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DIET OF THE SIXGILL SHARK *HEXANCHUS GRISEUS* OFF SOUTHERN AFRICA

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The sixgill shark *Hexanchus griseus* is a large, active, deep-water species that typically occurs along the outer continental shelves and their upper slopes. Stomach analysis was performed on 137 specimens collected off Namibia and South Africa. The major prey groups were cephalopods, teleosts, chondrichthyans and marine mammals. Dietary changes of sixgill sharks are related to growth. In most of their area of distribution, sixgill sharks have few comparable competitors, because sympatric squaloids and lamnoids of equivalent size feed at a lower trophic level.

Die seskiefhaai *Hexanchus griseus* is 'n groot, aktiewe diepwaterspesie wat tipies langs die buiterand van die vastelandsplat en die boonste gedeelte van die -helling voorkom. Die pensinhoud van 137 eksemplare wat teenoor Suid-Afrika en Namibië versamel is, is ontleed. Die hoofprooigroepe was koppotiges, beenvisse, kraakbeenvisse en seesoogdiere. Dieetveranderinge by seskiefhaaie staan in verband met groei. Oor die grootste deel van sy verspreidingsgebied het die seskiefhaai min vergelykbare mededingers omdat simpatriese skwaloïdes en lamnoïdes van soortgelyke grootte op 'n laer trofiese vlak voed.

The sixgill shark *Hexanchus griseus* is a large, active, deep-water species that typically occurs along the outer continental shelves and their upper slopes. It is perhaps the most common species of large, deep-water sharks, attaining a total length (*TL*) of 4,8 m (Isaacs and Schwartzlose 1975, Clark and Kristof 1990, Ebert 1990,). Sixgill sharks are usually found below a depth of 100 m (Ebert 1986a, b), and some have been recorded deeper than 2 500 m (Zhan *et al.* 1987). The sixgill shark occurs worldwide (Ebert 1990) and, with the pelagic blue shark *Prionace glauca*, is one of the most wide ranging of all shark species (Compagno 1984a).

Off southern Africa sixgill sharks occur from Angola southwards, around the tip of South Africa and up the East Coast to at least Moçambique (Pissaro and Sanches 1973, Bass *et al.* 1975, Compagno *et al.* 1989). It is particularly abundant along western southern Africa, especially off southern Namibia, which appears to be a nursery ground (Ebert 1990).

Despite their abundance off southern Africa very few data, other than those of Bass *et al.* (1975), exist on the natural history of this important deep-water predator. The sixgill shark feeds on a variety of prey items ranging from crustaceans and cephalopods to bony and cartilaginous fish, as well as on marine mammals (Bigelow and Schroeder 1948, Backus 1957, Compagno 1984b, Ebert 1986a, b, Clark and Kristof 1990), but most of this information is based on generalized accounts. The lack of feeding data is surprising given the sixgill shark's large size, relatively broad mouth and huge cutting teeth. This combination of morphological characteristics is indicative of a predator with a voracious appetite and one that must have a substantial impact on the prey organisms within its area of distribution. The purpose of this study was to investigate the feeding habits of the sixgill shark throughout most of its range around southern Africa.

MATERIALS AND METHODS

Field collections were made from Walvis Bay, Namibia, to northern Natal, South Africa, between October 1986 and May 1990. Sharks were collected by longline, rod and reel, and trawl, with the assistance of the Spanish commercial trawler M.F.V. *Chicha Touza* and the South African research vessels F.R.S. *Africana* and R.V. *Meiring Naudé*.

Shark stomachs containing prey items were removed. In the laboratory the contents were identified to the lowest possible taxon. Each species was identified and weighed to the nearest 0,1g. An index of relative importance (*IRI*), following Pinkas *et al.* (1971), was

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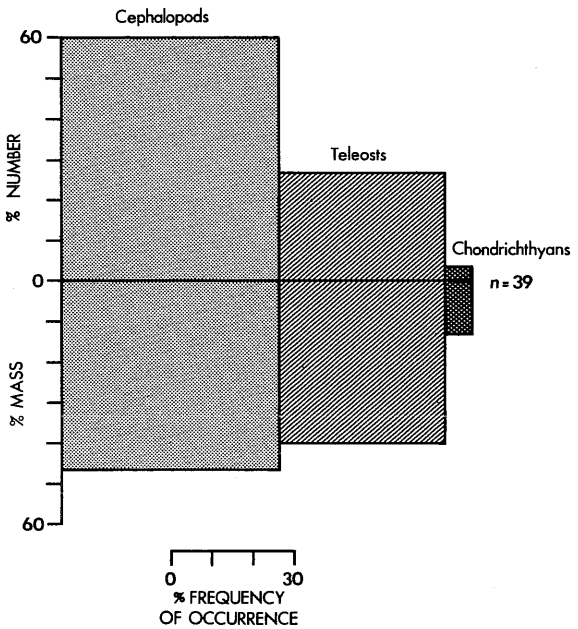

Fig. 1: Composition of the diet of sixgill sharks <1 200 mm *TL* off southern Africa by number, mass and frequency of occurrence

used to rank the prey items found. This index is calculated by summing the numerical and mass percentage values, and multiplying by the percentage frequency of occurrence. The equation reads as follows:

$$IRI = \%F(\%N + \%M) \quad ,$$

where *%N*, *%M* and *%F* are the percentage contributions of a species in terms of number, mass and frequency of occurrence in the stomachs examined.

Three arbitrary size-classes of sixgill sharks were used to investigate changes in the diet associated with growth. The size classes were <1 200 mm *TL*, 1 200–2 000 mm *TL*, and >2 000 mm *TL*.

Table I: Percentage composition of prey items given by number (*%N*), mass (*%M*) frequency of occurrence (*%F*) and index of relative importance (*IRI*) for prey species eaten by sixgill sharks of *TL* <1 200 mm

Prey item	*%N*	*%M*	*%F*	*IRI*
Cephalopoda				
Todarodes angolensis	60,0	47,7	53,8	5 794
Chondrichthyes				
Scyliorhinidae	4,0	12,4	5,1	84
Teleostei				
Diaphus sp.	4,0	3,3	2,3	17
Merluccius spp.	10,0	22,0	10,3	330
Sardinops sagax	2,0	1,7	2,3	9
Etrumeus whiteheadi	2,0	0,7	2,3	6
Unidentified teleosts	18,0	12,0	23,1	691

RESULTS

Analysis of stomach content was performed on a total of 137 sixgill sharks. Of those examined, 96 (70%) contained one or more prey items in the stomach.

Sixgills <1 200 mm *TL*

Of 57 sixgill sharks examined that were <1 200 mm *TL*, 39 (68%) contained prey items. Cephalopods were the most important prey group, with an *IRI* of 5 794 (Fig. 1, Table I). The cephalopod *Todarodes angolensis* was the most important prey item consumed and ranked highest in terms of *%N*, *%M* and *%F* (Table I). Teleosts were the second most important prey group, with an *IRI* of 3 100. Four teleost taxa were identified, hake *Merluccius* spp. being the most important (*IRI* = 330). Chondrichthyans were the third most important prey group, with an *IRI* value of 84. There were only two records of predation on chondrichthyans, both of which were on catsharks (Scyliorhinidae). There were no records of predation on invertebrates, other than cephalopods, or marine mammals.

Sixgills 1 200 – 2 000 mm *TL*

In all, 48 (71%) of the 68 sixgill sharks between 1 200 and 2 000 mm *TL* that were examined contained prey items. Teleosts, with an *IRI* of 2 179, were the most important prey group, followed by chondrichthyans (*IRI* = 1 666) and cephalopods (*IRI* = 1 362 — Fig. 2, Table II). *T. angolensis* was again the most important individual prey species recorded (Table II). Five species of teleost were identified, with hake the second most important prey species recorded. Five species of chondrichthyans were noted, of which the spiny dogfish *Squalus acanthias* and *S. megalops* were the most frequently observed. However, the biscuit skate *Raja* cf. *clavata* contributed the highest mass. Marine mammals were recorded in 13% of the stomachs examined, there being equal numbers of pinnipeds and cetaceans. Invertebrates, other than cephalopods, were recorded on three occasions, but they did not constitute a significant portion of the sixgill shark's diet.

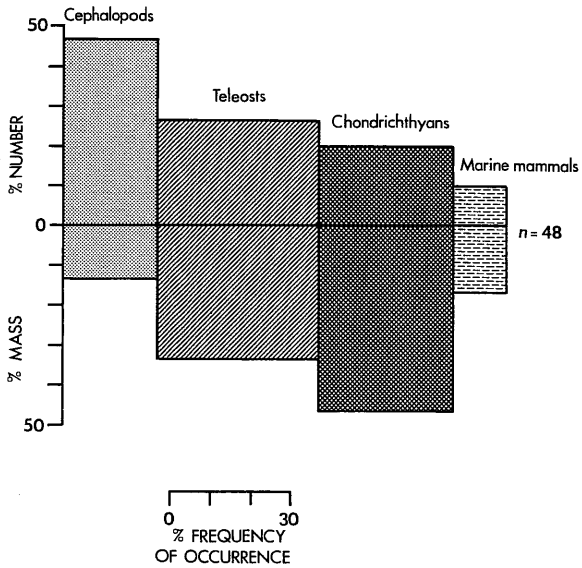

Fig. 2: Composition of the diet of sixgill sharks 1 200–2 000 mm *TL* off southern Africa by number, mass and frequency of occurrence

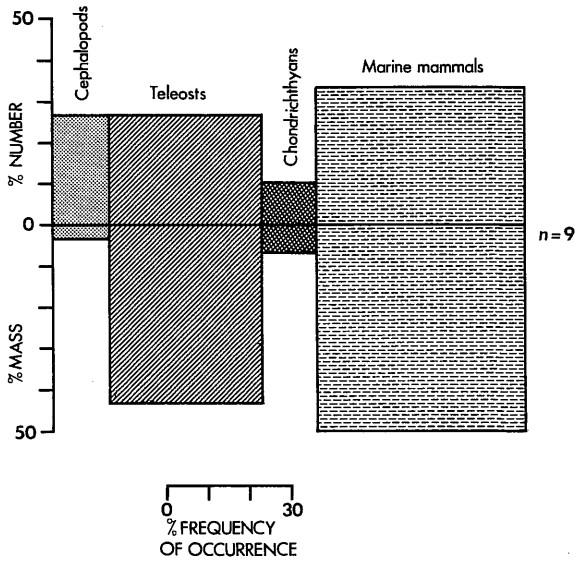

Fig. 3: Composition of the diet of sixgill sharks >2 000 mm *TL* off southern Africa by number, mass and frequency of occurrence

Table II: Percentage composition of prey items given by number (%*N*), mass (%*M*) frequency of occurrence (%*F*) and index of relative importance (*IRI*) for prey species eaten by sixgill sharks of *TL* 1 200–2 000 mm

Prey item	%*N*	%*M*	%*F*	*IRI*
Cephalopoda				
Todarodes angolensis	42,9	10,4	22,9	1 221
Gastropoda				
Unidentified gastropod	3,9	0,1	4,2	17
Crustacea				
Unidentified crustacean	1,3	0,2	2,1	3
Chondrichthyes				
Squalus acanthias	5,2	3,6	6,3	55
Squalus megalops	6,5	12,8	8,3	160
Mustelus mustelus	1,3	3,2	2,1	10
Raja cf. *clavata*	1,3	17,9	2,1	40
Callorhinchus capensis	1,3	1,8	2,1	7
Unidentified chondrichthyans	2,6	2,8	4,2	23
Teleostei				
Merluccius spp.	10,4	17,0	12,5	343
Coelorinchus sp.	1,3	1,2	2,1	5
Scomber japonicus	1,3	1,1	2,1	5
Thyrsites atun	1,3	1,1	2,1	15
Engraulis capensis	3,9	1,7	2,1	12
Unidentified teleosts	7,8	5,9	2,1	29
Cetacea				
Delphinidae	3,9	4,6	6,3	54
Pinnipeda				
Arctocephalus pusillus pusillus	3,9	9,7	6,3	86

Sixgills >2 000 mm *TL*

Of 12 sixgill sharks examined that had a *TL* >2 000 mm, nine (75%) contained prey items. Marine mammals (*IRI* = 3 756) were the most important prey group, and teleosts next, with an *IRI* of 2 311 (Fig. 3, Table III). Cephalopods and chondrichthyans were of minor importance. The most important prey taxa were the South African fur seal *Arctocephalus pusillus pusillus*, hake and dolphins (Table III). South African

Table III: Percentage composition of prey items given by number (%*N*), mass (%*M*) frequency of occurrence (%*F*) and index of relative importance (*IRI*) for prey species eaten by sixgill sharks of *TL* >2 000 mm

Prey item	%*N*	%*M*	%*F*	*IRI*
Cephalopoda				
Loligo vulgaris reynaudii	27,2	2,9	11,1	334
Chondrichthyes				
Callorhinchus capensis	9,1	6,7	11,1	175
Teleostei				
Helicolenus dactylopterus	9,1	32,3	11,1	460
Merluccius spp.	18,2	9,9	18,2	511
Cetacea				
Delphinidae	18,2	9,4	18,2	502
Pinnipeda				
Arctocephalus pusillus pusillus	18,2	38,8	18,2	1 037

fur seals contributed most by mass and, along with hake and dolphins (Delphinidae), appeared most frequently in stomachs.

The cephalopod *Loligo vulgaris reynaudii* contributed the highest percentage of individual prey organisms. Invertebrates, other than cephalopods, were not found. One additional record of predation on cetaceans came from a beached bottlenose dolphin *Tursiops truncatus* that had several bites taken out of it. The bites marks were identified as those of a sixgill shark. The bite radius suggested that the shark was in excess of 3 m *TL*.

DISCUSSION

A breakdown of the food habits of sixgill sharks by size-class revealed dietary changes associated with growth. Juveniles <1 200 mm *TL* preyed almost exclusively on cephalopods and teleosts. Sharks between 1 200 and 2 000 mm *TL* primarily consumed teleosts, chondrichthyans and cephalopods, but also fed on marine mammals. The largest sixgill sharks analysed (>2 000 mm *TL*) fed mainly on cetaceans and teleosts, with cephalopods and chondrichthyans of secondary importance.

The high occurrence of cephalopods in sixgill sharks <1 200 mm *TL* may reflect the habitat occupied by this size-class. All of the small sixgill sharks that had ingested cephalopods, specifically *T. angolensis*, were captured in an area off southern Namibia believed to be a nursery ground for this shark (Ebert 1990). Predation by sixgill sharks on their juveniles is reduced by the latter remaining on the outer continental shelves and upper slopes. In this habitat, the juveniles have few predators and no competitors of similar size with the same prey preference. Once the sixgill shark begins to mature, it moves down the continental slopes, where again it has no real predators and few competitors (Ebert 1990). Wetherbee *et al.* (1990) suggested that, in some shark species, juveniles have a restricted diet associated with a particular habitat, such as a nursery ground. A particularly abundant prey, or one that is easily caught, may dominate the diets of young sharks living on a nursery ground.

Sixgill sharks between 1 200 and 2 000 mm *TL* have an increased frequency of chondrichthyans and teleosts in their diet. This may reflect the broad range of habitats in which such sixgill sharks were captured. Individuals tended to be caught on the continental shelf and in some instances in water as shallow as 7 m. The prey items identified indicate that sixgill sharks in this size-class often come into shallow water to feed.

Unfortunately, data for the largest size-class (>2 000 mm *TL*) were limited, but from the information available it appears that the size and type of prey increases in proportion to the predator's size. Cetaceans and larger, more active teleosts become increasingly important in the diet of sixgill sharks as they grow. Small swordfish *Xiphias gladius* are a common prey item of sixgill sharks >4 m *TL* from the Azores (Ebert 1990, pers. obs.). Bigelow and Schroeder (1948) and Springer and Waller (1969) reported the occurrence of swordfish and marlin *Makaira* sp. in the stomachs of large sixgill sharks. Similarly, a shift in the diet of other large shark species to larger, more active prey items has been observed for the soupfin shark *Galeorhinus galeus* (Olsen 1954), shortfin mako shark *Isurus oxyrinchus* (Stillwell and Kohler 1982), great white shark *Carcharodon carcharias* (Tricas and McCosker 1984, Klimley 1985, Cliff *et al.* 1989), sevengill shark *Notorynchus cepedianus* (Ebert 1986a), sleeper shark *Somniosus pacificus* (Ebert *et al.* 1987), bull shark *Carcharhinus leucas* (Cliff and Dudley 1991) and tiger shark *Galeocerdo cuvier* (Simpfendorfer 1992). Energetically, it is beneficial for a large shark to capture one large prey item rather than numerous small items such as cephalopods. The energy expended by a large shark to catch smaller cephalopods might not be cost-effective. In addition, the large mouth and huge cutting teeth of a big sixgill shark are not suggestive of a predator that feeds exclusively on soft-bodied cephalopods.

Predator size in relation to prey size may play an important role in determining the hunting success for a sixgill shark. At least two Atlantic torpedo rays *Torpedo nobiliana* with sixgill shark scars were examined (pers. obs.). One, with a disc width of 315 mm, had a bite radius of 101 mm from a sixgill shark estimated to be approximately 1 000 mm *TL*. This species of torpedo ray is an active epibenthic predator and was probably attacked while swimming off the bottom. The attacking shark had apparently seized the ray directly on its electric organs and had received a shock. The size relationship between predator and prey suggests that the torpedo ray was able to fend off the shark's attack. A larger shark may have been more successful. Bigelow and Schroeder (1948) report sixgill sharks consuming torpedo rays in Spanish waters.

The occurrence of epibenthic, mesopelagic and epipelagic prey species indicates that the sixgill shark is a predator capable of foraging over a broad range of habitats. On the basis of identified prey species, it appears that sixgill sharks spend considerable time foraging off the bottom. Prey species like swordfish, cetaceans and dolphins *Coryphaena* sp. recorded in this study and elsewhere (Bigelow and Schroeder 1948, Backus 1957, Springer and Waller 1969, Ebert 1986a, b, Clark and Kristof 1990) indicate that sixgill

sharks are active hunters and often forage away from the bottom. Longline sets for swordfish made at several hundred metres occasionally catch large sixgill sharks (Bigelow and Schroeder 1948, Branstetter and McEachran 1986, pers. obs.). Forster *et al.* (1970) reported that 82% of the sixgill sharks they captured were taken 2,5 –10 m off the bottom. Bigelow and Schroeder (1948) reported that sixgill sharks come to the surface at night to feed.

The wide variety of prey items fed upon by the sixgill shark, reported here and elsewhere (Bigelow and Schroeder 1948, Springer and Waller 1969, Compagno 1984a, Ebert 1986a, b), includes several species of active fish and marine mammals. How these sharks were able to capture large active prey species is uncertain. The frequency of occurrence of many of the prey items in sixgill stomachs appears to be too high to be attributed solely to scavenging. An alternative means to scavenging would be to forage actively on live animals, as has been observed for the sevengill shark *Notorynchus cepedianus* (Ebert 1991). In foraging for prey, an apparently sluggish shark could position itself within range to make a short dash and overtake its prey.

It has yet to be confirmed, but the possibility exists that sixgill sharks can change their ground colour over a short time period. It would be advantageous for a wide-ranging predator to camouflage itself according to the habitat in which it was hunting. Sixgill sharks range from dark brown to dark silvery grey (Ebert 1990, Compagno *et al.* 1989). A silvery grey countershaded body would be advantageous for a mesopelagic predator, whereas darker hues would benefit a demersal hunter. A change in the intensity of light may lighten or darken the ground colour of these sharks as they move from one habitat to another. Other chondrichthyan species, such as the leopard catshark *Poroderma pantherinum* and the sevengill shark, have been observed to alter their ground colour over short time periods (pers. obs.). Moss (1981) noted that cryptic colouration in apparently lethargic sharks may allow them to approach fast-swimming billfish and tuna undetected. Similarly, Myrberg (1987) speculated that disruptive colouration may play a crucial role in the hunting behaviour of oceanic whitetip sharks *Carcharhinus longimanus*.

CONCLUSIONS

The sixgill shark is a eurytrophic predator that can exploit a broad spectrum of prey species and habitats. It readily forages in the deep demersal and midwater zones, but also nearshore. It is the dominant predator along the outer continental shelf and upper slope. Throughout most of its area of distribution it has few comparable competitors, because sympatric squaloids and lamnoids of similar size feed at a lower trophic level. Potential competitors include large squaloids such as the sleeper sharks *Somniosus* spp., which have a relatively small mouth in comparison to the sixgill shark. The sleeper shark, with its dagger-shaped upper teeth and low, short oblique lower teeth, large buccal cavity and moderate sized pectoral fins, is probably a less active hunter than the sixgill shark. The sleeper shark's large buccal cavity appears to act as a vacuum that inhales prey. The sleeper shark probably catches fast-swimming prey by lying in wait and ambushing them (Ebert *et al.* 1987). Of the deepwater lamnoids (Cetorhinidae, Megachasmidae, Mitsukurinidae and Odontaspididae), none combines a large body size with a large mouth and powerful jaws. The sixgill shark is also an active predator on other chondrichthyans, whereas these other species tend to feed exclusively on small teleosts and invertebrates.

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