscurus*. N/A = not available.

		Tagging			
Tag number	Sex	Fork length (cm) (estimated)	Age (estimated)	Time at liberty (years)	Total age (years)
63647	N/A	260	27 yr	12	39
YR200X	N/A	84	6 months	15.8	16.3
42204	F	130	4+ yr	11.9	16+
21367	F	73	Birth	11.6	11.6
48478	N/A	116	3+ yr	10.9	13.9+
39360	F	111	2+ yr	10.1	12.1+
F66 8802	M	73	Birth	11.8	11.8
37913	F	122	4 yr	14.5	18.5

is the best estimate available for the dusky shark. However, it should be kept in mind that the vertebral growth curve generated for the dusky shark may also underestimate age at maturity and maximum age.

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Literature cited

Anonymous.
1993. Secretarial shark fishery management plan for the Atlantic Ocean. U.S. Dep. Commer., NOAA, NMFS, Washington, D.C.

Bernard, D. R.
1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat. Sci. 38:233–236.

Bertalanffy, L., von.
1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10:181–213.

Branstetter, S.
1987. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Environ. Biol. Fishes 19:161–173.

Branstetter, S., and R. Stiles.
1987. Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ. Biol. Fishes 20:169–181.

Brothers, E. B.
1983. Summary of round table discussions on age validation. *In* E. D. Prince and L. M. Pulos (eds.), Proceedings of the int. workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks, p. 35–44. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

Brown, C. A., and S. H. Gruber.
1988. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral data. Copeia 1988:747–753.

Casey, J. G., and J. J. Hoey.
1985. Estimated catches of large sharks by U.S. recreational fishermen in the Atlantic and Gulf of Mexico. *In* Shark catches from selected fisheries off the U.S. coast, p. 15–20. U.S. Dep. Commer., NOAA Tech Rep. NMFS 31.

Casey, J. G., H. L. Pratt Jr., and C. E. Stillwell.
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42:963–975.

Casey, J. G., and L. J. Natanson.
1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 49:1474–1477.

Castro, J. I.
1983. The sharks of North American waters. Texas A&M Univ. Press, College Station, TX, 180 p.

Compagno, L. J. V.
1984. FAO species catalogues. Vol. 4: Sharks of the world. An annotated and illustrated catalogue of the shark species known to data, Parts 1 and 2. FAO Fish. Synopsis 125, 655 p.

Hoenig, J. M.
1979. Growth rates of large sharks determined by vertebral rings. Ph.D. diss., Univ. Rhode Island, Kingston, 85 p.

Hoenig, J. M., and S. H. Gruber
1990. Life-history patterns in the elasmobranchs: implications for fisheries management. *In* H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi (eds.), Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries, p. 1–16. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.

Hoey, J. J.
1983. Analysis of longline fishing effort for apex predators (swordfish, shark, and tuna) in the western North Atlan-

tic and Gulf of Mexico. Ph.D. diss., Univ. Rhode Island, Kingston, 288 p.

Holden, M. J.
1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164:360–367.

Humason, G. L.
1972. Animal tissue techniques, fourth ed. W. H. Freeman and Co., San Francisco, 661 p.

Lawler, E. F., Jr.
1976. The biology of the sandbar shark *Carcharhinus plumbeus* (Nardo, 1827) in the lower Chesapeake Bay and adjcent waters. M.S. thesis, College of William and Mary, VA, 49 p.

Majkowski, J., J. Hampton, R. Jones, A. Laurec, and A. A. Rosenberg.
1987. Sensitivity of length-based methods for stock assessment: report of Working Group III. *In* D. Pauley and G. R. Morgan (eds.), Length-based methods in fisheries research, p 363–372. ICLARM Conference Proceedings 13.

Marquardt, D. W.
1963. An algorithm for least-squares estimation of nonlinear parameters. J. Soc. Indus. Appl. Math. 11:431–441.

Musick, J. A., S. Branstetter, and J. A. Colvocoresses.
1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. *In* S. Branstetter (ed.), Conservation biology of elasmobranchs, p. 1–18. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 115.

Natanson, L. J., and G. M. Cailliet.
1990. Vertebral growth zone deposition in Pacific angel sharks. Copeia 1990:1133–1145.

Prager, M. M., S. B. Saila, and C. W. Recksiek.
1987. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science. Dep. Oceanography, Old Dominion Univ., Norfolk, VA., Tech. Rep. 87-10:1–37.

Ricker, W. E.
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479–541.

Rosenberg, A. A., and J. R. Beddington.
1987. Monte-Carlo testing of two methods for estimating growth from length-frequency data with general conditions for their applicability. *In* D. Pauley and G. R. Morgan (eds.), Length-based methods in fisheries research, p. 283–298. ICLARM Conference Proceedings 13.

Schwartz, F. J.
1983. Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks based on vertebral ring counts. *In* E. D. Prince and L. M. Pulos (eds.), Proceedings of the int. workshop on age determination of oceanic pelagic fishes; tunas, billfishes, and sharks, p. 167–174. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

Shepherd, J. G.
1987. A weakly parametric method for estimating growth parameters from length composition data. *In* D. Pauly and G. R. Morgan (eds.), Length-based methods in fisheries research, p. 113–119. ICLARM Conference Proceedings 13.

Shepherd, J. G., G. R. Morgan, J. A. Gulland, and C. P. Mathews.
1987. Methods of analysis and assessment: report of Working Group II. *In* D. Pauley and G. R. Morgan (eds.), Length-based methods in fisheries research, p. 353–362. ICLARM Conference Proceedings 13.

Skomal, G. B.
1990. Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. M.S. thesis, Univ. of Rhode Island, Kingston, 82 p.

Springer, S.
1960. Natural history of the sandbar shark, *Eulamnia milberti*. Fish. Bull. 61:1–38.

Walter, J. P., and D. A. Ebert.
1991. Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. S. Afr. J. Mar. Sci. 10:37–44.

Yoccoz, N. G.
1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. Bull. Ecol. Soc. Am. 71(2) 106–111.