

South African Journal of Marine Science



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

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To cite this article: G. Cliff (1995) Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The Great hammerhead shark *Sphyrna mokarran* (Rüppell), South African Journal of Marine Science, 15:1, 105-114, DOI: 10.2989/025776195784156331

To link to this article: https://doi.org/10.2989/025776195784156331



S. Afr. J. mar. Sci. 15: 105-114 1995

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SHARKS CAUGHT IN THE PROTECTIVE GILL NETS OFF KWAZULU-NATAL, SOUTH AFRICA. 8. THE GREAT HAMMERHEAD SHARK SPHYRNA MOKARRAN (RÜPPELL)

G. CLIFF*

Between 1978 and 1993, 209 great hammerhead sharks *Sphyrna mokarran* were caught in the shark nets which protect the swimming beaches of KwaZulu-Natal. This species constituted 0,97% of the total shark catch, with a mean annual catch of 13. Catch rates showed a significant decline during the period under review, from 0,66 to 0,09 sharks km-net-1 year-1. Most sharks were caught in the north of the netted region between January and May. Catches at Mzamba, the southern extremity of the netted region, represent the southernmost records of this species on the east African coast. The males ranged in size from 106 cm precaudal length (18 kg) to 264 cm (220 kg) and females from 140 cm (35 kg) to 326 cm (400 kg). Males matured at about 217 cm and females at 237 cm. Very few sharks were found in mating condition. Elasmobranchs were found in 82% of non-empty stomachs. There was a high incidence of stingrays (Dasyatidae), guitarfish (Rhinobatidae) and other bottom-dwelling fish in the diet.

Tussen 1978 en 1993 is 209 groothamerkophaaie *Sphyrna mokarran* gevang in die haainette wat die swemstrande van KwaZulu-Natal beskerm. Hierdie spesie het 0,97% van die die algehele haaivangs uitgemaak, met 'n jaarvangs van gemiddeld 13. Vangkoerse het beduidend gedurende die verslagtydperk afgeneem, van 0,66 tot 0,09 haaie 'km-net-1 a-1. Die meeste van dié haaie is tussen Januarie en Mei in die noorde van die netbeskermde gebied gevang. Die vangste by Mzamba, die verste suid waar nette aangebring is, verteenwoordig ook die suidelikste boekstawings van hierdie spesie aan die ooskus van Afrika. Mannetjies se groottes het van 106 cm prekoudale lengte (18 kg) tot 264 cm (220 kg) gestrek en dié van wyfies van 140 cm (35 kg) tot 326 cm (400 kg). Mannetjies het op sowat 217 cm geslagsrypheid bereik en wyfies op 237 cm. Baie min haaie is aangetref wat gereed was om te paar . Kraakbeniges is in 82% van die pense met inhoud gevind. Die voorkoms in die dieet van pylsterte (Dasyatidae), sandkruipers (Rhinobatidae) en ander bodemlewende visse was hoog.

The great hammerhead shark Sphyrna mokarran (Rüppell) is the largest of the nine members of the family Sphyrnidae. It is found in warm tropical waters throughout the world (Gilbert 1967, Compagno 1984). It is widespread in the south-west Indian Ocean (Fig. 1), but in South Africa it is confined to the KwaZulu-Natal coast, where it co-exists with the scalloped hammerhead S. lewini, also an inhabitant of the tropics, and the smooth hammerhead S. zygaena, which favours cooler waters (Bass et al. 1975). Sphyrna mokarran occurs close inshore but it may frequent deep water over continental shelves (Compagno 1984). Biological studies on this species have been conducted in Madagascar (Fourmanoir 1961), Florida (Clark and Von Schmidt 1965, Dodrill 1977), northern Australia (Stevens and Lyle 1989), west Africa (Cadenat 1957) and the east coast of South Africa (Bass et al. 1975).

Great hammerhead sharks are caught in the gill nets which protect the beaches of KwaZulu-Natal (formerly Natal) against shark attack (Wallett 1983). These nets, known locally as shark nets, are maintained by the Natal Sharks Board (NSB). This paper is the eighth in a series describing the general biology and catch statistics of each of the fourteen species of sharks commonly caught in the nets.

MATERIALS 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 distribution of nets is shown in Figure 1. In 1991, 1,3 km of nets was installed at Mbango, immediately north of St Michael's on Sea. The total length of netting at January 1993 was 44,4 km. Units of effort are kilometres of net per year.

Catch and biological data were recorded between 1978 and 1993. Earlier records were incomplete due to a failure to distinguish this species from its two congenerics. All lengths used in this report are precaudal lengths (PCL), because this is considered the most accurate measure of the length of a shark with a precaudal notch. Lengths cited from the literature were converted to PCL using the equations given below. Both precaudal length and fork length (FL) were measured as straight lines, parallel to the body, from the tip of the snout to the precaudal notch and to the fork of the tail respectively. The following relationship was found between these two length measurements:

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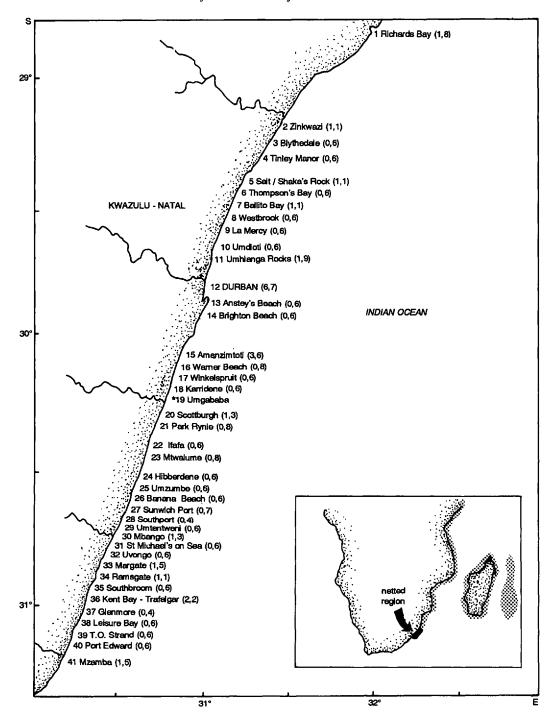


Fig. 1: Netted beaches on the KwaZulu-Natal coast and, in parentheses, the length of nets in kilometres in January 1993. * Nets were removed from Umgababa (No. 19) in 1990. Inset shows the locality of the netted region and the distribution of the great hammerhead shark in southern Africa

$$FL = 1,064 PCL + 6,09$$

(n = 40, r = 0,982, range: 133-306 cm PCL).

Bass et al. (1975) calculated total length (TL) as the sum of the precaudal length and 80% of the upper caudal length (UCL), while Dodrill (1977) used the sum of PCL and 85% of UCL. The UCL was measured as a straight line from the precaudal notch to the tip of the upper caudal fin. The relationship between UCL and PCL was linear:

$$UCL = 0.350 PCL + 17.10$$

(n = 140, r = 0.932, range: 106-306 cm PCL).

Total length (TOT) was measured by placing the upper caudal lobe parallel to the body axis, but the sample was too small (n = 12) to determine an accurate relationship with precaudal length. The following equation (Stevens and Lyle 1989) was used to convert from TOT to FL:

$$TOT = 1,29 FL + 3,58 (n = 261, r = 0,997)$$
.

Fork length was then converted to *PCL* using the equation given above.

Measurements of reproductive structures are given by Cliff et al. (1988) and criteria for visual assessment of maturity follow Bass et al. (1975).

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 onwards, 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; Hyslop 1980). Otoliths and cephalopod beaks were kept and identified against reference material in the collection of the Port Elizabeth Museum.

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

NET CATCHES

Annual variation

Between 1978 and 1993, 209 great hammerhead sharks were caught, with an annual mean of 13 (range 4–26). They constituted 0,97% of the total shark catch by number. During this period the annual catch rate ranged from 0,09 to 0,66 sharks km-net⁻¹ and showed a significant negative trend (r = -0.677,

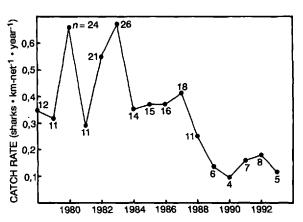


Fig. 2: Catch rates of great hammerhead sharks in the shark nets, 1978–1993

p < 0.005, Fig. 2). However, annual catch was low. The decline was unusual in that most shark species or species groups exhibited a drop in catch rate at the onset of widespread netting in the mid 1960s. This decline generally lasted until the early 1970s and no trend in catch rates was evident thereafter (Dudley and Cliff 1993a). Assuming that catch rate is an indicator of abundance off the KwaZulu-Natal coast, then there was a decline in numbers over the study period. In a species that is widely distributed in the tropical south-west Indian Ocean and is fished by the nets only at the southern extremity of its range, it is unlikely that mortalities from these nets alone are responsible for this decline.

Geographical and seasonal distribution

Great hammerhead sharks were caught at all but three net installations; the three were all in the south of the study region (Fig. 3). Catch rates of both sexes were highest to the north, with a peak at Zinkwazi (Beach 2, Fig. 1). Richards Bay, the northernmost beach, had the highest catch (23), followed by Zinkwazi with 18 sharks. Catches were made throughout the year, but they peaked in summer and remained high through May (Fig. 4); few sharks were caught in August and September. This geographical and seasonal catch pattern may be explained by the tropical distribution of S. mokarran. The sharks caught at Mzamba (Beach 41, Fig. 1, 31°08'S) represent the southernmost records on the east African coast, although the region immediately to the south of Mzamba is poorly sampled and great hammerhead sharks may occur there. The southern limit of this species on the east coast of Australia is 32°40'S (Stevens

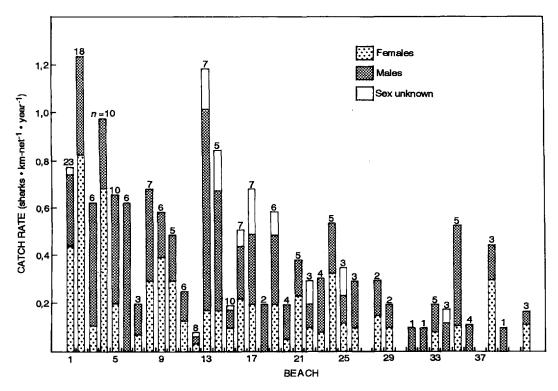


Fig. 3: Geographical distribution of annual catch rates of great hammerhead sharks in the shark nets, 1978–1993.

Beach numbers refer to Figure 1

and Lyle 1989).

In February 1984, following cyclone-induced floods, a hammerhead shark of about 4 m was seen in a small tributary of the Pongola River, which enters the sea in Maputo Bay, southern Moçambique. The shark was approximately 20 km from the sea. An NSB staff member saw the shark and identified it as a great hammerhead, because of its high dorsal fin. It may have been a scalloped hammerhead, but, irrespective of the identity, this incident appears to be the first reference to either species occurring in freshwater.

The shark net catch consisted of 109 males and 87 females; the sex ratio did not differ significantly from 1:1 (χ^2 test, p = 0,12). Females dominated the catches at three of the four northernmost beaches, but to the south more males were caught (Fig. 3). During the period January – April, the months of high catches, neither sex was more abundant, but from June to October very few females were caught (Fig. 4). Stevens and Lyle (1989) found significantly more males in their sample from northern Australia.

Only 4,8% of the 209 sharks caught were found

alive; none of these animals was tagged and released. Similarly low survival rates following capture in the nets were recorded for S. lewini and S. zygaena;

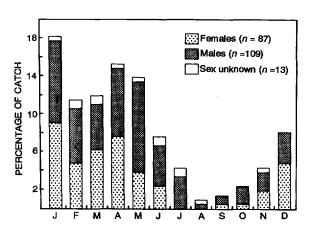


Fig. 4: Seasonal distribution of catches of the great hammerhead shark in shark nets, 1978–1993

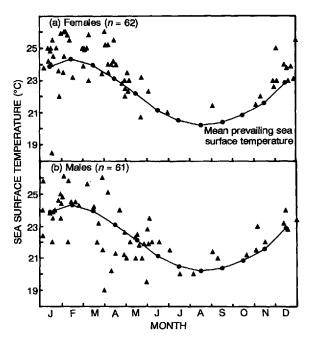


Fig. 5: Relationship between sea surface temperature and catches of (a) female and (b) male great hammer-head sharks between Richards Bay and Park Rynie

these values were the lowest for all sharks commonly caught in the nets (Cliff and Dudley 1992a). On three occasions, two great hammerhead sharks were found in the same net installation on the same day. No larger groups were encountered. Two of the pairs consisted of immature sharks of opposite sex. The third pair was a mature and an immature female. These results suggest that great hammerhead sharks are solitary, unlike the scalloped hammerhead and the smooth hammerhead, which may occur in large groups (Bass et al. 1975).

Environmental conditions at the nets

The sharks were caught in water with a surface temperature ranging from 18.5° C in January to 26.1° C in February and a mean of 23.1° C (n = 158). Most of the sharks (78%) were caught between Richards Bay and Park Rynie, a zone of relatively uniform temperature (Cliff et al. 1989). The mean monthly temperature (1981–1992) within this zone is shown in Figure 5. Significantly more females were caught there in water warmer than the monthly average than in cooler water (Fig. 5a, χ^2 test, p = 0.0001, n = 62). Males (n = 61) were caught in equal num-

bers in water warmer and cooler than the monthly mean (Fig. 5b).

Between October and December all sharks of both sexes were caught in water warmer than the average. This suggests that the sharks only move into the netted region at this time with the influx of warm water. Thereafter the sharks occurred in the netted region throughout summer, regardless of water temperature. With the water cooling in April and May, catches of females declined and sharks of this sex were rarely found in water cooler than 22°C. The males appeared more tolerant of cooler water, but by midwinter (August) they too were scarce in the netted region. Given the species' tropical distribution, it is assumed that great hammerhead sharks move north into warmer water in winter. As there were relatively small changes in the number of sharks caught from one month to the next (Fig. 4), it would seem that the presence of this species in KwaZulu-Natal is a seasonal expansion of its range rather than a migration. Populations of great hammerhead sharks off Florida and in the South China Sea also move polewards in summer (Taniuchi 1974, Compagno 1984).

The clarity of the water in which the sharks were caught ranged from 0 to 10 m, with a mean of 3,4 m (n = 162). There was no sex-related difference in the association between catch and clarity. At the two beaches with the highest catches, the mean water clarity at the time of capture was 1,2 m (n = 22) at Richards Bay and 2,6 m (n = 16) at Zinkwazi. The mean water clarity at these two beaches for the period 1981-1992 was 1,1 m at Richards Bay and 3,1 m at Zinkwazi. At Zinkwazi, the water is more turbid in summer when most of the sharks were caught, which accounts for the water at the time of capture being more turbid than the overall mean. The high catch at Richards Bay and Zinkwazi does not appear to be related to water clarity, but simply to the location of these beaches at the north of the study region.

Length distribution

There was no significant difference in the length: mass relationships of males and females (Student's t test, p > 0.05) and the data from the sexes were therefore combined (Fig. 6). The males examined in the laboratory ranged from 106 cm (18 kg) to 264 cm PCL (220 kg), with a mode of 201-210 cm (Fig. 7). The secondary mode of 151-160 cm may be an artifact of the small sample size. The females ranged from 140 cm (35 kg) to 326 cm PCL (400 kg), with a broad peak at 201-240 cm (Fig. 7). These maximum sizes are far smaller than those from northern Australia, where the largest sharks from a sample of

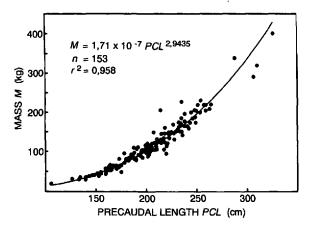


Fig. 6: Relationship between precaudal length *PCL* and mass *M* of the great hammerhead shark

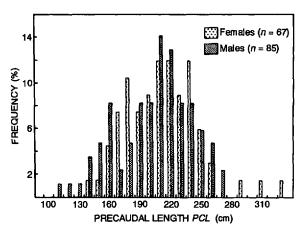


Fig. 7: Length frequency distribution of great hammerhead sharks caught in the shark nets, 1978–1993

1 334 were a male of 345 cm and a female of 315 cm (Stevens and Lyle 1989). The number of sharks sampled by the shark nets is too small to determine whether these geographical differences are real.

BIOLOGY

Reproduction

MALES

In males the length at 50% maturity was 217 cm (maximum likelihood estimation). The largest adolescent, based on its soft claspers, was 230 cm; the smallest mature male was 192 cm (Fig. 8). Two mature males, with large quantities of sperm in the ampulla of each ductus epididymidis, were caught in late November and January. These sharks were both considered to be close to mating condition. They had gonad indices (GI; gonad mass/shark mass \times 100) of 0,14 and 0,20% respectively. The value of 0,20% was the highest recorded among mature males (n = 13). There were insufficient data to check for a seasonal relationship in either GI or the hepatosomic index (HSI; liver mass/shark mass \times 100). The mean HSI of mature males was 8,2% (n = 15, SE = 0.69), which was significantly higher (Student's t test, p = 0.004) than that of immature males (6,1%, n = 32, SE =0,36).

Stevens and Lyle (1989) reported that males mature at about 155 cm, a value markedly lower than that obtained in this study. Those authors recorded the highest mean monthly GI values in October and November, 0,4 and 0,3 respectively, and they suggested that males mate at that time. The GI in male carcharhinid sharks peaked 2-3 months prior to the attainment of maximum ovum diameter in females (Cliff and Dudley 1992b) or to ovulation (Stevens and McLoughlin 1991). Although data on female S. lewini were few, the GI of mature males also appeared to peak 3-4 months before ovulation (Stevens and Lyle 1989). Given these observed lags, it would seem more likely that S. mokarran mate 2-4 months after the peak in male GI, and not during the peak, as suggested by Stevens and Lyle (1989).

FEMALES

In females the length at 50% maturity was 237 cm (maximum likelihood estimate) but, as in the males, there was considerable overlap in the size of adolescent and mature specimens. The largest adolescent was 246 cm, with narrow, tubelike uteri. The smallest mature shark was 218 cm. It had a regressed ovary with large bag-like uteri about 12 cm wide. The largest maximum ovum diameters (MOD), 15-20 mm, were found in females caught in March, April and June. The mean GI of mature females was 0,073 (n = 8). The highest GI (0,123) was recorded in a female caught in March, but the MOD was only 5 mm. The highest mean monthly MOD of 27 mm in the Australian study occurred in May (Stevens and Lyle 1989). Assuming that ovulation occurs when the ova exceed 25 mm, none of the females examined in the present study were in mating condition. Stevens and Lyle (1989) found that ovulation may take place

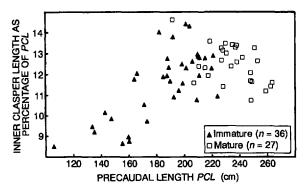


Fig. 8: Relationship between inner clasper length and precaudal length of male great hammerhead sharks

between February and July. Unless the females store sperm, this could mean a mating period of several months.

The *HSI* of immature females was 6,8% (SE = 0.35, n = 30), which was similar to that of immature males. The *HSI* of mature females was 9,0% (SE = 1.32, n = 6), not significantly different from that of mature males, but higher than that of immature females (Student's t test, p = 0.027).

Great hammerhead sharks of both sexes show marked geographical variation in size at maturity, the sharks from South Africa apparently maturing at the largest size. Stevens and Lyle (1989) found that females mature at 145 cm. The smallest of three pregnant great hammerhead sharks sampled by Dodrill (1977) off Florida was 187 cm, which was at least 40 cm shorter than the smallest pregnant female previously recorded from Florida (Clark and Von Schmidt 1965). Fourmanoir (1961) examined a pregnant female of 191 cm from Madagascar.

In the present study females matured at a far larger size (237 cm) than males (217 cm). This is a feature of many other carcharhiniform sharks (Compagno 1984), including *S. lewini* and *Eusphyra blochii* (Stevens and Lyle 1989). Therefore, the observation by Stevens and Lyle (1989) that female great hammerhead sharks mature when about 10 cm smaller than males is unusual.

Embryos

A single pregnant female of 223 cm was caught in November at Richards Bay and was examined only by the local NSB field officer. For this reason and because of its relatively small size, it is considered possible that the specimen may have been S. lewini.

The litter comprised 15 embryos, with three males and three females in the right uterus and four males and five females in the left uterus. The mean embryo length was 33,8 cm (0,39 kg), with a range of 31,0-35,5 cm (0,35-0,45 kg). Size at birth is reported to be about 30-45 cm, with litter sizes of 13-42 (Compagno 1984). Clark and Von Schmidt (1965) deduced that birth in Florida waters took place between late spring and early summer. Stevens and Lyle (1989) also reported that birth of *S. mokarran* occurred in spring-summer (December and January).

Feeding

A total of 147 stomachs was examined between 1978 and 1993; one was everted and food was found in 119 (82,5% of non-everted stomachs). The average mass of food found in 77 stomachs was 1940 g, 1,7% of the mean body mass. The average number of prey items was 2,1 per stomach. The incidence of nonempty stomachs was far higher than that encountered in other shark species found in the shark nets, e.g. blacktip shark Carcharhinus limbatus (50,9%, Dudley and Cliff 1993b), bull shark C. leucas (60,5%, Cliff and Dudley 1991) and great white shark Carcharodon carcharias (40%, Cliff et al. 1989). The results of the present study were similar to those from great hammerhead sharks in northern Australia, where Stevens and Lyle (1989) found food in 87,6% of 347 stomachs, also from sharks sampled in gill nets.

ELASMOBRANCHS

Over the 16-year study period elasmobranchs were found in 83,2% of stomachs that contained food. Between 1983 and 1993, they were found in 90,9% of stomachs and constituted 92,6% by mass and 76,1% by number. The prey was dominated by members of the superorder Batoidea (rays), in particular guitarfish (Rhinobatidae — 22,1%F) and stingrays (Dasyatidae — 18,9%F, Table I). Two families of sharks were represented: catsharks (Scyliorhinidae), often identified from the presence of egg cases together with soft and skeletal tissues, and requiem sharks (Carcharhinidae). The latter consisted of two species, the juvenile dusky shark Carcharhinus obscurus, which was the most common prey species (10.9%F), and the milk shark Rhizoprionodon acutus (9,2%F, Table I). Very few large (>1 m) sharks were found.

Dasyatid stingrays and guitarfish were identified by Stevens and Lyle (1989) as important prey of great hammerheads. Those authors also found batoid prey more frequently than they did sharks, as did

Table I: Stomach contents of great hammerhead sharks caught in the shark nets, expressed as percentages of the stomachs containing food (%F), the total mass of food (%M) and the number of prey items (%N). Totals represent number of stomachs (F), mass of prey items (M, kg) and number of prey items (N)

Prey category	1978-1982	1983-1993		
	%F	%F	%M	%N
ELASMOBRANCHS	64,3	90,9	92,6	76,1
Carcharhinidae (requiem sharks)		2.0	2.2	1.0
Unidentified requiem shark Carcharhinus obscurus (dusky shark)	2,4	3,9 15,6	3,2 30,7	1,8 8,6
Rhizoprionodon acutus (milk shark)	14,3	6,5	0,5	4,3
Scyliorhinidae (catsharks)	1	-,-	1,-	
Unidentified catshark		6,5	0,4	6,7
Halaelurus lineatus (banded catshark) Rajidae (skates)		1,3	0,1	0,6
Unidentified skate	1	1,3	0,0	0,6
Rhinobatidae (guitarfish)		1,5	·	,
Unidentified guitarfish	19,0	16,9	4,2	9,8
Rhinobatos annulatus (lesser guitarfish)	[[5,2	2,8	3,1
Rhinobatos leucospilus (greyspot guitarfish) Myliobatidae (eaglerays)		2,6	2,2	1,8
Pteromylaeus bovinus (bullray)		5,2	4,6	3,1
Mobulidae (mantas)		5,2	1,0	5,1
Manta birostris manta	[[1,3	4,7	0,6
Dasyatidae (stingrays)		440		
Unidentified stingray Dasyatis kuhlii (bluespotted stingray)	2,4	14,3 2,6	14,7 1,5	7,4 1,2
Himantura uarnak (honeycomb stingray)	2,4	2,0	1,5	1,2
Himantura gerrardi (sharpnose stingray)	}	5,2	10,1	1,8
Gymnura natalensis (backwater butterflyray)	2,4	3,9	3,8	2,5
Unidentified elasmobranch	4,8	2,6	0,1	1,2
Unidentified shark Unidentified batoid	26,2	1,3 22,1	0,6 4,8	0,6 13,5
Unidentified small shark	9,5	10,4	1,2	6,1
Unidentified large shark		1,3	2,1	0,6
TELEOSTS	42,8	35,1	7,3	20,9
Ariidae (seacatfish)	1	•		
Unidentified seacatfish	2,4			
Galeichthys feliceps (white seacatfish) Platycephalidae (flatheads)		1,3	0,1	0,6
Unidentified flathead	2,4	1,3	0,4	0,6
Triglidae (gurnards)	-,.	-,-	, , ,	0,0
Unidentified gurnard		1,3	0,0	0,6
Haemulidae (grunters) Unidentified grunter	1	1,3	0,3	1,2
Pomadasys commersonnii (spotted grunter)	2,4	5,2	3,3	2,5
Pomadasys kaakan (javelin grunter)		1,3	0,1	0,6
Pomadasys olivaceum (piggy)		1,3	0,0	0,6
Sciaenidae (kobs) Johnius dussumieri (small kob)	- }	1,3	0,1	0,6
Umbrina ronchus (slender baardman)		1,3	0,1	0,6
Oplegnathidae (knifejaws)				·
Oplegnathus conwayi (Cape knifejaw)		1,3	0,0	0,6
Echeneidae (remoras) Unidentified remora	2,4		ļ	
Pleuronectiformes (flatfish)	2,4			
Unidentified flatfish	4,8	6,5	1,5	4,9
Unidentified teleost	28,6	15,6	1,3	7,4
CEPHALOPODS	4,8	1,3	0,0	0,6
Sepia sp. (cuttlefish)	2,4	•		·
Squid		1,3	0,0	0,6
Unidentified cephalopods	2,4		\	
CRUSTACEANS		5,2	0,0	2,4
Brachyura (crabs)		1,3	0,0	0,6
Palinuridae (spiny lobsters)		3,9	0,1	1,8
Total	42	77	149,4	163

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Dodrill (1977) working in Florida. Dodrill (1977) reported a high incidence of stingrays, but no guitarfish. Cadenat (1957), working in west Africa, found the stingray *Trygon margarita* in 86% of stomachs and *Rhinobatos* in 2% of stomachs.

TELEOSTS

Teleosts were found in 37,8% of non-empty stomachs over the 16-year study period. Between 1983 and 1993, they occurred in 35,1% of stomachs, contributing 7,3% by mass and 20,9% by number. Over the study period, representatives from seven teleost families were found (Table I). The most important prey were grunters (Haemulidae) and flatfish (Pleuronectiformes). Otoliths without associated body tissue, and therefore not reflected in Table I, were found in nine stomachs between 1983 and 1993. All these otoliths belonged to species listed in Table I, the most common being the white seacatfish *Galeichthys feliceps* (3 stomachs) and the spotted grunter *Pomadasys commersonnii* (2 stomachs).

Stevens and Lyle (1989) reported that 87,5% of non-empty stomachs contained fish, both teleosts and elasmobranchs. In their study teleosts were the more important of the two fish categories, occurring in more than twice the number of stomachs that contained elasmobranchs. This result may be due to a higher incidence of small sharks in the Australian study, where the median size was about 150 cm. The median length of sharks in the present study was 208 cm. Small predators may be unable to handle larger prey, which would exclude many elasmobranchs from the diet of small great hammerhead sharks, a situation found in the bull shark by Cliff and Dudley (1991). On the other hand many teleosts, in particular the flatfish, may be too small to be of interest to the larger predators. Dodrill (1977) also found that teleosts were more important prey than elasmobranchs. Seacatfish (Ariidae) were the most common teleost prey in the studies of Cadenat (1957), Dodrill (1977) and Stevens and Lyle (1989).

OTHER PREY

Only two other prey groups, crustaceans, consisting mainly of swimming crabs, and cephalopods were encountered, each of which in fewer than 5% of stomachs. Cephalopod beaks without associated body tissue, and which were therefore omitted from the quantitative analysis, were found in four stomachs between 1983 and 1993. One of these stomachs contained the beaks of 32 squid from the family Octopoteuthidae and 21 Ancistrocheirus lesueuri (Enoploteuthidae). Stevens and Lyle (1989) found a much higher incidence of crustaceans (17,1%) but a similarly low incidence of cephalopods (4,6%).

DISTRIBUTION OF PREY

The most common prey families, the Rhinobatidae and the Dasyatidae, as well as the flatfish, are benthic inhabitants of sandy substrata. Juvenile dusky sharks are found throughout the water column. Milk sharks and grunters are found close to a sandy sea bed. Catsharks and seacatfish are demersal, usually associated with reef. It is clear that the great hammerhead feeds extensively on or very close to the bottom, particularly on soft substrata. Despite this habit, seaweed was not found in any stomachs. The fish ingested by northern Australian sharks were mainly demersal species (Stevens and Lyle 1989).

Ancistrocheirus lesueuri and cephalopods of the family Octopoteuthidae are large oceanic squid occurring in depths of 200 m and more. These pelagic, deep-water prey are unlikely to be common in sharks caught in the shark nets, which are only 400 m from the shore and in water 10–14 m deep. The presence of such prey therefore confirms that great hammerhead sharks do venture into deep water (Compagno 1984).

SIZE OF PREY

The largest prey item examined in this study was a manta *Manta birostris*, only part of which, consisting of 15 portions and weighing 7,0 kg, had been ingested by a shark of 215 cm. The manta remains, and those of a single large shark found in a predator of 235 cm, were the only prey which appeared to be larger than 1 m. All other prey items in which length was recorded were smaller than 1 m. The largest prey item swallowed whole was a dusky shark of 86 cm weighing 10,2 kg found in a shark of 253 cm. The heaviest item, ingested by a 306 cm great hammerhead, was a 12,0 kg sharpnose stingray *Himantura gerrardi* of 74 cm disc width. Both prey bore few tooth puncture marks, indicating that they had been swallowed with minimal biting.

Of 26 prey items in which the entire fish was found in the stomach, 7,7% (2) were ingested without any tooth puncture marks, 26,9% (7) were intact but bore tooth puncture marks, 34,6% (9) were intact but partially severed and 30,7% (8) were in two or more pieces. Strong et al. (1990) described how a great hammerhead repeatedly bit a stingray before swallowing it. From the present study it appears that such manipulation of the prey does not always take place and that prey of between 0,5 and 1 m can be swallowed whole.

SCAVENGING

There was no evidence of great hammerhead sharks being caught while scavenging on an animal

already captured in the nets. A guitarfish carcass was scavenged after the pectoral fins had been cut off by a fisherman. Another shark had ingested a small piece of cardboard.

ACKNOWLEDGEMENTS

The field staff of the Natal Sharks Board were responsible for providing specimens and information associated with their capture. Mr P. Mthembu dissected many of the sharks. Mrs B. Cunningham was responsible for data capture on computer and Mr S. F. J. Dudley commented on the manuscript. Dr M. J. Smale of the Port Elizabeth Museum identified the otoliths and beaks and Dr M. O. Bergh of OLRAC (Pty) Ltd provided the computer programme used to determine the maximum likelihood estimate of size at sexual maturity.

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