

## Short Communication

# The diet of the ragged-tooth shark *Carcharias taurus* Rafinesque 1810 in the Eastern Cape, South Africa

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The ragged-tooth shark *Carcharias taurus* is a large predator of inshore coastal waters in the Eastern Cape, South Africa. Born at about 1m long and attaining approximately 3m, stomach content analyses have shown that it feeds largely on teleosts and elasmobranchs, although cephalopods are taken to a lesser extent. Similar prey taxa were taken by small ( $\leq 2\text{m}$ ) and large individuals ( $> 2\text{m}$ ), although the larger predators broadened their trophic niche to include a greater

variety of elasmobranchs and more active prey. Maximum prey size increased with predator size. Both reef-associated and benthic fishes typical of sandy substrates were included in the diet and, in addition to inshore species, those typical of deeper shelf waters were also taken. Although *C. taurus* appear to prefer to swim around high relief reefs with caves and gullies by day, it is inferred that they must also hunt over soft substrates, possibly at night.

**Keywords:** grey nurse shark, Lamniformes, nursery areas, Odontaspidae, predator-prey, sand-tiger shark

## Introduction

*Carcharias taurus* (ragged-tooth, grey nurse or sand-tiger shark) is a widespread lamnid that has been recorded from the Western Atlantic, the Western and Eastern Indian and Western Pacific oceans (Compagno 2001). Bass *et al.* (1975) provided the first information on the biology of this species in southern Africa and described the migration of pregnant females to the Eastern Cape, where pups are born at about 1m long. Additional details of the nursery area were provided in a recent study by Smale (2002). This shark is listed as a Vulnerable species in the IUCN Red List of Threatened Species (Hilton-Taylor 2000) as a result of a reduction in their population size because of human fishing pressure, low reproductive rate (Springer 1948, Bass *et al.* 1975, Gilmore *et al.* 1983 and Gilmore 1993) and late age of maturation of about six years (Branstetter and Musick 1994). More recently, Goldman (2002) has shown that males mature at 6–7 years and females at 9–10 years. The present study was initiated as part of an investigation of the biology and ecology of elasmobranchs of South Africa and it represents the first detailed feeding study of *C. taurus* off the Eastern Cape.

## Material and Methods

Biological information, including stomach contents, were collected at angling competitions, from beached dead specimens, research fishing by line- and gillnets between 1978

and 2000 in the Eastern Cape between Port Alfred ( $33^{\circ}36'S$ ,  $26^{\circ}54'E$ ) and Storms River Mouth ( $34^{\circ}01'S$ ,  $23^{\circ}54'E$ ). Data collected from each animal included mass, total length — with the tail bent down in line with the body axis (Compagno 2001). Reproductive stages and information on the depth distribution and size range of material sampled are provided by Smale (2002). Prey from stomach contents were sorted and identified from whole animals or from fish otoliths (Smale *et al.* 1995) and cephalopod 'beaks' (Clarke 1986, Smale *et al.* 1993a) when prey were digested. Prey items were measured directly when undigested. Lengths of digested prey were calculated using regressions between cephalopod beak length and mantle length, or between otolith length and fish total length. Diet was quantified by: (i) frequency of occurrence (%F), the number of stomachs containing a particular prey to stomachs containing food, expressed as a percentage; (ii) numerical importance (%N), the number of each prey expressed as a percentage of the total number of prey items and (iii) gravimetric importance (%M), the wet mass of a prey category as a percentage of the total mass of the stomach contents (Hyslop 1980). By using all three methods of analysis, bias associated with the use of only one of these methods was avoided (Hynes 1950, Windell 1968, Hyslop 1980). No combination of methods (*sensu* Index of Relative Importance, Pinkas *et al.* 1971) was used because this may combine sources of error (Berg 1979). Reconstituted prey masses were not used,

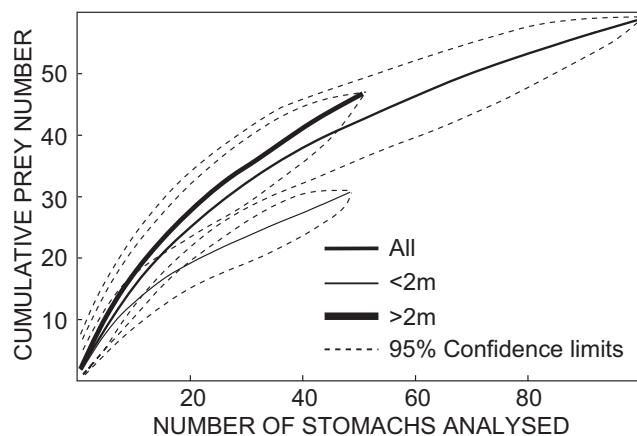
because bias may be introduced as a result of the different digestion and accumulation rates of fish otoliths and cephalopod beaks (Smale 1991). Consequently, the actual wet mass of each item in the stomachs was used in this study. Stomach contents were analysed in total then segregated by size to investigate differences in prey choice with size. An arbitrary size of 2m was chosen to differentiate between large and small sharks. The number of prey in principal prey groups (invertebrates, teleosts and elasmobranchs) in the two size-classes were tested using a contingency table and a log-likelihood ratio test (Crow 1982, Zar 1984) to investigate whether differences between the two groups were independent of size. Cumulative prey curves were constructed to determine if a sufficient number of stomachs had been collected to describe the diet adequately (Cortés 1997). The order in which the stomachs were analysed was randomised 100 times and the mean number of new species found consecutively in the stomachs and 95% confidence intervals were plotted against the number of stomachs examined.

## Results

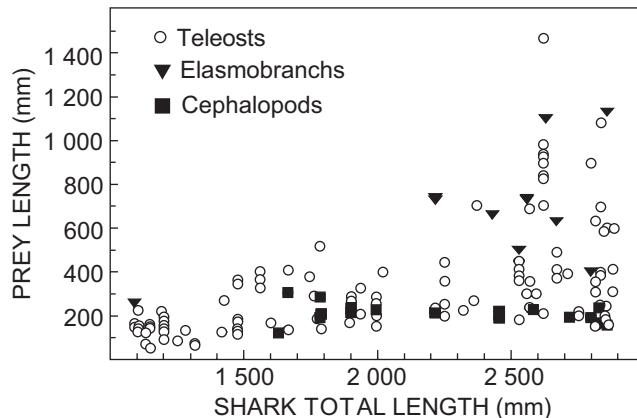
Cumulative prey frequency curves indicated that an asymptote in the number of prey had not yet been attained. This trend was more pronounced in larger sharks (Figure 1), possibly a result of the greater variety of prey taken by large animals compared to smaller sharks.

In all, 59 taxa were found in the stomach contents of 100 ragged-tooth sharks with prey (Table 1). In addition, 47 sharks were found with empty stomachs and two others had everted their stomachs. The broad spectrum of prey, and relatively low incidence of most of them, suggest a high degree of opportunist feeding. The wide spectrum of prey included species commonly found inshore, such as squids *Loligo vulgaris reynaudii*, guitarfish *Rhinobatos annulatus*, sea-catfish *Galeichthys feliceps*, grunter *Pomadasys commersonii* and the inshore sparid red tjor-tjor *Pagellus bellottii natalensis*. Prey included pelagic schooling species (e.g. horse mackerel *Trachurus trachurus capensis*, soft-bottom demersal and benthic fishes (e.g. *R. annulatus*, *G. feliceps*, *P. commersonii*), reef-associated species (e.g. *Sparodon durbanensis*, *Pachymetopon aeneum*, *Chirodactylus brachydactylus*) and prey associated with the mid- and outer-continental shelf (e.g. Cape hake *Merluccius capensis* and kingklip *Genypterus capensis*).

The small ( $\leq 2\text{m}$ ) sharks consumed a total of 31 taxa, 12 of which were not shared with the large ( $>2\text{m}$ ) sharks, whereas the latter group consumed a total of 47 prey taxa, 28 of which were found only in that group. Although both the large and small sharks had occasional crab remains, these may have been incidental prey taken while attacking other prey. The algae found in one stomach were probably ingested accidentally and is not included in the statistical analysis below. Small benthic and demersal fishes (e.g. sand tonguefish *Cynoglossus capensis*, *P. bellotti natalensis*, and kob *Argyrosomus inodorus*) were important to smaller predators. In the five smallest individuals examined (975–1 130mm), prey comprised *C. capensis*, *A. inodorus* and a small *R. annulatus* of 260mm TL.



**Figure 1:** Randomised cumulative prey curves for stomach contents of the entire sample, and two size groups ( $<2\text{m}<$ ) of *C. taurus*. The sequence of sampling was randomised 100 times and the means and upper and lower 95% confidence levels are plotted



**Figure 2:** Relationship between length of *C. taurus* and size of major prey taxa

Small *C. taurus* successfully attacked fish 5–20% of their length, but larger ragged-tooth sharks were able to consume larger sharks and teleosts, thereby broadening their trophic niche (Figure 2). Most prey were <40% of the predator total length, but the largest teleosts eaten were elongate kingklip, which were up to 56% of the predator length. These prey probably came from the edge of the continental shelf (Badenhorst and Smale 1991, Smale *et al.* 1993b).

Although there was overlap in 19 of the prey taxa taken by the two groups, elasmobranchs were more dominant prey of larger sharks (Figure 3). The number of invertebrates, elasmobranchs and teleosts taken by the small and large sharks differed significantly ( $p = 0.029$ ).

## Discussion

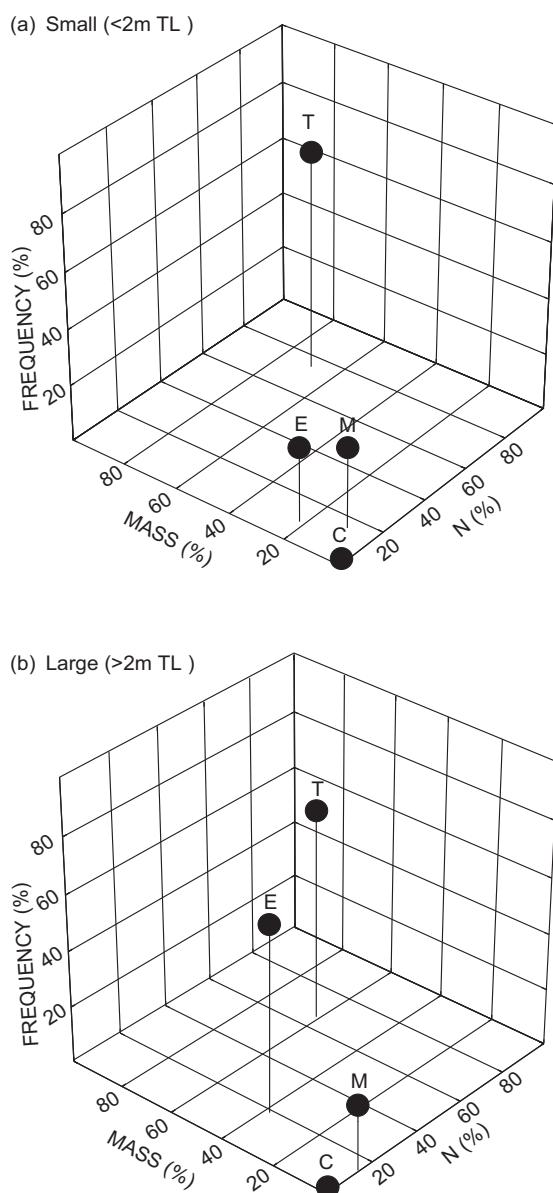
The Eastern Cape nursery ground of *C. taurus* has small individuals throughout the year in shallow inshore areas, where they are usually seen by divers or caught by anglers around high relief reefs with caves or gullies (Smale 2002).

**Table 1:** Prey items identified in the stomachs of *C. taurus* in the Eastern Cape and their percentage frequency by occurrence (%F), number (%N) and mass (%M) for small, large and all specimens combined

Species	All sizes			Small (<2m TL)			Large (>2m TL)		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
<b>CRUSTACEA</b>									
Crab leg	2.00	0.55	0.01	2.04	0.67	0.01	1.96	0.47	0.01
<b>MOLLUSCA</b>									
Gastropod	2.00	0.82	0.01	2.04	0.67	0.02	1.96	0.93	0.01
<i>Loligo vulgaris reynaudii</i>	19.00	11.26	1.27	16.33	10.67	7.89	21.57	11.68	0.43
<i>Sepia</i> spp.	8.00	2.20	0.18	10.20	3.33	1.29	5.88	1.40	0.04
<i>Octopus vulgaris</i>	1.00	0.27	<0.01	2.04	0.67	0.01			
<b>Chondrichthyes</b>									
Elasmobranch remains	9.00	2.47	2.06				17.65	4.21	2.32
<i>Squalus megalops</i>	2.00	0.55	0.49				3.92	0.93	0.56
<i>Carcharhinus brachyurus</i>	2.00	0.55	2.05	2.04	0.67	2.62	1.96	0.47	1.98
<i>Carcharhinus obscurus</i>	1.00	0.27	4.00				1.96	0.47	4.50
<i>Mustelus mustelus</i>	1.00	0.27	3.03				1.96	0.47	3.41
<i>Mustelus palumbes</i>	1.00	0.27	5.09				1.96	0.47	5.73
<i>Rhizoprionodon acutus</i>	1.00	0.27	2.42				1.96	0.47	2.73
<i>Triakis megalopterus</i>	1.00	0.27	3.64				1.96	0.47	4.10
<i>Halaehelurus natalensis</i>	3.00	0.82	0.47				5.88	1.40	0.53
<i>Poroderma pantherinum</i>	2.00	0.55	0.85				3.92	0.93	0.96
<i>Haploblepharus fuscus</i>	1.00	0.27	0.12				1.96	0.47	0.14
<i>Torpedo</i> sp.	1.00	0.27	0.23	2.04	0.67	2.07			
<i>Raja</i> remains	4.00	1.10	0.25	2.04	0.67	0.05	5.88	1.40	0.28
<i>Raja miraletis</i>	2.00	0.55	0.21	4.08	1.33	1.85			
<i>Rhinobatos annulatus</i>	15.00	4.67	8.95	18.37	6.00	15.19	11.76	3.74	8.16
<i>Myliobatis aquila</i>	2.00	0.55	1.55				3.92	0.93	1.75
Dasyatidae remains	5.00	1.37	0.93				9.80	2.34	1.05
<b>TELEOSTEI</b>									
Teleost remains	13.00	4.67	3.04	16.33	6.00	1.01	9.80	3.74	3.29
<i>Etrumeus whiteheadi</i>	1.00	1.10	0.12				1.96	1.87	0.14
<i>Sardinops sagax</i>	2.00	9.07	2.91				3.92	15.42	3.28
<i>Gonorhynchus gonorhynchus</i>	1.00	0.27	0.01	2.04	0.67	0.10			
<i>Galeichthys feliceps</i>	29.00	11.81	8.04	16.33	7.33	12.04	41.18	14.95	7.54
<i>Merluccius capensis</i>	4.00	1.37	0.35	4.08	2.00	2.56	3.92	0.93	0.07
<i>Genypterus capensis</i>	1.00	2.47	14.30				1.96	4.21	16.11
<i>Chelidonichthys</i> sp.	1.00	0.27	0.12				1.96	0.47	0.14
<i>Pomatomus saltatrix</i>	3.00	0.82	0.62	4.08	1.33	3.36	1.96	0.47	0.27
<i>Pomadasys commersonii</i>	12.00	3.57	9.72	6.12	2.00	2.18	17.65	4.67	10.67
<i>Pomadasys olivaceum</i>	7.00	2.75	0.11	14.29	6.67	1.00			
Sparidae?	1.00	0.27	0.05	2.04	0.67	0.45			
<i>Diplodus sargus</i>	3.00	0.82	0.33	2.04	0.67	0.09	3.92	0.93	0.36
<i>Lithognathus lithognathus</i>	4.00	1.10	1.57				7.84	1.87	1.77
<i>Pachymetopon aeneum</i>	2.00	0.55	0.21	2.04	0.67	0.54	1.96	0.47	0.16
<i>Pagellus bellottii natalensis</i>	6.00	4.12	1.40	2.04	6.67	10.61	9.80	2.34	0.23
<i>Pterogymnus lanarius</i>	2.00	0.55	0.33	4.08	1.33	2.92			
<i>Rhabdosargus holubi</i>	1.00	0.27	0.18				1.96	0.47	0.20
<i>Rhabdosargus sarba</i>	1.00	0.27	1.39				1.96	0.47	1.57
<i>Sarpa salpa</i>	1.00	0.27	0.01	2.04	0.67	0.11			
<i>Sparodon durbanensis</i>	3.00	0.82	8.29				5.88	1.40	9.34
<i>Spondylisoma emarginatum</i>	1.00	0.55	0.12	2.04	1.33	1.07			
<i>Argyrosomus inodorus</i>	9.00	3.57	1.37	12.24	4.67	5.47	5.88	2.80	0.85
<i>Argyrosomus japonicus</i>	2.00	0.55	2.57				3.92	0.93	2.89
<i>Umbrina ronchus</i>	1.00	0.27	0.11	2.04	0.67	0.96			
<i>Trachurus trachurus capensis</i>	3.00	0.82	0.46	2.04	0.67	3.01	3.92	0.93	0.14
<i>Remora remora</i>	1.00	0.27	0.33				1.96	0.47	0.37
<i>Chirodactylus brachydactylus</i>	1.00	0.27	0.72	2.04	0.67	6.46			
Mugilidae	1.00	0.27	0.09				1.96	0.47	0.11
<i>Liza richardsonii</i>	2.00	1.92	0.59				3.92	3.27	0.66
<i>Valamugil buchanani</i>	1.00	0.27	0.18				1.96	0.47	0.20
<i>Scomber japonicus</i>	1.00	0.27	0.24	2.04	0.67	2.18			
Bothidae ?	1.00	0.27	0.52				1.96	0.47	0.59

Table 1 cont.

Species	All sizes			Small (<2m TL)			Large (>2m TL)		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
<i>Arnoglossus capensis</i>	1.00	0.27	<0.01				1.96	0.47	<0.01
<i>Cynoglossus capensis</i>	13.00	10.16	1.09	24.49	24.00	8.37	1.96	0.47	0.16
<i>Austroglossus pectoralis</i>	6.00	2.47	0.70	10.20	5.33	4.50	1.96	0.47	0.21
ALGAE									
Algal remains	0.97	0.27	<0.01				1.96	0.47	<0.01
	100g	364g	82 517g	49g	150	9 260.90g	51g	214g	73 256g



**Figure 3:** Three-dimensional graphical representation of the percentage number, percentage mass and percentage frequency of occurrence of the major taxa in the diet of (a) small and (b) large *C. taurus*. T = teleosts, E = elasmobranchs, M = molluscs, C = crustaceans

They occur from the surf zone to at least 190m water depth (Bass *et al.* 1975, Compagno 2001, Last and Stevens 1994, Smale 2002). This study demonstrated that they consumed prey from inshore areas, mid-shelf (e.g. *M. capensis*) and the shelf edge (adult *G. capensis*), suggesting that deep-water feeding is not unusual. However, large numbers of this shark are caught by rod and line from the shore, and are usually seen on shallow reefs <15m. The fact that a large proportion of their prey occurs over soft substrates suggests that, although the sharks inhabit reefs by day, they may move into deeper water and hunt over soft substrates, possibly at night. Video records of *C. taurus* hunting in the vicinity of squid egg beds on sandy areas away from high relief reefs at night (Smale *et al.* 2001) support this hypothesis.

The sharks under study took similar types of prey to those reported by Bass *et al.* (1975) off the South African east coast and by Bigelow and Schroeder (1948) and Gelsleichter *et al.* (1999) in the western North Atlantic. This study also showed that the trophic spectrum increases with predator size, and that larger, more active prey are taken as the sharks grow, with the elasmobranch component becoming more dominant in larger individuals. *C. taurus* are opportunistic predators and they are likely to attack any suitable fish or squids they are able to consume. Their dentition (Bigelow and Schroeder 1948, Bass *et al.* 1975) is ideally suited for impaling their prey, which are then swallowed whole. Their dark body colouration and generally slow movement suggests that they are likely to hunt using ambush, then rush and strike, techniques.

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