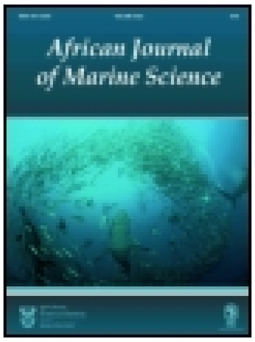

South African Journal of Marine Science

ISSN: 0257-7615 (Print) (Online) Journal homepage: http://www.tandfonline.com/loi/tams19

A preliminary estimate of age and growth of the dusky shark *Carcharhinus obscurus* from the South-West Indian Ocean, with comparisons to the western North Atlantic population

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S. Afr. J. mar. Sci. 17: 217–224
1996

A PRELIMINARY ESTIMATE OF AGE AND GROWTH OF THE DUSKY SHARK *CARCHARHINUS OBSCURUS* FROM THE SOUTH-WEST INDIAN OCEAN, WITH COMPARISONS TO THE WESTERN NORTH ATLANTIC POPULATION

L. J. NATANSON and N. E. KOHLER**

Age and growth of the dusky shark *Carcarhinus obscurus* from the South-West Indian Ocean was determined from bands in the vertebrae of 42 individuals. Age to maturity was estimated at 20,5 years for males and between 17 and 24 years for females. The oldest fish examined was a 34-year-old female. The Von Bertalanffy parameters calculated for the sexes combined were: L_∞ = 334, K = 0,047 and t_0 = –5,18. The growth rate of dusky sharks from the South-West Indian Ocean was similar to that of the western North Atlantic population.

The dusky shark *Carcharhinus obscurus* is a common, coastal pelagic species distributed worldwide in warm, temperate and tropical waters (Compagno 1984). In the South-West Indian Ocean (SWI), it is one of the most common species (D'Aubrey 1965). Adults occur primarily in the Moçambique Channel along the outer continental shelf, and (mainly large females) south to KwaZulu/Natal, South Africa (Fig. 1). They are occasionally reported inshore and have been caught as far south as Cape Recife (Bass 1978, Van der Elst 1979, Compagno *et al.* 1989, D. A. Ebert, U.S. Abalone, California, pers comm.). Newborn dusky sharks of 80–90 cm total length (*TL*) are generally found in a nursery area off the southern coast of KwaZulu/Natal, and as juveniles move out of this area when females come in to pup (Bass *et al.* 1973, Bass 1978, Compagno 1984). Dusky sharks from that region also undertake seasonal, temperature-related migrations, moving as far south as False Bay (Fig. 1) in spring and summer and returning north to KwaZulu/Natal in winter (Compagno *et al.* 1989, D. A. Ebert, pers. comm.).

In South Africa, dusky sharks are subject to mortality from both sportfishing and protective gillnetting. There was a sharp increase in the number of juvenile dusky sharks landed after 1968, which can be ascribed to sportfishing and which contributed to a general increase in the catches of elasmobranchs (Van der Elst 1979). A system of gillnets was placed off Durban on the KwaZulu/Natal coast in 1952 by the Natal Sharks Board to protect bathers from shark attacks. In the 1960s, the system was extended along the coast (Fig. 1) to beaches farther north to Richards Bay and south to Mzamba (Cliff *et al.* 1988). Although in recent years live sharks found in the nets have been tagged and released (Cliff *et al.* 1988), the nets do contribute to shark mortality (Van der Elst 1979). The removal of large, inshore sharks by gillnetting has decreased adult predation on juvenile dusky sharks, causing the apparent proliferation of small sharks in the 1970s (Van der Elst 1979).

The growth characteristics of elasmobranchs render them highly susceptible to exploitation (Holden 1973). Age and growth information on the western North Atlantic (WNA) population of dusky sharks indicates that they mature at 19–21 years of age and that individuals may live for up to 40 years (Natanson *et al.* 1995). The late age at maturation, combined with the low fecundity (mean 7,7 embryos per litter, Clark and Von Schmidt 1965), suggest that they may be particularly sensitive to fishing pressure. Musick *et al.* (1993) showed that the WNA population of dusky sharks has been declining since the mid-1960s.

The age and growth characteristics of the SWI population of dusky sharks are currently unknown. It is the aim of this study to determine these characteristics and to compare them with those of the WNA population.

MATERIAL AND METHODS

Dusky shark vertebrae were obtained from several sources. In all, 45 vertebrae were obtained from the Natal Sharks Board (NSB) and 12 from D. A. Ebert (California, U.S.A.). Samples were collected between 1984 and 1988 in all months except July, August, November and December off the south-east coast of South Africa between Zinkwazi Beach and False Bay (Fig. 1).

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Manuscript received: March 1996

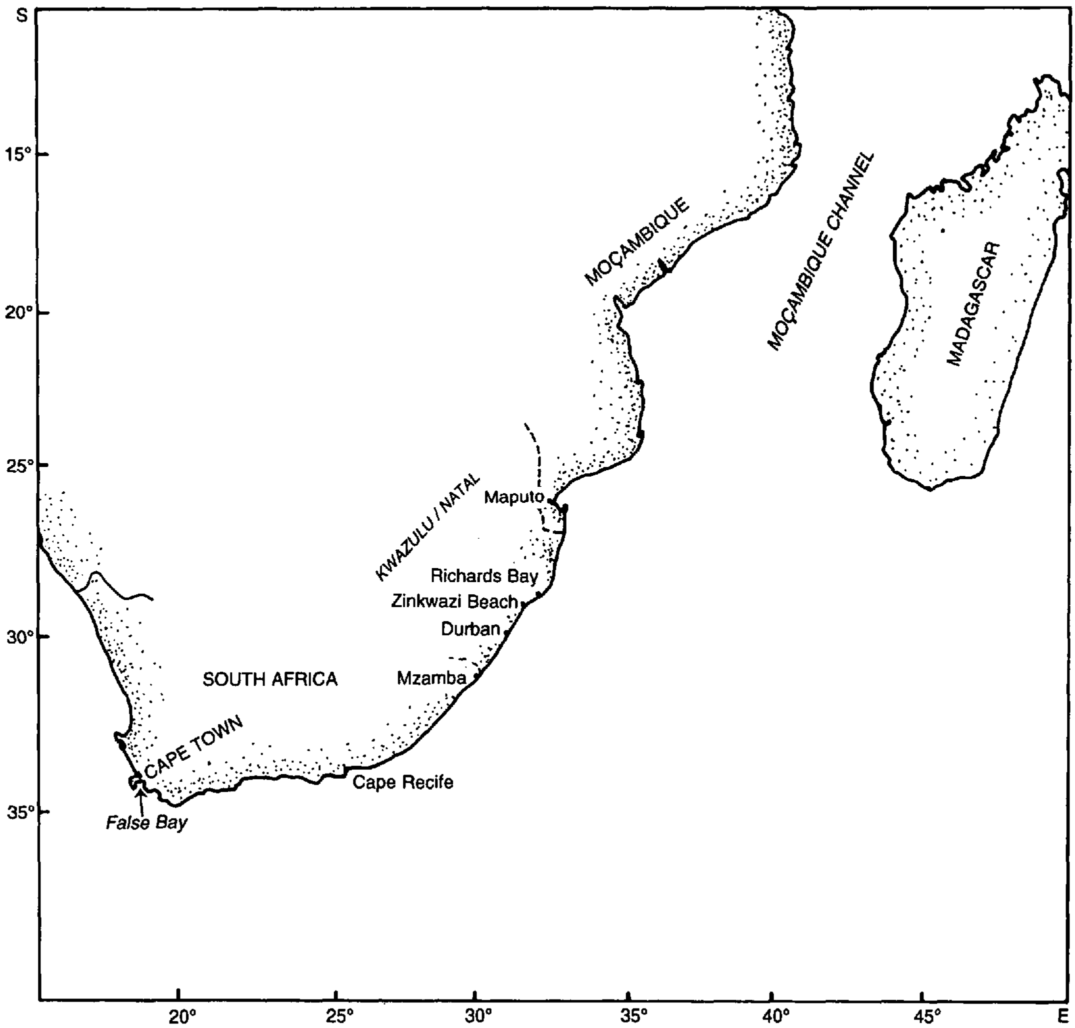

Fig. 1: Map of southern Africa showing the regions and loca- tions mentioned in the text

Length measurements

Precaudal lengths (*PCL*, cm) were measured in NSB samples from the tip of the snout to the distal edge of the precaudal pit, following Bass *et al.* (1973). Total lengths (*TL*, cm) were measured in the samples obtained from D. A. Ebert, following Compagno (1984). All measurements were converted to fork length (*FL*) using regressions obtained from dusky sharks caught in the WNA. The regressions were used interchangeably between the two populations as, based on proportional morphometric measurements, Compagno (1984) considered them to be the same species. *PCL* was converted to *FL* using the equation $FL = 1{,}09\ (PCL) + 0{,}10$ ($r^2 = 0{,}99$; $n = 24$). *TL* was converted to *FL* using the equation $TL = 1{,}17\ (FL) + 4{,}93$ ($r^2 = 0{,}99$; $n = 23$).

Vertebral samples

Sections of vertebral columns were removed from above the branchial chamber, trimmed of excess connective tissue and then dried in a refrigerator (NSB) or preserved in isopropyl alcohol (D. A. Ebert). Vertebrae were sent to the National Marine Fisheries Service (NMFS), Narragansett, U.S.A., for histological processing. Dried vertebrae were rehydrated for 48 hours and then stored in 70% ethanol. Fork length to vertebral radius (*VR*) regressions were calculated for each preservation method and *t*-tests were used to determine whether the preservation methods affected the size of the vertebrae differently. Two vertebrae from each specimen were processed histologically (Natanson *et al.* 1995)

Vertebral sections were read from images projected on a Summagraphics MM-1812 digitizing tablet (Skomal 1990). The same section from each centrum was read at least once by each of the current authors. If both authors considered a section unreadable, the sample was not used in the final analysis. The radius of each centrum was measured from the focus to the distal margin of the intermedialia. Measurements from the focus to each growth band were taken along the internal corpus calcareum. All measurements were digitized directly into an IBM PC-XT. Annual growth marks were defined following Casey *et al.* (1985) for the sandbar shark *Carcharhinus plumbeus*.

Two indices of precision: the average percentage error (*APE*) and the percentage error (*D*) were calculated to compare the reproducibility of age determinations between readers. The *APE* index calculates the error in ageing a specific fish as a fraction of the average of all age estimates for that fish (Beamish and Fournier 1981), whereas *D* is considered to be a more unbiased and consistent index of precision (Chang 1982).

The relationship between *VR* and *FL* was calculated to determine the equation for back-calculation of the size-at-age data. As this relationship was linear and did not pass through the origin, the Lee method of linear regression was considered more appropriate (Ricker 1969):

$$FL = a + (b \times VR) \quad ,$$

where a is the intercept on the length axis and b is the slope (Lagler 1956).

A growth curve was produced by fitting a Von Bertalanffy growth function (*VBGF*) to the age-length data using FISHPARM version 3.0 (Prager *et al.* 1987). FISHPARM implements Marquardt's algorithm for non-linear least-squares parameter estimation (Marquardt 1963), which allows the parameters of the non-linear equation to be directly estimated without transformation of the data.

Marginal increment analysis

Validation of the annual periodicity of band formation was attempted using the marginal increment ratio (*MIR*), calculated using the equation

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

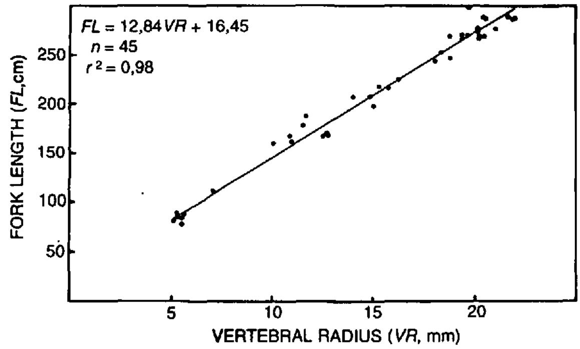

Fig. 2: Relationship between vertebral radius and fork length for male and female dusky sharks *Carcharhinus obscurus* from the South-West Indian Ocean (SWI)

where R_n is the last complete band near the vertebral edge.

The mean monthly *MIR* was then plotted against month to locate a periodic trend in band formation.

Growth comparisons between SWI and WNA populations

Using combined sexes, growth data (*FL* v. band number) for the SWI and WNA samples were linearized and the resulting regressions were compared using *t*-tests for slope and elevation (Zar 1974). Von Bertalanffy growth functions were then plotted and compared graphically. Also, Bernard's (1981) multivariate analysis was used to compare the SWI and WNA populations for the differences in *VBGF* parameters. This method also determined which of the *VBGF* parameters caused the most statistically significant differences in growth.

RESULTS

Vertebral samples

Of the processed vertebrae from the SWI population, six were eliminated because of lack of length data or because they were from embryos. Of the remaining 51 samples, nine (17,6%) were disregarded as unreadable, leaving 42 specimens (35 females and 7 males) aged between 0 and 34 years and ranging in size from post-partum young (80,5 cm *FL*) to a 298 cm *FL* adult. No significant difference was found between the *FL* : *VR* relationships for the different preservation methods ($p < 0,05$), and therefore all vertebrae were used inter-

Table I: Back-calculated and observed size-at-age data for dusky sharks *Carcharhinus obscurus* (sexes combined) from the South-West Indian Ocean population

Ring (age in years) 0 = birth	Size-at-age (mm)					
	Back-calculated			Observed		
	Mean	*SD*	*n*	Mean	*SD*	*n*
0	81,3	5,0	43	87,8	8,5	10
1	87,3	5,6	33			
2	94,7	6,5	33			
3	102,7	7,2	33			
4	110,3	8,3	33			
5	118,8	10,3	33			
6	126,0	11,2	33			
7	134,0	12,0	33	159,0		1
8	141,9	13,5	32	161,0		1
9	150,7	15,6	31			
10	160,0	16,2	31	171,0	6,1	3
11	168,9	17,5	28			
12	177,2	17,9	28	174,3	10,2	3
13	186,1	18,9	25	206,0		1
14	193,5	18,8	24	211,0	19,8	2
15	201,3	19,9	22	232,3	36,5	3
16	205,5	15,5	19			
17	214,0	15,6	19			
18	221,1	15,5	19	216,0		1
19	230,2	15,0	18			
20	238,1	15,1	18	268,0		1
21	243,1	15,6	17			
22	250,0	15,4	17	255,0	10,3	3
23	255,6	15,8	14	271,0	38,9	2
24	260,8	16,3	12	269,0	0,7	2
25	265,6	19,1	10	276,0	10,0	2
26	267,1	19,1	7	287,0	0,6	3
27	261,4	18,5	4	276,0		1
28	262,9	20,7	3	269,0		1
29	270,4	28,1	2	288,0		1
30	254,3		1			
31	260,7		1			
32	263,3		1			
33	268,4		1			
34	274,8		1	268,0		1

changeably. The *FL* : *VR* regression showed a strong, linear relationship (sexes combined, Fig. 2), indicating that vertebrae are suitable structures for age determination in dusky sharks.

The precision estimates (*APE* and *D*) provided similar results, ranging from 0 to 7,3% for individual fish with an overall sample mean of 3,3%. Therefore, owing to the close agreement in estimated age between the readers, the measurements for each specimen were averaged and the resulting values used for back-calculation.

When the back-calculated lengths were compared to the observed length-at-age data, Lee's phenomenon was observed (Table I), the magnitude of which increased with increasing length. Back-calculated length at the first band (81,3 cm *FL*) corresponded closely to the known size range at birth of 68–81 cm *FL* (Castro 1983, Compagno 1984). This indicates that the first band is formed at or near birth. The back-calculated *VBGF* fitted the observed data well for young and old fish, giving L_∞ and size-at-birth values close to known parameters (Table II). The portion of the back-calculated *VBGF* from just after size at maturity (218–235 cm *FL*, Bass *et al.* 1973) to approximately 25 years did not correspond closely to the data because of Lee's phenomenon. The back-calculated *VBGF* was used as the final curve because samples in the younger age-classes were lacking (Table I). Confidence intervals around the parameters were relatively low (Table II).

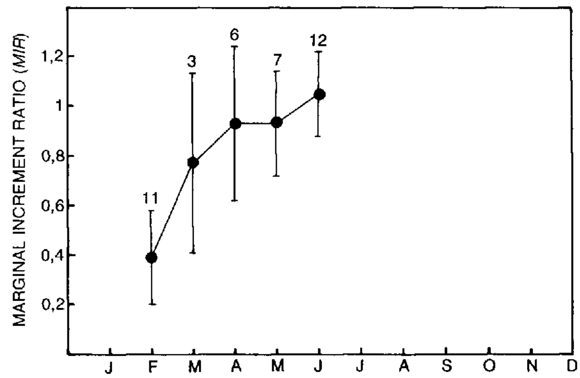

Fig. 3: Mean marginal increment ratio (± *SD*) and sample sizes (sexes combined) for dusky sharks *Carcharhinus obscurus* from the South-West Indian Ocean (SWI)

The scarcity of data for all months of the year prohibited an accurate determination of annual band formation. However, the *MIR* data showed a consistent increase between February and June (Fig. 3). This indicates that the band is formed between the beginning

Table II: Comparisons of Von Bertalanffy growth function parameters and 95% confidence intervals (*CI*) for dusky sharks *Carcharhinus obscurus* (sexes combined) from the South-West Indian Ocean (this study) and the western North Atlantic Ocean (after Natanson *et al.* 1995)

Population	Parameter						
	L_∞	*CI*	K	*CI*	t_0	*CI*	*n*
South-West Indian Ocean	334	29,22	0,047	0,01	-5,18	1,26	42
Western North Atlantic Ocean	352	15,54	0,040	0,004	-6,43	0,65	120

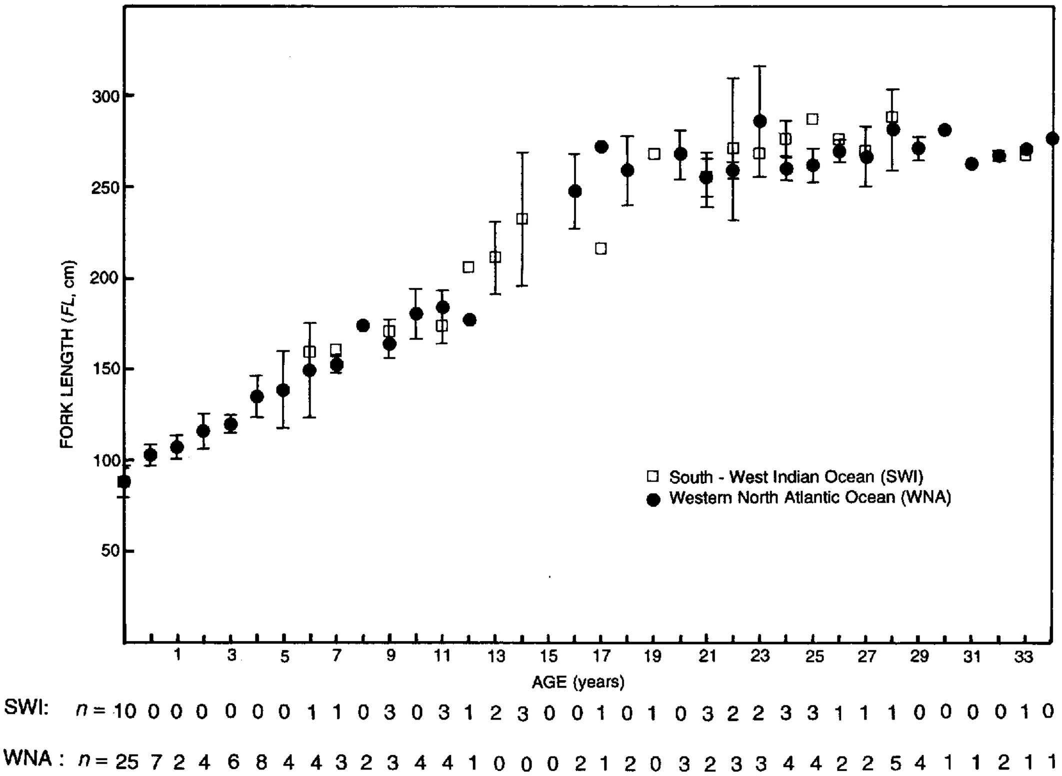

Fig. 4: Comparison of means and standard deviations of observed size-at-age data for dusky sharks *Carcharhinus obscurus* (sexes combined) from the South-West Indian Ocean (SWI) and western North Atlantic Ocean (WNA). Number of specimens (n) used in the calculations for each month are shown

of winter (June) and the beginning of summer (January), and is visible at the margin by February. June was used as an arbitrary month of band formation for the assignment of age-classes.

The results of the tests to compare the growth of dusky sharks between the SWI and the WNA populations differed. The growth plots of length-at-age (± *SD*) for the two populations overlapped considerably (Fig. 4), and no significant difference was found in the linearized size-at-age data ($p > 0{,}05$). However, Bernard's (1981) multivariate analysis showed a significant difference in the *VBGF* parameters between the two populations ($p < 0{,}05$), the t_0 values being the most dissimilar followed by K and L_∞. However, the differences appear slight when the Von Bertalanffy curves are plotted for the two populations (Fig. 5), a statement borne out by the fact that the *VBGF* parameters have overlapping confidence intervals (Table II).

DISCUSSION

The dusky shark is a long-lived, late-maturing species. The present value for L_∞ of 334 cm *FL* for combined data (Table II) is consistent with the maximum size of 300 cm *PCL* (328 cm *FL*) reported for a dusky shark from the SWI by Cliff and Wilson (1986). As L_∞ is the maximum theoretically attainable length for a species, it should be slightly larger than the maximum reliably reported length (Hoenig 1979). Based on the largest reported length and the Von Bertalanffy growth parameters obtained in the present study, individuals may live for longer than 70 years. Female and male sizes at maturity of 218–252 cm *FL* and 235 cm *FL* respectively (Bass *et al.* 1973) correspond to ages of 17–24 and 20,5 years respectively.

The length and age data for the dusky shark produced a typical Von Bertalanffy curve. Up to maturity,

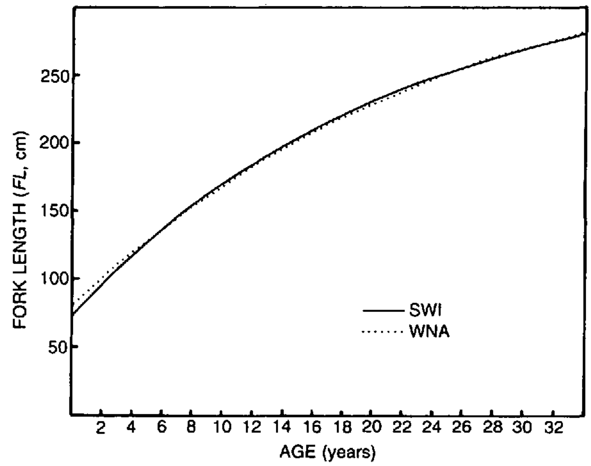

Fig. 5: Comparison of Von Bertalanffy growth curves derived from back-calculated vertebral data (sexes combined) for dusky sharks *Carcharhinus obscurus* from the South-West Indian Ocean (SWI) and the western North Atlantic Ocean (WNA)

the calculated *VBGF* fitted the observed data. However, from around the size of maturity to approximately 25 years, the *VBGF* lies below the observed data. The mean size at birth of the different populations predicted by the models (SWI = 81,3 cm *FL*, WNA = 82,5 cm *FL*) are well within the size range at birth reported for dusky sharks (Bass *et al.* 1973, Bigelow and Schroeder 1948, Castro 1983). Data from the present study show that growth of the dusky shark slows considerably after maturity, when individuals of the same size could vary in age by more than 15 years (Fig 3). This is not unusual in carcharhinids, but it appears extreme in dusky sharks. Therefore, although it may be possible to predict age from length using the *VBGF* up to size at maturity, this relationship is not reliable in mature dusky sharks.

In the present study, vertebral bands were analysed to reconstruct individual growth histories, which were then combined to derive a Von Bertalanffy growth curve for the dusky shark. Problems that arose from use of this method included the uncertainty of the periodicity of the bands (Beamish and McFarlane 1983), the potential for misinterpretation of bands v. checks (Casey *et al.* 1985), and the difficulty in reading the numerous, closely spaced bands at the centrum edge of large fish (Hoenig 1979). Marginal increment analysis provided a form of validation to determine the periodicity of band formation, which suggests that the SWI dusky shark population has annual periodicity in incremental growth. The use of multiple readers decreased the possibility of misinterpretation of bands. However, it should be borne in mind that the vertebral growth curves for carcharhinids may underestimate age at maturity and maximum age (Casey and Natanson 1992).

Cailliet *et al.* (1990) discussed the validity of comparing growth characteristics between two populations of the same species. They suggested that observed intra- and interspecific growth differences could be a result of varying techniques of preparation and readings of vertebrae, reader accuracy and precision, individual variation (which can be masked using a growth model), goodness-of-fit of a growth model, sample size and bias. In the present study, the above factors have been considered and attempts were made to limit their bias. Preparation and readings were done identically for each population, reader accuracy and precision for both populations were relatively high for a long-lived species, and individual variation was considered by comparing the observed size-at-age data. Other sources of error included the low sample size for the SWI population and the inability to represent all size-classes equally in either population. Additionally, length conversions using regression analysis is a possible source of variation.

Bernard's (1981) multivariate test showed significant differences in growth parameters between the populations. However, Cerrato (1990) cautioned that all test results from Von Bertalanffy growth parameter comparisons should be considered approximate, and that an important factor to consider was the influence of small sample sizes (< 300) on the accuracy of such tests. Although Cerrato (1990) recommended using the likelihood ratio test, he showed that Bernard's test differed from that test in only 4% of cases. Because of the small sample size in the present study, the reliability of the tests used should be viewed with caution.

Further, as the size-at-age confidence intervals overlapped between most age-classes of the two populations (Fig. 5), individual variation was therefore greater than any real difference between the populations. This variation is obscured when using a growth model (Cailliet *et al.* 1990) and is not taken into account when statistically testing the models (Labelle *et al.* 1993). The overlap of the confidence intervals around each parameter indicated that the error around the growth curves was enough to mask any real differences in the populations. This suggests that, although there is a statistical difference between the growth curves for the two populations, this may not be of any biological significance, a consideration that needs to be investigated (Yoccoz 1991, Labelle *et al.* 1993).

The life-history strategies of dusky shark populations from both the SWI and the WNA are similar, based on ages derived from the current growth curves

Table III: Comparisons of life-history information for dusky sharks *Carcharhinus obscurus* from the South-West Indian Ocean (SWI) and western North Atlantic Ocean (WNA)

Parameter	SWI	WNA
Mean number of pups per litter	9,9[1,3]	7,7[8]
Size at birth (cm *FL*)	54,8–81,3[1*]	68,7–81,2[4,5*]
Size at maturity (cm *FL*)		
Male	235[1,2*]	231[9*]
Female	218–252[1,2*]	235[9*]
Age at maturity (years)		
Male	20,5	19[6]–20
Female	17–24	17[6]–21
Maximum reported size (cm *FL*)		
Female		303[9*]
Sex not reported	328[7†]	
Age at maximum reported size (years)		
Female		43[10]–47[6]
Sex not reported	> 70	

* Calculated from *TL*
† Calculated from *PCL*
[1] Bass *et al.* (1973)
[2] Bass (1978)
[3] Van der Elst (1979)
[4] Castro (1983)
[5] Bigelow and Schroeder (1948)
[6] Natanson *et al.* (1995)
[7] Cliff and Wilson (1986)
[8] Clark and von Schmidt (1965)
[9] Springer (1960)
[10] Based on combined vertebral curve: this study

and from the literature. The only difference between them is that individuals from the SWI apparently grow to a slightly larger size than those from the WNA, and therefore, assuming similar population growth rates, a greater age (Table III). Also, the mean number of pups per litter is higher in the SWI population. The two populations have overlapping ranges for size at maturity and size at birth (Table III), and the corresponding ages at maturity are also similar.

In conclusion, there appears to be no marked difference in the biology of dusky sharks between the WNA and the SWI populations, despite their geographic isolation. This may be attributed to similarities in the physical environment off the South African and western North Atlantic coasts (Bass *et al.* 1973, Walford and Wickland 1968). Along both coasts, seasonal temperature changes induce dusky sharks to migrate. With increasing temperature in summer, they migrate north (in the WNA) and south (in the SWI), and in winter these migrations are reversed (Bass *et al.* 1973, J. G. Casey, NOAA/NMFS, Narragansett, U.S.A., unpublished data). Also, the different populations have similar diets, feeding primarily on benthic organisms (Bass *et al.* 1973, C. E. Stillwell, NOAA/NMFS, unpublished data). These ecological similarities may explain the similarity in growth rates between the two shark populations.

ACKNOWLEDGEMENTS

We thank Mr G. Cliff of the Natal Sharks Board (NSB), South Africa, and Dr D. A. Ebert of US Abalone, California, U.S.A., for providing the vertebral samples and data for this study. We also thank Dr G. Cailliet (Moss Landing Marine Laboratories, California, U.S.A.) for providing various computer programmes and, together with his students, for their discussions of the results. Ms C. Belcher (Department of Natural Resources, Georgia, U.S.A.) provided statistical help. Ms S. Wintner (NSB) provided much assistance, support and comments during the final stages of this study. Our colleagues Messrs J. Casey and H. W. Pratt, Ms P. Turner, Ms R. Briggs and the rest of the Apex Predator Investigation group provided valuable input.

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