CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2007, **58**, 127–134

Spatial and seasonal distribution patterns of juvenile and adult raggedtooth sharks (*Carcharias taurus*) tagged off the east coast of South Africa

M. L. Dicken[A,D], *A. J. Booth*[A], *M. J. Smale*[B] *and G. Cliff*[C]

[A]Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown, 6140, South Africa.
[B]Port Elizabeth Museum, PO Box 13147, Humewood, 6013, South Africa.
[C]Natal Sharks Board, Private Bag 2, Umhlanga Rocks, 4320, South Africa.
[D]Corresponding author. Email: raggedtoothshark@bayworld.co.za

Abstract. Understanding the movement patterns of raggedtooth sharks (*Carcharias taurus*) is crucial in defining habitat use and evaluating the effects of exploitation and anthropogenic activities. Between 1984 and 2004, 1107 *C. taurus* juveniles (<1.8-m TL) and 2369 *C. taurus* maturing subadults and adults (>1.8-m TL) were tagged and released along the east coast of South Africa. In total, 125 *C. taurus* juveniles and 178 *C. taurus* maturing subadults and adults were recaptured, representing recapture rates of 11.2% and 7.5% respectively. The average distance travelled by juvenile sharks was 18.7 km (95% CI = 10.8–26.6 km). Juvenile sharks displayed site fidelity to summer nursery areas. The average distance travelled by maturing and adult sharks was 342 km (95% CI = 275–409 km). One female shark, however, was recaptured 1897 km from its original release site. The average rate at which pregnant sharks moved south from their gestation to pupping grounds was 2.6 km day^{-1} (95% CI = 2.04–3.16 km day^{-1}). This study highlights the differences in movement patterns between *C. taurus* juveniles and adults and suggests philopatric behaviour in both life-history stages.

Additional keywords: life history stages, movement patterns.

Introduction

Crucial to effective fisheries management is a thorough understanding of the stock structure of a population. Understanding the spatial and seasonal distribution patterns of a species is necessary to define habitat use and evaluate the potential effects of exploitation and anthropogenic activities. This is particularly important for a species such as the raggedtooth shark (*Carcharias taurus* Rafinesque, 1810), whose life-history characteristics make it particularly susceptible to over-exploitation (Pollard *et al*. 1996; Smith *et al*. 1998; Compagno 2001). Exploitation, even at low levels for a slow-growing, late-maturing species that only produces two pups every other year, could reduce the population growth rate to values of $\lambda < 1.0$, resulting in severe population declines in a very short time period (Baum *et al*. 2003).

Raggedtooth sharks, commonly known as 'raggies' in South Africa, are also referred to as the sand tiger shark in North America and as the grey nurse shark in Australia. It is a wide-ranging coastal species found primarily in warm–temperate and tropical waters around the main continental landmasses, except in the eastern Pacific Ocean off North and South America (Last and Stevens 1994; Compagno 2001). Over-fishing, however, has resulted in dramatic population declines throughout much of its global range. In the north-western Atlantic, the population of *C. taurus* has declined by an estimated 80–90% since the 1970s (Musick *et al*. 1993, 2000). On the east coast of Australia, there are estimated to be less than 500, and possibly less than 300, individuals remaining. It has been estimated that the time to quasi-extinction for this population may be as short as 45 to 53 years (Otway *et al*. 2004). Dramatic declines have also been reported in the south-western Atlantic (Lucifora *et al*. 2002). *C. taurus* was once recorded in the Mediterranean; however, since 1980 there have been no records of this species, suggesting possible regional extinction (Fergusson *et al*. 2002). Owing to declining population trends worldwide, *C. taurus* is listed as a 'Vulnerable' species by the IUCN in its Red List of Threatened Animals (Hilton-Taylor 2000).

In South Africa, *C. taurus* has been occasionally reported from the west coast, but is more commonly found along the east coast from Cape Town to northern KwaZulu–Natal (KZN) (Bass *et al*. 1975; Smale 2002; Dicken *et al*. 2006*b*). Mature female sharks undergo a well defined biennial reproductive migration along the coast, which can be traced through the spatially and seasonally distinct phases of mating, gestating and parturition. Mating is thought to occur off the south coast of KZN from October to the end of November (Dicken *et al*. 2006*b*). Pregnant females then move northward to spend the early part of their gestation in the warmer waters of northern KZN and possibly southern Mozambique. 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; Dicken *et al*. 2006*b*), where they give birth to two pups from September to November (Smale 2002; Dicken *et al*. 2006*b*). The

 10.1071/MF06018 1323-1650/07/010127

pups are born at a total length between 95 and 120 cm (Cadenat 1956; Taniuchi 1970; Bass *et al*. 1975). The young-of-the-year and juvenile sharks remain in the geographically distinct nursery areas for their first 4–5 years of life, before joining the subadult and adult components of the population (Dicken *et al*. 2006*b*).

Although protected from commercial fishing in South Africa since 1998, bycatch in any fishery potentially poses a realistic threat to the survival of *C. taurus*. Because *C. taurus* typically inhabits shallow inshore areas, it is rarely, if ever, caught by the large-scale industrial fisheries operating on the high seas. Its near-shore distribution, however, makes it susceptible to small-scale multi-species fisheries as well as recreational fishermen, spearfishers and the bather protection nets of the Natal Sharks Board (NSB). Although the broad-scale distribution and migratory habits of *C. taurus* have been inferred for parts of its range, little is known on the fine-scale movement patterns, particularly within the nursery areas. This information is crucial in defining habitat use and evaluating the effects of commercial and recreational exploitation and anthropogenic activities on the juvenile (<1.8-m TL) and adult (>1.8-m TL) components of the population.

The present paper presents information on the spatial and temporal movement patterns of *C. taurus* juveniles and adults using tag–recapture data from both the Oceanographic Research Institute (ORI) and Port Elizabeth Museum (PEM) tagging programs. Movement patterns were used to confirm the geographical extent and seasonal utilisation of nursery areas by juvenile sharks. They were also used to investigate aspects of site fidelity and philopatric behaviour of adult sharks. This information is necessary for effective fisheries management to ensure that the South African population does not suffer the marked declines that are evident in almost all other areas of its global distribution.

Materials and methods

Study area

Two major ocean currents border the South African coast: the warm Agulhas Current, which flows southwards past the east and south-east coasts, and the cool Benguela Current, which flows northwards along the west coast. As a consequence of these two major oceanic currents, three biogeographical zones can be broadly recognised along the South African coastline based on water temperature: a cool temperate west-coast zone extending from Cape Town northwards; a warm temperate south-coast zone; and a subtropical east-coast zone from approximately east London northward (Turpie *et al*. 2000).

For the purposes of this study, the South African coastline was subdivided into 28 100-km coastal areas (Fig. 1). This scale of division was considered sufficient to identify the major trends and patterns in the spatial movement patterns of *C. taurus* juveniles and adults. Area 14 encompasses the Tsitsikamma Marine Protected Area and, consequently, no sharks were tagged or recaptured within this area.

Tagging

Different tag types, A-, B- and C-type tags, have been used to tag *C. taurus* by members of the ORI and PEM tagging programs. A- and B-type tags are Hallprint manufactured dart tags (Hallprint, Victor Harbour, SA, Australia), and consist of a monofilament vinyl streamer attached to either a plastic barb (A-type) or stainless steel pointed head (B-type). All pertinent tag information, including the tag number, return address and telephone number of the tagging program are printed on the streamer. Sharks were caught and tagged by shore and boat anglers in the NSB nets and by scientific divers underwater. Because juvenile sharks are restricted to the Eastern Cape

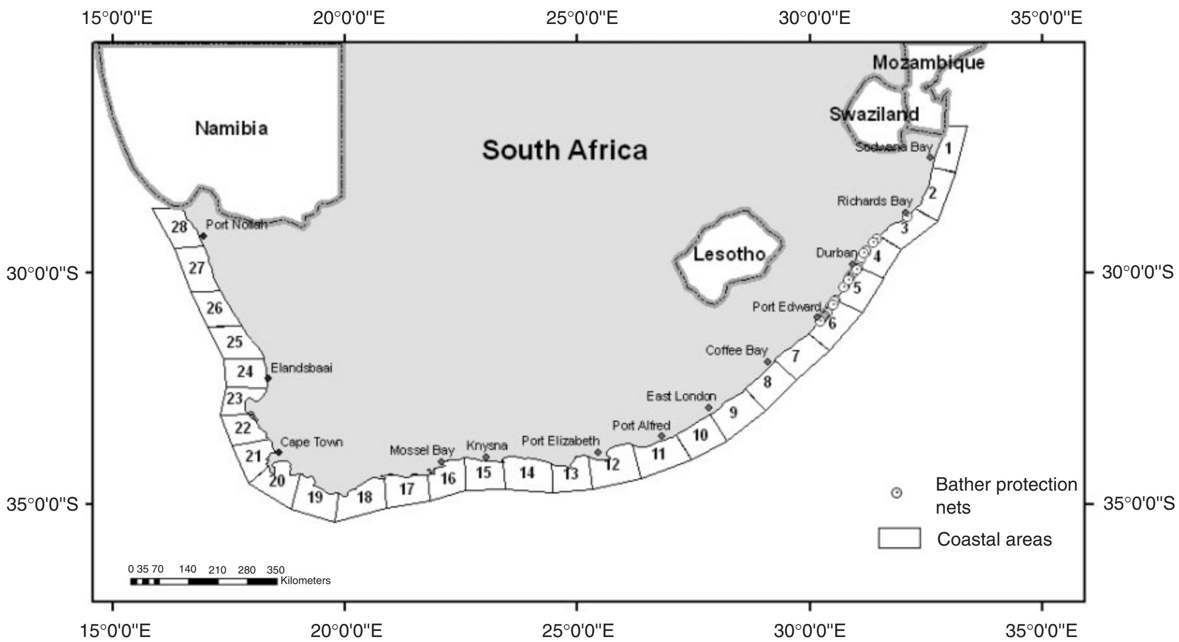

Fig. 1. Map of South Africa showing the location of the 28 100-km coastal areas used to analyse the spatial movement patterns of *Carcharias taurus* inferred from tag–recapture data.

nursery areas, only the adult component of the population is subject to catches in the NSB nets.

Fishermen and the NSB net operators applied the tags with a stainless steel tagging needle, which was used to drive the pointed head of the tag into the dorsal musculature at the base of the first dorsal fin. Once inserted, the tags were pulled gently to ensure that they were securely attached. If they had not been inserted correctly, they were reapplied. Taggers were instructed to apply the tag at an angle of $\sim 45°$ so that the streamer would stay alongside the shark while swimming in an attempt to minimise hydrostatic drag. Scientific divers tagged sharks underwater using a Hawaiian sling. C-type tags are locally manufactured (Durban, South Africa) plastic disk tags, similar in design to the Jumbo Rototag. The tag is applied with an applicator, through a hole created by a leather punch towards the base of the first dorsal fin. The tag comprises two plastic disks (a male and female component) that are placed on either side of the hole and then clipped together. All tag information was printed on the outside of the disk. The issue of this tag type to anglers was curtailed in 2001 owing to excessive biofouling growth and fin damage (Bullen and Mann 2004). Despite this fact, anglers who already possessed this tag type continued using it to tag sharks.

Taggers were asked to record the following data when tagging a shark: tag number, date, locality, sex, weight, precaudal and total length and the taggers name and address. This data was then mailed on a pre-addressed data card back to the ORI program or emailed or faxed to the PEM program, depending on which organisation the angler was affiliated with. Unfortunately, many of the anglers in the ORI program failed to report all of the requested information, which limited data analysis. To improve the reporting rate of tag recoveries, this study was advertised in newspaper articles, posters and radio interviews. It also featured in the 'Tagging News', a tag-and-release information pamphlet distributed to members of the ORI tagging program. A series of workshops were also held at fishing clubs throughout the country, encouraging fishermen to record and report any tag–recaptures.

Movement patterns

Area of recapture, minimum travel distance (MTD) and the number of days at liberty were determined for all shark recaptures. MTD was defined as the distance travelled between the tagging and recapture locality. Localities were defined as the distance in kilometres along the coast from the Mozambique/South African border according to Bullen and Mann (2004). Because of the generally north–south orientation of the South African coastline, movements from the tagging site included strong northward or southward directional components. Northward movements greater than 20 km for juvenile sharks and 50 km for adult sharks were defined as positive displacements, and southward movements of the same magnitudes were defined as negative displacements.

Few juvenile sharks were tagged or recaptured outside of the summer fishing season (September to May). As a result, the data were inadequate to investigate seasonal movement patterns. An analysis of competitive shore angling catches (Dicken *et al.* 2006*b*) suggested that juvenile sharks exhibited site fidelity to summer aggregation sites. To test this hypothesis, a 90-day season was chosen, such that recaptures made within 0 to 45 days of tagging, or within ± 40 days of a tagging anniversary, were classed as 'in season' and recaptures made outside these periods were classed as 'out of season'. A two-sample *t*-test, assuming unequal variances, was then used to compare the distances travelled between the seasons. The test was repeated using a shorter 60-day season. A two-sample *t*-test was also used to compare the average MTD between juvenile male and female sharks.

To test the hypothesis that mature female sharks undergo a biennial breeding migration, a 360-day season was selected. Recaptures made within 0 to 180 days of tagging or within ± 180 days of a tagging anniversary were classed as 'in season' and recaptures outside these periods were defned as 'out of season'. Tests using shorter season lengths were not possible because of the small number of recaptures. It was not possible to compare the movement patterns between adult male and female sharks because of the low number of male recaptures.

Results

From 1984 to 2004, 1107 *C. taurus* juveniles and 2364 *C. taurus* adults were tagged and released. In total, 125 juvenile (11.3%) and 177 adult (7.5%) sharks were recaptured. The time at liberty for recaptured juvenile sharks ranged from 1 day to 5.2 years, with an average of 372 days (95% CI = 350–394 days). The time at liberty for adult sharks ranged from 1 day to 10.8 years, with an average of 929 days (95% CI = 791–1067 days).

C. taurus juveniles were tagged and released between coastal Areas 6 to 20. The majority (86.0%) were tagged between Areas 10 and 13. Adult sharks were tagged along the entire coast from Areas 1 to 20. All movements greater than 20 km made by juvenile tagged sharks are shown in Fig. 2. Of the 125 sharks recaptured, 74 (59.0%) were re-caught within 5 km of the original tagging locality and 115 (92.0%) were re-caught within 50 km. The average distance travelled was 18.7 km (95% CI = 10.8–26.6 km). Only eight recaptured juvenile sharks had moved to a different coastal area, involving a movement of over 100 km. Four of these recaptures were to the north of the original tagging locality and four were to the south. The greatest movement observed for a recaptured juvenile was 268 km. The shark had moved from the 'Dredges' in Area 10 to Port St. Johns in Area 7 and was at liberty for 269 days. Because of the restricted movement patterns exhibited by juvenile sharks, the majority of recaptures (83%) were made between Areas 10 to 13. Surprisingly, no recaptures were reported in Areas 15 or 16, despite the fact that 24 juvenile sharks had been tagged and released within this 200-km stretch of coast.

The mean distances travelled by recaptured *C. taurus* juveniles classified by season and sex are given in Table 1. A two-sample *t*-test indicated there was no significant difference between the distance travelled 'in season' and 'out of season' for either a 60- ($P = 0.80$) or 90-day season ($P = 0.85$). There was also no significant difference between the distance travelled between male and female sharks ($P = 0.95$). Despite these results, plots of MTD against days at liberty (Fig. 3) suggest that *C. taurus* juveniles may make cyclic annual movements to and from summer nursery areas and/or exhibit some degree of seasonal site fidelity.

The maximum rate of travel recorded was 5.6 km day^{-1} for an unsexed juvenile shark. The shark travelled 168 km in 30 days

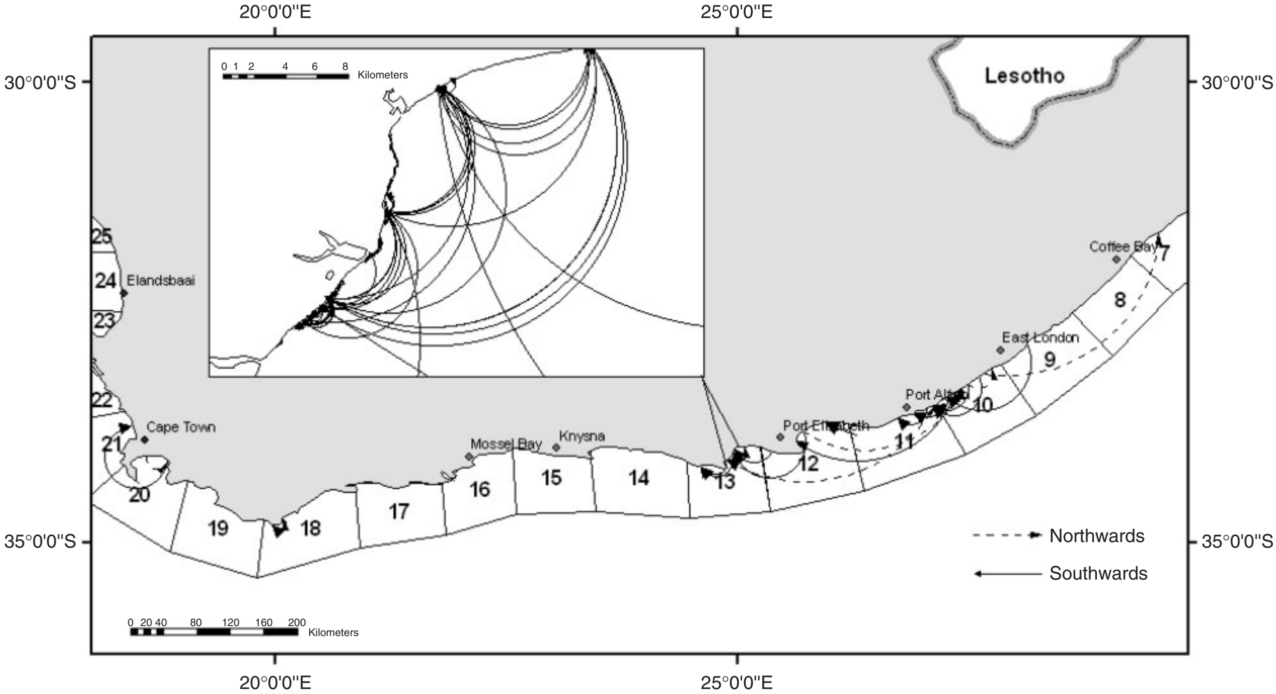

Fig. 2. Movements (>20 km) of *Carcharias taurus* juveniles from tag–recapture data 1984 to 2004. The insert, a 30-km section of Area 13, shows the fine-scale movement of the majority of juvenile recaptures.

Table 1. Minimum travel distance of recaptured juvenile *Carcharias taurus*, shown as mean ± s.e. classified by season and sex
Sample size is shown in parentheses

60-days season		90-days season		Sex	
In-season	Out-of-season	In-season	Out-of-season	Male	Female
19.9 ± 8.2 (41)	18.2 ± 4.5 (84)	17.6 ± 6.3 (54)	19.6 ± 5.2 (71)	18 ± 9.5 (30)	17.3 ± 6.4 (51)

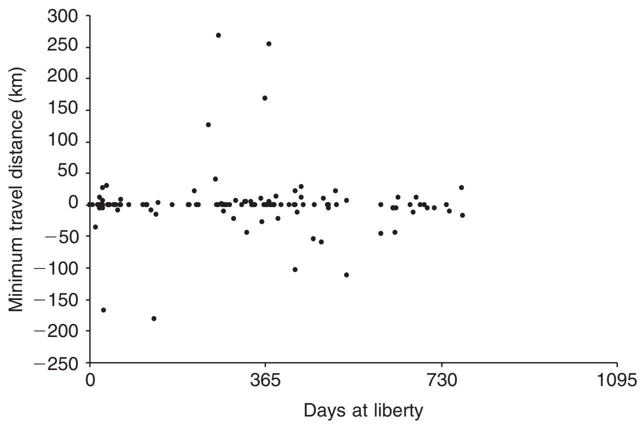

Fig. 3. Relationship between minimum travel distance and days at liberty for recaptured *Carcharias taurus* juveniles. Positive and negative values reflect a northward or southward movement respectively.

from the Strand in Area 20 to Bontkop in Area 21. This was the only *C. taurus* specimen (tagged or untagged) to be caught on the west coast of South Africa and this exceptionally high displacement velocity should be viewed with caution. The next two fastest rates of travel were 2.7 km day^{-1} and 1.4 km day^{-1}. All other recaptures, 122 (96%), had travelled at a rate below 1.0 km day^{-1}. Rates of travel are minimal, since the juvenile sharks may have travelled further than the MTD between the tagging and recapture sites.

All movements greater than 50 km made by adult tagged sharks are shown in Fig. 4. Of the 177 sharks recaptured, 72 (40.7%) were re-caught within 100 km of the original tagging locality, 136 (76.8%) within 500 km and 152 (85.9%) within 1000 km. The average distance travelled was 342 km (95% CI = 275–409 km). The greatest movement observed for a recaptured adult was 1897 km. This was a female shark that had moved from 'raggy reef' in Area 2 to the Strand in Area 20, and was at liberty for 1377 days. Adult sharks, particularly females, are highly migratory. Female sharks move northwards to breed and gestate and southwards to pup. As a result, sharks recaptured after a time at liberty greater than 12 months may have travelled a greater distance than their recapture site.

The majority (56.5%, $n = 100$) of recaptured sharks were female and only four sharks were males (2.3%). All other recaptures (41.3%, $n = 73$) were unsexed. The distances that recaptured adult sharks moved displayed no apparent cyclic movement pattern (Fig. 5). A weak biennial movement pattern

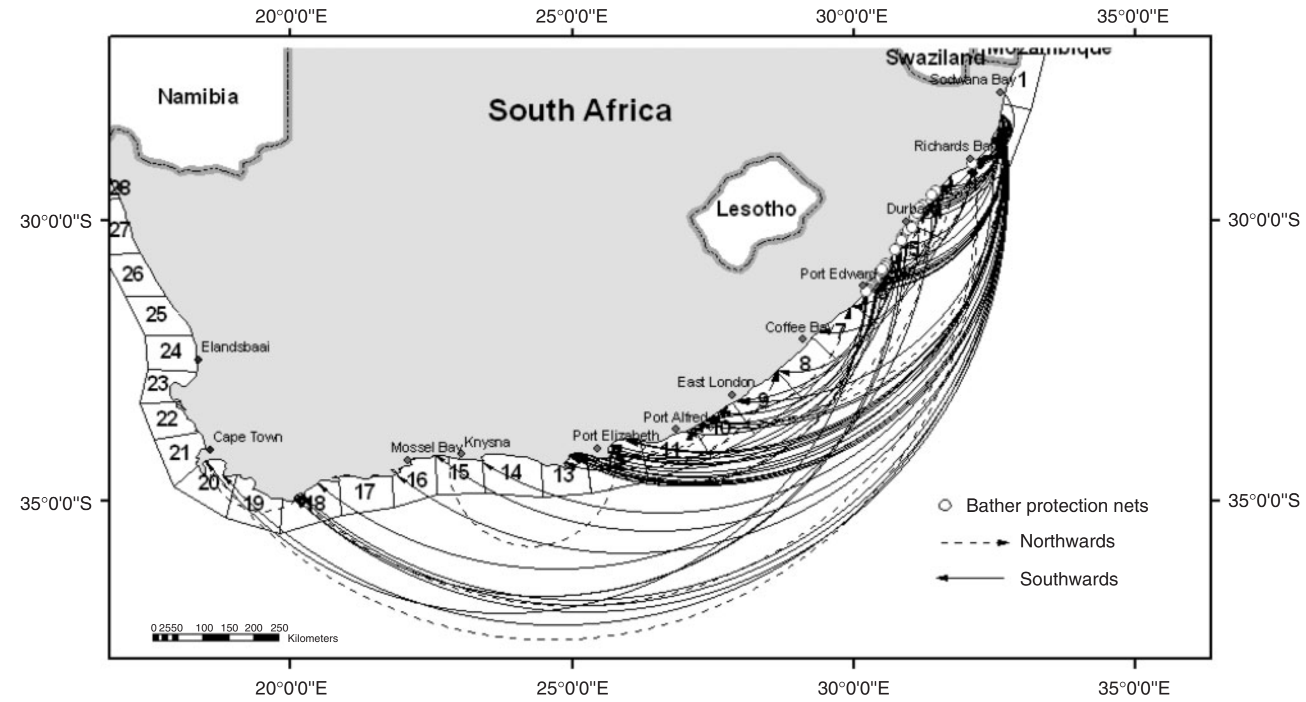

Fig. 4. Movements (>50 km) of *Carcharias taurus* adults from tag–recapture data 1984 to 2004.

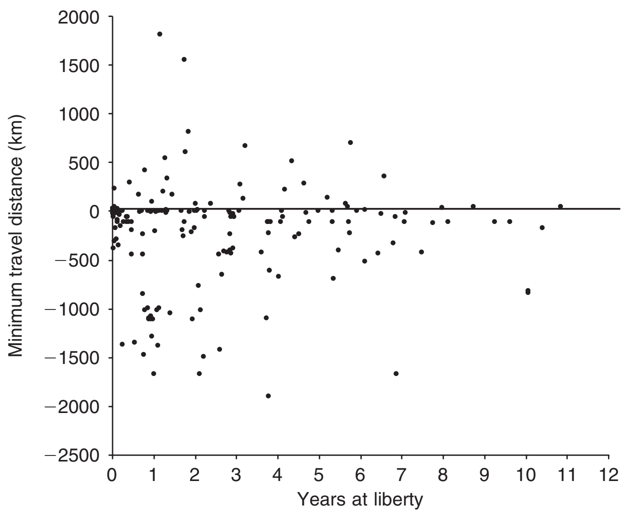

Fig. 5. Relationship between minimum travel distance and years at liberty for recaptured *Carcharias taurus* adults. Positive and negative values reflect a northward or southward movement respectively.

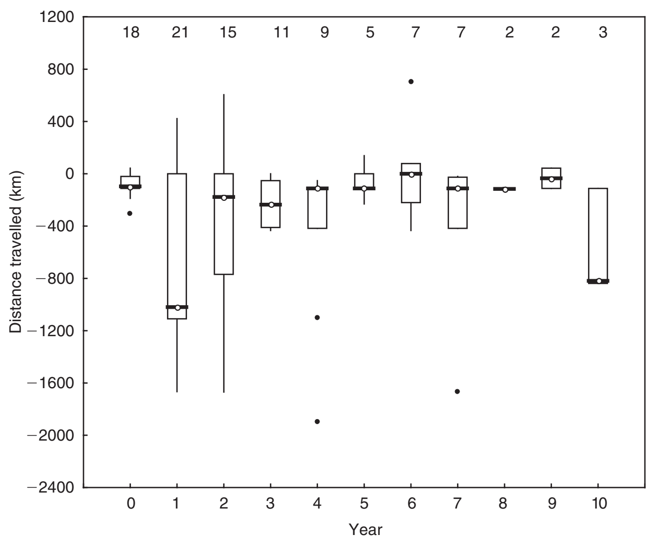

Fig. 6. Box plots of minimum travel distance against time at liberty for mature *Carcharias taurus* females. Boxes illustrate the interquartile range for minimum travel distance with the median distance represented by the solid bar and open circle. Whiskers are drawn to the shortest distance travelled, not beyond 1.5 times the interquartile range. Solid points indicate the maximum distance travelled. Numbers show sample sizes larger than 1.

was observed, however, when distances were correlated with times at liberty for only recaptured female sharks (Fig. 6). The mean distance that female sharks were recaptured from their original tagging locality in-season and out-of-season for a 360-day season was 288.5 km ($n = 54$) and 487.6 km ($n = 46$) respectively. A two-sample *t*-test indicated that this seasonal difference was marginally significant ($P = 0.042$).

In total, 71 gestating sharks were tagged in Areas 1 and 2. Recaptures of these sharks within a 12-month period indicated their movement southwards to pup in the nursery Areas 9 to 20. The majority of these sharks were recaptured in Areas 10 to 13 (66.6%) compared with Areas 14 to 20 (30.4%). The average rate at which pregnant sharks moved south was 2.6 km day^{-1} (95% CI = 2.04–3.16 km day^{-1}). One recaptured female, however, travelled 383 km in 13 days, from Cape Vidal in Area 2 to Uvongo in Area 6, at rate of 29.5 km day^{-1}. In total, 37 recaptured sharks had moved northwards from their original tagging site. Only one female shark, however, was recaptured within a time at liberty of less than 12 months. This shark had moved 422 km from Gamtoos in Area 13, to Mazeppa Bay in Area 8 at rate of 1.45 km day^{-1}.

Discussion

The overall recapture rate for *C. taurus* (8.7%) was higher than for the majority (55%) of the 52 shark tagging studies reviewed by Kohler and Turner (2001), which reported return rates of less than 5%. The return rate for *C. taurus* specimens tagged in the Atlantic by the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program (CSTP) was only 5.5% (Kohler *et al*. 1998). Recapture rates, however, are influenced by a variety of factors, which can limit the validity of the inferences that may be drawn from these data. Recapture rates are influenced by the life-history characteristics of the species. *C. taurus* is an inshore species of shark that is readily caught by recreational anglers. Some species occur farther offshore in deeper waters and are not present in areas during the primary fishing season, or are not readily caught. *C. taurus* juveniles remain in nursery areas for extended periods of time. They are less migratory than adult sharks and are consequently more prone to capture and recapture. This may be a possible explanation for their higher recapture rate (11.3%) compared with adult sharks (7.5%).

Recapture information indicated that the movements of *C. taurus* juveniles were limited. Few sharks, less than 8%, had moved more than 50 km, suggesting that little mixing may occur between juvenile sharks inhabiting different areas within the nursery grounds. Recreational shore anglers target *C. taurus* throughout the geographical range of its nursery area (Dicken *et al*. 2006*a*). Fishing effort is not constant throughout the year, however, and is limited to the summer months (September to May) due to unfavourable weather conditions in the winter. This, combined with few offshore releases by recreational and commercial ski-boat fishers, severely restricts the analysis of movement patterns. As a result, the observed movements of recaptured juveniles may not be true, but a reflection of variable fishing effort.

Annual recaptures of juvenile sharks provided weak evidence of a cyclic annual movement to and from summer nursery areas. The proximity of recaptures to the original release site in the same months, 1 year, 2 years or 3 years after tagging suggests that juvenile sharks may exhibit natal nursery homing. This behaviour has also been observed for juvenile sandbar sharks, *Carcharhinus plumbeus*, (Merson and Pratt 2001), juvenile blacktip sharks, *Carcharhinus limbatus*, and juvenile blacknose sharks, *Carcharhinus acronotus* (Hueter *et al*. 2004). For philopatric species, the specific areas they return to must confer some form of competitive advantage. Focussed studies on shark nursery areas (Branstetter 1990; Castro 1993; Merson and Pratt 2001; Heupel and Hueter 2002) suggest that predator avoidance and prey abundance are the critical factors influencing habitat choice. The greater number of pregnant female recaptures and the higher abundance of juvenile sharks in the nursery Areas 10 to 13 compared with 14 to 20, suggests that water temperature also plays an important role.

In temperate zones, cold winter temperatures force YOY (young of the year) and juvenile sharks into deeper offshore or warmer water (Castro 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 (Dicken *et al*. 2006*b*). The location of the winter nursery areas remains uncertain. During the winter, it is possible that juvenile sharks move into deeper offshore water. Alternately, they may move northwards towards the northern part of the Eastern Cape and southern KwaZulu–Natal.

Movements of *C. taurus* adults were much more extensive than the juveniles. Movements were associated primarily with reproduction, with one pregnant female travelling 1897 km from the gestating areas in northern KwaZulu–Natal to the parturition areas in the Eastern Cape to pup. The maximum distance travelled by *C. taurus* specimens tagged in the Atlantic by the NMFS CSTP was 1187 km (Kohler *et al*. 1998). The movement of pregnant females south along the South African coast to pup is rapid. The fastest movement observed was 29.5 km day^{-1}. This shark had been at liberty for 13 days and had travelled 383 km. Stevens *et al*. (2000) recorded a similar maximum rate of travel (25 km day^{-1}) for *Carcharhinus tilstoni*, tagged off northern Australia. Tagging studies in New Zealand have reported maximum rates of travel of 21 km day^{-1} for *Mustelus lenticulatus* (Francis 1989) and 23 km day^{-1} for *Galeorhinus galeus* (Hurst *et al*. 1999). In contrast, the maximum rate of travel for *C. taurus* specimens tagged in the Atlantic was only 5.4 km day^{-1} (Kohler *et al*. 1998).

The majority of female sharks in gestation (66.6%) tagged in Areas 1 and 2 were recaptured within the nursery Areas 9 to 13, compared with Areas 14 to 20, during the pupping season between September and February. The fishing effort within these two regions was similar, 8477 and 7789 fishing days year^{-1} respectively (Dicken *et al*. 2006*a*). Assuming that the non-reporting rate is the same in both regions, then the observed movement patterns are probably unbiased and not a reflection of variable fishing effort. This spatial recapture pattern was not surprising, given that the majority (94.2%) of YOY sharks collected in a survey of competitive shore anglers were recorded within Areas 10 to 13 (Dicken *et al*. 2006*a*).

Recaptures of female sharks closer to their original tagging site in alternate years provided weak evidence of a biennial reproductive cycle. Evidence for a 2-year reproductive cycle with a resting stage in between has also been observed for *C. taurus* populations in the North Atlantic (Branstetter and Musick 1994) and the South Atlantic (Lucifora *et al*. 2002). Successful reproduction in captivity over the last 10 years also supports a 2-year reproductive cycle hypothesis (Henningsen *et al*. 2004). Few adult male sharks were recaptured. As a result, their movement patterns in relation to the female breeding migration and their whereabouts outside of the breeding season remains unclear.

Recaptures of gestating sharks in the same areas that they were originally tagged, in the same months, every other year suggests that female sharks may be philopatric to their gestating areas in northern KZN. Concern has been expressed in recent years that increased diver pressure may be impacting the number of sharks seen in these areas. Such is the concern, that all SCUBA diving and spearfishing was temporarily suspended at one particular reef (Quatermile reef) in December 2005, pending the arrival and acclimation of the sharks (K. Sink, South African Institute Aquatic Biodiversity, personal communication).

There were an insufficient number of recaptures to investigate the possibility of philopatry to the mating or pupping areas. A female shark tagged as a juvenile in Area 10 was recaptured 8 years later as an adult, only 34 km from the originally tagging site. Unfortunately, there were no data on the reproductive state of the female, but it is possible that this shark had returned to its natal nursery area to pup. In other shark species, nuclear and mitochondrial DNA markers have been used to indicate strong to moderate signals of natal philopatry for the lemon shark, *N. brevirostris* (Feldheim *et al*. 2002) and the blacktip shark (Keeney *et al*. 2003).

The effects of over-fishing, anthropogenic activities and environmental perturbations will have a more dramatic effect on populations whose individuals are philopatric and depend on a specific locality, compared with those that are part of a larger homogeneous stock. For philopatric species, the specific areas they return to must confer some form of competitive advantage. Why some reefs are chosen over others, despite similar physical characteristics, at this stage remains unclear. If suitable habitat is limited, the identification of aggregation sites, particularly those associated with the reproductive activities of mating, pupping and gestation, are essential for effective fisheries management to ensure the conservation of *C. taurus* in South Africa.

Acknowledgements

This work would not have been possible without the cooperation of volunteer anglers from both the Oceanographic Research Institute and Port Elizabeth Museum cooperative tagging programs. In particular we would like to thank R. King, T. Herbst, K. Lennox, M. Spies, M. Peterson, M. Potgieter, A. Hayward, T. Radloff and T. Nazgoole. Special thanks to R. Martin and R. Smit for the development of the Port Elizabeth Museum cooperative shark-tagging program. We thank the Port Elizabeth Museum Director and staff for their support and infrastructure, the National Research Foundation (NRF) and Marine and Coastal Management (MCM) for funding and Bayworld Centre for Research and Education for administering the study. We gratefully acknowledge the data supplied by both the Natal Sharks Board and the Oceanographic Research Institute.

References

Bass, A. J., D'Aubrey, J. D., and Kistnasamy, N. (1975). Sharks of the east coast of southern Africa IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Investigative report 39. Oceanographic Research Institute, Durban, South Africa.

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., and Doherty, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**, 389–392. doi:10.1126/SCIENCE.1079777

Branstetter, S. (1990). Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. NOAA Technical Report 90. pp. 17–28. National Marine Fisheries Service, Washington, DC.

Branstetter, S., and Musick, J. A. (1994). Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. *Transactions of the American Fisheries Society* **123**, 242–254. doi:10.1577/1548-8659(1994)123<0242:AAGEFT>2.3.CO;2

Bullen, E. M., and Mann, B. Q. (2004). Sedgwicks/ORI/WWF tagging programme: Spotted ragged-tooth shark (*Carcharias taurus*). Report 2004.1. Oceanographic Research Institute, Durban, South Africa.

Cadenat, J. (1956). Note d'ichtyologie ouest-africaine. XIV. Remarques biologiques sur le Requin-sable Carcharias (Odontaspis) taurus Rafinesque 1810. *Bulletin de l'institute Français de l'Afrique Noire* **18**, 1249–1256.

Castro, J. I. (1993). The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes* **38**, 37–48. doi:10.1007/BF00842902

Compagno, L. J. V. (2001). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Vol. 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). (Food and Agriculture Organization of the United Nations: Rome.)

Dicken, M. L., Smale, M. J., and Booth, A. J. (2006*a*). Shark fishing effort and catch of the raggedtooth shark (Carcharias taurus) in the South African competitive shore angling fishery. *African Journal of Marine Science* **28**(3), 589–601.

Dicken, M. L., Smale, M. J., and Booth, A. J. (2006*b*). Spatial and seasonal distribution patterns of the raggedtooth shark (*Carcharias taurus*) along the coast of South Africa. *African Journal of Marine Science* **28**(3), 603–616.

Feldheim, K. A., Gruber, S. H., and Ashley, M. V. (2002). The breeding biology of lemon sharks at a tropical nursery lagoon. *Proceedings of the Royal Society of Biological Science, London, Series B* **269**, 1655–1661.

Fergusson, I. K., Vacchi, M., and Serena, F. (2002). Note on the declining status of the sandtiger shark *Carcharias taurus* in the Mediterranean sea. In 'Proceedings of the 4th meeting of the European Elasmobranch Association, 27–30 November 2002, Livorno, Italy'. (Eds M. Vacchi, G. La Mesa, F. Serena and B. Seret.) pp. 73–76. (Association Societe Francaise d'Ichtyologie (SFI): Paris.)

Francis, M. P. (1989). Exploitation rates of rig (*Mustelus lenticulatus*) around the South Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **23**, 239–245.

Henningsen, A. D., Smale, M. J., Gordon, I., Garner, R., Marin-Osorno, R., and Kinnunen, N. (2004). Captive breeding and sexual conflict in elasmobranchs. In 'Elasmobranch Husbandry Manual: Proceedings of the First International Elasmobranch Husbandry Symposium 2001'. (Eds M. Smith, D. Warmolts, D. Thorney and R. Heuter.) pp. 239–250. (Ohio Biological Survey: Columbus, OH.)

Heupel, M. R., and Hueter, R. E. (2002). Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Marine and Freshwater Research* **53**, 543–550. doi:10.1071/MF01132

Hilton-Taylor, C. (2000) – (Compiler) 2000. IUCN red list of threatened species. The IUCN Species Survival Commission, Gland, Switzerland.

Hueter, R. E., Heupel, M. R., Heist, E. J., and Keeney, D. B. (2004). Evidence of philopatry in sharks and implications for the management of shark fisheries. *e-Journal of Northwest Atlantic Fishery Science* V35, article 7.

Hurst, R. J., Bagley, N. W., McGregor, G. A., and Francis, M. P. (1999). Movement of the New Zealand school shark, *Galeorhinus galeus*, from tag returns. *New Zealand Journal of Marine and Freshwater Research* **33**, 29–48.

Keeney, D. B., Heupel, M. R., Hueter, R. E., and Heist, E. J. (2003). Genetic heterogeneity among blacktip shark, *Carcharhinus limbatus*, continental nurseries along the U.S. Atlantic and Gulf of Mexico. *Marine Biology* **143**, 1039–1046. doi:10.1007/S00227-003-1166-9

Kohler, N. E., Casey, J. G., and Turner, P. A. (1998). NMFS cooperative shark tagging program, 1962–1993: an atlas of shark tag and recapture data. *Marine Fisheries Review* **60**, 1–87.

Kohler, N. E., and Turner, P. A. (2001). Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes* **60**, 191–223. doi:10.1023/A:1007679303082

Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne.)

Lucifora, L. O., Menni, R. C., and Escalante, A. H. (2002). Reproductive ecology and abundance of the sand tiger shark, *Carcharius taurus*, from the southwestern Atlantic. *ICES Journal of Marine Science* **59**, 553–561. doi:10.1006/JMSC.2002.1183

Merson, R. R., and Pratt, H. L. (2001). Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. *Environmental Biology of Fishes* **61**, 13–24. doi:10.1023/A:1011017109776

Musick, J. A., Branstetter, S., and Colvocoresses, J. A. (1993). Trends in shark abundance from 1974–1991 for the Chesapeake Bight region of the U.S. mid Atlantic coast. NOAA Technical Report 115. National Marine Fisheries Service, Washington, DC.

Musick, J. A., Harbin, M. M., Berkeley, G. H., Burgess, G. H., Eklund, A. M., *et al.* (2000). Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of salmonids). *Fisheries* **25**(11), 6–30. doi:10.1577/1548-8446(2000)025< 0006:MEADFS>2.0.CO;2

Otway, N. M., Bradshaw, C. J. A., and Harcourt, R. G. (2004). Estimating the rate of quasi-extinction of the Australian grey nurse shark (*Carcharias taurus*) population using deterministic age- and stage classified models. *Biological Conservation* **119**, 341–350. doi:10.1016/J.BIOCON.2003.11.017

Pollard, D. A., Smith Lincoln, M. P., and Smith, A. K. (1996). The biology and conservation status of the grey nurse shark (*Carcharias taurus* Rafinesque 1810) in New South Wales, Australia. *Aquatic Conservation: Marine & Freshwater Ecosystems* **6**, 1–20. doi:10.1002/(SICI)1099-0755(199603)6:1<1::AID-AQC177>3.0.CO;2-#

Smale, M. J. (2002). Occurrence of *Carcharias taurus* in nursery areas of the Eastern and Western Cape, South Africa. *Marine and Freshwater Research* **53**, 551–556. doi:10.1071/MF01129

Smith, S. E., Au, D. W., and Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**, 663–678. doi:10.1071/MF97135

Stevens, J. D., West, G. J., and McLoughlin, K. J. (2000). Movements, recapture patterns, and factors affecting the return rate of carcharhinid and other sharks tagged off northern Australia. *Marine and Freshwater Research* **51**, 127–141. doi:10.1071/MF98158

Taniuchi, T. (1970). Variation in the teeth of the sand tiger shark, *Odontaspis taurus* (Rafinesque) taken from the East China Sea. *Japanese Journal of Ichthyology* **17**(1), 37–44.

Turpie, J. K., Beckley, L. E., and Katua, S. M. (2000). Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biological Conservation* **92**, 59–72. doi:10.1016/S0006-3207(99)00063-4

Wallett, T. S. (1973). Analysis of shark meshing returns off the Natal coast. M.S. Thesis, University of Natal, South Africa.

Manuscript received 30 January 2006, accepted 23 October 2006