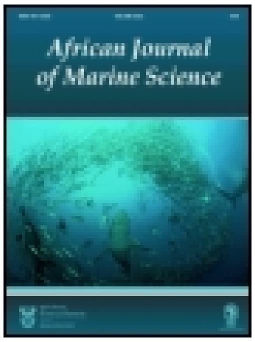

African Journal of Marine Science

ISSN: 1814-232X (Print) 1814-2338 (Online) Journal homepage: https://www.tandfonline.com/loi/tams20

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To cite this article: ML Dicken , MJ Smale & AJ Booth (2006) Spatial and seasonal distribution patterns of the ragged-tooth shark *Carcharias taurus* along the coast of South Africa, African Journal of Marine Science, 28:3-4, 603-616, DOI: 10.2989/18142320609504210

To link to this article: https://doi.org/10.2989/18142320609504210

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African Journal of Marine Science 2006, 28(3): 603–616
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AFRICAN JOURNAL OF MARINE SCIENCE
EISSN 1814–2338

Spatial and seasonal distribution patterns of the ragged-tooth shark *Carcharias taurus* along the coast of South Africa

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Catches from competitive shore-anglers, inshore boat-based anglers and sightings by spearfishers and divers were used to infer the spatial and seasonal movement patterns of young-of-the-year (<1.2m TL), juvenile (1.2–1.8m TL), sub-adult (1.8–2.4m TL) and adult (>2.4m TL) ragged-tooth sharks *Carcharias taurus* along the coast of South Africa. Adult sharks inhabited the entire coast between Maputaland in the east and St Helena Bay on the West Coast. The geographical range of sharks at earlier life-history stages decreased with size. The vast majority (93.8%) of young-of-the-year sharks recorded from competitive shore-angling club records were between East London and St Francis Bay on the East Coast, suggesting this region to be the primary nursery area for *C. taurus*. Estuarine systems, although utilised by young-of-the-year and juvenile *C. taurus*, do not form an important component of their nursery area in South Africa. Catches of pregnant and *post partum* females taken during the same time of year and in different areas indicated a biennial reproductive cycle. *C. taurus* appears to display a high degree of affinity for particular reefs. The reason some reefs are chosen over others, despite having similar physical characteristics, remains unclear. A significant increase in the number of *C. taurus* caught in competitions held by the Border Rock and Surf Angling Association between 1984 and 2004 suggests an increase in the abundance of *C. taurus*.

Keywords: boat-anglers, *C. taurus*, competitive shore-angling, distribution patterns, estuaries, habitat, South Africa, spearfishers

Introduction

Off South Africa, the ragged-tooth shark *Carcharias taurus* has been occasionally reported from the West Coast, but it is more commonly found along the East and South coasts from Cape Town to northern KwaZulu-Natal (KZN) (Bass *et al.* 1975, Smale 2002). Mating is thought to occur off the south coast of KZN from October to late November (G Cliff, Natal Sharks Board, unpublished data). Pregnant females then move northward to spend the early part of their gestation in the warmer waters of northern KZN and possibly southern Moçambique. During July and August, the near-term pregnant females begin to move southwards towards the cooler waters of the Eastern Cape (Wallett 1973, Bass *et al.* 1975, G Cliff, unpublished data), where they give birth from September to November (Smale 2002). After parturition, many of the females migrate back to KZN. The whereabouts of mature males outside of the mating season is unclear. These broad-scale distribution and migratory habits for *C. taurus* have been inferred from limited catch records obtained for only parts of its range along the South African coast.

C. taurus has never been specifically targeted by any commercial fishery in South Africa, and the limited data available indicates that it is rarely caught as a bycatch, with the exception of the commercial handline fishery (Kroese *et al.* 1995). *C. taurus* are regularly caught in the bather protection nets of the Natal Sharks Board (Wallett 1973, Dudley and Cliff 1993, Dudley 2002) and the recreational linefishery (Coetzee *et al.* 1989, Smale 2002, Pradervand and Govender 2003). The recreational linefishery comprises four components: shore-anglers, skiboat-anglers, light-tackle boat-anglers (LTB) and spearfishers. Shore-anglers are the primary component to actively target sharks and catch *C. taurus.* Catch data from this fishery are voluntarily submitted to the National Marine Linefish System (NMLS) for collation and analyses. Unfortunately, because of the high levels of non-reporting, only 466 *C. taurus* have been recorded over the past 20 years, most of which were from the Eastern Cape (Smale 2002). The existing catch records vastly underestimate the total catch of this species along the coast and provide only limited information on their spatial and seasonal distribution patterns for only part of its geographical range.

The other components of the recreational fishery rarely target sharks and invariably regard them as a nuisance and return them to the water either dead or alive. As a result, this catch is not reported and remains unidentified. In past

Published online 08 Jan 2010

surveys of these fisheries, few *C. taurus* have been recorded (Smale and Buxton 1985, Hecht and Tilney 1989, Brouwer and Buxton 2002, Fennessy *et al.* 2003). However, these incidental captures, including those of the commercial handline fishery, are important. They provide information on the seasonal and spatial distribution of *C. taurus* in the deeper offshore waters that are not fished by the shore-angling sector. These catches also provide additional information on fishing mortality. Sighting by spearfishers and SCUBA divers provide information on the distribution patterns of *C. taurus* in areas that are not fished by any sectors of the recreational or commercial linefishery, and in areas they are not feeding. This is particularly so in regions such as northern KwaZulu-Natal, where it has been suggested that gestating pregnant females cease feeding and do not take baited hooks (G Cliff, unpublished data).

This study aims to complement past surveys (Wallett 1973, *Bass et al.* 1975, Smale 2002) by providing detailed information on the spatial and seasonal distribution patterns of *C. taurus* for its entire distributional range along the South African coast. This was achieved through the collection of historical club catch records from competitive shore-anglers, from a survey of the inshore boat-based linefishery and a survey of divers and spearfishers.

Material and Methods

Study area

For the purposes of this study, the South African coastline was subdivided into twenty-eight 100km-long coastal areas (Figure 1). This scale of division was considered sufficient to identify the major trends and patterns in the spatial and seasonal distribution patterns of *C. taurus*. A summary of the environmental characteristics and processes operating along the South African coast is provided in Dicken *et al.* (2006).

Surveys

Competitive shore-angling fishery

Recreational shore-anglers who are registered to the South African Shore Angling Association (SASAA) actively target sharks in competitions to earn club points. Because of its distinctive dentition, this species is rarely recorded as a misidentified shark. Given the high frequency of club competitions, catch records from organised angling provide a good source of information on catches of *C. taurus.* Previous studies that have used competition data to assess various aspects of the South African shore-fishery have all recorded catches of *C. taurus* (Coetzee and Baird 1981, Coetzee *et al.* 1989, Smale 2002, Pradervand and Govender 2003, Pradervand 2004). These surveys, however, have been limited to only small sections of the coast. In addition, sample sizes have been inadequate for any meaningful sub-regional analysis on the seasonal or spatial distribution of sharks.

SASAA is composed of 11 regional fishing provinces (rather than current political provinces — see Dicken *et al.* 2006) and in 2005 had a membership of 2 699 anglers (E Holmes, SASAA secretary, pers. comm.). An introductory letter was sent to the Chairperson and Records Officer of each fishing province asking for their co-operation and participation in the collection of competition catch data for *C. taurus* for as far back as their records existed. Individual fishing clubs were contacted telephonically and asked for any catch records that their club possessed. Because of the large number of clubs registered in KwaZulu-Natal, it was not feasible to contact all of them, so 20 were selected at random. In most instances, club catch records consisted of the date, place of capture and the weight of the shark. In order to obtain historical catch data, as well as complete catch information for the 2002/2003 fishing season, the survey was conducted over a three-month period from May to July 2003. Additional information on the spatial distribution of catches was obtained from the Oceanographic Research Institute (ORI) and the Port Elizabeth Museum (PEM) co-operative tagging programmes. Many of these records provided information not only on the weight of the shark but its sex, precaudal length (PCL) and total length (TL).

Inshore boat-based linefishery

The inshore boat-based linefishery comprises commercial linefish, and recreational skiboat and light-tackle boat components. Although catches of *C. taurus* are rarely recorded, anglers within this fishery have a good local ecological knowledge (LEK) on the seasonal occurrence of this species in the areas they fish. This information has been accumulated over many years of observations while fishing for other species of fish.

Light-tackle boat clubs are affiliated to the South African Light Tackle Boat Association (SALTBA) and 75% of recreational skiboat clubs to the South African Deep Sea Angling Association (SADSAA) (van der Elst 1989). All commercially licensed boats are registered with the Marine and Coastal Management (MCM) branch of the Department of Environmental Affairs and Tourism and, in most cases, are associated to a regional commercial forum. A list of affiliated clubs and commercial forums was obtained from each of the relevant organisations and used as the sampling frame for telephone surveys, which were conducted from September 2002 to March 2003. Information collected in these surveys was supplemented with additional data obtained through key informant interviews with fishers who were deemed to be the most knowledgeable and willing to provide information.

The chairpersons of each of the coastal clubs registered to SALTBA and SADSAA and of each commercial linefish forum were sent an introductory letter describing the purpose of the survey and their co-operation was sought in the collection of information related to the catch and distribution of *C. taurus*. Only coastal-affiliated clubs were contacted because anglers within these clubs were considered to have a superior LEK compared with inland anglers who only occasionally fish at the coast. A follow-up telephone call was made a few days after the letter had been posted to assess the willingness of the club to participate in the survey. Each chairperson was asked to discuss the survey at their next club or association meeting to obtain information on the areas that their anglers fished and any catches of *C. taurus*. If any *C. taurus* were caught, the club anglers were asked to provide information on the size and

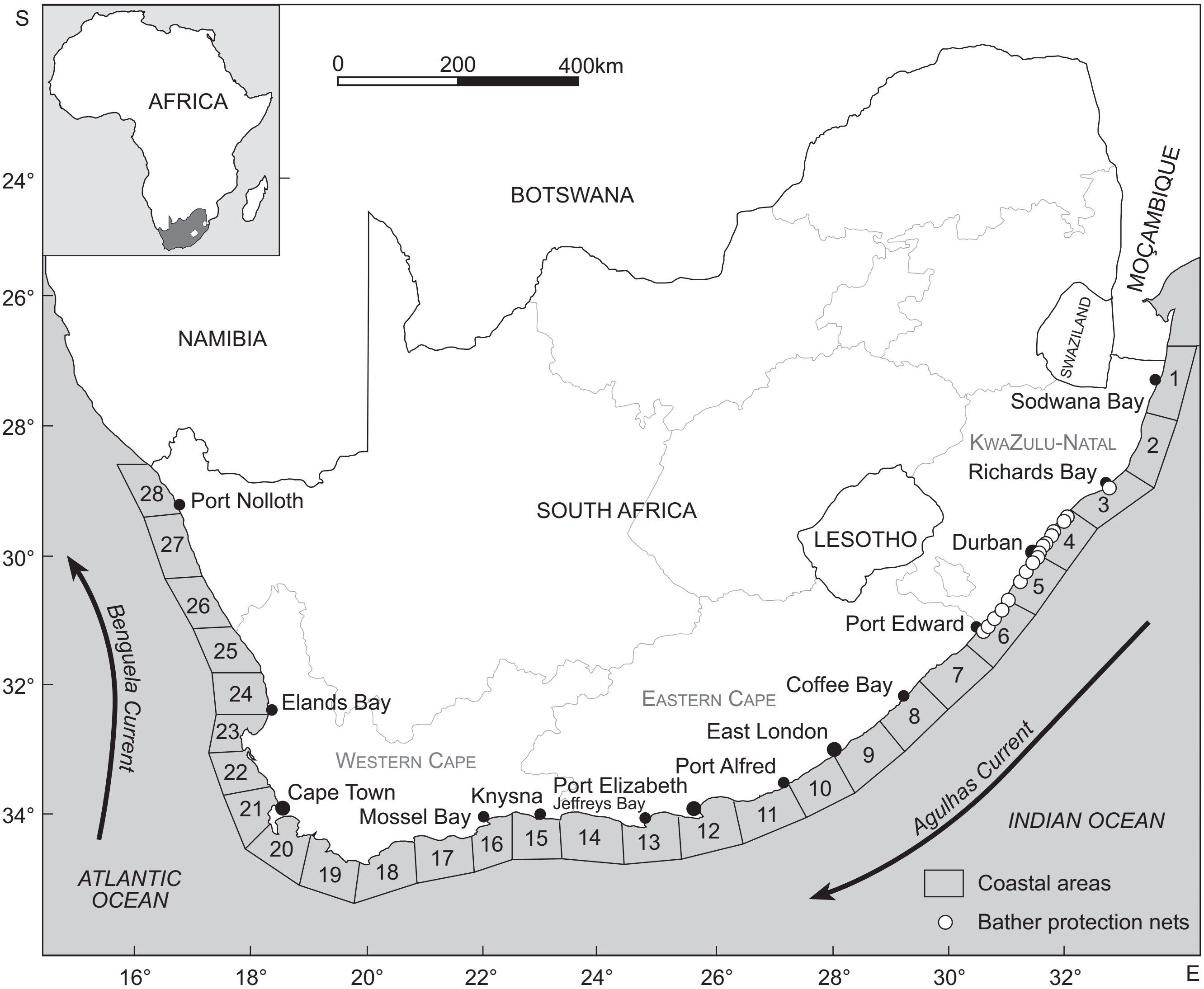

Figure 1: Map of South Africa showing the locations of the 28 coastal areas used in the analyses

date of the catches, the fate of the catch (released alive or dead) and whether or not any of the sharks that were caught had been tagged. Clubs that were willing to participate in the survey were contacted a month later to collect the information they had gathered from their members.

Key informant interviews were conducted with 'local experts' previously identified by each of the clubs. These anglers were posted a South African Navy (SAN) chart of the area that they commonly fished and had knowledge of, and were asked to mark on the chart the areas that they fished, together with any catch details of *C. taurus*. Interviews with these anglers were deliberately 'open' in an attempt to solicit as much information as possible.

Spearfishers and divers

There are an estimated 7 000 participants in the spearfishing industry, of which around 900 are registered to clubs affiliated to the South African Spearfishing Federation (Mann *et al.* 1997). There are approximately 100 000 SCUBA divers in South Africa, and their numbers are increasing rapidly (Booth and Hecht 2000). In South Africa, SCUBA divers are qualified under three main bodies: (a) the National Association of Underwater Instructors (NAUI); (b) the Professional Association of Dive Instructors (PADI); and (c) the Confederation Mondial des Activites Subaquatiques (CMAS). Once qualified, most SCUBA divers dive with a local dive operator or club, which is affiliated to one of these organisational bodies. Some SCUBA diving and spearfishing clubs are also registered to the South African Underwater Union (SAUU). A list of affiliated SCUBA diving and spearfishing clubs was obtained from each of the relevant organisations, and these lists were used as the target population to be interviewed. Because the members dive continually throughout the year, monthly shark sightings would not be greatly masked by differing seasonal diving activity.

Between January and August 2003, 91 questionnaires were posted to all coastal SCUBA diving operators listed in a local diving magazine (including 10 operators in Moçambique). Another 100 questionnaires were posted to SCUBA diving instructors and spearfishing clubs selected at random from lists supplied by PADI and the South African Spearfishing Federation respectively. In the absence of postal addresses, an additional 231 questionnaires were also e-mailed to CMAS-affiliated dive instructors.

Divers regularly record their observations of *C. taurus* in logbooks, reducing the recall bias of sightings inherent in many surveys (Essig and Holliday 1991). In an attempt to improve the response rate of the mail survey, a telephone call was made to each of the dive clubs or divers before the questionnaire was posted. Unfortunately, this protocol could not be followed for the CMAS divers, because the list of instructors that had been supplied did not contain contact phone numbers. If the questionnaire was not returned within a month, follow-up calls (or e-mails) were made once every month for a three-month period. The questionnaire was advertised on the South African Spearfishing website at www.spearfishingsa.co.za. A link to a more detailed questionnaire on a 'fishwatch' website was also advertised at the top of each of the postal questionnaires.

Because spearfishers commonly cover large areas while diving, it was often impractical on the postal questionnaire for them to list specific dive sites where *C. taurus* were observed. To alleviate this problem, South African Navy charts were posted to spearfishers who were deemed to have the most knowledge. These experienced spearfishers were identified by members of their own club who had already filled out a postal questionnaire. Spearfishers were asked to mark on the charts the areas where they dived and to note *C. taurus* sightings. They were also asked to provide information on sizes and any tagged individuals. In some instances, respondents completed questionnaires containing information for the same reefs. Where the information differed slightly in the size or timing of shark sightings, an average of the recorded data was made and used as a single database entry.

Length-weight conversions

Based on the present knowledge of the life history of *C. taurus* in South Africa, four size-classes were identified: young-of-the-year (<1.2m TL), juvenile (1.2–1.8m TL), sub-adult (1.8–2.4m TL) and adult (>2.4m TL). These size-classes were used to compare spatial and temporal distribution patterns between the different life-history stages. The approximate ages that correspond to each of these size-classes, based on the age-length relationship of Goldman (2002), are given in Table 1.

The four life-history stages were categorised by total length. However, competition catch records collected in the survey of the shore-angling fishery and from the PEM and ORI tagging programmes were a combination of weights, precaudal lengths and total lengths. To standardise units of measurement, all precaudal lengths and weights were converted to total length. Using length and weight measurements from the Natal Sharks Board (NSB; n = 100) and the PEM tagging programme (n = 625), where total length was calculated with the tail bent down to the perpendicular, following Compagno (2001), the following relationships were estimated:

Males: $TL = 1.333PCL + 68.555$ ($n = 287$, $r^2 = 0.99$)
Females: $TL = 1.290PCL + 115.560$ ($n = 438$, $r^2 = 0.99$)
Combined: $TL = 1.299PCL + 104.507$ ($n = 725$, $r^2 = 0.99$)

The relationships between weight (kg) and TL (mm) were:

Males: $W = 3.349 \times 10^{-10} TL^{3.394}$ ($n = 267$, $r^2 = 0.98$)
Females: $W = 2.337 \times 10^{-10} TL^{3.445}$ ($n = 433$, $r^2 = 0.98$)
Combined: $W = 1.296 \times 10^{-9} TL^{3.205}$ ($n = 700$, $r^2 = 0.98$)

Significant differences were found between male and female PCL-TL (ANCOVA, $p = 0.001$) and length-weight (ANCOVA, $p = 0.001$) relationships. The increased sample size of this study (particularly for larger individuals) improves the accuracy and precision of the length-weight relationship, compared with the equation given by Smale (2002), whose equation underestimates the weight of individuals larger than 2 500mm TL.

Results

Competitive shore-angling fishery

A total of 7 337 *C. taurus* catches was collected from competitive club records and the NMLS, as well as from the ORI and PEM tagging databases. Part of the ORI database consisted of sharks that had been caught, tagged and released from the bather protection nets of the NSB (n = 972) between Area 3 and Area 6 (Figure 1). These records were included in the following analyses owing to the lack of shore-angling catches in this region and the proximity of the nets to the coast.

The collected catch data, in the absence of information on effort, do not accurately portray patterns of abundance. The data are biased by seasonal variations in fishing effort and regional variations in the quality of club and provincial records. Despite these limitations, the data collected in this

Table 1: Four size-classes and corresponding ages of *C. taurus* (based on parameters from the North-West Atlantic, Goldman 2002) used for a comparison in spatial and seasonal distribution patterns along the South African coast

			Age (years)	
Size-class	Category	Total length (m)	Male	Female
1	Young-of-the-year	<1.2	0–1	0–1
2	Juvenile	1.2–1.8	1–5	1–5
3	Sub-adult	1.8–2.4	5–10	5–14
4	Adult	>2.4	>10	>14

survey were considered to reflect spatial and seasonal distribution patterns better than the catch per unit effort (cpue) obtained in a telephone survey of coastal club-affiliated shore-anglers (Dicken *et al.* 2006), because of the larger sample size. Catch records collected in this study also provided information on the sex of the shark, allowing a comparison of distribution patterns between sexes. If the number of recorded catches for any coastal area was <10, they were not presented in Figures 2–5. This was done to reduce the size of the proportional monthly catch bubbles, to allow a more accurate graphical representation of trends in the other coastal areas.

Young-of-the-year sharks

A total of 1 120 catch records of young-of-the-year (YOY) sharks was collected from the combined datasets. The smallest individual reliably recorded was 3kg (750mm TL). YOY sharks were recorded in Areas 7–20, but mostly (93.8%) in Areas 10–13, suggesting that this was the primary nursery area. YOY sharks were recorded in every month, but were most abundant from October to February (Figure 2). The sex ratio between the number of female (n = 116) and male sharks (n = 77) was significantly different from a 1:1 sex ratio (χ^2, $p < 0.05$).

Juvenile sharks

A total of 2 995 catch records of juvenile sharks was collected from the combined datasets. Catches were recorded in Areas 6–20, with the majority (89.2%) in Areas 10–13 (Figure 3) exhibiting a seasonal distribution pattern similar to YOY sharks. In Areas 6–9, catches were also recorded in the winter (July and August). The sex ratio between the number of

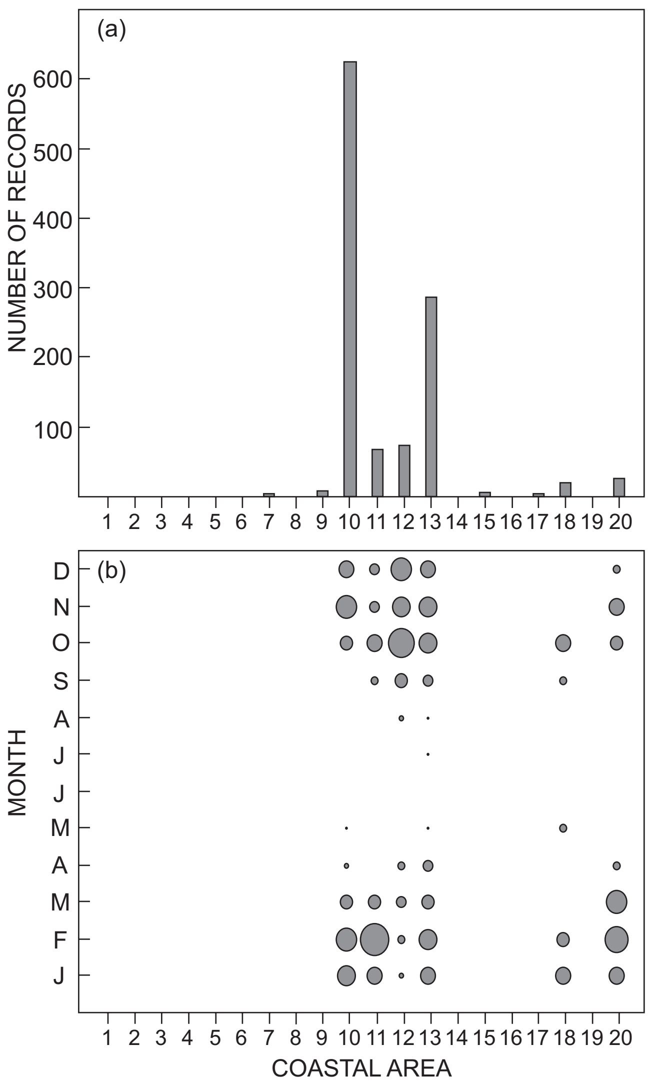

Figure 2: (a) Frequency of catch records of young-of-the-year *C. taurus* collected from club records and the ORI and PEM tagging databases, and (b) the corresponding monthly catch proportions, where monthly catch is scaled to sum to unity for each coastal area

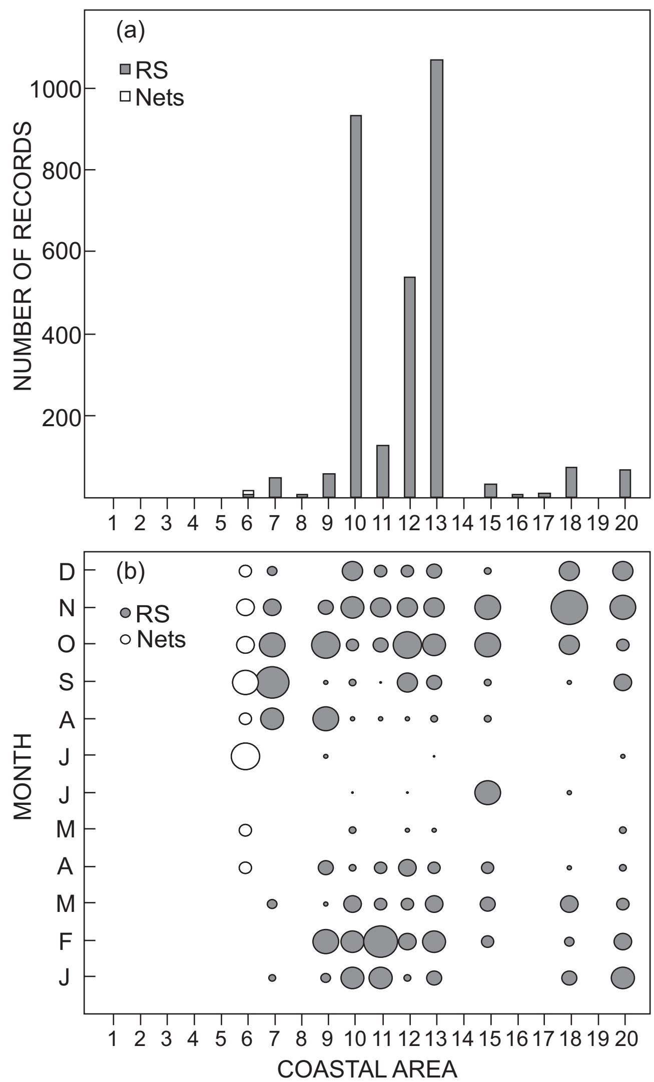

Figure 3: (a) Frequency of catch records of juvenile *C. taurus* collected from club records and the ORI and PEM tagging databases, and (b) the corresponding monthly catch proportions, where monthly catch is scaled to sum to unity for each area. RS = rock- and surf-anglers

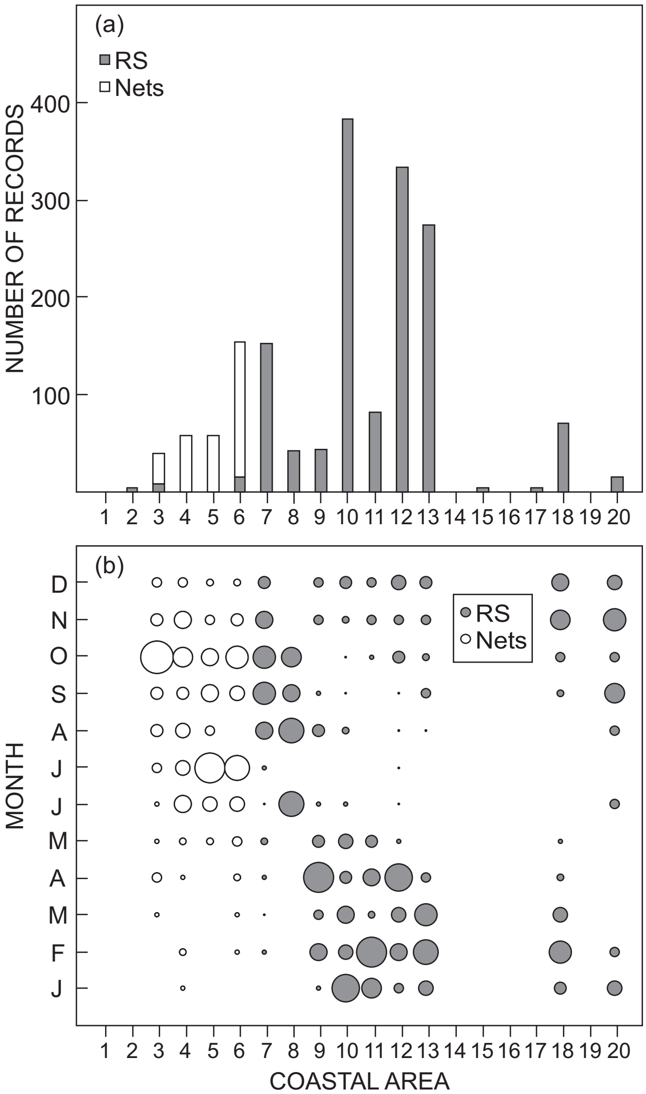

Figure 4: (a) Frequency of catch records of sub-adult *C. taurus* collected from club records and the ORI and PEM tagging databases, and (b) the corresponding monthly catch proportions, where monthly catch is scaled to sum to unity for each coastal area. RS = rock- and surf-anglers

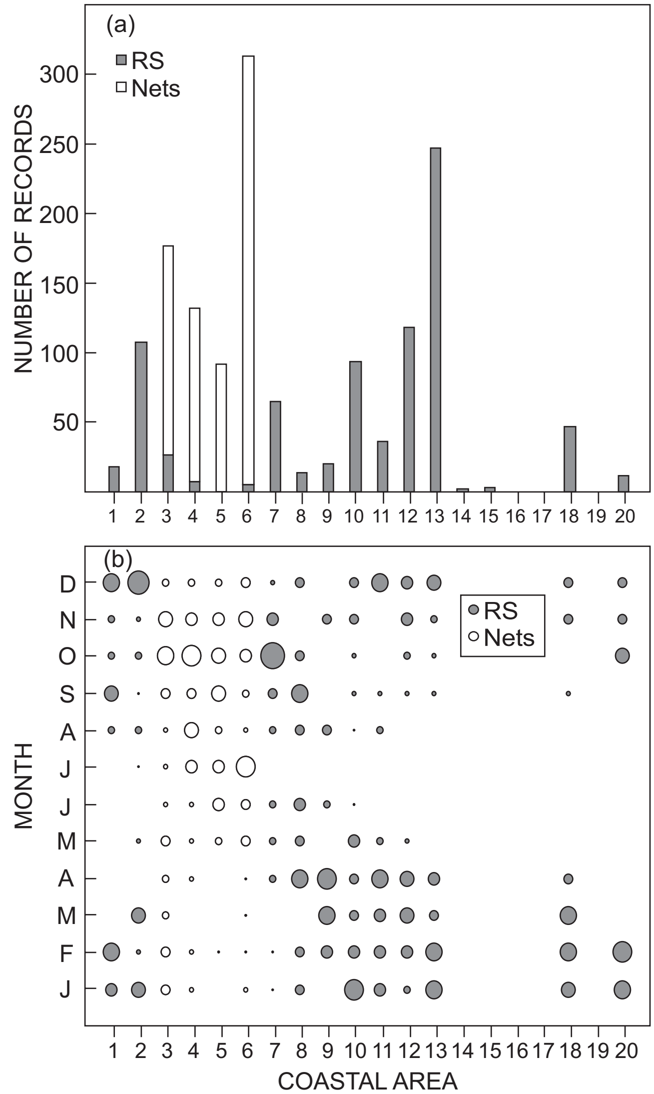

Figure 5: (a) Frequency of catch records of adult *C. taurus* collected from club records and the ORI and PEM tagging databases, and (b) the corresponding monthly catch proportions, where monthly catch is scaled to sum to unity for each coastal area. RS = rock- and surf-anglers

female (n = 346) and male sharks (n = 243) was significantly different from a 1:1 sex ratio (χ^2, $p < 0.05$).

Sub-adult sharks

In all, 1 723 catch records of sub-adult sharks were recorded from the combined datasets in Areas 3–20. Although they were recorded from the same coastal areas as YOY and juvenile sharks, 32.1% of catches were from Areas 3–9. Most were caught in Areas 9–13 from January to May, and in Areas 3–8 from June to November, suggesting a seasonal movement northward in winter and southward in summer (Figure 4). There were spatial differences in the sex ratio of catches between areas. In Area 8, sexes were obtained from 19 sharks, the majority (69.2%) being male. The greater number of male (n = 13) compared with female sharks (n = 6) was not significantly different from a 1:1 sex ratio (χ^2, $p > 0.05$). In contrast, the majority of sharks caught in Area 13 were female (80.0%). The ratio between the number of female (n = 73) and male sharks (n = 18) caught was significantly different from 1:1 sex ratio (χ^2, $p > 0.05$).

Adult sharks

In all, 1 499 catch records of adult sharks were collected in the survey. The largest shark that was reliably recorded was 3 260mm TL. Catch records were collected along the entire coast (Areas 1–20, Figure 5). Adults were the most prevalent size-class in Areas 1–6 and dominated the catch in the bather protection nets from Areas 3–6. Adult sharks exhibited a seasonal movement pattern similar to that of sub-adults. Catches in Areas 1–3 and in Areas 10–13 were highest between November and February, and catches were dominated by females (92.2%) in Areas 1–3 (n = 226) and in Areas 10–13 (79.3%, n = 53). The ratio between the numbers of female and male sharks caught in both these regions were significantly different from 1:1 sex ratio (χ^2, $p > 0.05$). Females caught in Areas 1–3 were pregnant (G Cliff, unpublished data) and were *post partum* in Areas 10–13 (Smale 2002). These findings suggest that *C. taurus* have a biennial reproductive cycle. Catches of adults in Areas 10–13 from November to February coincide with an increase in catches of YOY sharks during that period. Only 57 adult males were recorded in the survey and their distribution pattern is unclear. The majority of males (78.9%) were caught between February and April in Areas 10–13.

Habitat utilisation

All size-classes of sharks were caught within the primary nursery (Areas 10–13). To investigate the possibility that size-classes within this area were segregated by habitat type, mean lengths of catches from areas of rocky reef were compared with those from sandy beach areas in Areas 12 and 13. The length-frequency distribution of catches made in each habitat is given in Figure 6. Sub-adult and adult sharks dominated the catch from areas of sandy beach (53.1%), whereas catches in rocky reef were mostly (86.9%) YOY and juvenile sharks. The mean length of sharks caught from beach areas (1 915mm) was significantly larger than those caught in reef areas (1 536mm; t-test, $p < 0.05$). A contingency table indicated a significant relationship between size-class and habitat ($p < 0.001$).

Temporal catch trends

The Border Rock and Surf Angling Association (BRSAA) was the only province from which a comprehensive record of competitive catches of *C. taurus* was available. A regression analysis of the temporal trend in the number of *C. taurus* caught showed a significant increase ($p < 0.05$) over the period 1982–2003 (Figure 7). The temporal distribution of competition effort has remained relatively constant over this period, as has the format of the competitions, the number of competing anglers and the target species preference for elasmobranchs (Pradervand and Govender 2003). As such, the catch records can be used as a general index of relative abundance.

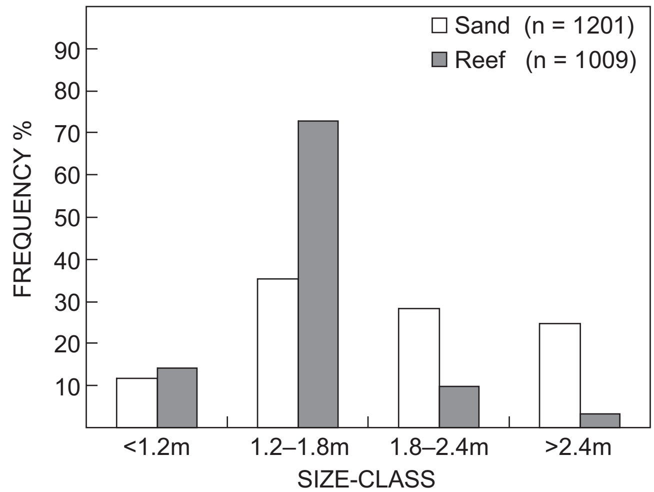

Figure 6: Comparison of the size composition of *C. taurus* caught from areas of sandy beach and rocky reef in Areas 12 and 13

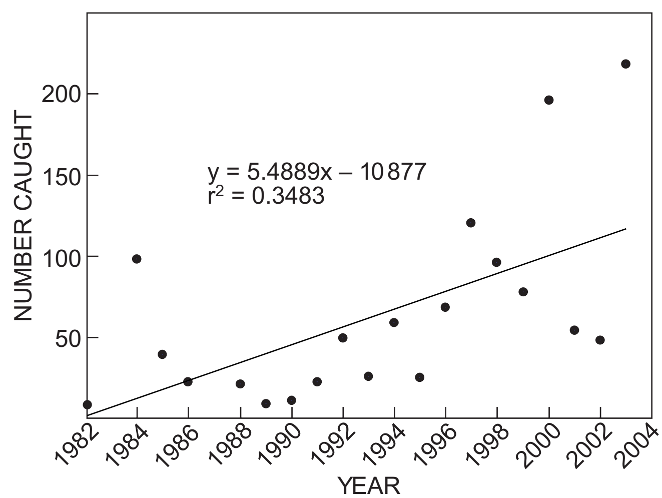

Figure 7: Temporal trends in competition catches of *C. taurus* from the Border Rock and Surf Angling Association for the period 1982–2003

Inshore boat-based linefishery

Light-tackle boat

Of the 34 LTB clubs contacted, *C. taurus* were only caught by clubs registered to Border and the Eastern Province. Anglers in these two provinces operate in local estuaries and in an area approximately 5km north and south to a distance of one nautical mile offshore from the East London and Port Elizabeth harbours respectively. The estuaries are all small shallow systems open to the sea. *C. taurus* were only actively targeted by anglers during club competitions, which are held 3–4 times a year. Anglers stated that, outside of competitions, they fished almost exclusively for non-cartilaginous species. Competition catch records for the past 10 years were unavailable for either Border or the Eastern Province. On average, however, <5 *C. taurus* are caught annually in all bay and estuarine competitions by Border (M Arentsen, pers. comm.) and <10 in the Eastern Province (J Beukes, pers. comm.). Although anglers practice a catch-and-release ethic, it is common practice for anglers to 'subdue' the sharks that they catch before bringing them aboard the boat to be weighed. As a result, the mortality rate of released sharks is probably high.

A list of all the estuaries fished by LTB-anglers that were interviewed and those in which *C. taurus* had been recorded is given in Figure 8. Anglers stated that *C. taurus* were most commonly caught in the Kariega and Kromme estuaries in summer from December to March, ranging in weight from 5kg to 30kg. Catches in the other estuaries were infrequent. Anglers reported catching the majority of sharks at the estuary mouth, but catches were recorded as

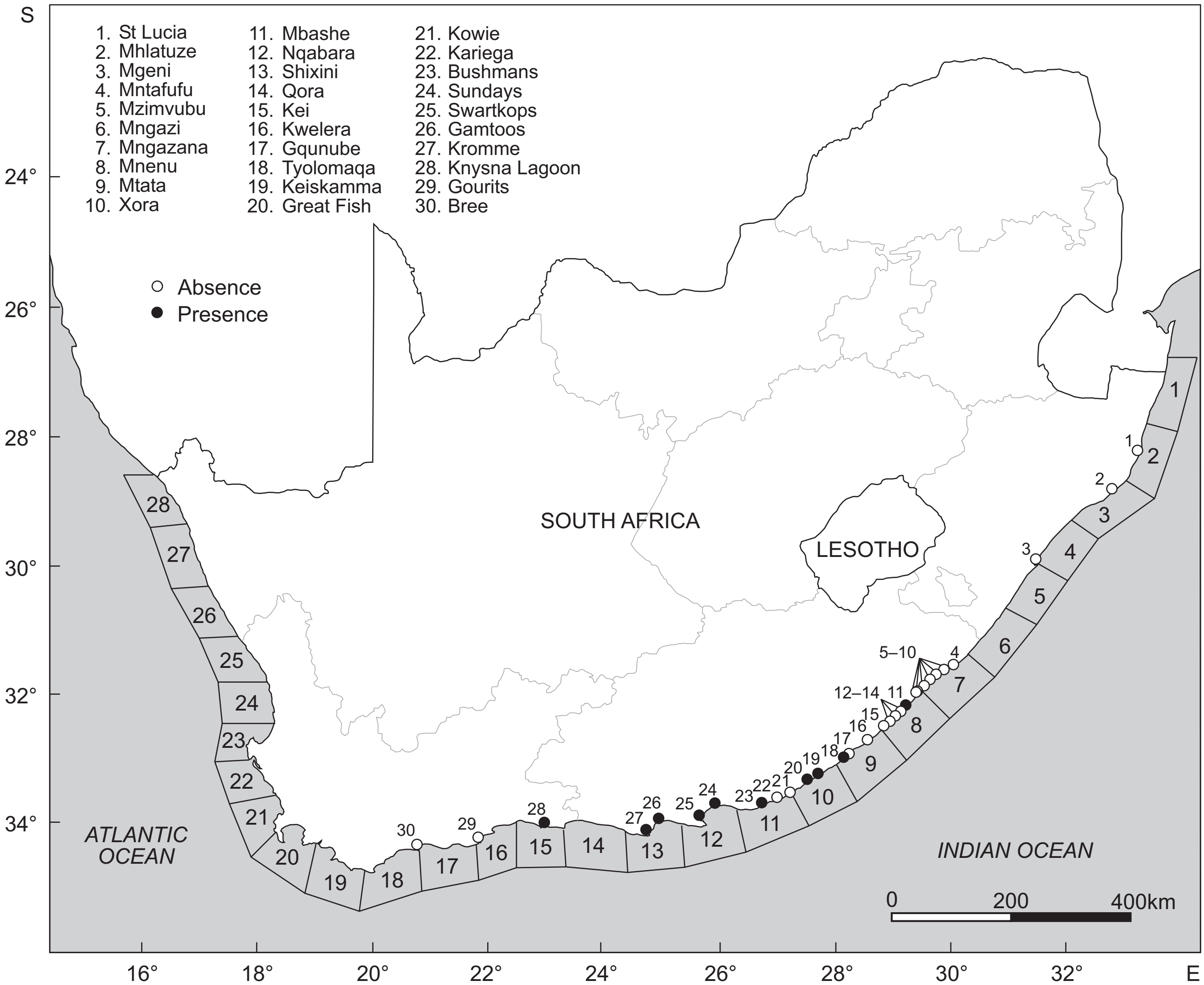

Figure 8: Map of South Africa showing the location of the 30 estuarine rivers fished by light-tackle boat-anglers. Those rivers in which *C. taurus* were caught are indicated

far as 3km from the mouth of the Gonubie Estuary and 4km from the mouth of the Knysna Estuary.

Skiboat and commercial handline

Totals of 75 skiboat clubs and 25 commercial linefish operators were contacted, of which roughly half (33 and 15 respectively) were willing to supply catch information. Possible explanations for this poor response rate include (a) fishers are often reluctant to reveal their 'best kept' fishing spots; (b) since the banning of vehicles on beaches in December 2001, many boat-launching sites have been closed, which has resulted in a feeling of animosity to the scientific community; and (c) the widely held perception of many anglers that the catch information they supply will eventually be used as a tool against them to place further restrictions on catch quotas.

In all, 1 095 fishing co-ordinates were collected in the survey from Area 1 to Area 23. However, *C. taurus* were only recorded at 209 of the sites, in Areas 2–18, and of those most catches were made at only a few reefs. *C. taurus* were most commonly caught at depths between 20m and 40m, although catches were reported as deep as 80m while fishing for hake *Merluccius capensis* in Areas 15 and 16. None of the anglers interviewed specifically targeted shark species. Any *C. taurus* that were caught were accidentally taken while targeting non-cartilaginous fish species, particularly geelbek *Atractoscion aequidens*, in Areas 2–7, kob *Argyrosomus* spp. and yellowtail *Seriola lalandi* in Areas 8–13, and kob and hake in Areas 15–18.

YOY sharks were not recorded by boat-anglers at any of the deeper reefs fished. This suggests that they are segregated from the rest of the population within their nursery areas by depth. The spatial and seasonal distributions of catches of the other three size-classes were similar to those recorded by the shore-angling fishery. One notable difference, however, was that boat-based anglers reported catching *C. taurus* at a number of reefs in Areas 4–6. This stretch of coast is protected by NSB bather protection nets and is an area in which shore-anglers reported rarely catching *C. taurus*. The spatial distribution pattern of *C. taurus* catches by boat-based fishers may be biased on account of greater fishing effort in the summer because of more favourable weather conditions. There is also a seasonal change in target species by recreational anglers in Areas 3–6. In the summer, anglers tend to use lures and target game fish species such as king mackerel *Scomberomorus commerson*. In winter, baited hooks are used to catch bottom-feeding reef fish such as slinger *Chrysoblephus puniceus*. Therefore, the bottom-fishing techniques used in winter have a greater chance of catching *C. taurus* than does midwater trolling in the summer.

All of the recreational fishers interviewed stated that they preferred to 'cut the line' and release any *C. taurus* that had been accidentally caught rather than try to land them on the boat. In contrast, commercial fishers admitted that *C. taurus* were regarded as an unwanted pest when fishing for more valuable non-cartilaginous fish species and on occasion they would be killed rather than released alive. Despite the commercial ban on this species, and its poor market value, anglers recalled fishers that actively targeted *C. taurus* to sell in order to supplement their income. The consensus among the interviewees was that this trend was increasing as a direct response to the reduction of allocated linefish licences in 2004. These aspects of fishing mortality cannot be accurately assessed, but the result of the interviews suggests that mortality is greater from boat-based fishing than from either the bather protection nets (Dudley 2002) or from the shore-angling fishery (Dicken *et al.* 2006) (Table 2). Fishing mortality from all fishery components is highest in Areas 3–6. Fishing mortality within this area will only impact the adult component of the population because the distribution of juvenile sharks is limited to nursery areas located primarily within Areas 10–13 (Dicken *et al.* 2006).

Boat-based anglers reported incidental seasonal catches of *C. taurus* of 2–3 per day and up to 20 per night at some reefs in Algoa Bay (Area 12). Despite these high capture rates, only four anglers (in Areas 3, 10 and 13) reported catching a tagged shark, and none of them had been able to read the tag number or reported the recapture to the relevant tagging organisation. One angler recalled one fisher who had caught four tagged sharks in a day in (Area 13) and another who had caught three tagged sharks in Area 12, but none of these recaptures had been reported. Therefore, sharks that have been tagged by shore-anglers or released from the bather protection nets appear to move into deeper waters where they are fished by recreational and commercial skiboat fishers. The high non-reporting of tagged sharks in this fishery hampers investigations into their offshore movement patterns. The development of educational and outreach programmes has dramatically improved recovery percentages in co-operative tagging programmes in Australia (Pepperell 1990, Kohler *et al.* 1998). Such an approach might encourage better reporting by anglers within the boat-based fishery in South Africa.

Table 2: Estimated number of *C. taurus* killed within different South African fisheries in 2004

Areas	Number killed: Skiboat angling	Shore-angling (Dicken et al. 2006)	NSB nets (Dudley 2002)
1–2	NI	7	–
3–6	180	9	128
7–11	NI	55	–
12–13	160	38	–
15–18	70	13	–
19–28	0	2	
Total	410	124	128

NSB = Natal Sharks Board
NI = No information

Spearfishers and divers

In all, 124 (64.9%) of the 191 questionnaires posted to SCUBA divers and spearfishers were returned. This response rate was markedly higher than the 16% obtained from a postal survey of KwaZulu-Natal spearfishers by Mann *et al.* (1997). Brown (1991) recommended a response rate of between 60% and 75% for effective surveys. Of the 231 questionnaires that were e-mailed to CMAS-affiliated dive instructors, only 23 (10%) were returned. This poor response rate highlights the necessity and effectiveness of integrating the postal survey with a personal introduction and, if necessary, follow-up phone calls.

A total of 557 reef locations was recorded in the survey from Area 1 to Area 28. Divers had observed *C. taurus* at 203 of the sites in Areas 1–20 (39.3%), and at only one site (Area 23) in Areas 21–28 (2.5%). These results provide further evidence that the distribution of *C. taurus* west of Cape Point is a rare and anomalous occurrence. Dive locations and sightings of *C. taurus* ranged in depth from 3m to 40m. Divers sighted YOY sharks within Areas 10–20, inhabiting the same reefs as larger sub-adult and adult sharks. The YOY sharks were typically observed swimming at depths of between 5m and 10m within protective rocky gullies and the larger sharks in deeper water on the outskirts of the reef.

The seasonal distribution of shark sightings within each coastal area (Figure 9) was based on the reef where the majority of interviewed divers had observed the greatest number of sharks. The distributional patterns and size-classes of sharks observed were very similar to those inferred from catch records obtained in the other surveys. Shore-anglers caught few YOY or juvenile sharks during winter. As a result, it was suggested that these life-history stages might move into deeper offshore water in response to declining water temperatures. Although spearfishers and SCUBA divers were active throughout the year, they observed few of these sharks at any of the reefs where they dived during winter. The whereabouts of the winter nursery areas of *C. taurus* remains unknown.

Although *C. taurus* were observed at reefs in Areas 1–23, no more than five individuals were ever sighted on reefs in Areas 19–23. In Areas 4–6, in which the bather protection nets are deployed, *C. taurus* had never been observed at

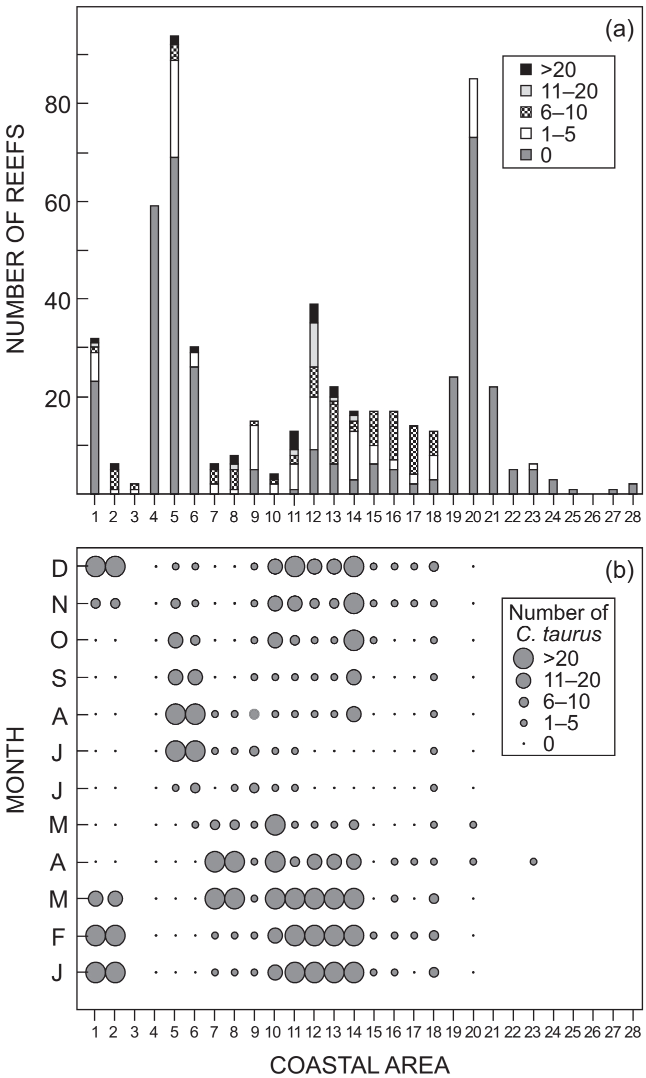

Figure 9: (a) The maximum numbers of *C. taurus* observed at all of the reefs recorded in the survey of divers within each of the coastal areas and (b) monthly sightings of *C. taurus* at reefs in Areas 1–28

any of the 59 reefs dived in Area 4. They were seen at 25 (26.6%) of the 94 reefs in Area 5 and at only four (13.3%) of the 30 reefs in Area 6. These observations suggest that the protection nets may potentially prevent the sharks' utilisation of inshore reefs. Sharks in these areas may be forced to inhabit deeper offshore reefs such as Aliwal Shoal and Protea Banks. Both these reefs are located over 5km offshore and were the only two sites in Areas 5 and 6 at which more than five sharks had been observed. At 23 of the 32 (71.9%) reefs that interviewees had dived in Area 1, *C. taurus* were never seen, whereas at one site (Quarter Mile) over 20 sharks were commonly observed in some years from December to March. Diver observations are biased by water clarity, the popularity of the dive site and seasonal effort. This selective pattern of reef preference, however, was evident at reefs along the entire coast.

Tagged sharks were observed at only a few diving sites, and only the shape and colour, but not the tag number, were identifiable. As a result, these sightings provided little useful information on the identification of offshore movement patterns. Scientific monitoring of *C. taurus* over a wide geographical area and over a long time period is financially and logistically unfeasible. The LEK available from recreational SCUBA divers and spearfishers, although limited to simple observations, is a potentially valuable source of information.

In Moçambique waters, divers observed *C. taurus* at Ponta do Oura on the South African border and farther north at Ponta Malongane, Inchaca Island, Inhambane and Bazaruto Island. *C. taurus* were observed infrequently and only in small groups comprising of one or two large individuals. These results are in marked contrast to observations made some 30 years ago by Condon (1970), who reported seeing aggregations of up to 30 individuals in the vicinity of Inhaca Island. In the 1960s and 1970s spearfishers were paid per shark and up to four sharks were shot every weekend around Inchaca Island alone (N Gomez, ORI, pers. comm.). The results of this present survey suggest that the *C. taurus* population in Moçambique has been dramatically reduced over the past 2–3 decades. Wallett (1973) and Bass *et al.* (1975) believed that male sharks, outside of the mating season, reside in southern Moçambique. However, the results from the present survey do not support this theory.

Discussion

Nursery areas

Catch records and underwater sightings indicate that the Eastern Cape is the primary nursery area for YOY and juvenile *C. taurus*. Although YOY and juvenile sharks were recorded in Areas 6–20, 93% of YOY sharks and 89% of juvenile sharks caught by shore-anglers were recorded in Areas 10–13. Variation in abundance is likely related to sea temperature, which is considered to be the most important factor governing the distribution of fish populations along the South African coast (van der Elst 1989, Turpie *et al.* 2000). Juvenile sharks ranged over a broader area than YOY sharks. This may be attributable to the former having a greater tolerance to temperature variations or alternatively to an increased choice in habitat utilisation owing to a reduced risk of predation.

The primary characteristics of a nursery area may be predator avoidance (Holland *et al.* 1993, Morrissey and Gruber 1993, Merson and Pratt 2001, Heupel and Hueter 2002) and an abundant food source (Branstetter 1990, Castro 1993, Simpfendorfer and Milward 1993). Although there is no evidence of predation on smaller conspecifics, other elasmobranchs become increasingly important in the diet of larger *C. taurus* (Bass *et al.* 1975, Gelsleichter *et al.* 1999, Smale 2005). Other potential predators that inhabit the nursery region are the great white shark *Carcharodon carcharias*, bull shark *Carcharhinus leucas*, dusky shark *C. obscurus*, bronze whaler shark *C. brachyurus* and spotted sevengill cow shark *Notorynchus cepedianus*. YOY and juvenile sharks were typically caught by anglers in areas of high profile reef. In contrast, sub-adult and adult sharks comprised <13% of shore-angling catches in such areas. These results may be biased by the greater likelihood of losing larger sharks in areas of reef, but suggest that rocky reef areas may provide safety from larger sharks by access restriction (Springer 1967, Branstetter 1990, Castro 1993).

The absence of young sharks from catches by boat-based anglers and sightings by divers suggests that they may be utilising shallow-water reefs as a refuge from larger species of sharks. Water depth may therefore play an important role in the distribution of the different life-history stages. YOY and juvenile sharks are known to feed on species such as kob *Argyrosomus* spp. and guitarfishes *Rhinobatus annulatus* (Smale 2005), which are commonly found over sandy substrates. However, a large proportion of their prey, consists of shallow reef-dwelling species such as white musselcracker *Sparodon durbanensis*, blue hottentot *Pachymetopon aenum* and twotone fingerfin *Chirodactylus brachydactylus* (Smale 2005). The distribution and habitat utilisation of reef areas by YOY and juvenile sharks may reflect the abundance of these prey species.

The sex ratio of YOY and juvenile sharks of 1 male:1.5 females in the shore-anglers' catches was similar to the sex ratio obtained by Smale (2002). However, Merson and Pratt (2001) reported an almost equal male:female ratio in juvenile sandbar sharks *C. plumbeus*. It is relatively common, while fishing for *C. taurus,* to catch more than five in quick succession. This observation does not explain whether the animals are moving together or are simply drawn to the bait in a relatively confined area. Aggregation behaviour, however, may have biased the sample sex ratio.

Shore-angling catches indicated that YOY sharks appeared in the nursery areas at the end of September, with the greatest numbers caught (76%) between November and February. The increase in the number of YOY sharks coincided with an increased catch of mature sharks, many of them females (76%). There were no apparent regional variations in the arrival of female sharks or the onset of pupping within the nursery areas. This is surprising, considering the differences in the distances migratory pregnant females have to travel from their gestation grounds in northern KwaZulu-Natal to pup in Areas 10–20. The earliest catches of juvenile sharks coincided with the appearance of YOY sharks, when the water temperature typically ranged between 18°C and 22°C. The latest month in which both size-classes were encountered was May, when the water temperature dropped to between 15°C and 18°C. These observations are consistent with those of Castro (1993) and Merson and Pratt (2001), which suggest that water temperature is the cue to the onset and conclusion of the *C. taurus* pupping and summer nursery season.

In temperate zones, cold winter temperatures force YOY and juvenile sharks into deeper offshore and warmer water (Castro 1993). In the north-western Atlantic, juvenile *C. taurus* occupy summer nurseries from North Carolina to Cape Cod and winter nurseries in the warmer waters between North Carolina and northern Florida (Gilmore *et al.* 1983, Gilmore 1993). Few YOY or juvenile sharks were either caught or sighted by shore-anglers, boat-anglers or divers anywhere along the entire east coast of South Africa between May and August. The location of the winter nursery areas remains uncertain. It is possible that, during the winter, juvenile sharks move into deeper offshore water. Alternately, they may move northwards towards the Transkei Coast between the Eastern Cape and KwaZulu-Natal. However, that coastline is rarely dived or fished, because of its inaccessibility and often poor diving conditions.

Estuaries are utilised by *C. taurus* as nurseries off the east coast of America, because of the abundance of food and reduced predatory pressures there (Gilmore 1993). Estuaries in South Africa, however, are typically small and shallow. Although *C. taurus* were caught by light-tackle boat-anglers in 11 of the 30 estuarine rivers that they fished, they were only regularly caught in the Kariega and Kromme rivers. Paterson and Whitfield (2000) estimated that juvenile *C. taurus* comprised 2.3% of the channel ichthyofauna in the Kariega River, but were absent from the shallower eelgrass and creek areas of the estuary. The present results suggest that estuarine systems, although utilised by YOY and juvenile *C. taurus*, do not form an important component of the nursery habitat in South Africa.

Adult population

Adult *C. taurus* were recorded along the entire survey area from Area 1 in northern KwaZulu-Natal to Area 23 on the West Coast. Their occurrence west of Cape Point, however, is rare and anomalous, and effectively signals their southernmost distributional range. Sub-adult sharks were rarely recorded north of the Tugela River (Area 3) in shore-angling catch records. The seasonal occurrence of adult sharks along the coast is related to the breeding migration of predominantly female sharks, which is well defined and can be traced through spatially and seasonally distinct phases of mating, gestating and parturition (Bass *et al.* 1975, G Cliff, unpublished data).

Based on catches from the bather protection nets, Bass *et al.* (1975) and G Cliff (unpublished data) postulate that mating takes place off the south coast of KwaZulu-Natal (Areas 4 and 6) between October and December. Aggregations of male and female *C. taurus* are commonly observed by divers at Aliwal Shoal (Area 5) from July to October, and most of the sharks are mature or maturing males, with many of the females displaying mating scars (B Allen and VM Peddemors, University of KwaZulu-Natal, unpublished data). The predominance of male sharks (64%) in shore-angling catches suggests male aggregations during the same periods in Areas 7 and 8. Anglers also reported catching mature female sharks with pre-copulatory scarring on their flanks as far south as Coffee Bay (Area 8) during June, July and August. Therefore, it appears that mating takes place earlier in the year and over a broader geographical range than was previously believed. The seasonal timing of mating of *C. taurus* is similar to that observed for the species in the north-western Atlantic (Gilmore 1993). In the south-western Atlantic, however, mating in *C. taurus* occurs during the summer, in much cooler water of 12°–16°C than off the east coast of South Africa (Lucifora *et al.* 2002). The male:female sex ratio during the mating season in the south-western Atlantic was 2:1 (Lucifora *et al.* 2002). The lower sex ratio observed in this survey and that of Allen and Peddemors suggests a much lower level of male competition for females in South Africa.

The survey results confirm the findings of Wallett (1973) and Bass *et al.* (1975) that pregnant females move northwards after mating, into the warmer waters of northern KwaZulu-Natal to gestate. A similar movement northwards to gestate has been observed for *C. taurus* in the south-western Atlantic (Lucifora *et al.* 2002). However, in the north-western Atlantic, mating and gestating occurs in a similar area (Gilmore 1993). Catch records indicate that gestating females begin to migrate southwards in March, towards the Eastern and Western Cape nursery areas to pup. Wallett (1973) and Bass *et al.* (1975) found that during the period of June-August most of the female sharks caught in the protection nets were pregnant and carrying two full-term embryos. In the south-western Atlantic, however, parturition is believed to occur in the same warm subtropical waters as the gestation grounds in southern Brazil (Lucifora *et al*. 2002). The presence of pregnant females in Areas 1 and 2 between November and March, and of mature but non-pregnant females at the same time of year in Areas 10–13, provides further evidence of a biennial reproductive cycle as proposed by G Cliff (unpublished data). A biennial cycle has also been proposed for *C. taurus* in the north-western Atlantic (Branstetter and Musick 1994) and the south-western Atlantic (Lucifora *et al.* 2002). The presence of sub-adult sharks and possibly non-breeding adult females (in their resting year) in Areas 3–6, between June and November may well represent a range extension from Areas 10–13.

The whereabouts and movement patterns of mature males outside of the mating season remains uncertain. Wallett (1973) and Bass *et al.* (1975) suggested that males reside in northern KwaZulu-Natal and southern Moçambique, but the results from this survey do not support this theory. Gilmore (1993) suggested that male *C. taurus* in the north-western Atlantic inhabit deeper offshore water outside their mating season. A similar hypothesis has been proposed for male *C. taurus* in the south-western Atlantic (Lucifora *et al.* 2002) and in Australian waters (Otway and Parker 2000). Approximately half (51%) of the sub-adult and adult sharks caught by anglers in Areas 9 and 10 during the pupping season were males, compared with only 20% in Area 13. These findings suggest that male sharks may move south after mating into the northern part of the juvenile nursery area. Mature male *C. taurus* have also been shown to occupy part of the nursery area off the east coast of America (Gilmore 1993).

Prey density may be a cue for habitat choice, particularly for sub-adult and adult sharks. Silvester (1977) suggested that the northward movement of *C. taurus* in Australia might be linked to the migration of flathead mullet *Mugil cephalus*. In South Africa, geelbek *Atractoscion aequidens*, yellowtail *Seriola lalandi* and other predatory species migrate northwards from the Western Cape to KwaZulu-Natal in winter during the 'sardine run'. The event is an annual phenomenon that takes place between June and August. Sardine *Sardinops sagax* extend their geographical distribution from the Southern and Eastern Capes eastwards, in response to decreasing water temperatures (Armstrong *et al*. 1991). Anglers, particularly in Areas 6–9, reported increased catches of *C. taurus* associated with the sardine run. The breeding migration of *C. taurus* along the coast is not intrinsically associated with the movement of sardines. However, sardine are likely to affect spatial distribution patterns of *C. taurus* on a smaller scale.

There has been concern recently that breeding aggregations of *C. taurus* at Aliwal Shoal and Protea Banks (Areas 5 and 6) are declining because of increased diver pressure there (AM van Tienhoven and VM Peddemors, University of KwaZulu-Natal, unpublished data). Diver pressure has also been linked to a reduction in the number of *C. taurus* sightings at Quarter Mile Reef in Area 1, an important gestation area. As a consequence, all SCUBA diving and spearfishing was temporarily suspended at this site, pending the arrival and acclimation of the sharks to the reef in December 2005 (K Sink, South African Institute of Aquatic Biodiversity, pers. comm.). The results presented here indicate that *C. taurus* display a high degree of affinity for particular reefs. Why some reefs are chosen over others, despite them having similar physical characteristics, remains unclear. If suitable habitat is limited, the identification of aggregation sites, particularly those associated with the reproductive activities of mating, pupping and gestation, is essential for effective fisheries management to ensure the conservation of *C. taurus* in South Africa.

Temporal trends

The considerable increase in the number of *C. taurus* caught in angling competitions in the Border fishing province (Areas 9 and 10) from 1984 to 2004 suggests that the population of *C. taurus* has increased over the past two decades. This is supported by results from angler interviews, the majority (77%) being of the opinion that the population of *C. taurus* has remained relatively stable or has even increased over the past 20 years (Dicken *et al.* 2006). Similarly, trends in catch rate and size of *C. taurus* in the bather protection nets between 1978 and 2003 show no indications of a population decline (Dudley and Simpfendorfer 2006). The number of *C. taurus* caught in the nets has reduced markedly in recent years with a reduction in the number of netted beaches and their removal during the annual sardine migration (Dudley 2002). Fishing mortality has also decreased in the competitive shore-fishery with the advent in the past decade of a catch-and-release ethic by the majority of anglers. A reduction in fishing effort and associated mortality has also been evident in response to the vehicle beach ban in 2001. As a result of the ban, the number of registered club anglers decreased by 30% (E Holmes, SASAA, pers. comm.). In addition, many of the remaining club anglers now target non-cartilaginous species (Dicken *et al.* 2006). Therefore, indications are that fisheries-related mortality of this species will continue to decrease rather than increase in the future. Of concern, however, is the increased targeting of *C. taurus* by commercial skiboat-anglers in response to the reduction in the number of allotted linefish licences, a trend that is likely to increase in the future.

Acknowledgements — This work would not have been possible without the cooperation of SASAA, SALTBA, SADSAA, PADI, CMAS, SAUU, and the South African Spearfishing Federation. In particular, we thank the following shore-anglers: B Wareham, N Heath, D Pretorius, T Herbst, M Pautz, E Klur, R King, K Lennox, M Sumner, J van Niekerk, M Spies, M Peterson, M Potgieter, A Hayward, S Muller, J Strauss, A Dames, J La Grange, S Gomes and T Flossy. Thanks are due to the following boat-based anglers: M Arentsen, J Beukes, J Bester, R Thompson, J Rance, P Petry, L Alkers, M Roos, M Bahrain, W Watts, M Schiller, M Fraser, J Josling, S Stamatis, C de Beer, L Edwards, V de Villers, T Whitton, J Bath, D Sharp, H Daniel, V Cirrini and T Mengels. Thanks are also due to the following dive operators and spearfishers: R Bester, M Addison, K van der Walt, L van Aardt, L Boshoff, G Plagiani, C Robertson, T Botha, M Jackson, F Burger, Y Lechanteur, B Ackerman, E Hayman, A Heydorn and TH Hand. Special thanks are give to R Martin and R Smit for the development of the Port Elizabeth Museum co-operative shark tagging programme. We thank the Port Elizabeth Museum Director and staff for their support and infrastructure, the National Research Foundation (NRF) and Marine and Coastal Management for funding, and Bayworld Centre for Research and Education for administering the study. We acknowledge with thanks the data supplied by both the Natal Sharks Board and the Oceanographic Research Institute.

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Manuscript received January 2006; accepted July 2006