S. Afr. J. mar. Sci. 24: 1–8
2002

AGE AND GROWTH OF THE SPINNER SHARK *CARCHARHINUS BREVIPINNA* (MÜLLER AND HENLE, 1839) OFF THE KWAZULU-NATAL COAST, SOUTH AFRICA

B. R. ALLEN and S. P. WINTNER†*

Age and growth of the spinner shark *Carcharhinus brevipinna* off the KwaZulu-Natal coast of South Africa was investigated from vertebral growth ring counts of 67 specimens (54–213 cm precaudal length, *PCL*). Counts were made from sectioned vertebral centra by two readers. There was a statistically significant difference between the growth functions of both sexes and Von Bertalanffy growth functions were L_∞ = 196.3 cm, k = 0.146 year^{-1} and t_0 = -2.3 year for males; L_∞ = 232.8 cm, k = 0.1 year^{-1} and t_0 = -2.9 year for females. This difference was thought to be attributable to initially faster growth rate of males until maturity, after which their growth rate slowed below that of females. Number of growth rings at maturity was 8–10 for both males (150 cm *PCL*) and females (160 cm *PCL*). The oldest female and male in the sample had 17 (213 cm *PCL)* and 19 growth rings (192 cm *PCL*) respectively. Annual growth ring deposition could not be validated using marginal increment ratio analysis because of the small sample size. Geographic variation in growth rate and maximum attainable size was evident between the spinner shark populations of the Indian and Atlantic oceans. Although *C. brevipinna* grow slowly, the protective nets off the KwaZulu-Natal coast do not appear to have any detrimental effect on the population.

Key words: age, *Carcharhinus brevipinna*, growth, KwaZulu-Natal, shark, vertebra

The spinner shark *Carcharhinus brevipinna* (Müller and Henle, 1839) is a common coastal-pelagic species along the continental and insular shelves of warm-temperate and tropical areas of the western and eastern Atlantic and the Indo-West Pacific (Compagno 1984). In the south-west Indian Ocean it has been recorded off the west coast of Madagascar (Fourmanoir 1961), southern Moçambique (Bass *et al.* 1973), the east coast of southern Africa (Bass *et al.* 1973, Allen and Cliff 2000) and as far south as Mossel Bay (Smith 1951).

On average, 136 spinner sharks are caught in the gill-nets of the Natal Sharks Board (NSB; Allen 1999). That organization maintains the nets off the KwaZulu-Natal coast of South Africa to protect bathers at popular beaches from shark attack (Cliff *et al.* 1988, Dudley and Cliff 1993). The nets have been in place since 1952 and, to assess their possible impact on the C. *brevipinna* population, life history parameters such as fecundity and lifespan need to be determined.

Although much is known about the general biology of C. *brevipinna* (Clark and Von Schmidt 1965, Sadowsky 1967, Bass *et al.* 1973, Dodrill 1977, Branstetter 1981, Stevens and McLoughlin 1991, Allen and Cliff 2000), the only available information on age and growth is given by Branstetter (1987), who examined 15 specimens from the Gulf of Mexico. This study uses vertebral growth ring counts from 67 animals to elucidate the age and growth of the species from the east coast of South Africa and compares the results with those of Branstetter (1987).

MATERIAL AND METHODS

Sampling

Spinner sharks were collected between 1991 and 1998 from the NSB nets. Each net was 106 m long and 6.3 m deep, with a stretched mesh size of 50 cm. Nets are laid in two rows and run parallel to the shore, at a distance of 300–500 m offshore, in water 10–14 m deep. Further details of the netting operation are provided by Cliff *et al*. (1988).

Each spinner shark was sexed, weighed and the precaudal length (*PCL*) measured in a straight line from the tip of the snout to the precaudal notch. For comparison with Branstetter (1987), who used total length (*TL*), and other authors who used fork length (*FL*), the following equations were used to convert *TL* and *FL* to *PCL*:

$$PCL = 0.779\ TL - 9.07\ (n = 376,\ r^2 = 0.98)$$
$$PCL = 0.944\ FL - 3.21\ (n = 382,\ r^2 = 0.99)\quad .$$

Assessment of sexual maturity followed the criteria

* Formerly Natal Sharks Board, Private Bag 2, Umhlanga Rocks 4320, South Africa
† Natal Sharks Board (correspondence author). E-mail: wintner@shark.co.za

Manuscript received January 2000; accepted September 2000

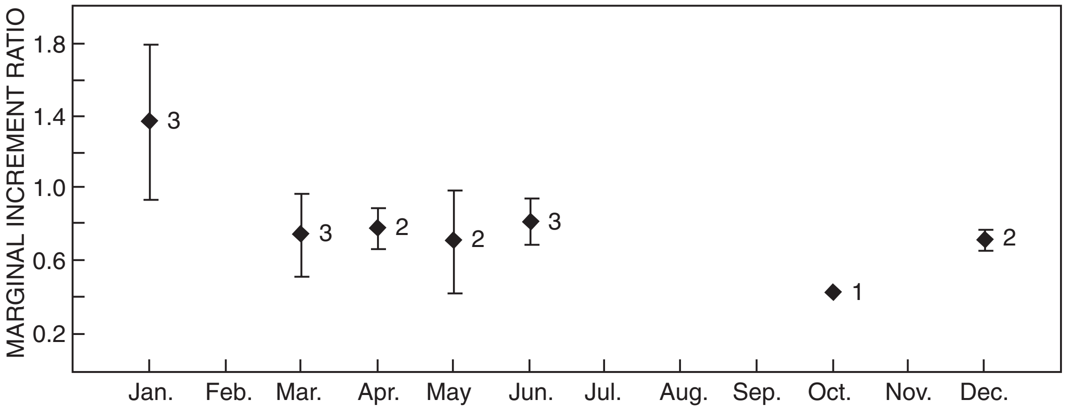

Fig. 1: Mean monthly marginal increment ratios (±*SD*) for *C. brevipinna* with eight growth rings or less

of Bass *et al.* (1973). Males were considered mature when claspers were rigid from calcification and females were considered mature if there were distinct ova in the ovary and the uteri were expanded from a thin tube-like state to form loose sacs.

Vertebral samples of 8–10 vertebrae from 35 males and 47 females, including four male and four female embryos close to term, were collected anterior to the origin of the first dorsal fin. All vertebrae were stored frozen, except for 10 that were stored in 70% isopropanol.

Ring-enhancing methods and ring counts

Several techniques were investigated to determine the best ring-enhancing method: viewing clean unstained vertebra with transmitted light and dark field (Wintner and Cliff 1996); staining whole and sectioned vertebra with either crystal violet (Schwartz 1983) or cobalt nitrate (Hoenig and Brown 1988) or silver nitrate (Stevens 1975) and the "bow tie" method (Branstetter and McEachran 1986). The clearest results were obtained with the "bow-tie" method, in which a sagittal section was cut from the centrum and polished using 200-grit sandpaper. The section was mounted on a glass slide and successively sanded to a thickness of approximately 0.5 mm using 200-, 400- and 600-grit sandpaper. It was then viewed under a dissecting microscope at a magnification of 63×, using transmitted light and dark field.

In this study, a growth ring was defined as a pair of bands consisting of a darker opaque and a lighter translucent band (Cailliet *et al.* 1983, Cailliet and Radtke 1987). Following the centrum face outward from the centre (focus), a distinct change in the angle of the centrum was visible, and this was defined as a zero growth ring. Any ring observed before this birthmark was defined as a pre-birth mark. The diameter of the birthmark and the centrum diameter (*CD*) were measured dorso-ventrally along the sagittal plane through the focus using vernier calipers.

Counts were made independently by two readers without prior knowledge of the length of the animal. Samples with unclear growth rings were defined as unreadable and were discarded. To accept a count, the counts of the two readers had to be either identical or differ by one growth ring; in the case of the latter, the lower of the two was taken in an attempt to be conservative. Non-accepted counts were recounted and the same procedure was applied. Samples not accepted after a second count were counted a third time, but only those counts that were identical were accepted; all others were discarded. For samples accepted on the third count, the precision of age determination was determined using the method of average percentage error (*APE*), as described by Beamish and Fournier (1981). An arbitrary upper limit of 10% was set and any sample above this limit was discarded.

The von Bertalanffy growth function (VBGF) was computed using the nonlinear regression programme of STATGRAPHICS®:

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

where L_t is the length at age t in years, L_∞ the maximum theoretical length, k the rate at which L_∞ is reached and t_0 is the theoretical age at length zero.

To test for significant differences in the VBGF of males and females, the data for both sexes were lin-

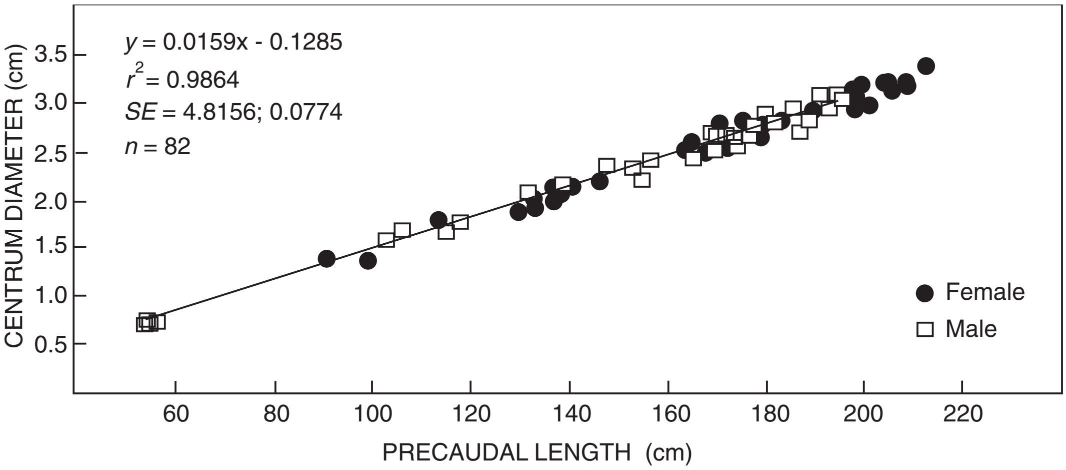

Fig. 2: Relationship between centrum diameter and precaudal length (*PCL*) for *C. brevipinna*

earized and an analysis of covariance (ANCOVA) was performed.

Centrum analysis

The width of each growth ring was measured using an ocular micrometer. Verification of the periodicity of band deposition was attempted by comparing the nature, i.e. opaque or translucent, of the last band with the month of capture (Kusher *et al.* 1992) and by calculating monthly marginal increment ratios (*MIR*; Hayashi 1976, Skomal 1990). The equation used to calculate the ratios was

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

where *VR* is the vertebral radius, R_n the width of last complete growth ring and R_{n-1} is the width of the second-to-last complete growth ring.

A relationship between *CD* and *PCL* was investigated and the Dahl-Lea method of back-calculation (Carlander 1969) was used following the equation:

$$PCL_t = CD_t \times PCL_c / CD_c \quad ,$$

where PCL_t is the length at age *t*, CD_t the centrum diameter at age *t*, PCL_c the length at capture and CD_c is the centrum diameter at capture.

RESULTS

Of the discarded samples, five were unreadable, seven had no agreement after three counts and three had *APE*s >10%, resulting in an overall usable sample of 67. The samples stored in alcohol had much poorer resolution of growth rings than those stored frozen, and of the five unreadable samples, four were stored in alcohol.

Pre-birth marks were observed in 9% of the samples. In 59% of the samples, a thin translucent band was observed immediately after the birthmark. The nature of the last band in specimens with more than eight growth rings was difficult to determine and was therefore abandoned. *MIR* analysis was hampered by a lack of samples from July to December, and by the difficulty in measuring the thin growth rings near the centrum edge, which were smaller than the smallest unit of the ocular micrometer (0.08 mm). *MIR* analysis was therefore performed on samples with fewer than eight growth rings because those samples could be measured more accurately (Fig. 1). A *MIR* peak in January and subsequent low *MIR*s at the end of the year were visible. However, annual deposition of growth rings could not be verified because of the small sample size and overlap of monthly standard errors.

There was a linear relationship between *CD* and *PCL* (Fig. 2) and no significant difference between sexes (Student's *t*-test, $p > 0.05$). Because the *y*-intercept was close to zero (-0.1285), no correction factor such as that of the Fraser-Lee method (Carlander 1969) was required. Mean back-calculated length at zero growth rate was 57 cm, close to the observed value of 55 cm (Table I). Lee's phenomenon, a tendency for back-calculated lengths of older fish in the earlier years of

Table I: Back-calculated and observed lengths at number of growth rings for *C. brevipinna*

Number of growth rings	Back-calculated *PCL* (cm)					Observed *PCL* (cm)				
	Mean	Min.	Max.	*n*	*SD*	Mean	Min.	Max.	*n*	*SD*
0	57	44	82	58	6	55	54	57	8	1
1	75	61	114	58	9	–			0	
2	89	69	116	57	8	114			1	
3	103	84	137	55	11	95	91	100	2	6
4	115	94	145	53	12	126	115	137	2	16
5	124	103	157	50	11	137	133	141	3	4
6	133	111	158	47	10	145	130	157	3	14
7	142	120	166	46	10	133			1	
8	150	130	173	41	10	155	139	166	5	11
9	157	134	183	41	10	–			0	
10	165	140	188	39	10	151	137	165	2	20
11	171	151	195	37	10	171	169	174	2	4
12	178	160	201	33	11	170	165	175	4	4
13	183	165	205	30	11	179	176	183	3	4
14	188	169	209	20	12	184	170	205	10	12
15	190	173	211	14	12	192	172	209	6	13
16	192	175	213	10	11	195	175	209	4	14
17	188	177	195	5	7	200	186	213	5	10
18	189	187	192	2	3	188	177	195	3	10
19	–			0		189	187	192	2	3

life to be systematically lower than those of younger fish at the same age (Carlander 1969), was not evident.

Because there was a significant difference between the VBGF of both sexes ($F = 15.172$, $p < 0.05$), separate VBGF were calculated for males and females (Fig. 3). A combined VBGF for comparative purposes was also calculated and the parameter estimates are given in Table II.

The predicted growth rate of males and females at one growth ring was 19 and 17 cm respectively. Males and females were mature at 8–10 growth rings (Table II), after which the annual growth rate slowed from 7 to 2 cm for males and from 8 to 4 cm for females. The oldest animal analysed was a 192 cm

Table II: Comparison of the calculated Von Bertalanffy growth parameters (sexes combined) and other parameters from this study with those of Branstetter (1987)

Parameter	Present study				Branstetter (1987)			
k (year^{-1})	0.127				0.212			
L_∞ (cm)	209				158			
t_0 (years)	-2.52				-1.94			
n	67				14			
Size at birth	55				40			
Maximum length (cm)	220				166			
	Male		Female		Male		Female	
	PCL (cm)	Number of growth rings	*PCL* (cm)	Number of growth rings	*PCL* (cm)	Number of growth rings	*PCL* (cm)	Number of growth rings
Smallest	115	4	91	3	84	2.4	81	1.5
Youngest	115	4	114	2	84	2.4	81	1.5
Largest immature	157	6	165	10	115	5.6		
Maturity	150	8–10	160	8–10	123	7.5	131	7.5–8.5
Smallest mature	155	8	164	8	127	7.7	135	7.5
Largest	196	17	213	17	141	8.5	153	11.8
Oldest	192	19	213	17	141	8.5	153	11.8
Pregnant			193–209	14–16				
Post-partum							153	11.8

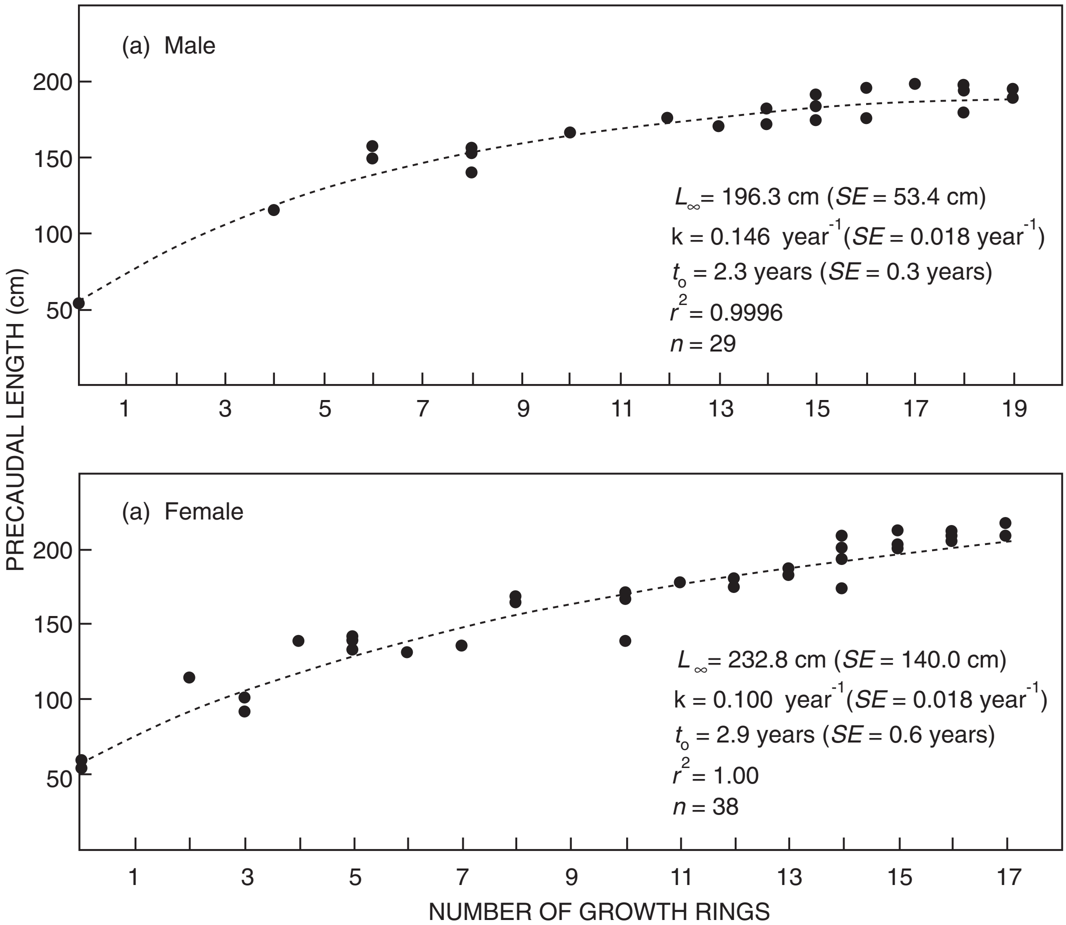

Fig. 3: Von Bertalanffy growth curve and parameter estimates for (a) male and (b) female *C. brevipinna*

male with 19 growth rings, and the largest was a 213 cm female with 17 rings.

DISCUSSION

Pre-birth marks have been found in a number of carcharhinids (Casey *et al.* 1985, Branstetter and Stiles 1987, Batista and Silva 1995). Few samples in this study (9%) possessed pre-birth marks. Branstetter (1987) reported that at least one annulus was formed during embryonic development in *C. brevipinna* from the Gulf of Mexico. That author suggested that this was common among placental species, occurring as a result of nutrient increases at the onset of placentation. However, Batista and Silva (1995) also observed pre-birth marks in aplacental species. Casey *et al.* (1985) suggested that these marks could also be formed in the embryo's vertebrae as a result of migrations and/or winter marks of its mother, which may affect the development of the embryo.

In 59% of the samples, a thin translucent band was present immediately after the angle change. Wintner and Cliff (1996) found the same pattern in *C. limbalus* from the east coast of South Africa and suggested that the thin translucent band is representative of the first winter growth and that subsequent opaque bands are deposited every summer. This would provide a plausible explanation for *C. brevipinna,* because full-term females from South Africa are caught in winter between May and July (Bass *et al.* 1973, Allen 1999).

MIR analysis is commonly used to verify the periodicity of band deposition in elasmobranchs (Branstetter and Stiles 1987, Killiam and Parsons 1989, Batista and Silva 1995, Natanson *et al.* 1995, Wintner and Cliff 1998). Difficulties in distinguishing the last band and measuring the widths of the outermost bands in older specimens of sharks were also found by Casey *et al.* (1985), Ferreira and Vooren (1991) and Goosen and Smale (1997). Because of this, Killiam and Parsons (1989) used juveniles 2–3 years old in their *MIR* analysis. Owing to the scarcity of animals under study with two or three growth rings, animals with eight rings or less were used. However, the results of the *MIR* analysis are not conclusive enough to suggest the possibility of annual growth ring deposition. Branstetter (1987), on the basis of absolute marginal increments, suggested that growth rings begin to form between October and December and are completed by late summer (September). However, the samples (n = 12) were only collected between late May and late September, preventing distinct annual growth ring deposition from being verified.

The linear relationship between *CD* and *PCL* is common for many carcharhinids (Casey *et al.* 1985, Davenport and Stevens 1988, Killiam and Parsons 1989). Branstetter (1987) also found such a relationship for *C. brevipinna* in the Gulf of Mexico. Mean back-calculated length at zero growth rings (57 cm *PCL*) corresponded to a size at birth of 50–60 cm (Allen 1999), suggesting that the angle change is formed at or close to birth. These birth sizes were larger than the 38–45 cm *PCL* reported by Branstetter (1987) for the same species.

Differences in VBGF parameters between males and females have been found in other carcharhinids (Natanson *et al.* 1995, Sminky and Musick 1995). It appears that male *C. brevipinna* off South Africa initially grow faster than females, but that the growth rate then slows below that of females after maturity is reached. Branstetter (1987), using a sample of six males and nine females, found no difference in growth rate between sexes. The present number of growth rings at maturity (8–10) was the same for both sexes (Table II). Branstetter (1987) also found similar ages at maturity for both sexes of *C. brevipinna* (Table II) and suggested that males reach maximum length at 10.5–15.5 growth rings and females at 15.5–20.5 rings. The asymptote for the VBGF of both sexes occurs at 17 rings in the present study. This falls within the range of the females, but is larger than that of males of the species from the Gulf of Mexico.

The combined VBGF calculated here differs from that of Branstetter (1987; Table II). The present L_∞ value of 209 cm is larger than the 158 cm calculated by Branstetter (1987), a result of the maximum attainable size of the South African *C. brevipinna* (220 cm), being larger than that from the Gulf of Mexico (166 cm). The value of k in this study (0.127 year^{-1}) represents initially slow growth for juveniles, with neonates doubling their length after approximately three years. Branstetter (1987) attributed his findings of a large value of k (0.212 year^{-1}) to the rapid growth rate of juveniles, with neonates doubling in length in the first six months.

According to Branstetter (1990), to ensure survival, neonates must attain a length of approximately 70 cm to deter predators by allowing for escape through increased swimming capabilities. He stated that two different strategies are employed by elasmobranchs to achieve this objective. First, young of the species exposed to predators in their nursery grounds will usually grow fast (k > 0. 1). Second, those with slower growth rates (k < 0.1) inhabit more protected nursery areas, or have higher fecundities. According to Bass *et al.* (1973), the KwaZulu-Natal coast serves as a nursery ground for newborn *C. brevipinna.* Dudley and Cliff (1993) found an abundance of predatory shark species along the KwaZulu-Natal coast, many of which prey on small sharks, including *C. brevipinna.* The Gulf of Mexico also has an abundance of large coastal shark species (Branstetter 1981) that may prey on newborn *C. brevipinna* using shallow bay areas as nurseries (Branstetter 1987). Branstetter (1990) categorized *C. brevipinna* as employing the first strategy in the Gulf of Mexico. The slower growth rate of *C. brevipinna* in South Africa may therefore be compensated for by their larger size at birth. The 70 cm "survival size" suggested by Branstetter (1990), would therefore be reached by both populations after approximately one year.

There are clear differences in age and growth between C. *brevipinna* populations from the Gulf of Mexico and those off South Africa. It must be noted, however, that factors such as small sample size, sampling bias, enhancing techniques and reader accuracy may also play a role in the differences observed. Further analysis, incorporating the use of multiple methods, including tag-and-recapture and tetracycline studies (Beamish and McFarlane 1983), are needed to verify and validate the age and growth of *C. brevipinna* from the northern and southern hemispheres.

Spinner sharks are fairly long-lived, exhibiting both slow growth rate and late maturation, making them susceptible to overfishing. Between 1978 and 1997, 2 728 *C. brevipinna* were caught in NSB nets, 10.27% of the total catch of sharks. Analysis of trends in NSB catch data has shown that this species has exhibited significant increases in *PCL* of mature and pregnant females over the period 1966–1998 (Dudley 1999). Such a trend was also evident for tiger shark

Galeocerdo cuvier and, although the cause is unknown, the phenomenon may be attributable to competitive advantage that these species have over other sharks caught by the NSB fishery (Dudley 1999). The current catch rate of *C. brevipinna* in NSB nets appears to be sustainable. However, the extent of other forms of fishing mortality (e.g. commercial/recreational fisheries) elsewhere in its range is unknown.

ACKNOWLEDGEMENTS

The field staff of the Natal Sharks Board (NBS) were responsible for providing specimens and information associated with their capture. Messrs P. Methembu and P. Zungu (NSB) dissected many of the sharks for collecting and storing the vertebrae.

LITERATURE CITED

ALLEN, B. R. 1999 — Abundance, reproduction, feeding and age and growth of the spinner shark, *Carcharhinus brevipinna,* from KwaZulu-Natal, South Africa. M.Sc. thesis, University of Port Elizabeth, South Africa: 94 pp.

ALLEN, B. R. and G. CLIFF 2000 — Sharks caught in the protective gillnets off KwaZulu-Natal, South Africa. 9. The spinner shark *Carcharhinus brevipinna* (Müller and Henle). *S. Afr. J. mar. Sci.* **22**: 199–215.

BASS, A. J., D'AUBREY, J. D. and N. KISTNASAMY 1973 — Sharks of the east coast of southern Africa. 1. The genus *Carcharhinus* (Carcharhinidae). *Investl Rep. oceanogr. Res. Inst. S. Afr.* **33**: 168 pp.

BATISTA, V. S. and T. C. SILVA 1995 — Age and growth of juveniles of junteiro shark *Carcharhinus porosus* in the coast of Maranhão, Brazil. *Rev. Brasil. Biol.* **55**: 25–32.

BEAMISH, R. J. and D. A. FOURNIER 1981 — A method for comparing the precision of a set of age determinations. *Can. J. Fish. aquat. Sci*. **38**: 982–983.

BEAMISH, R. J. and G. A. McFARLANE 1983 — The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**(6): 735–743.

BRANSTETTER, S. 1981 — Biological notes on the sharks of the north central Gulf of Mexico. *Contrib. mar. Sci.* **24**: 13–34.

BRANSTETTER, S. 1987 — Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. *Copeia* **1987**(4): 964–974.

BRANSTETTER, S. 1990 — Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries. Proceedings of the Second United States-Japan Workshop.* Pratt, H. L., Gruber, S. H. and T. Taniuchi (Eds). *NOAA tech. Rep.* **NMFS 90**: 17–28.

BRANSTETTER, S. and J. D. McEACHRAN 1986 — Age and growth of four carcharhinid sharks common to the Gulf of Mexico: a summary paper. In *Indo-Pacific Fish Biology – Proceedings of the Second International Conference on Indo-Pacific Fishes*. Uyeno, T., Arai, R., Taniuchi, T. and K. Matsuura (Eds). Tokyo; Ichthyological Society of Japan: 361–371.

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**(3): 169–181.

CAILLIET, G. M., MARTIN, L. K., KUSHER, D., WOLF, P. and B. A. WELDEN 1983 — Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, Miami, February 1982.* Prince, E. D. and L. M. Pulos (Eds). *NOAA tech. Rep.* **NMFS 8**: 157–165.

CAILLIET, G. M. and R. L. RADTKE 1987 — A progress report on the electron microprobe analysis technique for age determination and verification in elasmobranchs. In *Age and Growth of Fish.* Summerfelt, R. C. and G. E. Hall (Eds). Ames; Iowa State University Press: 359–369.

CARLANDER, K. D. 1969 — *Handbook of Freshwater Fishery Biology* **1**. Ames, Iowa; State University Press: 752 pp.

CASEY, J. G., PRATT, H. L. 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.

CLARK, E. and K. VON SCHMIDT 1965 — Sharks of the central Gulf coast of Florida. *Bull. mar. Sci.* **15**(1): 13–83.

CLIFF, G., DUDLEY, S. F. J. and B. DAVIS 1988 — Sharks caught in the protective gill nets off Natal, South Africa. 1. The sandbar shark *Carcharhinus plumbeus* (Nardo). *S. Afr. J. mar. Sci.* **7**: 255–265.

COMPAGNO, L. J. V. 1984 — F.A.O. species catalogue. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. (2) Carcharhiniformes. *F.A.O. Fish. Synop*. **125**: 250–655.

DAVENPORT, S. and J. D. STEVENS 1988 — Age and growth of two commercially important sharks (*Carcharinus tilstoni* and *C. sorrah*) from northern Australia. *Aust. J. mar. Freshwat. Res.* **39**(4): 417–433.

DODRILL, J. W. 1977 — A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida, M.Sc. thesis, Florida Institute of Technology: 304 pp.

DUDLEY, S. F. J. 1999 — Shark catch trends in the KwaZulu-Natal shark nets 1966–1998. Unpublished Report, Natal Sharks Board, South Africa **2/99**: 27 pp.

DUDLEY, S. F. J. and G. CLIFF 1993 — Some effects of shark nets in the Natal nearshore environment. *Environ. Biol. Fishes* **36**: 243–255.

FERREIRA, B. P. and C. M. VOOREN 1991 — Age, growth and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. *Fishery Bull., Wash.* **89**: 19–31.

FOURMANOIR, P. 1961 — Requins de la côte ouest de Madagascar. *Mém. Inst. scient. Madagascar, Ser. F* **4**: 1–81.

GOOSEN, A. J. J. and M. J. SMALE 1997 — A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). *S. Afr. J. mar. Sci.* **18**: 85–91.

HAYASHI, Y. 1976 — Studies on the growth of the red tilefish in the East China Sea. 2. Estimation of age and growth from otolith-reading. *Bull. Jap. Soc. scient. Fish.* **42**(11): 1243–1249.

HOENIG, J. M. and C. A. BROWN 1988 — A simple technique for staining growth bands in elasmobranch vertebrae. *Bull. mar. Sci.* **42**: 334–337.

KILLIAM, K. A. and G. R. PARSONS 1989 — Age and growth of the blacktip shark, *Carcharhinus limbatus*, near Tampa Bay, Florida. *Fishery Bull., Wash.* **87**: 845–857.

KUSHER, D. I., SMITH, S. E. and G. M. CAILLIET 1992 — Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environ. Biol. Fishes* **35**: 187–203.
NATANSON, L. J., CASEY, J. G. and N. E. KOHLER 1995 — Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fishery Bull., Wash*. **93**: 116–126.
SADOWSKY, V. 1967 — Selachier aus dem Litoral von Sao Paulo, Brasilien. *Beitr. Neotrop. Fauna* **5**: 71–88.
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 *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, Miami, February 1982*. Prince, E. D. and L. M. Pulos (Eds). *NOAA tech. Rep*. **NMFS 8**: 167–174.
SKOMAL, G. B. 1990 — Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. M.Sc thesis, University of Rhode Island, Kingston: 103 pp.
SMINKEY, T. R. and J. A. MUSICK 1995 — Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* **1995**: 871–883.
SMITH, J. L. B. 1951 — A new galeorhinid shark from South Africa, with notes on other species. *Ann. Mag. nat. Hist. Ser*. **124**(37): 86–93.
STEVENS, J. D. 1975 — Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *J. mar. biol. Ass. U.K.* **55**(3): 657–665.
STEVENS, J. D. and K. J. McLOUGHLIN 1991 — Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. *Aust. J. mar. Freshwat. Res.* **42**(2): 151–199.
WINTNER, S. P. and G. CLIFF 1996 — Age and growth determination of the blacktip shark, *Carcharhinus limbatus,* from the east coast of South Africa. *Fishery Bull., Wash.* **94**: 135–144.
WINTNER, S. P. and G. CLIFF 1998 — Age and growth determination of the white shark, *Carcharodon carcharias,* from the east coast of South Africa. *Fishery Bull., Wash.* **97**: 153–169.