

SHARKS CAUGHT IN THE PROTECTIVE GILL NETS OFF KWAZULU-NATAL,
SOUTH AFRICA. 9. THE SPINNER SHARK *CARCHARHINUS BREVIPINNA*
(MÜLLER AND HENLE)

B. R. ALLEN* and G. CLIFF†

A total of 2 728 spinner sharks *Carcharhinus brevipinna* was caught in nets that protect the swimming beaches of KwaZulu-Natal between 1978 and 1997. The species constituted 10.3% of the total shark catch during that period. An average of 136 spinner sharks was caught annually, with no trend in catch rate over the study period. The species was caught throughout the year, predominantly in the south and mainly from February to July. Males matured at approximately 150 cm precaudal length and females at 154 cm. Gonad indices in mature males were highest during December and January and in females during February and March. Mating takes place between January and March. The hepatosomic index of pregnant females was highest at the onset of pregnancy and lowest at parturition. Evidence suggests a two-year reproductive cycle in females, with a gestation period of 13–18 months. The average litter size was nine, with an estimated length at birth of between 50 and 60 cm. Near-term pregnant females were caught mainly in the north, indicating the possibility of a nursery there. Both large and small pregnant females produce pups of the same length, but larger females generally have larger litters. Regional, seasonal and size variations were evident in the diet, with teleosts being the most frequently eaten prey.

The spinner shark *Carcharhinus brevipinna* (Müller and Henle) is a common coastal-pelagic species in warm-temperate and tropical areas of the Western and Eastern Atlantic and the Western Indo-Pacific (Compagno 1984). In the South-West Indian Ocean, it has been recorded from the west coast of Madagascar (Fourmanoir 1961) and off southern Mozambique (Bass *et al.* 1973). In South Africa, it occurs off KwaZulu-Natal (Bass *et al.* 1973) and as far south as Mossel Bay (Smith 1951). Biological studies have been conducted on this species from the east coast of South Africa (Bass *et al.* 1973), the Gulf of Mexico (Branstetter 1981), Florida (Clark and Von Schmidt 1965, Dodrill 1971), southern Brazil (Sadowsky 1967) and northern Australia (Stevens and McLoughlin 1991).

C. brevipinna are frequently caught in the gill nets (commonly known as shark nets) that protect the beaches of KwaZulu-Natal against shark attack (Walleit 1983) and are maintained by the Natal Sharks Board (NSB). This paper is the ninth in a series describing the general biology and catch statistics of each of the 14 species of sharks commonly caught in the nets.

MATERIAL AND METHODS

The shark nets, which have a mesh of 25-cm bar, are set parallel to the shore (300–500 m offshore) in water 10–14 m deep. Details of the netting operation are given by Cliff *et al.* (1988). The nets are distributed

along a 326-km stretch of coastline, between Mzamba in the south and Richards Bay in the north (Fig. 1). In January 1997, the total length of netting was 44.4 km. Units of effort are expressed as kilometres of net per year.

Catch and biological records were regarded as having been reliable since 1978. Before then, *C. brevipinna* was frequently confused with the blacktip shark *Carcharhinus limbatus*, a problem encountered elsewhere (Bigelow and Schroeder 1948, D'Aubrey 1965, Branstetter 1982) and possibly in the present study when sharks were not returned to the laboratory for further examination.

All shark lengths used in this report, including those cited from the literature, are precaudal lengths (*PCL*), measured in centimetres. *PCL* is considered to be a more precise measurement than the more commonly used total length (*TL*). Precaudal length and fork length (*FL*) were measured in a straight line, parallel to the body (i.e. connecting perpendiculars to the reference points), from the tip of the snout to the precaudal notch and the fork of the caudal fin respectively. Upper caudal length (*UCL*) was measured in a straight line from the precaudal notch to the tip of the upper caudal fin. Total length was measured in a straight line from the tip of the snout to the tip of the upper caudal lobe, with the upper caudal lobe placed parallel to the body axis (Compagno 1984). In order to compare measurements with those in the literature, the following equations were used to convert *TL* and *FL* to *PCL*:

* Formerly Zoology Department, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6000, South Africa, and Natal Sharks Board

† Natal Sharks Board, Private Bag 2, Umhlanga Rocks 4320, South Africa. E-mail: cliff@shark.co.za

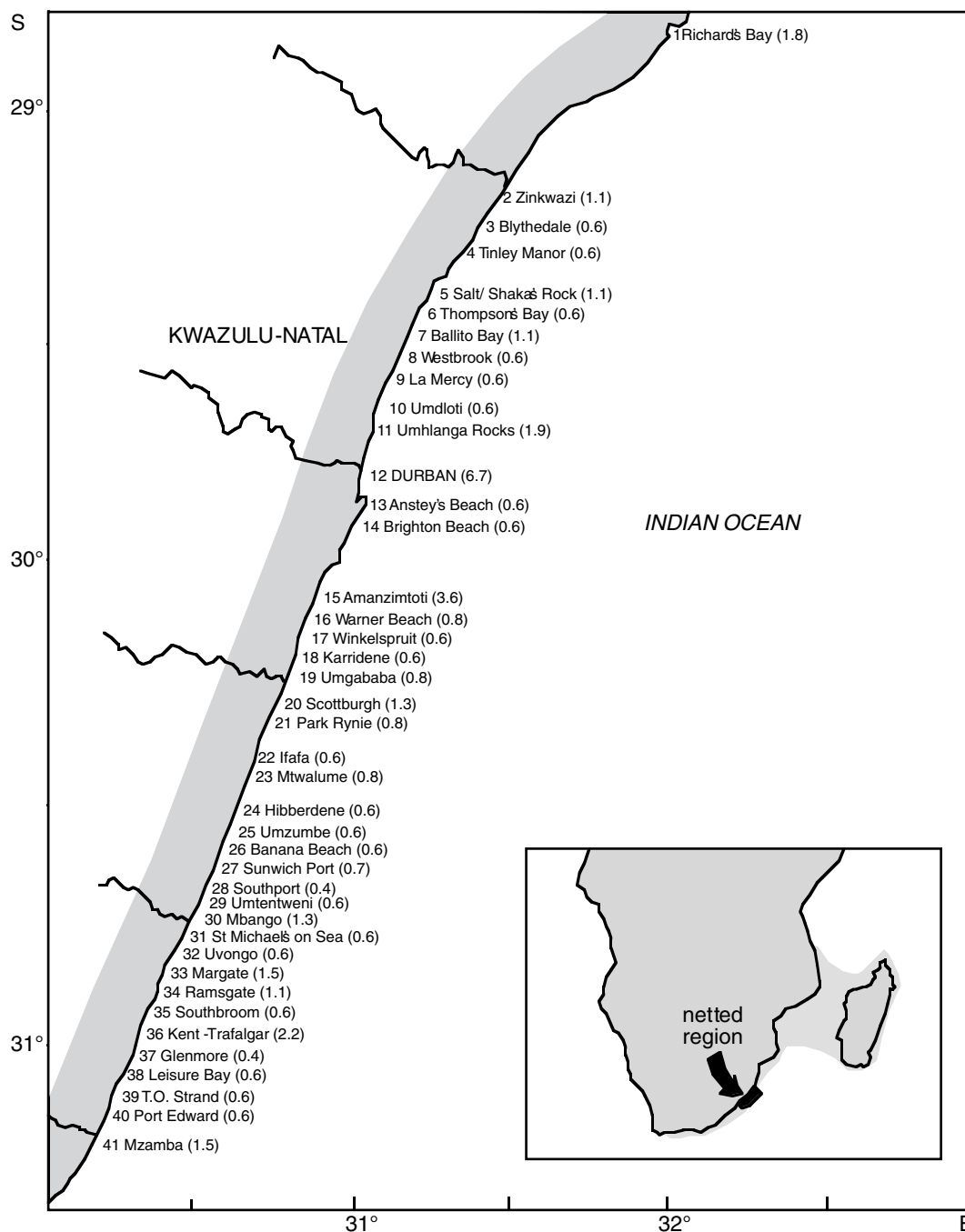


Fig. 1: Netted beaches on the KwaZulu-Natal coast and, in parenthesis, the length of nets in kilometres. Nets were removed from Umgababa (Beach 19) in 1990 and from Ifafa (Beach 22), Mtwalume (Beach 23) and Tinley Manor (Beach 4) in 1994. Inset shows the locality of the netted region and the distribution of *C. brevipinna* in southern Africa

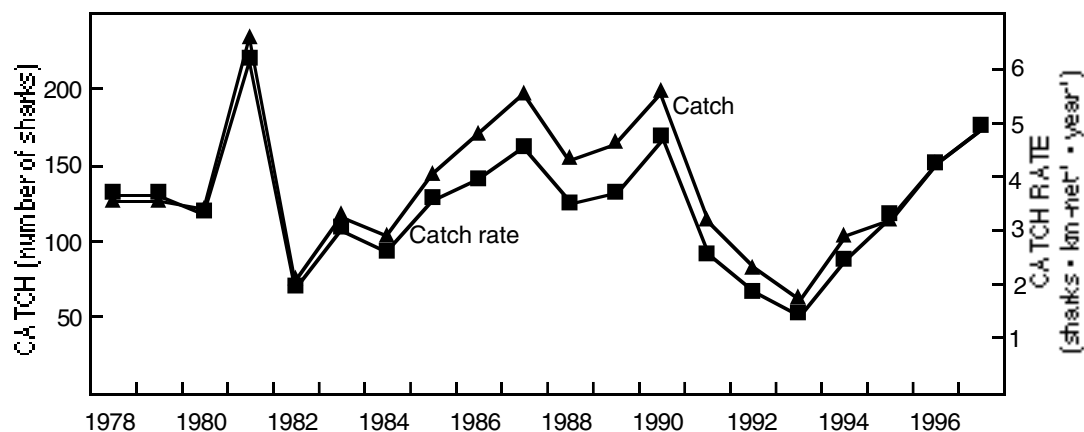


Fig. 2: Catches of *C. brevipinna* in the shark nets, 1978–1997

$$PCL = 0.779 TL - 9.07$$

$$(n = 376, r^2 = 0.98) ;$$

$$PCL = 0.944 FL - 3.21$$

$$(n = 382, r^2 = 0.99) .$$

Bass *et al.* (1973) used the equation $TL = PCL + 0.8 UCL$ to convert PCL to TL for *C. brevipinna*. The equation $PCL = 0.8159 TL + 5.72$ ($n = 202, r^2 = 0.96$) was therefore generated to make comparison with measurements reported in Bass *et al.* (1973).

Measurements of reproductive structures are according to Cliff *et al.* (1988) and criteria for visual assessment of maturity follow Bass *et al.* (1973). Length-at-50% maturity was calculated using a maximum likelihood estimation.

Stomach contents were sorted to the lowest possible taxon and expressed as frequency of occurrence (%F). Stomachs containing only otoliths, cephalopod beaks or elasmobranch egg cases were regarded as empty. From 1983, the items in each group were counted and a wet mass was obtained, making it possible to express stomach contents in terms of percentage by mass (%M) and by number (%N). The dietary importance of each food item was calculated using the “index of relative importance” (IRI) – Hyslop (1980):

$$IRI = (\%N + \%M) \times (\%F) .$$

Otoliths and cephalopod beaks were identified against reference material in the collection of the Port Elizabeth Museum.

At each net installation, sea surface temperature was measured, and water clarity was estimated using the meshes of the net as a guide whenever the nets were checked.

NET CATCHES

Annual variation

A total of 2 728 *C. brevipinna* was caught between 1978 and 1997, with an annual mean of 136 (range 62–234, Fig. 2). This constituted 10.3% of the shark catch in the nets. The mean catch rate was 3.4 sharks·km-net⁻¹·year⁻¹ and, despite considerable inter-annual variation, showed no significant trend ($r^2 = 0.012, p > 0.05$). A lack of trend in annual catch rate has been found for a number of shark species caught in the nets (Dudley and Cliff 1993a).

Geographical and seasonal distribution

Both mature (>150 cm) and immature (≤150 cm) *C. brevipinna* were caught throughout the study area all year round (Fig. 3). The catch of mature sharks ($n = 1 579$) was almost double that of immature sharks ($n = 857$). The highest catch rate of mature sharks was at Richards Bay (Beach 1), but catch rates were also high at the southern extremity of the study area. Immature sharks were caught mainly at the southern beaches, with the highest catch rate at Umgababa (Beach 19). Catches of mature sharks increased sharply in February and decreased to a minimum in November and December. Immature sharks showed less seasonal variation, peaking in January and February and declining to a minimum in October and November (Fig. 4). The overall sex ratio of immature sharks did not differ from 1:1 (χ^2 test, $p > 0.05$). Mature females outnumbered mature males by 1.4:1 (χ^2 test,

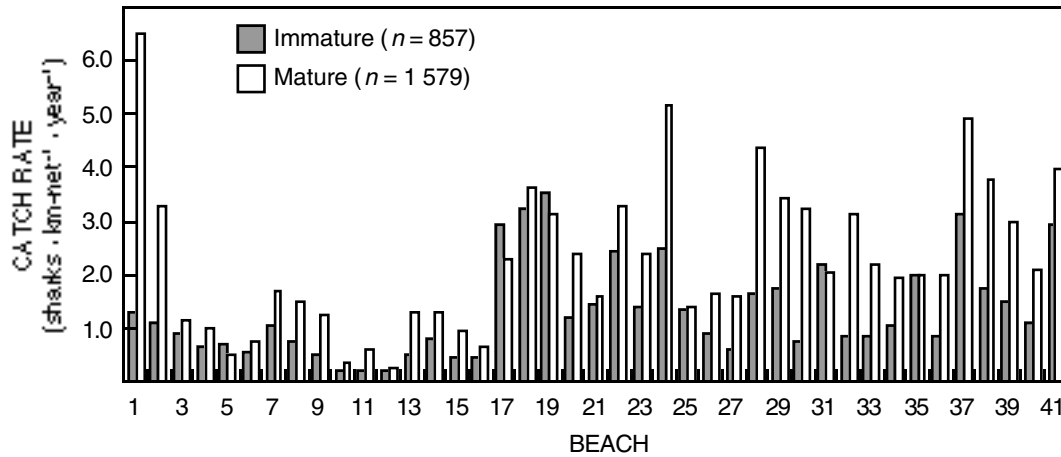


Fig. 3: Geographic distribution of *C. brevipinna* in the nets, 1978–1997. Beach numbers refer to Figure 1

$p < 0.05$), although more males were caught than females in February. The monthly variation in numbers of mature males was greater than that of mature females.

The scarcity of both mature and immature *C. brevipinna* in the second half of the year may be attributable to sharks either moving north (Bass *et al.* 1973) or offshore. Sampling in deeper water, offshore of the netted region, was conducted using longlines (Bass 1968), by which method 13 *C. brevipinna* were

caught, some at depths up to 27 m. *C. brevipinna* in the Gulf of Mexico are highly migratory, moving inshore in summer to breed and offshore, into deeper waters (up to 75 m), in winter (Compagno 1984).

TAGGING

Between 1978 and 1997 a total of 132 *C. brevipinna* was tagged and released from the nets. Only one was

Table 1: Captures of groups ($n \geq 5$) of *C. brevipinna* caught on a single day in a single beach installation

Beach number	Date	Catch	Sex ratio male:female	Size range (cm)	Common prey item
3	18/01/84	5	2:3	117–142	Empty
7	19/01/90	5	2:3	118–174	Empty
1	17/02/86	5	4:1	164–195	Empty
1	14/02/95	5	All males	168–179	Empty
1	21/02/86	12	1:2	157–194	Empty
7	04/02/89	6	1:2	135–171	<i>Scomber japonicus</i>
41	29/02/88	5	4:1	172–186	Empty
33	30/03/87	6	2:1	135–169	Empty
7	22/05/96	5	All females	152–204	Teleosts
18	19/06/84	6	1:5	128–211	<i>Sardinops sagax</i>
31	30/06/79	10	2:3	153–187	<i>S. sagax</i>
36	15/06/84	5	3:2	148–210	<i>S. sagax</i>
36	27/06/81	10	7:3	156–191	<i>S. sagax</i>
40	26/06/81	9	7:2	159–214	<i>S. sagax</i>
18	7/07/80	5	1:4	161–218	<i>S. sagax</i>
37	24/07/78	28	2:5	129–216	<i>S. sagax</i>
40	24/07/78	6	5:1	165–187	<i>S. sagax</i>
15	21/09/83	7	6:1	172–189	<i>S. japonicus</i>
17	23/09/83	7	All males	175–194	<i>S. japonicus</i>
18	23/09/83	7	5:2	122–191	<i>S. japonicus</i>
7	4/10/95	5	All females	204–212	<i>S. sagax</i>

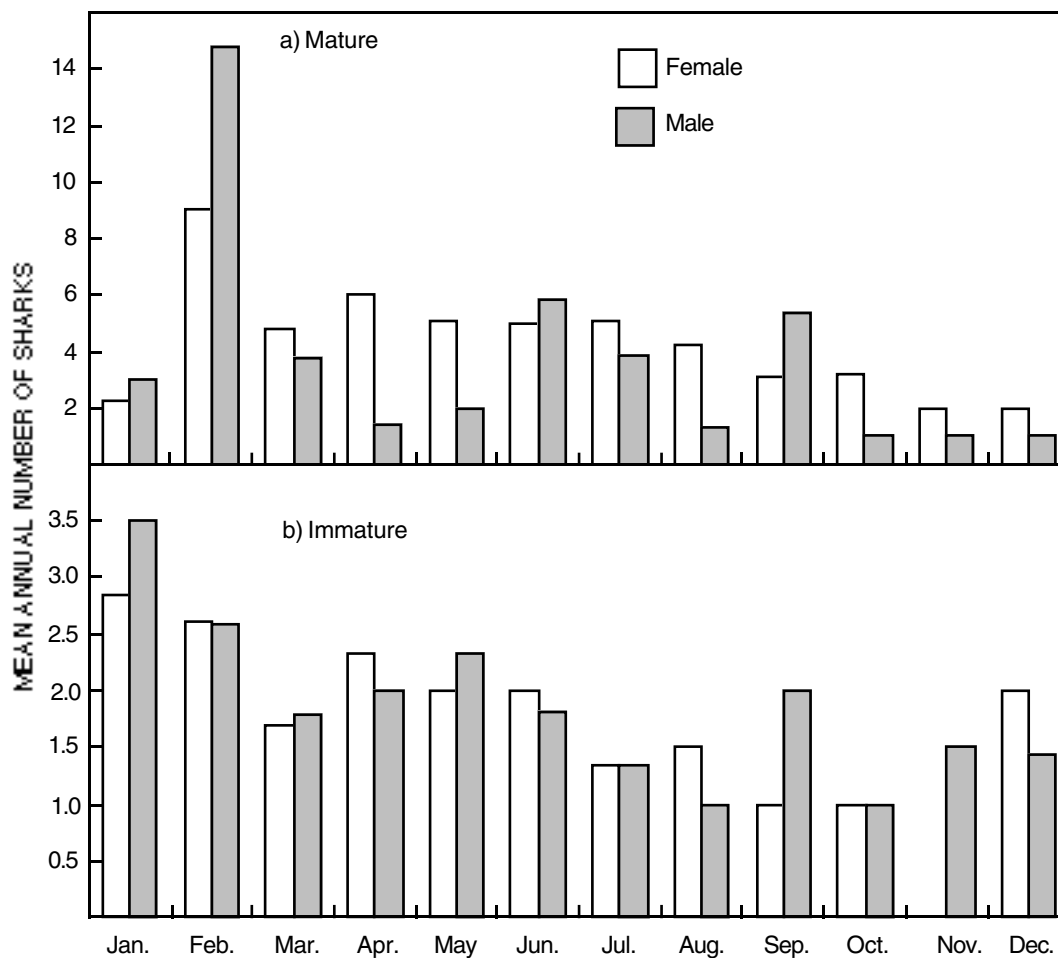


Fig. 4: Seasonal distribution of (a) mature and (b) immature *C. brevipinna* in the nets, 1978–1997

recaptured, at the same net installation where it was tagged, three days after release. This low recapture rate may be attributable to fast-moving sharks succumbing to capture stress after being released. Davies and Joubert (1967) conducted a tag evaluation study at Durban (Beach 12) in November and December 1964. A total of 183 *C. brevipinna* ranging in size from 37 to 58 cm were tagged, of which 73 were recovered. The authors concluded that juvenile *C. brevipinna* move northwards. However, a tagging study conducted later by Bass *et al.* (1973) revealed that newborn sharks ranging in size from 40 to 62 cm ($n = 960$) moved southwards, out of the KwaZulu-Natal area, when water temperatures decreased.

Group occurrence

On 21 occasions between 1978 and 1997, groups of five or more *C. brevipinna* were caught together in a single net installation (Table I). The largest group, consisting of 28 sharks, was taken at Blythedale in 1978 (Beach 3). Fourteen groups consisted only of mature sharks, suggesting that size segregation may take place. Five of the 21 groups, consisting of both mature males and females in mating condition, were caught in January and February, suggesting that *C. brevipinna* may form aggregations during the mating season. Some of the groups caught may have been a result of feeding aggregations, particularly in winter when sar-

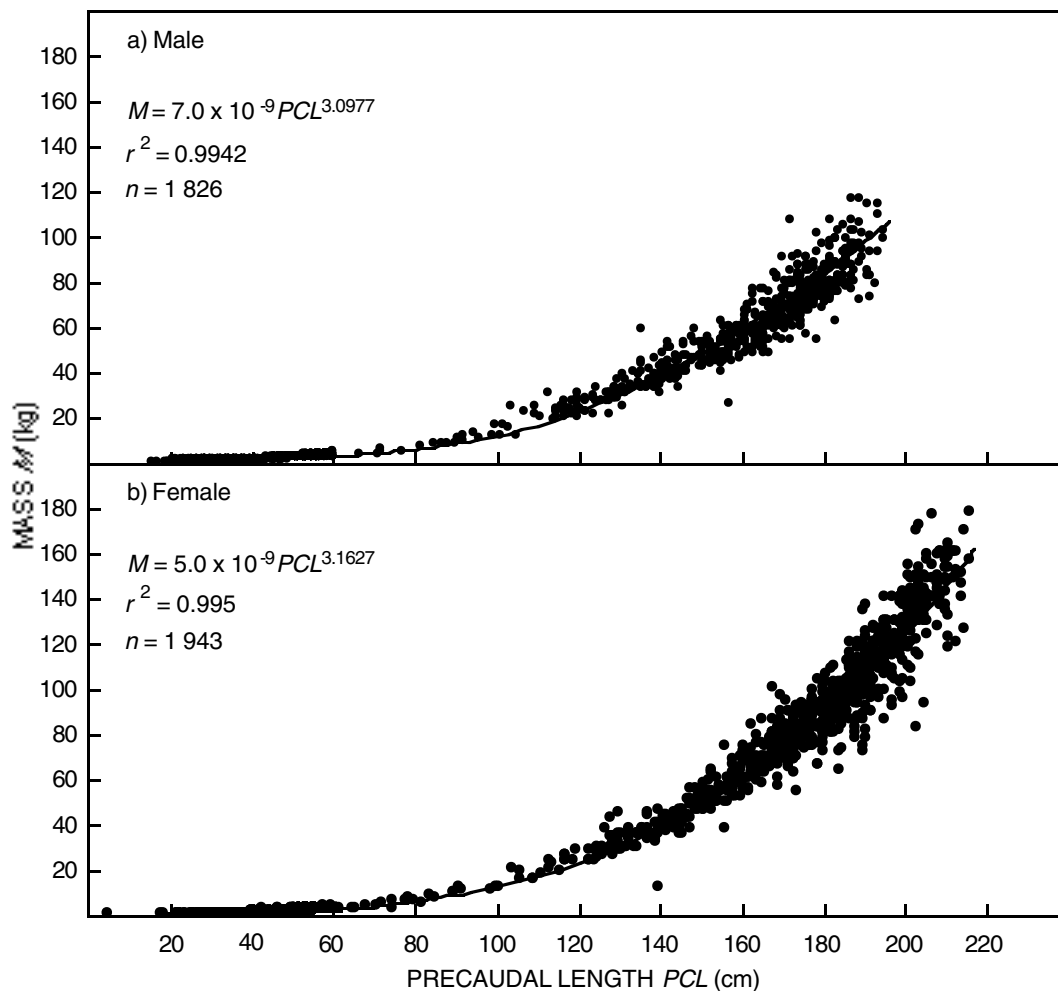


Fig. 5: Relationship between precaudal length and mass of (a) male and (b) female *C. brevipinna*

dine *Sardinops sagax* are common in KwaZulu-Natal coastal waters. *C. brevipinna* is described as a schooling shark (Compagno 1984) and has been reported to form "packs" behind shrimp boats in Florida (Dodrill 1971).

Length distribution

The length-mass relationships for males and females (Fig. 5) were significantly different (t -test, $p < 0.05$). The smallest and largest male caught measured 51 and 195 cm and weighed 1.3 and 98 kg respectively. The smallest and largest female measured 52 and

220 cm and weighed 1.4 and 176 kg respectively. Males and females had respective modal size-classes of 173–177 and 183–187 cm (Fig. 6). The length frequency distribution of both males and females was negatively skewed, most likely a result of the size selectivity of the nets. Geographical variation in size is evident between the southern and northern hemisphere *C. brevipinna* populations (Table II).

Environmental conditions at the nets

Nearshore surface temperatures associated with catches of *C. brevipinna* ranged from 17.2°C in Sep-

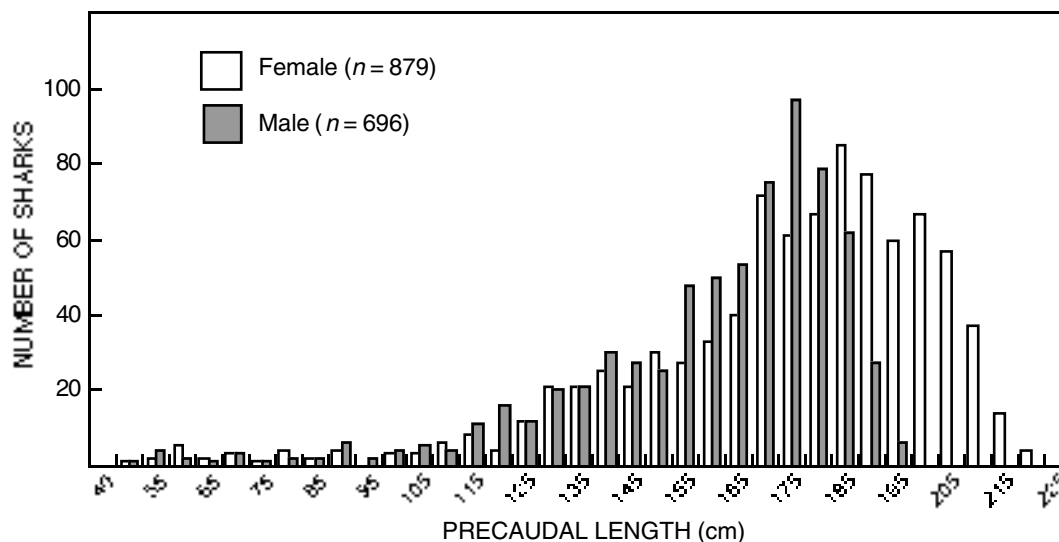


Fig. 6: Length frequency distribution of *C. brevipinna* caught in the nets, 1978–1997

temper to 27.3°C in February (mean = 22.5°C, $n = 2\,253$). Although *C. brevipinna* was caught throughout the year, there was a direct relationship between mean monthly water temperature and monthly catches ($r^2 = 0.675$). Largest catches were recorded during the warmest months (February/March) and smaller catches during the coolest months (August/September). Cliff *et al.* (1989) and Armstrong *et al.* (1991) reported seasonal differences in water temperature in the study region.

Mean water clarity associated with catches was 2.5 m (range 0–15 m, $n = 2\,253$), which differed ($p < 0.001$) from the annual mean of 3.3 m for the study area (1981–1991). Mean water clarity varied from 1.8 m in February and March, when catches of *C. brevipinna* were greatest, to 4.2 m in July, when catches were smallest. The higher turbidity in summer can be attributable to increased river outflow into the sea at such times.

BIOLOGY

Reproduction

MALES

Length-at-50% maturity, based on clasper calcification (Fig. 7), was calculated at 150 cm (95% confidence limits of 148 and 152 cm). This value differs

markedly from that given by Bass *et al.* (1973) for South African *C. brevipinna*, as well as from most other estimates made elsewhere (Table II). The largest adolescent (177 cm) that was caught during the present study had uncalcified claspers, 15.4% of its length. Of the 690 males examined, 475 (69%) were mature. The smallest mature male (144 cm) had calcified claspers, 17.3% of its length.

Most mature males were caught in summer (January–March) in the southern part of the study area, although numbers peaked at Richards Bay (Beach 1) in the north. A summer mating season was indicated by the presence of males with enlarged testes, seminal fluid in the seminal vesicles, and swollen, bleeding claspers at that time.

There were significant monthly differences in the gonad index ($GI = \text{gonad mass/shark mass} \times 100$) of mature male sharks (Kruskal-Wallis H -test, $p < 0.01$). From March to October (with the exception of one shark caught in May), mean GI values for mature males remained fairly low, at between 0.03 and 0.2% (Fig. 8a). However, it must be noted that the sample size was small between April and November. Gonad activity peaked in December ($GI = 0.79\%$), then began decreasing at the onset of mating between January and March. A peak in GI two to three months prior to mating was also recorded for *C. limbatus* (Dudley and Cliff 1993b) and *C. brachyurus* (Cliff and Dudley 1992).

Significant monthly differences were also found in the hepatosomic index ($HSI = \text{liver mass/shark mass}$

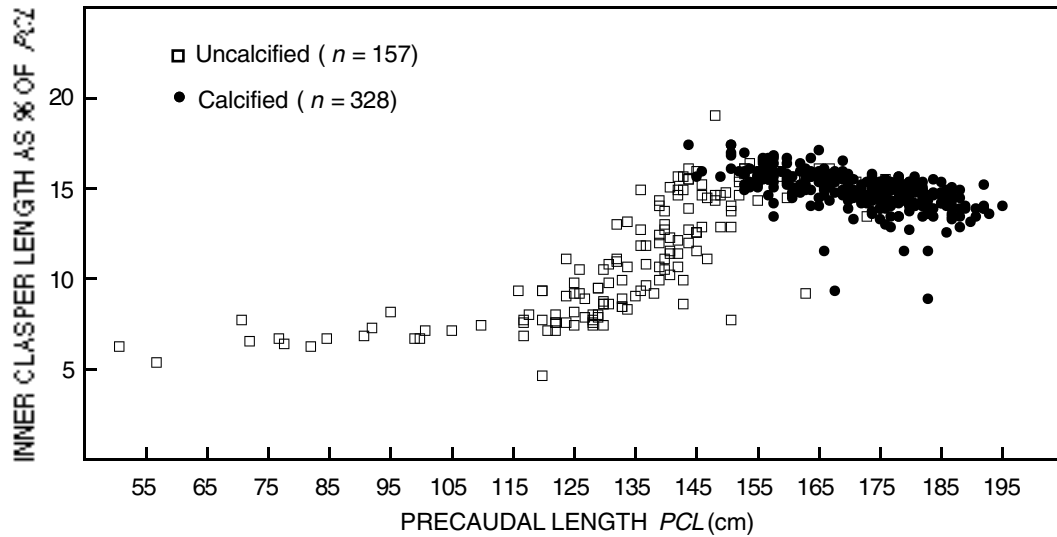


Fig. 7: Relationship between precaudal length and inner clasper length (expressed as a percentage of *PCL*) of male *C. brevipinna*

$\times 100$) of mature males (Kruskal-Wallis *H*-test, $p < 0.01$). The mean *HSI* values of mature males were $<10\%$ from January to April and again in September (Fig. 8b). *HSI* values were highest in June and July, which may be attributable to increased availability of food from the annual winter migration of sardine into the study region (Armstrong *et al.* 1991). *HSI* values

for both sexes combined fluctuated between 4 and 11%, with no seasonal pattern (Fig. 8c).

FEMALES

The length-at-50% maturity was calculated at 154 cm (95% confidence limits of 152 and 156 cm), based

Table II: Comparison of the precaudal length of reproductive parameters for *C. brevipinna* from different geographical regions

Parameter	Precaudal length (cm)						
	East coast of South Africa (present study)	East coast of South Africa (Bass <i>et al.</i> 1973)	Northern Australia (Stevens and McLoughlin 1991)	Southern Brazil (Sadowsky 1967)	Florida (Clark and Von Schmidt 1965, *Dodrill 1971)	Gulf of Mexico (Branstetter 1981)	South Carolina (Castro 1993)
<i>Males</i>							
Maturity	150	169	143	115–119	137–149	124	
Largest adolescent	179	153	120				
Smallest mature	144	169	143		137	124	
Largest mature	195	196	194	163	149	132	
<i>Females</i>							
Maturity	154	169	159	123–172		131	
Largest adolescent	176	167				123	
Largest mature	220	222	206	172		156	148
Smallest pregnant	154	179	187	123	155*	135	148
Mating	Jan.–Mar.	Jan.–May	Mar./Apr.	Nov.–Jan.		Jun./Jul.	
Parturition	Mar./Aug.	Apr./May	Mar./Apr.	Nov.–Jan.		May/Jun.	Jun.–Sep.
Size at birth	50–60	59–67	45–53			38–45	38–49
Mean litter size	9	10.7	11	6	8*	7	
Gestation period (months)	13–18	12–15	12	≈ 12		11–12	

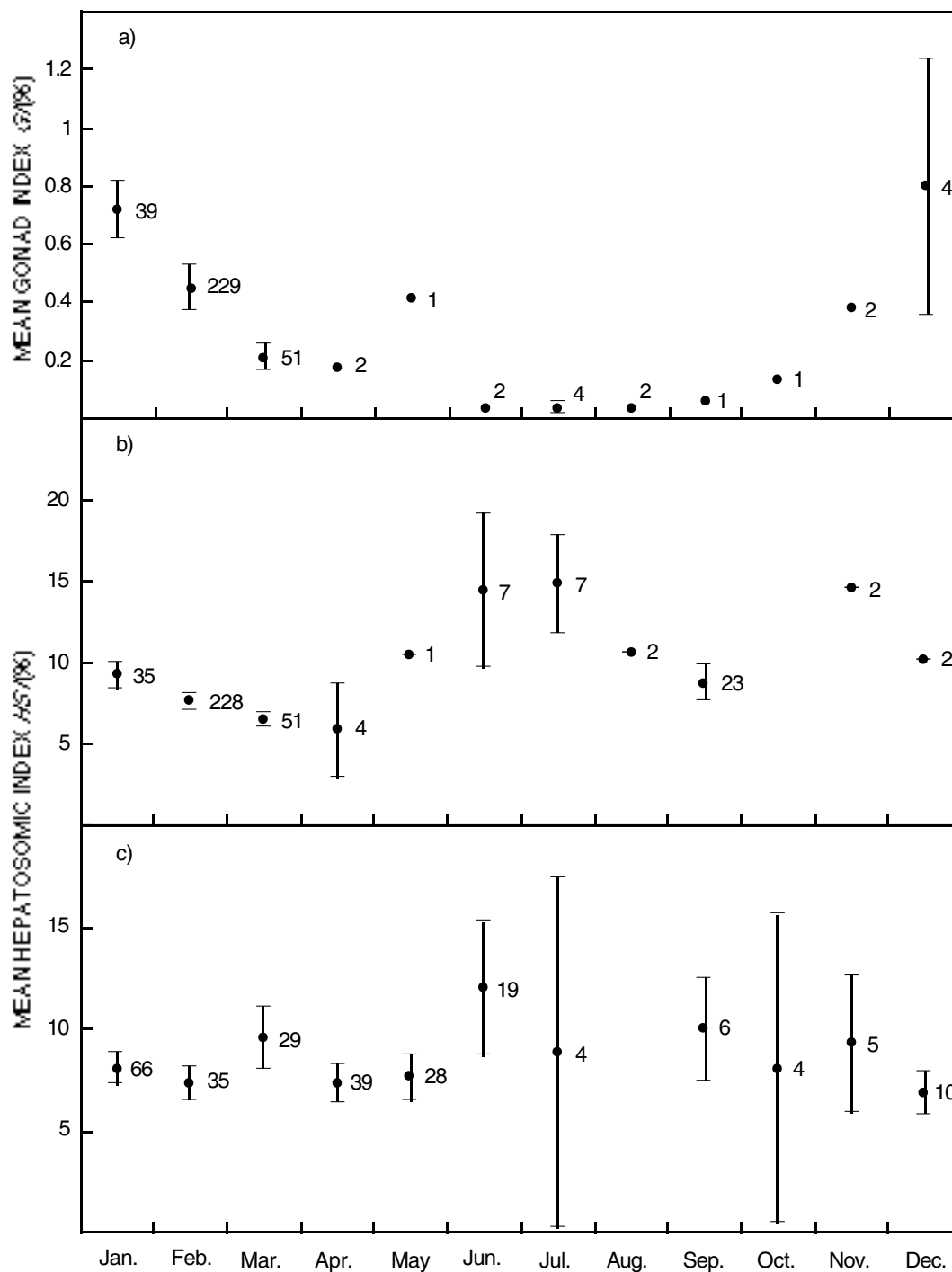


Fig. 8: Mean monthly (a) gonad indices and (b) hepatosomic indices of mature males and (c) mean monthly hepatosomic indices for immature combined sexes of *C. brevipinna*. Bars represent 95% confidence limits and numbers are sample size

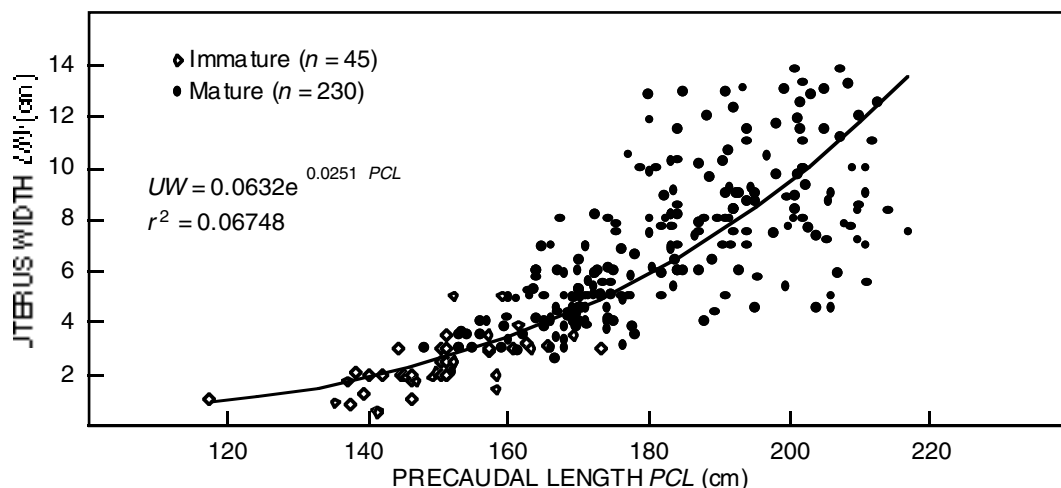


Fig. 9: Relationship between uterus width and precaudal length of non-pregnant female *C. brevipinna* (excluding post-partum females with uterus widths >15 cm)

on the presence of distinct ova in the ovary and loose, sac-like uteri. The smallest mature female was 148 cm, with the smallest and largest pregnant sharks being 154 and 220 cm respectively. Comparative lengths for *C. brevipinna* from southern Brazil and the Gulf of Mexico were smaller than those from Australia and South Africa (Table II).

The largest adolescent female (176 cm) had developing ova in the ovary. Immature females had uterus widths ranging from 0.8 to 5 cm ($n = 48$). There was an exponential relationship between uterus width and PCL in mature females, excluding pregnant and post-partum individuals (Fig. 9). A similar relationship was found by Dudley and Cliff (1993b) for mature *C. limbatus* females.

Significant monthly differences were found in both *GI* and *HSI* values for mature females ($p < 0.01$). Mean monthly maximum ovum diameter (*MOD*) and *GI* values (Fig. 10) were plotted for mature, non-pregnant females. *MOD* values were arbitrarily divided at 15 mm. Two distinct groups were evident between January and June, the ova in one group developing to 30–40 mm in February, whereas those in the other group exhibited little enlargement and remained at around 10 mm. Dudley and Cliff (1993b) obtained similar results for *C. limbatus*. There was a marked peak in *GI* values in February/March (0.47%). *MOD* and *GI* values both decreased in winter to 10–20 mm and <0.1% respectively. *MOD* increased gradually from September to February and *GI* values rose sharply from January to February. An exponential relationship between *GI* and *MOD* (Fig. 11) was also found for *C. limbatus*. However, this relationship was

linear in *C. brachyurus* (Cliff and Dudley 1992).

Mating females and those in the initial stages of pregnancy caught in February and March had high *HSI* values of between 12 and 23% (Fig. 12). These values decreased during pregnancy to around 5% at parturition (March–August), but the sample size of females at mid pregnancy was small. Rossouw (1987) found maximum *HSI* values in the lesser guitarfish *Rhinobatos annulatus* coinciding with their peak breeding activities. An inverse linear relationship ($r^2 = 0.7293$, $n = 70$) was found between the *HSI* of pregnant *C. brevipinna* females and mean embryo length. A two-year reproductive cycle would therefore allow the post-partum females about nine months between pregnancies to regenerate their energy reserves in preparation for the following mating season. Dudley and Cliff (1993b) suggested the possibility of a three-year reproductive cycle for the blacktip shark, based on the presence of mature females in summer that were neither in mating condition nor post-partum. The present findings support the possibility of a three-year reproductive cycle for *C. brevipinna*, because of the small number ($n = 22$) of mature females caught in the first half of the year that were neither pregnant nor had ova large enough to be fertilized in the January/February mating season (Fig. 12). However, in view of the small number of such females, it is also possible that some females that pupped the previous winter may fail to undergo ovum development in the ensuing summer.

The body position and frequency of occurrence of mating bites was recorded from 127 females (Fig. 13). The highest frequency of bites (52.8%) was on the

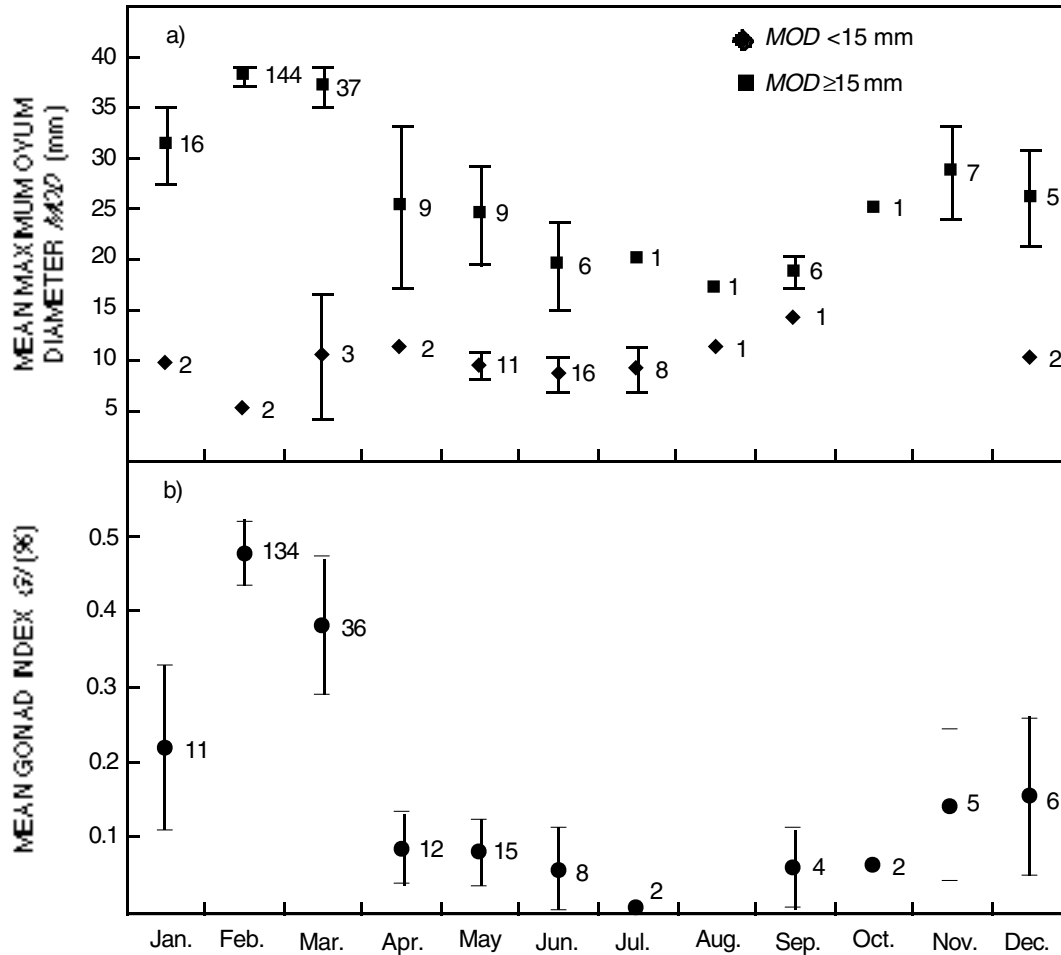


Fig. 10: Seasonal development in mean monthly (a) maximum ovum diameter with an arbitrary split at 15 mm and (b) gonad indices of mature, non-pregnant female *C. brevipinna*. Bars represent 95% confidence limits and numbers are sample size

central and lower flanks of female sharks, with only 16.6 and 13.4% on the pectoral fins and stomach respectively. In some cases, older, healed scars were observed in conjunction with fresh scars, indicating that *C. brevipinna* may mate several times throughout their lifetime (Springer 1960).

Mating and post-partum females were distributed throughout the study area, with the latter caught mainly in June. Of the 290 pregnant females caught, 185 (64%) were caught between March and May, mainly in the northern half of the study area. Three different stages of pregnancy were found (Fig. 14). Females caught in February had fertilized but undeveloped eggs *in utero*, whereas those caught between June and December

had developing embryos, ranging in length between 20 and 45 cm. Females caught between March and August of the following year had near or full-term embryos, ranging in length between 45 and 65 cm. Mating between January and March, followed by parturition between March and August, indicates a gestation period of between 13 and 18 months. The fact that some 50% of the mature females examined were pregnant provides further evidence that *C. brevipinna* reproduce every second year. Similar gestation and parturition periods were found by Bass *et al.* (1973) for South African *C. brevipinna*. However, shorter periods have been reported for this species elsewhere (Table II).

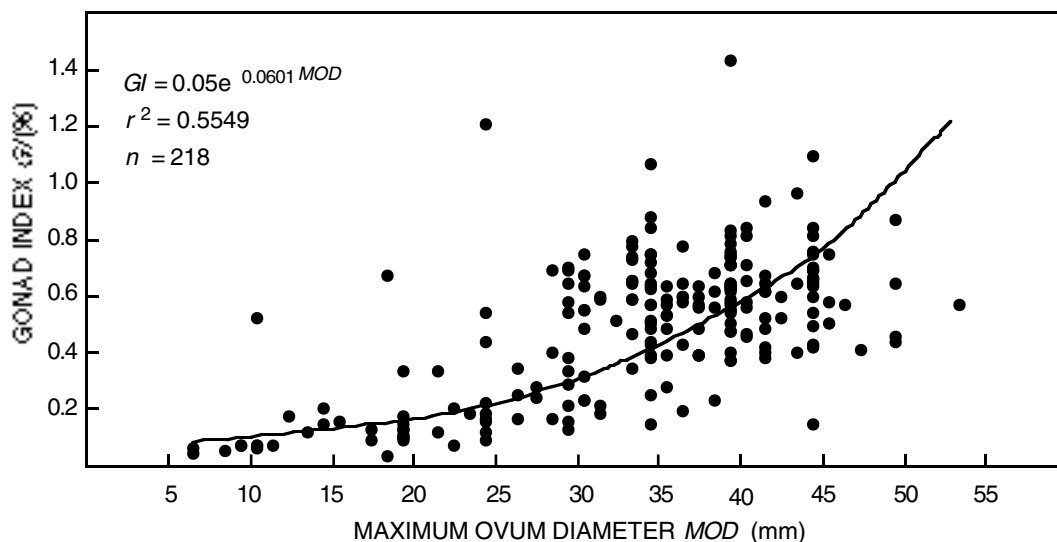


Fig. 11: Relationship between maximum ovum diameter and gonad index of *C. brevipinna*

Embryos and nursery grounds

The smallest embryo found in a litter was 15.8 cm, weighing 100 g. This was considered to be a runt because the size range of the remainder of the litter ranged between 28.7 and 30.9 cm. The largest and heaviest embryo was 62 cm, weighing 2.6 kg. There was an exponential relationship between embryo length and embryo mass ($r^2 = 0.9641$, $n = 262$).

Mean litter size was nine, with a maximum of 17 ($n = 273$ litters). There were weak relationships between mother length and litter size ($r^2 = 0.373$; $n = 273$) and litter mass ($r^2 = 0.493$, $n = 148$). The number of embryos in the right and left uterus, and the sex ratio were equal (χ^2 test, $p > 0.5$, $n = 2\ 467$). Size at birth ranged between 50 and 60 cm, based on the mean length of the largest full-term embryos.

Near-term females, which made up 69% (200) of the

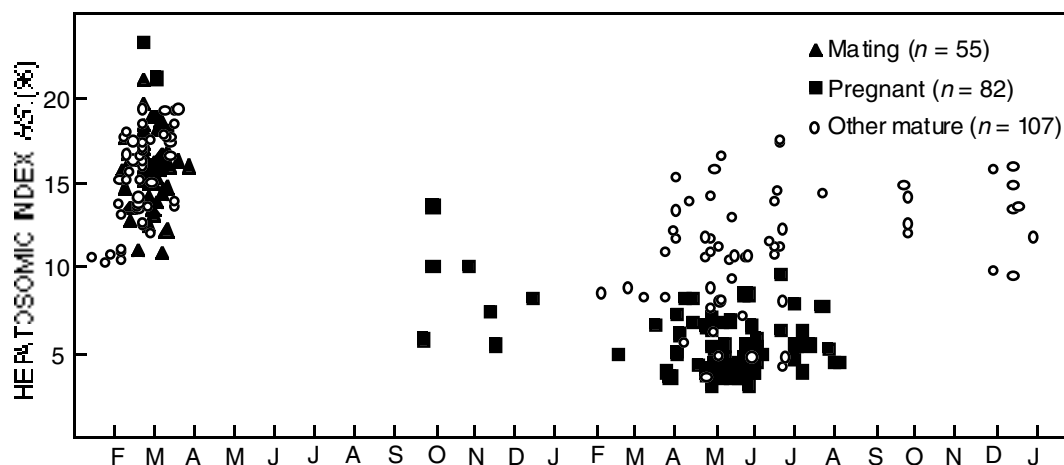


Fig. 12: Seasonal cycle in hepatosomatic index in mature female *C. brevipinna*

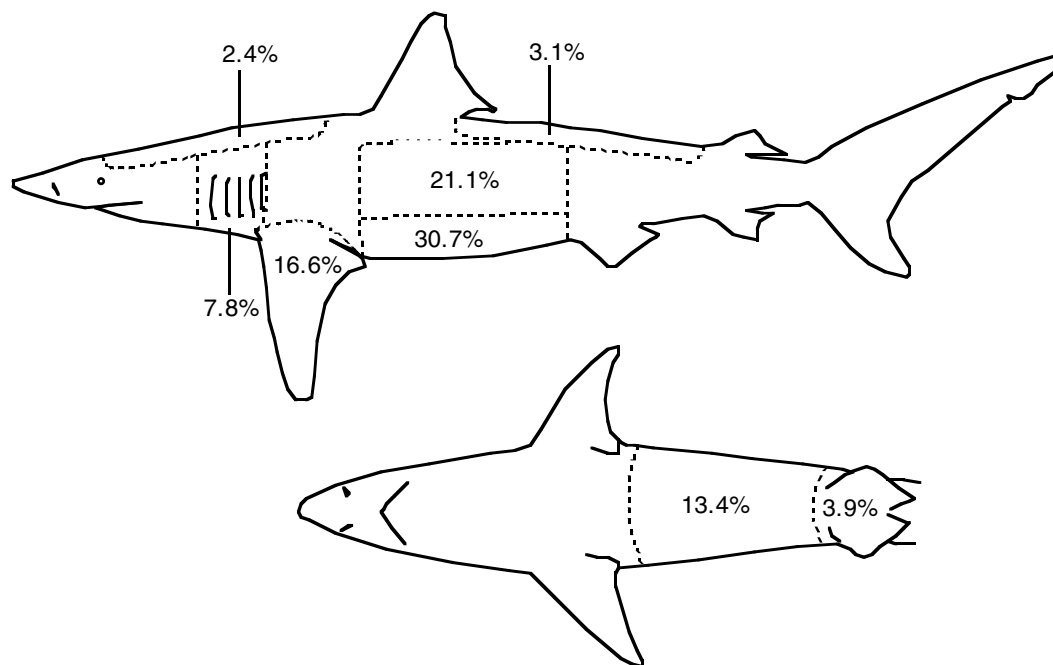


Fig. 13: Position and frequency of occurrence of mating bites on 127 mature female *C. brevipinna* (areas with frequencies <1% are not included)

total catch of pregnant females (290), were taken mainly at Richards Bay (Beach 1) and Zinkwazi (Beach 2), indicating the possibility of a northern nursery area. According to Castro (1993), nurseries of viviparous sharks are usually identified by the presence of gravid

females, neonates and small juveniles. *C. brevipinna* <100 cm were rare in the nets because of the size selectivity of the mesh. Bass *et al.* (1973) found large numbers of young *C. brevipinna* <70 cm between June and December from the central region of the present

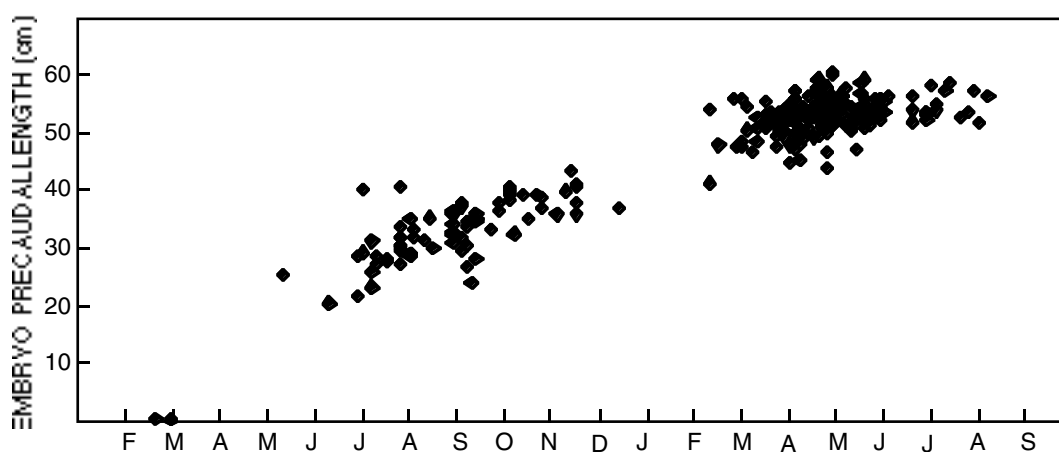


Fig. 14: Relationship between time of year and precaudal length of embryo *C. brevipinna*

Table III: Stomach contents of *C. brevipinna* caught in the Natal shark nets, 1983–1997. Totals represent number of stomachs (*F*), number of prey items (*N*) and mass of prey (*M*, kg) respectively. The index of relative importance (*IRI*) is also given

Prey category	% <i>N</i>	% <i>M</i>	% <i>F</i>	<i>IRI</i>
Teleosts	96.7	96.7	79.6	15 394.6
Ariidae (seacatfish)			0.5	
Carangidae		0.1	0.3	
<i>Carangoides armatus</i> (longfin kingfish)			0.3	
<i>Decapterus macrosoma</i> (slender scad)	1.6	0.1	0.5	0.9
<i>Trachurus delagoa</i> (African horse mackerel)	2.8	4.1	6.3	43.5
Clupidae				
<i>Etrumeus teres</i> (East Coast roundherring)	1.1	0.7	1.8	3.2
<i>Etrumeus whiteheadi</i> (round herring)	0.3		0.5	
<i>Sardinops sagax</i> (South African sardine)	37.8	44.4	15.3	1 257.7
<i>Hilsa kelee</i> (kelee shad)			0.3	
Engraulidae	9.7	0.5	2.4	24.5
<i>Sardonella albella</i> (white sardonelle)			0.3	
<i>Engraulis capensis</i> (Cape anchovy)	18.5	3.9	0.8	17.9
<i>Thryssa vitrirostris</i> (glassnose orangemouth)	3.7	0.9	0.8	3.7
Gerreidae (purse mouth)	0.3		0.3	
Haemulidae			0.3	
<i>Pomadasys commersonnii</i> (spotted grunter)			0.3	
<i>Pomadasys olivaceum</i> (piggy)	0.6	0.1	2.6	1.8
Leiognathidae		0.1	0.3	
<i>Secutor insidiator</i> (slender soapie)	0.2	0.1	0.3	0.1
Monodactylidae				
<i>Monodactylus</i> sp. (moony)			0.3	
Mugilidae (mullet)		0.1	0.3	
Mullidae (goatfish)			0.3	
Pleuronectiformes (flatfish)			0.3	
Pomacanthidae (angelfish)			0.3	
Pomatomidae				
<i>Pomatomus saltatrix</i> (elf)	0.1	0.2	1.1	0.3
Sciaenidae				
<i>Johnius</i> sp. (small kob)	1.2	0.3	1.0	1.5
<i>Otolithes ruber</i> (snapper kob)			0.3	
Scombridae	0.1	5.4	1.3	7.2
<i>Katsuwonus pelamis</i> (skipjack tuna)		0.2	0.3	
<i>Scomber japonicus</i> (chub mackerel)	1.7	22.8	7.4	181.3
<i>Scomberomorus commerson</i> (king mackerel)	0.1		0.3	
Sparidae			0.3	
<i>Pagellus bellottii natalensis</i> (red tjor-tjor)	4.0	0.6	2.4	11.0
<i>Sarpa salpa</i> (strepie)	1.2	1.0	0.3	0.7
Sphyrnidae (barracuda)	0.2		0.8	
Synodontidae			0.3	
<i>Saurida undosquamis</i> (lizardfish)			0.3	
Trichiuridae	0.1	0.1	0.8	0.2
<i>Trichiurus lepturus</i> (cutlass fish)	0.1	1.4	0.8	1.2
Trigilidae				
<i>Cheilidonichthys queketti</i> (lesser gurnard)			0.3	
Soleidae				
<i>Aesopia cornuta</i> (unicorn sole)			0.3	
Unidentified teleost	11.3	9.6	25.6	535.0

(continued)

(Table III continued)

Prey category	%N	%M	%F	IRI
Elasmobranchs	0.1	1.0	1.7	1.9
Sphyrnidae (hammerhead shark)		0.3	0.3	
Carcharhinidae				
<i>Carcharhinus obscurus</i> (dusky shark)		0.1	0.3	
Rhinobatidae				
<i>Rhinobatos annulatus</i> (lesser guitarfish)		0.1	0.3	
Unidentified small shark (<1 m)	0.1	0.5	0.5	0.3
Unidentified large shark (>1 m)			0.3	
Molluscs	2.0	1.9	17.5	68.3
Unidentified cephalopod	0.1	0.1	1.1	0.2
Cephalopoda				
<i>Octopus</i> spp. (octopus)	0.1	0.6	1.6	1.1
Teuthoidea	0.3		2.6	
<i>Sepia</i> spp. (cuttlefish)	1.1	1.0	9.5	20.0
<i>Loligo duvaucelli</i> (squid)	0.1	0.1	1.1	0.2
Enoploteuthidae (enope squid)				
<i>Ancistrocheirus leseuri</i> (sharpear enope squid)	0.1	0.1	0.3	0.1
Gastropoda	0.2		1.3	
Crustaceans	0.2		1.9	
Brachyura (crabs)	0.1		0.8	
Anomura (hermit crab)			0.3	
Othes decapods	0.1		0.8	
Miscellaneous items				
Stones	0.1		0.3	
Total	3 400	158	379	

study area and suggested that a nursing ground existed there. Van der Elst (1979) reported large catches ($n = 1\ 637$) of milk sharks *Rhizoprionodon acutus* by anglers during May between Richards Bay (Beach 1) and Amanzimtoti (Beach 15). *R. acutus* are similar in size and appearance to newborn *C. brevipinna*, so anglers may have confused the two species. It is therefore likely that many of the *R. acutus* caught in May in the northern part of the study area were in fact newly born *C. brevipinna*, as this corresponds with the occurrence of full-term pregnant *C. brevipinna* in the area.

C. brevipinna inhabit estuarine waters off South Carolina, where there is an abundance of neonates and juveniles (Castro 1993). Branstetter (1987) reported that young of both *C. brevipinna* and *C. limbatus* utilize shallow beaches and bay areas of the Gulf of Mexico as nursery areas. Although immature *C. limbatus* are common in the present study area, newborns are uncommon, and it is suggested that the nursery area for

C. limbatus may be north of the study area, near Moçambique (Bass *et al.* 1973). By having different nursery locations, competition between the two species is therefore reduced. However, there may be competition between juvenile *C. brevipinna* and similar-sized mature *Rhizoprionodon acutus*, which are abundant throughout the year in the shallow, inshore waters of KwaZulu-Natal (Bass *et al.* 1975).

Feeding

A total of 1 230 stomachs of *C. brevipinna* was examined, of which 851 (69%) were empty and 31 (2.5%) were everted. The mean mass of the contents from the 379 stomachs containing food was 416 g, equating to 0.6% of the mean body mass. The mean number of prey items per stomach was nine. In all, 27 families and 34 species of prey were identified (Table III).

Table IV: Frequency of occurrence (%F) of the six major prey species of *C. brevipinna* by predator size, season and region, 1983–1997

Prey species	%F							
	Immature	Mature	Season				Region	
			Summer Dec.–Feb.	Autumn Mar.–May	Winter Jun.–Aug.	Spring Sep.–Nov.	North (warm)	South (cool)
<i>Sardinops sagax</i>	7.9	30.6	0.7	4	60	25	9.7	22.2
<i>Sepia</i> spp.	2.6	1.4	13.1	11.7	1.7	4.7	3.9	15.7
<i>Scomber japonicus</i>	5.3	18.1	2	1		35.9	9.7	6.5
<i>Trachurus delagoa</i>	21.1	9.7	8.5	6.8	3.3	1.6	11.1	
<i>Pomadasys olivaceum</i>	10.5		3.3	2.9		1.6	3.9	0.9
<i>Pagellus bellottii natalensis</i>	5.3		4.6	1		1.6	3.4	1.9

North = Beaches 1–21
South = Beaches 31–44

TELEOSTS

C. brevipinna fed primarily on teleosts, which were found in 79% of the stomachs containing food and accounted for 97.1% by mass and 97.6% by number. Representatives from 22 teleost families and 26 species were identified. The three most frequently eaten were sardine *Sardinops sagax* (15.3%), chub mackerel *Scomber japonicus* (7.4%) and African horse mackerel *Trachurus delagoa* (6.3%). Bass *et al.* (1973) found teleosts in 95% of the *C. brevipinna* stomachs they examined and in northern Australia, the species also consumes mainly teleosts (Stevens and McLoughlin 1991).

OTHER PREY

Cephalopods were found in 15.8% of stomachs that contained food. Cuttlefish, *Sepia* spp., were the most frequently eaten and the second most common prey item. Crustaceans and elasmobranchs were in 1.9 and 1.6% of stomachs respectively. Cephalopods were found in 3% of the stomachs examined by Bass *et al.* (1973) and Stevens and McLoughlin (1991) encountered them in 8% of stomachs they examined from northern Australia. *C. brevipinna* consumed shrimp in the Gulf of Mexico (Burgess 1985) and have been observed foraging behind shrimp trawlers in Florida (Dodrill 1971).

VARIATION IN DIET

Although the most common prey items were small pelagic, shoaling fish, the presence of demersal prey such as *Sepia* and red tjor-tjor *Pagellus bellottii natalensis* (Table IV) indicates that *C. brevipinna* are capable of feeding near the bottom. *T. delagoa* were the most common prey item in immature sharks, whereas

S. sagax were more frequently eaten by mature sharks. The majority (83%) of the prey were <30 cm long; the size of prey being largely determined by limitations due to the small, narrow-cusped teeth of *C. brevipinna*.

The proportions of the six major prey items differed significantly between seasons (χ^2 test, $p < 0.001$). The most common prey item in summer and autumn was *Sepia* spp., in winter *Sardinops sagax* and in spring *Scomber japonicus* (Table IV). Seasonal variation in diet is common in many species of shark (Wetherbee *et al.* 1990) because of seasonal changes in the availability of their prey. *S. japonicus* undergo seasonal migrations (Van der Elst 1988), which may explain their absence in the diet in winter. The presence of large shoals of *S. sagax* during winter ("the sardine run") off the KwaZulu-Natal coastline, (Armstrong *et al.* 1991) would explain their dietary importance to *C. brevipinna*, as well as in the copper shark *C. brachyurus* (Cliff and Dudley 1992) and the blacktip shark *C. limbatus* (Dudley and Cliff 1993b) at that time.

The most common prey of sharks in the warmer, northern region from Richards Bay to Park Rynie (Beaches 1–21) was *T. delagoa*. However, this species was absent in the diet of sharks from the cooler, southern region from St Michaels-on-Sea to Mzamba (Beaches 31–41), where *S. sagax* were most frequently eaten. Dudley and Cliff (1993b) found a similar dietary pattern for blacktip sharks.

ACKNOWLEDGEMENTS

We thank the field staff of the Natal Sharks Board (NSB) for providing specimens and information associated with the capture. Messrs P. Methembu and

P. Zungu of the NSB dissected many of the sharks. Mrs B. Cunningham (NSB) was responsible for data capture. Dr M. J. Smale of the Port Elizabeth Museum identified the otoliths and beaks and Dr M. O. Bergh of Ocean and Land Resource Assessment Consultants provided the computer programme used to determine the maximum likelihood estimate of size at sexual maturity. Finally, I (GC) acknowledge the efforts of the first author, Bryce Allen, who was tragically killed in June 2000.

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