Cephalopod Biodiversity, Ecology and Evolution
Payne, A. I. L., Lipiński, M. R., Clarke, M. R. and M. A. C. Roeleveld (Eds). *S. Afr. J. mar. Sci. 20: 241–253*
1998

CEPHALOPODS IN THE DIETS OF FOUR SHARK SPECIES (*GALEOCERDO CUVIER*, *SPHYRNA LEWINI*, *S. ZYGAENA* AND *S. MOKARRAN*) FROM KWAZULU-NATAL, SOUTH AFRICA

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The cephalopod components of the diets of four species of shark, tiger *Galeocerdo cuvier*, smooth hammerhead *Sphyrna zygaena*, scalloped hammerhead *S. lewini* and great hammerhead *S. mokarran*, were examined to reveal patterns of prey choice. Although these sharks were caught in the inshore gillnets used in KwaZulu-Natal to protect bathers from shark attack, prey included neritic and oceanic taxa that were pelagic, epibenthic or benthic. In all, 3 387 lower beaks were found in the stomach contents. A total of 15 families was identified from 117 tiger sharks with cephalopod lower beaks in their stomachs. Sepiidae, Octopodidae and Ancistrocheiridae were most numerous and dominated in terms of mass. Of the 422 scalloped hammerheads with lower beaks in their stomachs, Octopodidae, Octopoteuthidae and Ancistrocheiridae were the most dominant of the 12 families identified. The cephalopod prey items of 258 smooth hammerheads were dominated by Loliginidae. Sepiidae and Ancistrocheiridae were also major components of the 12 families identified. The prey items of seven great hammerheads were dominated by Ancistrocheiridae and Octopoteuthidae, and only six families were recorded. Neritic cephalopods were relatively more important in smaller sharks of each species analysed, whereas pelagic and epibenthic taxa from offshore were more dominant in larger individuals, these findings thus supporting information on shark behaviour derived from previous feeding and telemetry studies. There was overlap in cephalopod taxa taken by these sharks and by marine mammals in the same area, and the high numbers of some of the cephalopods in stomach contents, such as Sepiidae, Octopodidae, Ancistrocheiridae and Octopoteuthidae, suggest that they may be very abundant in the study area.

Analyses of stomach contents provide information on prey of individual predators, which is the usual aim of such studies. Broader-based feeding studies may provide a richer understanding of different components and of interrelationships in ecosystems (Randall 1967). More unusual are studies that use the predators as samplers of the ecosystem to help reveal aspects of the distribution and biology of taxa such as cephalopods (Clarke 1980, Rancurel and Intes 1982, Dunning *et al*. 1993). This is partly a consequence of the difficulty in recognizing partially digested prey (Smale 1996). Fish remains are more often identified to species or family level either because ichthyologists are involved in the feeding analyses of other fish or because there is a relative wealth of identification guides to fish. On the other hand, cephalopods are often left at the Class level in part because the group is less well understood than are fish. However, this difficulty has been overcome for some localities, and there are now several publications that provide guides to the cephalopod fauna (Clarke 1962, 1980, 1986, Smale *et al*. 1993). Neverthe-less, such work usually lags behind systematic studies that are in themselves less advanced than studies of fish, for example.

In this paper, information is presented on the cephalopods eaten by four species of shark. Initial studies had suggested that the four species took a variety of cephalopods from inshore and offshore, but little had been published. Teleosts and other prey items are excluded from this study and will be dealt with in greater detail elsewhere. The reason for this focus is threefold. First, the cephalopod prey of KwaZulu-Natal sharks is poorly known and the present focus allows a more direct investigation and analysis. Second, the study provides an opportunity to compare the cephalopod prey of sharks with that of sperm whales *Physeter macrocephalus* studied in the same area over a considerable time (Clarke 1980), and with that of common *Delphinus delphis* and bottlenose *Tursiops truncatus* dolphins (Cockcroft and Ross 1990, Young and Cockcroft 1994) sampled from the same nets. It was reasoned that this approach would augment interpretation of the findings in this study because these mammals and sharks appear to feed at a similar trophic level. Finally, it was hoped that the study would throw additional light on the cephalopod fauna of southern Africa and thereby stimulate other studies on sharks and their prey. Hopefully, realization may dawn that there is a wealth of information in stomachs so that thorough, if time-consuming, analyses can advance knowledge of the predators, as well as provide information on prey rarely encountered using traditional

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Manuscript received: September 1997

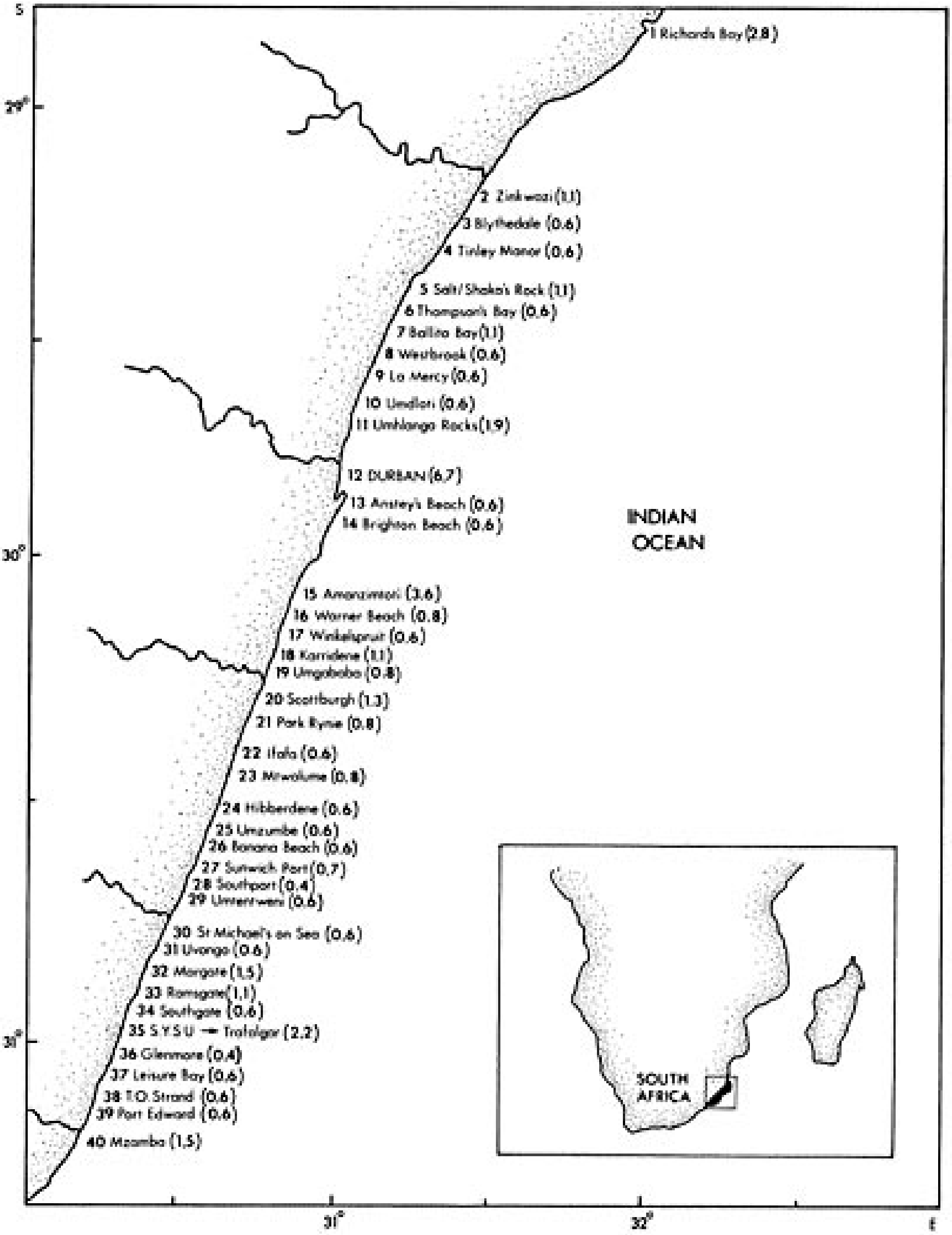


Fig. 1: Locator map of the KwaZulu-Natal coast along which shark nets are deployed. Installations and, in parenthesis, length of nets (km) in January 1990 are indicated (after Cliff and Dudley 1991)

Table I: Material examined in this study for the period 1983–1995

Predator	Empty	With food	With cephalopod remains	With beaks
Tiger shark	15	299	160	119
Scalloped hammerhead	242	1 035	577	433
Smooth hammerhead	178	490	310	258
Great hammerhead	12	89	11	7

sampling techniques. It was hoped that this multi-species, crossdisciplinary approach would augment understanding of predator/prey interactions in the field, where direct studies are extremely expensive and time-consuming.

METHODS

Sharks were collected between 1983 and 1995 from inshore gillnet installations deployed along the coast of KwaZulu-Natal for bather protection. The region is subtropical and the continental shelf narrow (Fig. 1). Details of the net locations, numbers and servicing methods are given by Cliff and Dudley (1992). Sharks were removed, labelled and returned to Natal Sharks Board (NSB) headquarters, where identifications were checked, precaudal length (*PCL*) measured and biological data gathered. The full sample is listed in Table I. Stomach contents were sorted and hard parts of prey, notably fish otoliths and cephalopod beaks, saved for later identification. Cephalopod beaks were preserved in formalin and sent to the Port Elizabeth Museum (PEM) for identification. Beaks were identified against material held in the PEM collections and using literature (Clarke 1980, 1986, Smale *et al.* 1993). Effort was focused on the lower beaks for identification and measurement (Clarke 1986), but upper beaks were identified where possible because these structures can sometimes assist in confirming identifications (e.g. in the Ommastrephidae). Beaks were counted and measured, and morphometric relationships in the literature or developed at the PEM were used to estimate the dorsal mantle lengths (*DML*) and masses of each using either rostral length (*RL*) for squid or crest length (*CL*) for Octopodidae and Sepiidae (Clarke 1980, 1986, Smale 1983, Smale *et al.* 1993).

To investigate the capture behaviour of the predators, the cephalopods were broadly divided into neritic and oceanic (including epipelagic, mesopelagic, bathypelagic and benthic) forms. For the purposes of this paper, the families Octopodidae, Loliginidae and Sepiidae were considered neritic, and the rest oceanic. Changes in prey choice with growth were investigated, as a preliminary exercise only, by splitting the size range of predators available after preliminary analyses suggested the approximate size at which prey choice appeared to change. No attempt was made to investigate changes in prey choice by gender.

The use of hard parts of prey in diet analyses has potential to introduce bias when different prey groups are examined, because of the varying influence of digestion on each prey type. This factor was probably of minor influence in the current study because only cephalopods were compared. However, a factor that is very difficult to eliminate is the retention of beaks by these sharks of prey consumed by lower level predators, such as other fish and birds prior to their being taken by the sharks. Although this may account for some of the material, the influence is likely to be minor, judging by the fact that cephalopods are routinely recorded in relatively fresh condition from shark stomach contents.

RESULTS

Tiger shark *Galeocerdo cuvier*

In all, 119 specimens had cephalopod beaks in their stomachs, but two had upper beaks only and were excluded from further analyses. The predators were 1 140–2 650 mm *PCL*. Lower beaks examined numbered 472, representing a prey total wet mass of 189 kg (Fig. 2).

Neritic cephalopods made up 60% by number and 45% by mass of the prey. Octopods (*Octopus* cf. *vulgaris*, *O. cyanea* and at least two other forms of *Octopus* beaks were recognized) and sepiids were the dominant shelf species recorded. The size range of octopods was estimated to be 30–246 mm *DML* (mean 85 mm, *SD* 45 mm, $n = 81$). Sepiids could not be identified to species level, but they were estimated to measure 83–501 mm *DML* (mean 206 mm, *SD* 93 mm, $n = 191$). Loliginids were left at the level of family because of difficulties in the systematics of this group off KwaZulu-Natal.

Oceanic prey constituted 40% by number and 55% by mass of prey and were dominated by ancistro-

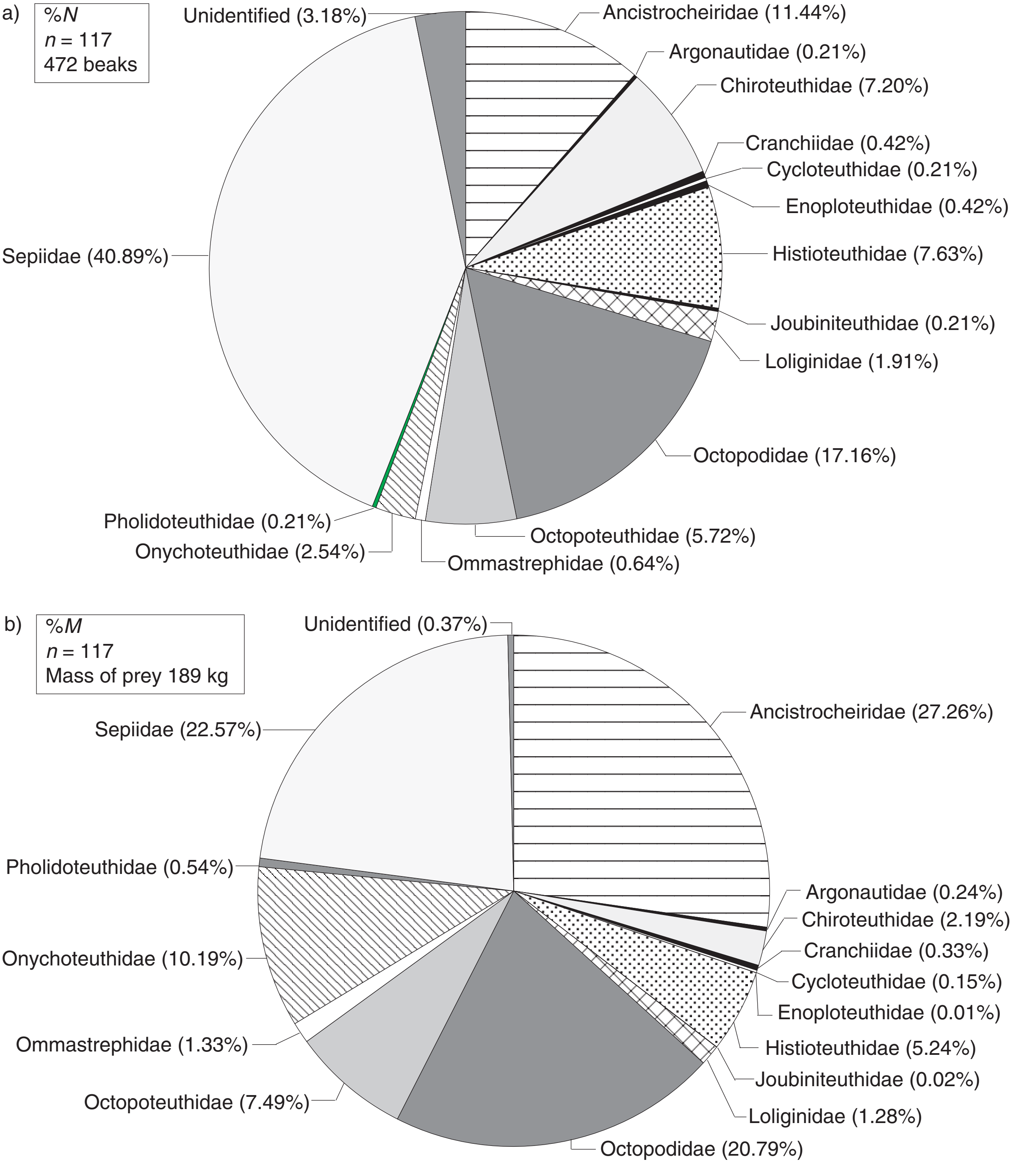


Fig. 2: Prey of tiger sharks according to (a) lower beak numbers and (b) calculated wet mass, expressed as a percentage

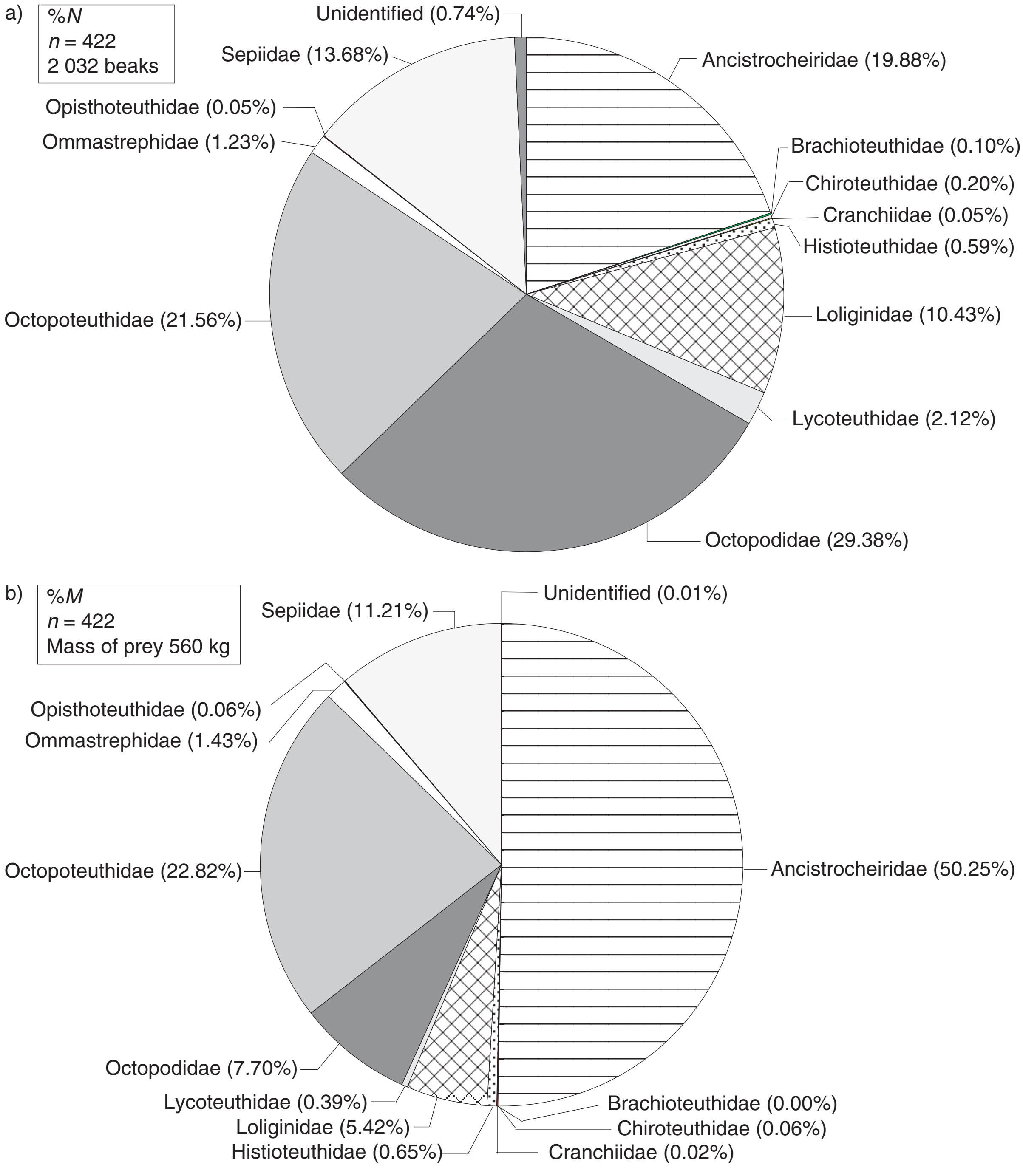


Fig. 3: Prey of scalloped hammerhead sharks according to (a) lower beak numbers and (b) calculated wet mass, expressed as a percentage

cheirids (*Ancistrocheirus lesueuri),* that were estimated to measure 122–358 mm *DML* (mean 239 mm, *SD* 60 mm, *n* = 54). Octopoteuthids were represented mainly by *Octopoteuthis sicula*, which measured 140–209 mm *DML* (mean 170 mm, *SD* 24 mm, *n* = 26), only one *Taningia danae* estimated at 797 mm *DML* being found. Ommastrephids were not common, but they included *Ornithoteuthis volatilis* and *Sthenoteuthis oualaniensis*. Chiroteuthids and cranchiids were not identified below family level. Histioteuthids identified were *Histioteuthis meleagroteuthis*, *H. bonnellii corpuscula, H. miranda* and *H. dofleini,* and this group measured 58–162 mm *DML* (mean 113 mm, *SD* 25 mm, *n* = 34). Onychoteuthids (*Moroteuthis robsoni* and *Onychoteuthis* sp.) were less dominant prey. Minor prey included *Abralia* sp., *Joubiniteuthis* sp. and *Pholidoteuthis boschmai*. A single *Argonauta argo* was recorded. One large upper beak of *Architeuthis* was collected, but it is not reflected in Figure 2 because the lower beak was not collected.

A difference in prey choice was found with different sizes of sharks. Neritic prey were more dominant (75%*N*, 69%*M*) than oceanic prey (25%*N*, 31%*M*) in 81 sharks < 2 m *PCL*. In the 36 sharks 2 m and larger, a higher proportion was oceanic prey (67%*N*, 79%*M*) than neritic. Many of the oceanic species were mesopelagic or epibenthic and it appears that the larger sharks were feeding more frequently in deeper water than smaller conspecifics.

Scalloped hammerhead shark *Sphyrna lewini*

This shark was the most numerous sampled, 433 specimens having cephalopod beaks in their stomachs, although 11 had upper beaks only and were excluded from further analysis. The predators measured 695–2 430 mm *PCL* and a total of 2 032 lower beaks was recorded. The calculated wet mass of prey was 560 kg (Fig. 3).

Neritic cephalopods made up 53% by number and 24% by mass of the prey. Octopodids dominated and there were more than two forms of beaks, including some identified as *Octopus* cf. *vulgaris*. They were estimated to measure 22–191 mm *DML* (mean 50 mm, *SD* 15 mm, *n* = 597). Sepiids were not identified below the level of family and it is possible that a small number of sepiolids were included in this group. They measured 39–471 mm *DML* (mean 218 mm, *SD* 86 mm, *n* = 278). At the present stage of knowledge of these groups in the study area and given the poor representation of vouchered specimens in the beak collection of the Port Elizabeth Museum, it was not possible to separate the sepiids and the sepiolids. Loliginid beaks appeared to belong to several species, including *L. duvaucelii* and *Loligo vulgaris reynaudii,* but they could not be identified confidently to species in most cases.

Oceanic cephalopods made up 47% by number and 76% by mass of prey. Ancistrocheirids (*A. lesueuri)* and octopoteuthids (*Otopoteuthis* and a single *Taningia danae*) dominated (Fig. 3). *Ancistrocheirus* measured 97–362 mm *DML* (mean 213 mm, *SD* 58 mm, *n* = 404) and *Octopoteuthis* measured 128–221 mm *DML* (mean 185 mm, *SD* 17 mm, *n* = 437). Other taxa identified were *Argonauta* (an upper beak), *Brachioteuthis*?, *Chiroteuthis* spp., Cranchiidae (*Teuthowenia*) and Histioteuthidae (including *H. miranda* and *H. dofleini*). Also recorded were lycoteuthids (*Lycoteuthis lorigera* – a senior synonym of *L. diadema*) and ommastrephids (*O. volatilis, S. oualaniensis, Todarodes* sp. and unidentified Ommastrephidae). One beak was listed as ?*Grimpoteuthis*.

There was a tendency for larger sharks to prey more on oceanic cephalopods than on neritic forms. In 385 sharks <1 500 mm *PCL,* neritic cephalopods constituted 58%*N* and 28%*M* and oceanic cephalopods the balance. In the 37 sharks >1 500 mm *PCL*, oceanic taxa dominated (85%*N*, 91%*M*).

Smooth hammerhead shark *Sphyrna zygaena*

This was the second most numerous species sampled. In all, 258 specimens had cephalopod beaks in their stomachs, but 20 contained upper beaks only and were excluded from further analysis. Sharks measuring 600–1 189 mm *PCL* had a total of 833 lower beaks, and these made up an estimated wet prey mass of 248 kg (Fig. 4).

Neritic cephalopods dominated the prey by number (73%) and mass (65%). Loliginids dominated and were estimated to measure 52–338 mm *DML* (mean 230 mm, *SD* 46 mm, *n* = 455). A large proportion was probably *L. v. reynaudii* or *L. duvaucelii*, but other unidentified species were also found. Sepiids were also important prey in terms of number and mass, but again it is possible that sepiolids were included in this group because of the difficulty of distinguishing between them in the study area at present. They measured 18–429 mm *DML* (mean 147 mm, *SD* 66 mm, *n* = 143). Octopodids were minor prey represented by *O.* cf. *vulgaris* and at least three other forms.

Oceanic cephalopods constituted 27% by number and 35% by mass of prey (Fig. 4). These taxa were dominated by *Ancistrocheirus* of 109–334 mm *DML* (mean 217 mm, *SD* 66 mm, *n* = 69). O*mmastrephes bartramii, Ornithoteuthis volatilis, Sthenoteuthis oualaniensis, Todarodes filippovae* and *Todarodes* sp. were the ommastrephids identified, and members of this family measured between 76 and 452 mm *DML*

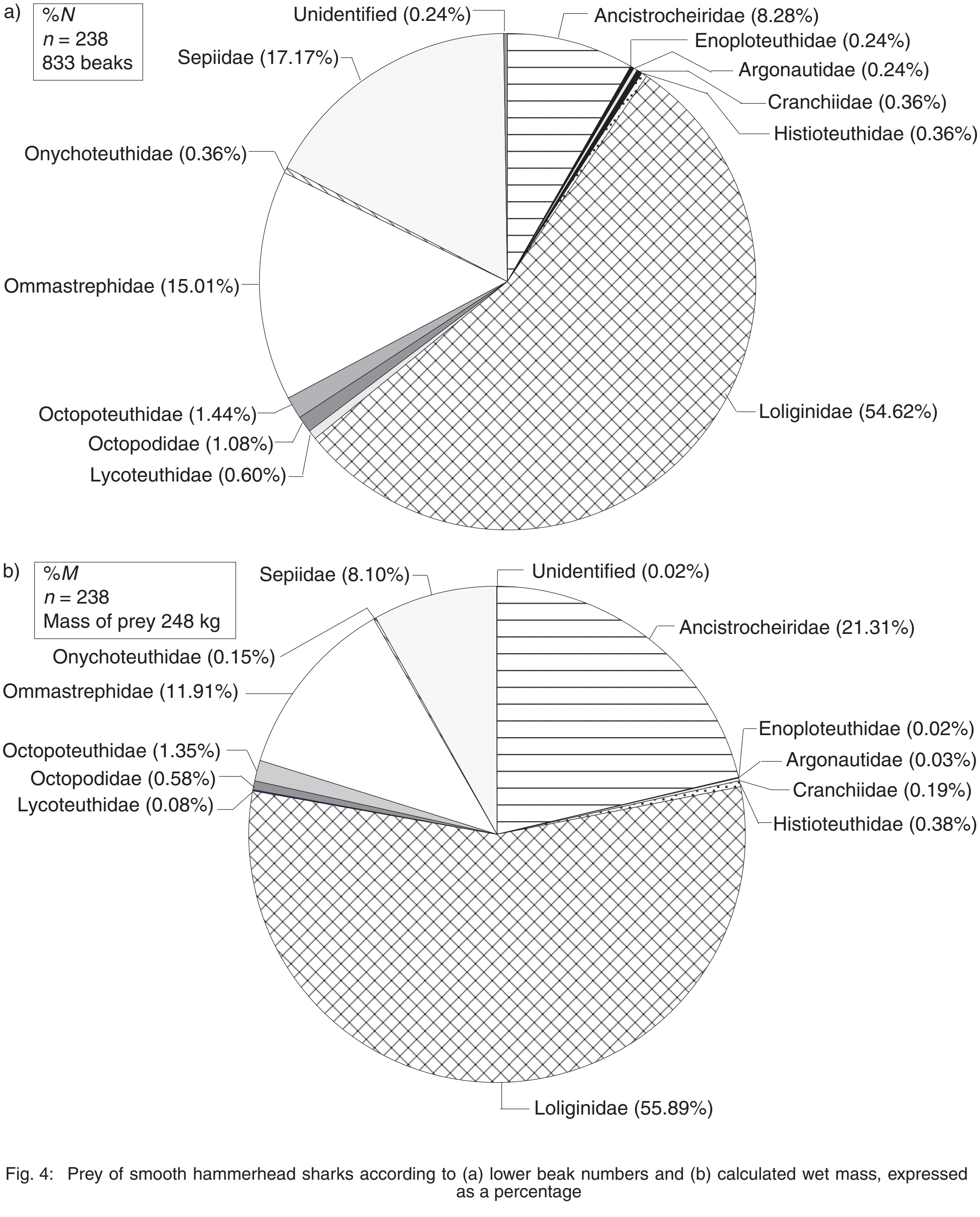
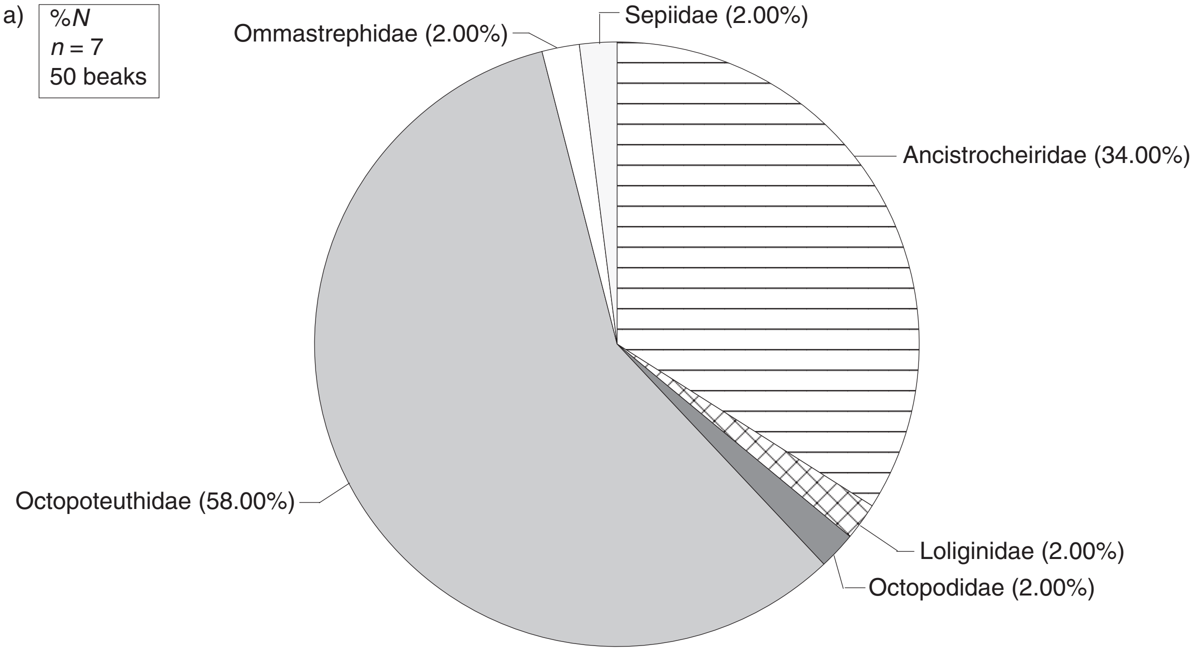


Fig. 4: Prey of smooth hammerhead sharks according to (a) lower beak numbers and (b) calculated wet mass, expressed as a percentage



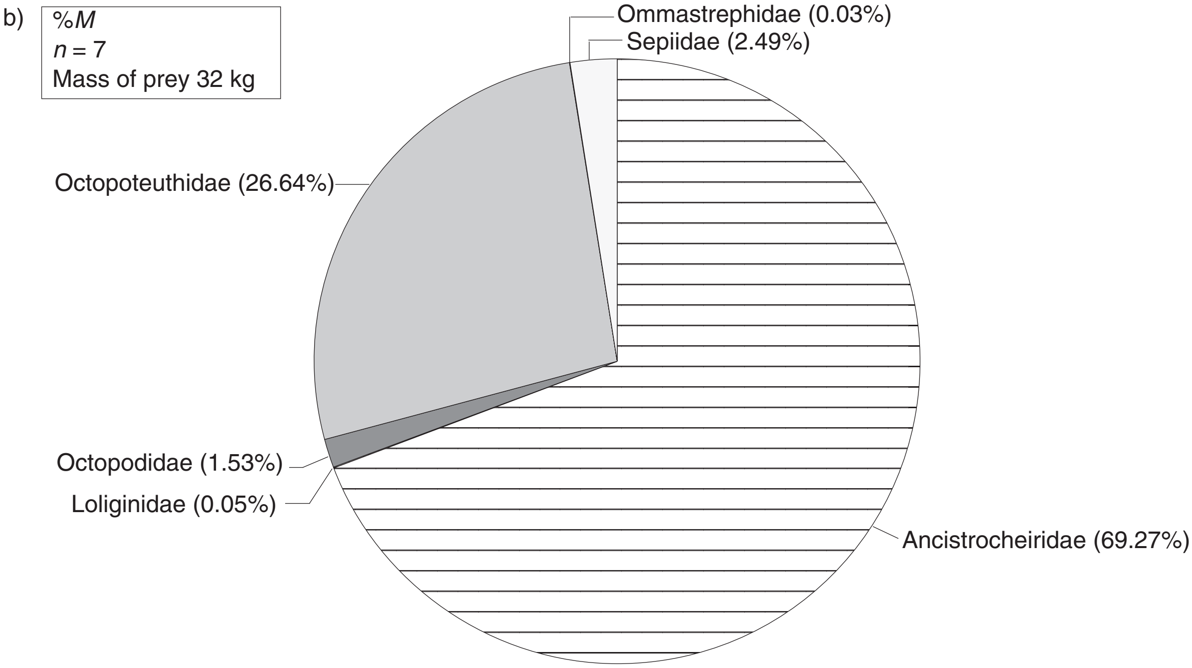


Fig. 5: Prey of great hammerhead sharks according to (a) lower beak numbers and (b) calculated wet mass, expressed as a percentage

(mean 193 mm, *SD* 63 mm, *n* = 120). Other taxa identified included *Argonauta argo* and *Liocranchia*. *Abralia*? and *Enoploteuthis* were identified from the family Enoploteuthidae, but *Histioteuthis miranda* was the only member of the Histioteuthidae identified. *Lycoteuthis lorigera* and ?*Selenoteuthis* were identified from the family Lycoteuthidae, but only 12 *Octopoteuthis* (Octopoteuthidae) were taken. The only onychoteuthid recognized was *Onychoteuthis* sp.

There was a tendency for larger sharks to feed more on oceanic cephalopods. In 169 smooth hammerheads <1 000 mm *PCL*, neritic prey made up 88% by number and 78% by mass of prey and oceanic cephalopods the balance. Neritic prey were less important (44%*N*, 41%*M*) in 69 sharks of ≥1 000 mm.

Great hammerhead *Sphyrna mokarran*

Only 7 of the 101 great hammerheads analysed had cephalopod beaks in their stomachs (Table I). The predators measured 1 730–2 370 mm *PCL*. A single stomach from a shark of 2 186 mm *PCL* contained all the *Ancistrocheirus* and *Octopoteuthis*, the others contained one cephalopod beak each. That single stomach had a considerable influence on the results because those two taxa made up the bulk of the prey (Fig. 5). *Octopoteuthis* measured 171–216 mm *DML* (mean 193 mm, *SD* 9.6 mm, *n* = 29). *Ancistrocheirus* measured 118–342 mm *DML* (mean 261 mm, *SD* 79 mm, *n* = 17). The *Sepia* sp. measured 287 mm *DML*. The octopod was identified as *O. cyanea* and estimated to weigh 500 g, although the beak was broken.

DISCUSSION

Prey

Ancistrocheirus was found in all four shark species and the beaks were darkened at all sizes down to 4 mm *RL*. The size range of beaks found in this study (3.4–9.9 mm *RL*) was similar to that recorded by Clarke (1980) from sperm whales. Their presence in these sharks and in sperm whales, that are known to feed in deep water (to c. 2 000 m, Clarke 1980), suggests that these squid are a dominant component of the fauna in deep water and would themselves be dominant predators off south-eastern Africa. This squid is poorly known, despite its importance in foodwebs, but it has been shown that the tissues contain ammonia that would provide buoyancy (Clarke *et al.* 1979). There is also some evidence that they may spawn from June to October off South Africa (Clarke 1980). Squid in this study included both juveniles and adults.

Histioteuthids identified were mainly *H. bonnellii corpuscula, H. miranda* and *H. dofleini* (Clarke 1986), although there were additional taxa in stomachs that could not be confidently attributed to species; they probably belonged to the same three species. Taxa grouped as "B" by Clarke (1980, 1986) were rarely recorded here. Except in the case of tiger sharks, histioteuthids were minor components of the diets of the four sharks studied here, whereas they are important prey of sperm whales in the same region (Clarke 1980).

Ommastrephids were not found frequently except in smooth hammerheads. In that case, *Ornithoteuthis volatilis* was the most dominant, although several other species were found and a few could not be identified below the family level. Ommastrephids are important prey of this shark off Australia (Dunning *et al.* 1993), suggesting that the result may reflect hunting behaviour and prey choice. Alternatively (or in addition), their relatively low importance in scalloped hammerheads and tiger sharks may suggest their relative scarcity off KwaZulu-Natal compared to that of other cephalopods there.

Loliginids were important prey of all four species of shark analysed, as has been found in studies off the Eastern Cape (Sauer and Smale 1991, Smale 1991). Initial attempts to identify prey to species level were often thwarted by features of the beak shape and darkening of some material that suggested that additional taxa not represented in the PEM beak collection were present. A greater diversity of loliginids off southern Africa, than hitherto thought, was realized after a recent research cruise to Moçambique; now at least 10 loliginid species have been identified (Roeleveld 1998). Until the status of these species is established in KwaZulu-Natal and beaks acquired for collections, reliable beak identifications can only be to family level.

Despite a recent regional advance in octopod beak identification (Smale *et al.* 1993), many of the octopod beaks could not be identified with confidence to species level and were consequently reported only at the level of family. Although numerous beaks had features that conformed to those characters described in Smale *et al.* (1993), juveniles were particularly difficult to resolve to species, and some beaks found in stomachs were obviously not included in that work. This is a reflection of the state of knowledge of southern African octopods (Roeleveld 1998), and further advances in beak identification will depend on advances in the systematics of the family from this region.

Sepiids and sepiolids may have been grouped in this study, but the vast majority of the material appeared to belong to the Sepiidae. A few small beaks had features that suggested that they may have been sepiolids, but

East Coast sepiolids are not represented adequately in the PEM collection. Therefore, because of their similarity to sepiids, they were grouped together. More work is needed on the systematics and beaks from these families before identifications of beaks can be attempted with confidence, although beaks of both families are difficult to resolve below the family level without reliable vouchers (Clarke 1986, pers. comm.). Nevertheless, sepiids are ecologically important off KwaZulu-Natal, as is reflected by these results and dolphin feeding studies (Cockcroft and Ross 1990).

Many neritic and oceanic cephalopods were preyed on by the sharks analysed. Despite the cryptic behaviour used by cephalopods to deceive predators (Hanlon and Messenger 1996), these sharks were able to detect and prey on them. The differences in proportions of various cephalopods consumed by the four shark species suggest that there may be differences in prey preference, possibly resulting from differences in hunting behaviour and habitat use by the different sharks. The material was collected over more than a decade, but it is strongly biased because all the sharks were caught in shallow gillnets off a KwaZulu-Natal coastline of several hundred kilometres. Nevertheless, both offshore and nearshore prey were recorded, no doubt partly because of the resistance of the chitinous beaks to digestion, allowing evidence of past meals to accumulate. The differences in prey recorded suggest real differences in the prey targeted by each of the predators and that these sharks can provide considerable information on the relative abundance of such prey species. Furthermore, there was a consistent pattern of intraspecific variation, larger predators taking a higher proportion of offshore prey than smaller ones, indicating that predatory behaviour changes with growth.

Where and when the predators attack their prey is less certain. A number of squid species are known to undertake vertical migration (Clarke and Lu 1974, Lu and Clarke 1975a, b, and see review by Hanlon and Messenger 1996, p. 160). This behaviour may make squid that normally inhabit deep water during part of the day more readily available to predators hunting in the water column when they rise, often at night. This would make them vulnerable to nocturnal predators that need not necessarily penetrate deep water, although at least some of the sharks are known to be able to enter deep, cooler water, as is discussed below.

Predators

The catholic feeding habits of tiger sharks are legendary (Bass *et al.* 1975, Compagno 1984, Stevens 1984, Randall 1992, Simpfendorfer 1992, Lowe *et al.* 1996). Although considered scavengers by many authors, tiger sharks are powerful top predators capable of taking a wide range of prey. Stevens and McLoughlin (1991) found that 16% of 98 specimens from northern Australia had cephalopod prey (*Sepia* and unidentified cephalopods) compared to 62% with fish, 58% with reptiles and 16% with crustaceans. Simpfendorfer (1992) found that ontogenetic changes in diet included increasing importance of sea snakes and turtles with growth and a decline in squids and teleosts, in terms of frequency of occurrence. However, Lowe *et al.* (1996) showed an increase in the frequency of cephalopods in the diets of larger tiger sharks from Hawaii, as did Rancurel and Intes (1982) in New Caledonia. The latter authors also suggested that larger tiger sharks were feeding in deeper water than small animals, based on the finding of crabs and pelagic squid in larger sharks. The results of the present study support that hypothesis. Dunning *et al.* (1993) found that tiger sharks took cephalopods from both coastal and deep offshore water, as was found in this study of a considerably larger sample size than was available to them.

Tiger sharks can penetrate relatively deep water and an individual of 2.5 m total length (*TL*) has been recorded on the sea floor at a baited cage in 305 m off Cayman in the early evening (Clark and Kristof 1990). Telemetry work has shown that they also hunt inshore at the surface, near reefs, and in midwater to at least 250 m in water where the bottom is as deep as 800 m (Tricas *et al.* 1981). Their wide range of hunting behaviour in a variety of habitats and catholic prey choice explains the wide range of cephalopods found in this study.

Scalloped hammerheads have inshore pupping grounds, often in turbid bays, but they move out to reefs at night to feed (Clarke 1971). They are thought to move farther offshore after a few months (Clarke 1971). Holland *et al.* (1992) tracked scalloped hammerheads for up to 13 days and found that pups hovered as a school about 1–3 m off the lagoon floor in defined "core areas" by day but became more active at night, when they expanded their range, returning next day to the core area. In Hawaii the young pups fed mainly on fish and crustaceans (Clarke 1971), probably at night.

Adult scalloped hammerheads have also been tracked using telemetry and they have been found to refuge over seamounts by day, but they may disperse individually up to 8 km from their diurnal site (Klimley and Nelson 1984, Klimley *et al.* 1988). They aggregate by day but do not feed then, even though schools of potential prey and bait may be encountered (Klimley and Nelson 1981). They move into the pelagic environment at night, and vertical excursions from 100 to 450 m deep were recorded by Klimley (1993). The same author reported that the hammerheads often swam in midwater away from the surface or bottom at 25–300 m by day and at 125–400 m by night in the case of one individual. Klimley (1987) recorded females ≤1 600 mm *TL* feeding on a higher percentage of pelagic prey than males of the same size. Also, the female diet recorded was less benthic (15%) than that of males (40.9%) in terms of the index of diet used. Prey changed with size, octopods being more important in smaller sharks whereas *Ancistrocheirus* and *Mastigoteuthis* were more common in larger individuals (Klimley 1987), a trend consistent with the results of the present study.

Sharks are able to detect their prey using a variety of senses, including chemoreception (Hodgson and Mathewson 1978), vision (Gruber and Cohen 1978) and bioelectric detection using the ampullae of Lorenzini (Kalmijn 1978). Scalloped hammerheads have been filmed hunting at night, taking prey on or in sediments, probably using their bioelectric sensory system and other senses. These highly developed sensory systems would make benthic prey, including octopods and sepiids, particularly vulnerable to both hammerheads and other sharks. Such hunting behaviour would explain how inactive, retiring prey (Clarke 1971) could nevertheless be vulnerable to sharks, even when fossorial.

Smooth hammerheads are less studied than tiger and scalloped hammerheads, although they are known to take both pelagic and benthic prey (Bass *et al.* 1975, Stevens 1984, Smale 1991). Loliginids were considerably more important than ommastrephids in this study, in marked contrast to a study off eastern Australia (Dunning *et al.* 1993), probably reflecting different geographical abundance of the two groups. Smooth hammerheads are more typical of temperate waters, and the occurrence of loliginid beaks identified as *L.v. reynaudii* in stomach contents suggests that the sharks had migrated north to KwaZulu-Natal before being taken in the gillnets, because this squid is rare in the study area. Off the Eastern Cape, *L.v. reynaudii* is a dominant prey of smooth hammerheads inshore near squid spawning grounds (Sauer and Smale 1991).

Great hammerheads are less well known than the other two hammerhead species, although they are regularly taken in tropical waters (Compagno 1984). Cliff (1995) found that great hammerheads off KwaZulu-Natal preyed mainly on batoids and other elasmobranchs. Teleosts were less important, whereas cephalopod remains were mainly represented by beaks and were therefore of minimal overall importance in the region. Stevens and Lyle (1989) found that cephalopods (only squid, cuttlefish and some unidentified taxa) occurred in only 4.6% of 186 stomachs with food. The present study revealed that both inshore and oceanic species were taken, although cephalopods are probably of minor importance to this shark (Cliff 1995).

Previous studies of other predator groups have shown that similar prey species are taken. Feeding studies of coastal bottlenose dolphins have suggested that *Sepia* spp., *Loligo* spp. and *Octopus* spp. may be abundant in KwaZulu-Natal because they were the dominant cephalopods in the diets of those dolphins (Cockcroft and Ross 1990). These dolphins are known to feed inshore, rarely being sighted beyond the 30 m isobath (Cockcroft and Ross 1990). Their prey selection supports sighting data of their depth distribution, because the cephalopods taken are typical of the continental shelf. The schooling and more pelagic-feeding common dolphin also eats *Sepia*, *Loligo* spp. and *Lycoteuthis lorigera* (Young and Cockcroft 1994), their prey including species found offshore on the edge of the shelf.

On the other hand, Clarke's (1980) studies of sperm whales revealed that a variety of cephalopods, including *Histioteuthis*, *Ancistrocheirus* and *Chiroteuthis* that were also recorded in this study, were important prey of those cetaceans. Clearly the sperm whales have little influence, if any, on coastal cephalopod communities off KwaZulu-Natal, whereas they are significant predators on deep-living cephalopods.

Evidently, the sharks examined in this study took prey also eaten by common and bottlenose dolphins over the continental shelf and they also preyed on offshore fauna, some of which are preyed on by deep-diving sperm whales. Because relatively few species of cephalopod made up the bulk of the prey in different taxa, it appears that some cephalopods may be highly abundant off KwaZulu-Natal and some of those may in future become components of fisheries in that region.

In conclusion, it has been shown that the sharks in this study prey on cephalopods from the continental shelf (*Octopus* spp., *Sepia* spp., Loliginidae) and on deep-water species such as *Ancistrocheirus lesueurii* and *Histioteuthis* spp. Some of the prey may have been taken close to the bottom, but the influence of vertical migration making deep-sea squid more available to pelagic-hunting predators is unknown, although the subject deserves further investigation. This study has shown that detailed stomach content analyses can provide additional information on the cephalopod fauna of a region and that predators can provide insight into the fauna not possible with traditional sampling methods (e.g. Roeleveld *et al.* 1992), although more information on the prey would be derived were it possible to retain and study soft tissues in addition to the beaks. Undoubtedly, cephalopods are important and influential components of marine ecosystems (Boyle and Boletzky 1996, Clarke 1996). They clearly deserve more attention, particularly because they are increasingly being targeted as a food resource for humans.

ACKNOWLEDGEMENTS

We are grateful to the staff of the Natal Sharks Board for collecting the material reported here. Dr M. R. Clarke (Plymouth, U.K.) kindly examined a small subsample of beaks at our request and Ms T. Nuneman (formerly Port Elizabeth Museum) assisted in sorting, identifying and measuring a portion of the sample. Dr L. J. V. Compagno (South African Museum) and an anonymous referee provided comments on an early draft of this paper.

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