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Fine scale movements and activity areas of white sharks (*Carcharodon carcharias*) in Mossel Bay, South Africa

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Abstract Previous work on white sharks indicate the species show seasonally limited movement patters, at certain aggregation sites small areas may play vital roles in the life history of a large amount of the population. Acoustic telemetry was used to estimate habitat use of white sharks, *Carcharodon carcharias,* while aggregating at Mossel Bay, South Africa. Total range of all shark tracks combined accumulated 782 h and covered an area of 93.5 km^2 however, within this range, sharks were found to highly utilise a core habitat (50 % Kernel, K50) of just 1.05 km^2 over a reef system adjacent to a river mouth. Individual tracks revealed additional core habitats, some of which were previously undocumented and one adjacent to a commercial harbor. Much was found to be dependent on the size of the shark, with larger sharks (>400 cm) occupying smaller activity areas than subadult (300–399 cm) and juvenile (<300 cm) conspecifics, while Index of Reuse (IOR) and Index of Shared Space (IOSS) were both found to increase with shark size. Such results provide evidence that larger white sharks are more selective in habitat use, which indicates they have greater experience within aggregation sites. Furthermore, the focused nature of foraging means spatially restricted management strategies would offer a powerful tool to aid enforcement of current protective legislation for the white shark in similar environments of limited resources and capacity.

Keywords Acoustic telemetry · Manual tracking · Home range · Kernel analysis · Habitat use · White sharks

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Introduction

The white shark *Carcharodon carcharias* (Linnaeus, 1758) is globally threatened and has been listed under Appendix II of the Convention on International Trade in Endangered Species (CITES) and the World Conservation Union (IUCN) (Fergusson et al. 2005). It is of particular interest due to their tendency to aggregate close to shore and the perceived danger they represent to humans (Kock et al. 2012). The species is protected by both local and international legislations (Compagno 1991; Dulvy et al. 2008). However, widespread public support for this legislation has been difficult to generate, often due to fear of shark attacks (Peschak 2006). The species can make large-scale oceanic migrations whilst displaying patterns of site fidelity, often linking aggregation sites, occupying previously unforeseen areas and entering waters which may not fall under their protection (Bonfil et al. 2005; Bruce et al. 2006; Weng et al. 2007; Nasby-Lucas et al. 2009; Jorgensen et al. 2010; Duffy et al. 2012; Jorgensen et al. 2012). Despite the legislations, trade in white shark products has continued; particularly of those fished offshore in international waters by the shark finning industry (Shivji et al. 2005). Other threats include incidental by-catch in commercial fisheries and mortalities in shark nets or drumlines set at popular swimming beaches in South Africa, Australia and Singapore (Compagno et al. 1997; Baum et al. 2003; Dudley and Simpfendorfer 2006). Along with other species, white sharks have now gained commercial value in tourist trade, since the advent of shark diving in the late 1980's and early 1990's (Gallagher and Hammerschlag 2011).

Within South Africa, aggregation sites are often coastal and associated with pinniped colonies (Compagno et al. 1997). Such aggregations are particularly well documented in the South Western Cape at three locations; Seal Island, False Bay (Kock and Johnson 2006); Dyer Island, Gansbaai (Johnson 2003; Wcisel et al. 2010) and Seal Island, Mossel Bay (Johnson et al. 2009). Movements of individuals between these sites and others along the coastline have been confirmed with acoustic and satellite telemetry as well as visual identification (Bonfil et al. 2005; Johnson and Kock 2006).

In order to protect a species we must first understand their movements and habitat use patterns (Simpfendorfer et al. 2010). In the marine environment acoustic telemetry systems have lead to a better understanding of sharks' role as apex predators in ecosystems (Sundström et al. 2001; Voegeli et al. 2001). Such studies allow for a better understanding of concepts such as home range (the day to day, spatial extent or outside boundary which an animal utilises Burt 1943; McNab 1963) to be explored and have often formed the basis for assessing the boundaries and potential effectiveness of marine protected areas (Heupel et al. 2004; Bruce et al. 2005; Meyer and Holland 2005; Hearn et al. 2010). These protected areas are considered vital tools for science based protection of marine species (Heupel and Simfendorfer 2005; Simpfendorfer et al. 2010). Active tracking has the advantage over passive monitoring in that it can reveal fine scale movement patterns, particularly in areas which are frequented by an individual for long periods of time (Johnson et al. 2009; McCord and Lamberth 2009). It also produces tracks of a finer scale than satellite telemetry, which is limited by the water column itself (Teo et al. 2004; Jewell et al. 2011). The obvious disadvantage with active tracking is the long hours involved in collecting data and the limitation of weather conditions; as such finding a study site with some protection from the ocean is often preferable (Johnson et al. 2009).

Previous studies indicate that white sharks may limit their activity areas while foraging on pinnipeds; Goldman and Anderson (1999) and Klimley et al. (2001) documented foraging of white sharks at the Farallon Islands over mulit-day periods, whilst Johnson et al. (2009) tracked tagged white sharks for several months in Mossel Bay. In a separate study Johnson (in prep) found white sharks year round in Mossel Bay and over 40 % were found to be seasonal residents, being detected by an acoustic array at least 50 % of days during a study of the seven month high season. Such studies used Rate of Movement (ROM) Swimming Linearity (LI) to assess movement patterns (Goldman and Anderson 1999; Sundström et al. 2001) and we further examine habitat use with home range analysis (Kernel and Minimum Convex Polygon; Silverman 1986). We define the activity areas projected as at least temporary or seasonal home ranges as many of the individuals have been documented to return to Mossel Bay over many years (Johnson unpubl. data), however it is important to note that during its entire life history a white shark may roam many thousands of km spanning entire oceans.

We report on the seasonal home range size and overlap of acoustically tagged and manually tracked white sharks utilising Mossel Bay, South Africa. We further determine whether home range size and overlap is independent of shark size (total length). Already established as an important habitat for this protected and vulnerable species, we examine if a marine protected area in Mossel Bay, and similar systems, could be a viable and effective tool to aid the survival of white sharks.

Materials and methods

Study site

Mossel Bay lies approximately 400 km to the east of Cape Town on the Indian Ocean side of South Africa's Western Cape (Fig. 1; S′34°10, E′22°10). The bay provides an ideal study site for acoustic telemetry surveys as it is partially protected from the winter prevailing winds from the west and south west by the Cape St. Blaize peninsula, and fully protected to the north and east by the curvature of the bay. The bay is home to a moderate sized colony of Cape fur seals *Arctocephalus pusillus pusillus* (Schreber 1775) of *circa*, 4500–5000 individuals (excluding pups of the year), which reside on Seal Island (Kirkman pers. comm.). There are three river mouths within the bay (Hartenbos, Kleinbrak and Grootbrak), each with reef systems adjacent to them.

Acoustic telemetry

All relevant permit and ethics approval were obtained prior to initial tagging from Marine and Coastal Management (MCM now operating under Oceans and Coasts) and University of Pretoria Animal Use and Care Committee. A total of 13 sharks were tagged with acoustic transmitters and tracked by research vessels in Mossel Bay between June 2005 and October 2008 (Table 1). Sharks were attracted to a research vessel with the use of bait and chum in order to be tagged externally while free swimming (as described in Johnson et al. 2009). Body markings and any other individual traits such as dorsal fin ID and shark total length (TL) were recorded to recognise each shark throughout the study. Total length was estimated by comparison to known dimensions of research vessels as sharks swam close. Sharks were tagged with VEMCO V16 frequency-specific continuous transmitters (pinging rate every 1000–2000 ms), with the use of a tagging pole. These sharks were then actively tracked by a boat-mounted hydrophone connected to a VEMCO VR60 (GWS's 1–3) or VEMCO VR100 (GWS's 4–13) acoustic receiver. Every 10 min, the tracking boat would position itself 30–40 m (equivalent to signal strength of about 70 dB) from the shark to approximate the shark's position in comparison to the onboard GPS's position. The vessel would not try to follow the shark closer than 20–30 m (*circa* 80 dB) to minimise any potential interaction between the shark and the tracking vessel. Time and position of the shark were recorded manually every 10 min, while the VR100 recorded boat's GPS positions continuously.

When conditions permitted, sharks were continuously tracked for a minimum of 24 h. Crew changes involved a second research vessel in order to minimise disruption to the continuity of the track. When a second vessel was unavailable for crew change, the research vessel would dock in the harbor, which led to

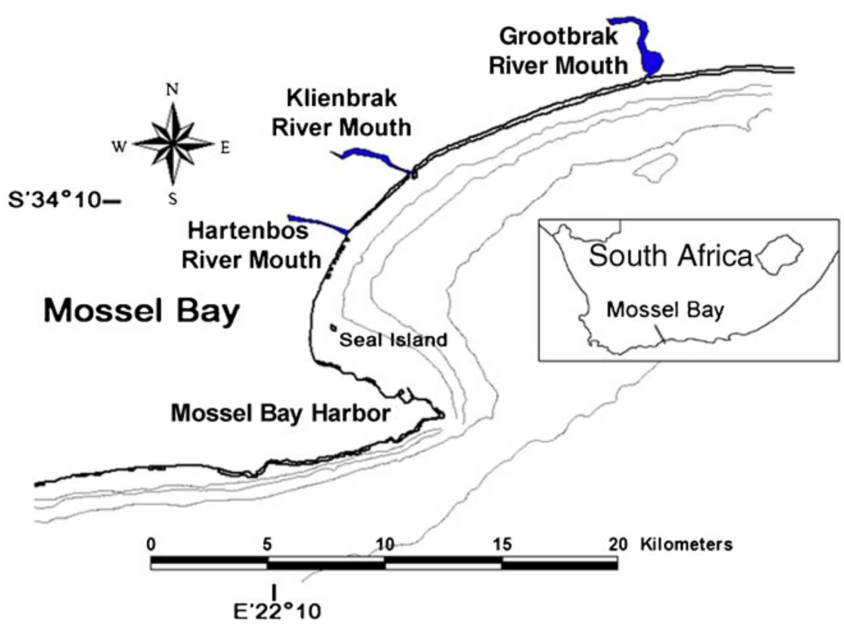


Fig. 1 Mossel Bay, South Africa study site

Table 1 Individual shark tagging details, tracks and analysis; a total of 13 sharks were tagged with tracking efforts from 1 h to 337 h, tracks 37 and 38 were measured from detections from an anchored vessel rather than active tracking and as such no further analysis has been used

Shark ID	TL	Sex	Track	Tag Location	Start date	Duration (hr)	MCP (km^2)	Kernel		Distance (km)	IOR	Linearity (*r*)
								95 % (km^2)	50 % (km^2)			
GWS-01			1	Hartenbos	08-Jul-05	10	1.7	2.18	0.48	22.20	–	0.032
	420	F	2		09-Jul-05	9	0.3	0.16	0.03	8.30	0.14	0.057
			3		10-Jul-05	9	0.1	0.10	0.02	7.00	0.38	0.126
			4		12-Jul-05	24	5.0	3.71	0.56	45.10	0.05	0.043
			5		18-Jul-05	17	0.4	0.36	0.05	22.6	0.00	0.054
			6		26-Jul-05	78	3.9	0.93	0.19	89.50	0.58	0.014
			7		16-Aug-05	103	4.6	1.14	0.21	160.00	0.53	0.006
			8		08-Sep-05	4	1.2	2.80	0.38	8.50	0.47	0.152
			9		07-Oct-05	11	2.7	3.43	0.31	20.50	0.77	0.071
			10		18-Oct-05	18	2.7	2.90	0.44	31.90	0.79	0.014
			11		22-Oct-05	54	8.8	4.68	1.22	126.80	0.76	0.016
			Total			337	41.8	5.08	0.71	542.40	0.52	–
			12	Hartenbos	09-Sep-05	8	0.6	0.75	0.09	13.90	–	0.049
GWS-02	360	F	13		16-Sep-05	13	5.6	4.96	0.43	24.80	0.26	0.041
			14		21-Sep-05	14	0.5	0.39	0.09	9.30	0.15	0.075
			15		22-Sep-05	6	1.4	2.35	0.33	11.90	0.28	0.167
			16		28-Sep-05	2	0.2	0.23	0.03	2.60	–	0.241
			17		02-Oct-05	24	3.8	4.76	0.78	51.30	0.51	0.037
			18		09-Oct-05	10	0.8	0.76	0.07	13.40	0.00	0.088
			19		13-Oct-05	12	3.3	5.19	0.72	32.20	0.68	0.211
			20		21-Oct-05	12	38.5	34.53	3.98	36.50	0.24	0.333
			21		30-Oct-05	11	19.8	25.76	4.68	29.90	0.65	0.445
			22		04-Dec-05	4	3.5	7.35	3.59	10.10	0.24	0.189
			Total			110	55.5	15.60	2.14	236.00	0.38	–
			23	Grootbrak	14-Nov-05	13	27.7	8.80	2.20	25.30	–	0.027
GWS-03	280	F	Total			13	27.7	8.80	2.20	25.30	–	–
			24	Hartenbos	01-Aug-07	6	6.4	3.00	0.40	8.43	–	0.400
GWS-04	400	F	Total			6	6.4	3.00	0.40	8.43	-	-
			25	Seal Island	31-Jul-07	2	1.6	3.60	0.50	5.18	–	0.552
GWS-05	300	F	Total			2	1.6	3.60	0.50	5.18	–	–
			26	Grootbrak	17-Mar-08	5	4.6	5.80	1.19	8.99	–	0.373
GWS-06	270	F	27		18-Mar-08	6	3.5	3.97	0.32	12.40	0.08	0.121
			28		19-Mar-08	2	1.1	2.36	0.49	5.65	–	0.182
			29		20-Mar-08	2	0.5	1.85	0.44	6.58	–	0.047
			30		24-Mar-08	3	3.1	6.30	2.57	7.24	–	0.354
			31		27-Mar-08	24	20.4	25.47	2.06	48.44	0.27	0.007
			Total			42	27.7	21.15	3.23	89.30	0.20	–
			32	Hartenbos	21-May-08	6	3.6	9.01	1.42	11.19	–	0.451
GWS-07	300	F	33		21-May-08	10	6.2	9.53	1.42	16.90	0.76	0.014
			34		22-May-08	31	30.4	22.23	5.29	64.85	0.57	0.050
			35		05-Jun-08	24	1.9	1.03	0.16	32.94	0.09	0.010

Table 1 (continued)

Shark ID	TL	Sex	Track	Tag Location	Start date	Duration (hr)	MCP (km^2)	Kernel 95 % (km^2)	Kernel 50 % (km^2)	Distance (km)	IOR	Linearity (*r*)
			36		20-Jun-08	24	10.9	2.97	0.39	65.64	0.01	0.073
			Total			101	39	9.90	2.24	191.52	0.35	–
			37	Hartenbos	12-Jun-08	1*	–	–	–	–	–	–
GWS-08	260	F	38		14-Jun-08	2*	–	–	–	–	–	–
			39		16-Jun-08	3	1.6	0.60	0.06	5.18	–	0.183
			Total			6	5	2.10	0.40	5.18		–
			40	Hartenbos	03-Jul-08	5	12.4	29.58	6.09	13.50	–	0.839
GWS-09	420	F	41		04-Jul-08	29**	67.4	43.80	5.30	67.70	–	0.330
			Total			34	151.5	–	–	81.20	–	–
			42	Seal Island	07-Jul-08	1	–	–	–	0.87	–	0.276
GWS-10	230	F	43		14-Jul-08	28	12.1	9.80	0.79	69.41	–	–
			Total			29	12.1	9.80	0.79	70.28	–	–
			44		12-Aug-08	5	3.7	1.70	0.20	9.17	–	0.290
GWS-11	220	F	Total			5	3.7	1.70	0.20	9.17	–	–
			45	Seal Island	11-Sep-08	33	15.1	16.60	4.00	83.93	–	0.041
GWS-12	320	F	46		17-Sep-08	9	4.7	4.50	0.64	13.23	0.39	0.244
			47		24-Sep-08	5	5.2	8.40	1.76	8.67	0.37	0.692
			Total			46	22.1	13.20	0.71	105.83	0.36	–
			48	Hartenbos	16-Oct-08	1	–	–	–	–	–	–
GWS-13	400	F	49		17-Oct-08	5	0.8	1.10	0.14	6.34	–	0.309
			50		19-Oct-08	5	0.2	0.20	0.03	3.83	0.00	0.055
			51		20-Oct-08	40	13.8	2.05	0.38	49.03	0.55	0.142
			Total			51	18.3	3.52	0.88	59.20	0.55	–

* Presence detected from anchored vessel

**29 h tracked, 20 within bay, 9 travelling away from bay

gaps of 40–70 min in tracking data. When sea conditions deteriorated or the tag signal was lost, tracking was abated until favourable conditions returned. On occasions a tagged shark would be picked up opportunistically by the research vessel while on unrelated excursions and tracking would recommence.

Data analysis

Home range analysis

Data of tracked sharks was filtered to one data point for every 10 min as in Johnson et al. (2009). Home ranges were determined using both Minimum Convex Polygon (MCP) and Kernel (K) methods using the 'Animal Movement' extension of ArcView 3.2 (Hooge and Eichenlaub 2000). We defined 'activity area' from MCP, 'home range' from K95% and 'core-area' from K50%. Kernels of both 95 % and 50 % (K95/K50) were derived using limited cross validation smoothing parameters as suggested by Warton (1995) and Carr and Rogers (1998). In the event that a kernel extended over land, the land was clipped using the X-tools extension of ArcView as in Heupel et al. (2004).

Total range

Separate tracks of the same shark were synthesised (i.e. calculated as if they were continuous) to produce a cumulative track for each shark. These cumulative tracks were then synthesised for all the tracked white sharks to give a total range of tracking efforts. This range was then tested for activity area, home range and core area use.

Size class/home range

Individual tracks of each shark were subjected to home range analysis and then tested against size class with one-way Analysis of Variance (ANOVA) to determine if home range estimates varied significantly between different size classes of shark. We determined size class after Bruce (1992), who considered sharks under 300 cm as juvenile and presumed to have diet and physiology more adapted to teleost and cephalopod prey (Ferrara et al. 2011; Smale and Cliff 2012; $n=5$). Subadult white sharks are expected to be 300–450 cm, however, our size range only extended to 420 cm and there is much debate on exactly what size white sharks become mature (it is impossible to tell visually while free swimming). As a result we avoided the term 'mature' and rather determined 'large' sharks at≥400 cm ($n=4$) and 'subadult' between 300 and 399 cm ($n=4$).

Activity area over time

A comparison for activity area over time was plotted in a similar way to Goldman and Anderson (1999). We used the observation-area curve recommended by Winter and Ross (1982) and used by Rechisky and Weatherbee (2003) to determine optimal tracking time (the time at which the animal reaches the full extent of it's movement and home range estimates become more accurate) for white sharks in Mossel Bay, based on 5 % activity area change.

Swimming linearity

Linearity of sharks' individual tracks were determined using the Linearity Index (LI) of Bell and Kramer (1979):

$$LI = (Fn - F1)/D$$

Where Fn is the last position taken for the shark, F1 is the first position taken for the shark, and D is the total distance travelled by the shark. A linearity of 1 indicates linear movements without returning to the vicinity (i.e. straight line travel). A LI near zero indicates little movement from the area with a great deal of overlap and reuse of the activity space. LI was determined after every 5 h of tracking on individual tracks lasting longer than 10 h as in Johnson et al. (2009).

Index of reuse

Index of Reuse was used to determine the level of reuse from one day-to-day movement to the next. Home ranges (K95), determined from individual tracks of less than 24 h, were overlapped with each other, and those from longer tracks periods (12 or 24 h) were compared as in Rechisky and Weatherbee (2004):

$$IOR = [OV(A1 + A2)]/(A1 + A2)$$

Where [OV(A1+A2)] is the area of overlap between two home ranges (K95), and (A1+A2) is the total area of both home ranges ((Morrissey and Gruber (1993) modified from Cooper (1978) and McKibben and Nelson (1986)). The effect of shark body size was measured with Linear Regression from TL and IOR.

Home range overlap

We developed an Index of Shared Space (IOSS) from home range overlap using methods of Bull and Baghurst (1998) and Morrissey and Gruber (1993), K95 overlap from one individual's home range with each of the other sharks' home range was calculated using the X-tools feature of Arc View:

$$IOSS = OV/[(A1 + A2)/2]$$

Where OV is the area of overlap from one conspecific's home range to another and A1 and A2 are the total home ranges of the two conspecifics (K95). The mean home range overlap was used to describe individual's general level of home range overlap with con-specifics (Table 2). Kruskal-Wallis test was used to determine if home range overlap was inversely correlated to TL.

Migration away from Mossel Bay

Most tracks ranged from the harbor mouth to the Grootbrak River Mouth, but one shark (GWS-9) moved out of Mossel Bay using a near linear swimming pattern (Fig. 2a). The shark was not detected during any research operations in the bay for the following two months but was sighted back in Mossel Bay later on the 2 July 2008, by which time the tag had ceased transmitting. As the study's focus was to examine home range of sharks whilst residing in Mossel Bay, the track of this shark was cut to the point at which it began moving away from Mossel Bay.

Table 2 Level of overlap from one sharks home range to each of the others in the study as determined by IOSS

Shark Id	Average	St Er
GWS-01	0.400	0.067
GWS-02	0.351	0.040
GWS-03	0.134	0.054
GWS-04	0.331	0.067
GWS-05	0.361	0.068
GWS-06	0.142	0.061
GWS-07	0.389	0.056
GWS-08	0.292	0.059
GWS-09	0.240	0.044
GWS-10	0.201	0.042
GWS-11	0.234	0.055
GWS-12	0.323	0.056
GWS-13	0.147	0.037

Results

The total activity area of the thirteen sharks, as determined by MCP, encompassed an area of 93.5 km^2 (Fig. 2b). This extended from Mossel Bay harbor to past the Grootbrak river mouth. The area was primarily restricted to near shore coastal habitat within the natural boundary of Mossel Bay. The home range (K95) within this area comprised 10.19 km^2 covering the habitats of Seal Island, Hartenbos, the waters adjacent to Kleinbrak and Grootbrak river mouths. The core area was 1.05 km^2 and located in the Hartenbos area.

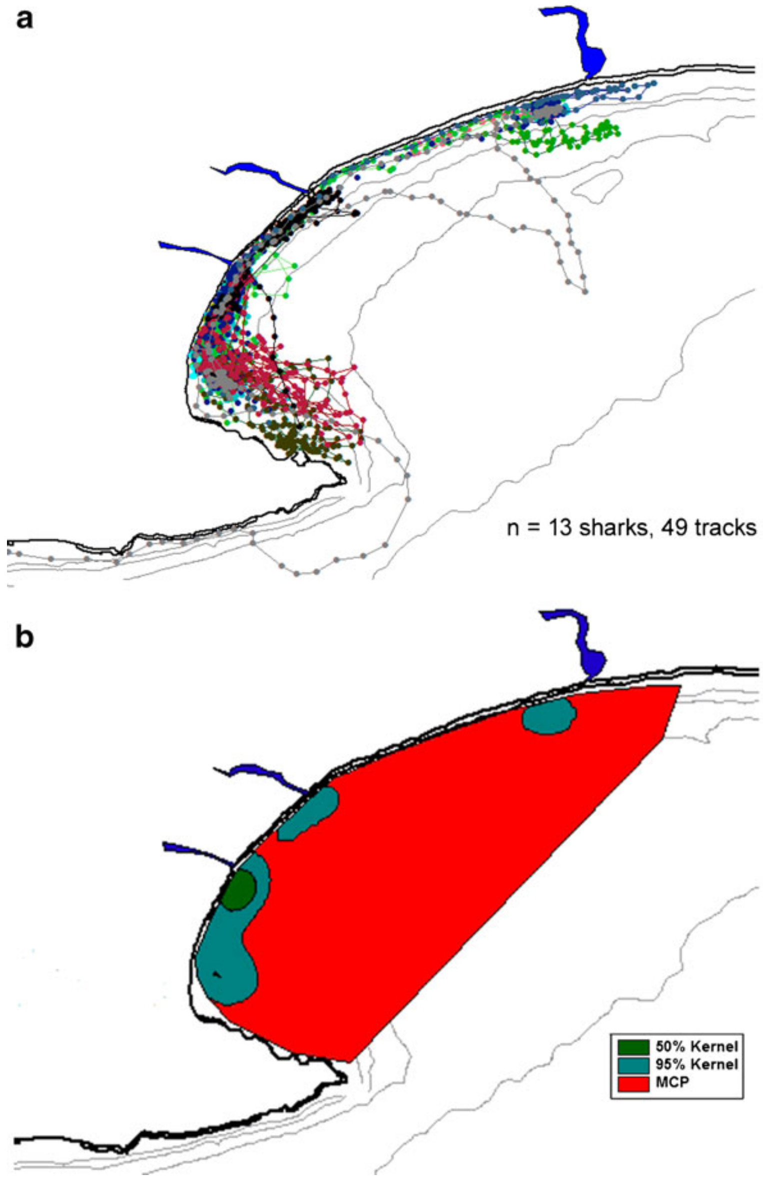
Individual activity areas ranged from 6.4 km^2 (GWS-05) to 55.5 km^2 (GWS-02) (Table 1), whilst home range (K95) of these individuals varied from 3.52 km^2 (GWS-13) to 21.15 km^2 (GWS-06). Ten of the sharks confined their home range to one, or more, of the previously identified core habitats, namely Seal Island, Hartenbos, Kleinbrak and Grootbrak (Fig. 3). Two sharks (GWS's 10 and 12) displayed fidelity to an area adjacent to Mossel Bay harbor and one (GWS-09) moved into an area offshore of the Grootbrak. Incidentally GWS-10 also adopted an anomalous behaviour of entering the harbor during tracking and remaining within the harbor for several hours. Whilst at the harbor mouth, GWS-12 frequently circled a sardine purse-seine fishing vessel as it apparently cleaned its fish holds (as determined by the presence of a chum type slick).

Linearity varied depending on the sharks movements either away from core areas (higher) or remaining within them (lower). When GWS-09 moved into the area of Grootbrak its movement in this area was linear (LI=0.696) before returning back to the coast and continuing to move linearly (LI=0.495–0.454) until reaching Seal Island where linearity lowered (0.045). After 11 h in this area (22:00–09:00 h) the shark began to move directly out of the bay heading south west (LI=0.698). In comparison both sharks using the harbor mouth area showed low levels of linearity while there (LI of 0.019 and 0.041 respectively). Several other tracks also displayed high linearity; GWS-06 (LI=0.885 between hours 5–15) which travelled from Hartenbos to Grootbrak and back to Seal Island and GWS-12 track 3 (LI=0.692) which extended from Seal Island to Kleinbrak. Each of these movements followed costal routes from and back to the island or reef systems. GWS-13 moved from Kleinbrak towards the harbor, possibly as the shark moved away from Mossel Bay (LI=0.777, the shark was not detected again despite several search transects in the weeks following). Lowest levels of LI were observed when tracks remained in core areas (GWS-01, Track 7; 0.006; GWS-06, Track 32; 0.007; GWS-07, Track 36; 0.010).

LI was independent of TL (ANOVA, $F_{(2,36)}=1.488$, $P>0.5$, $n=39$), but significantly related to K95 (*t*-test $p<0.01$, $n=39$). However, the home range of individual tracks were found to be dependent on TL (ANOVA, $F_{(2,36)}=4.315$, $P<0.05$, $n=39$) with large sharks using a more refined home range in comparison to small and medium sized individuals (Fig. 4a). IOR was found to be a function of size with larger sharks showing higher levels of reuse (Fig. 4b; Linear regression; $r^2=0.896$, $P<0.01$, $n=6$). In particular GWS-01 and GWS-13 showed high fidelity to the areas of Hartenbos and Kleinbrak respectively with the former repeatedly returning to the same site and the latter remaining at the same site for 80 % of its total track. In contrast, GWS-06 used several different areas of the same reef system at Grootbrak which resulted in low levels of reuse.

IOSS revealed an average of 0.273 (equivalent to less than 30 %) shared space between one individual to all other conspecifics tracked, and showed a significant relationship to body size (Table 2; Fig. 5; Kruskal-Wallis$_{(7,156)}=21.65$, $P<0.1$, $n=13$ sharks, 156 IOSS values). Highest levels of shared space were recorded between sharks at Hartenbos and were particularly high between two sharks tagged and tracked within the same 24 h (GWS-04 and GWS-05; 0.692). GWS-01 had the highest level of shared space with all other conspecifics at 0.400. Cases of zero overlap occurred between

Fig. 2 Active tracks of 13 white sharks tagged at Mossel Bay (**a**) and combined home range and core habitat use of thirteen white sharks acoustically tracked within the confines of Mossel Bay (**b**). Estimates determined by K95 (grey), K50 (*green*) and MCP (*outer*, *red*) calculations



individuals whose tracks were either confined to one area (GWS-03) or several areas which did not include the Hartenbos reef system (GWS- 06 and GWS-10). Duration of tracking did not appear to play a major role in degree of overlap with several sharks tracked for just one shift showing higher overlap than others tracked for several days. GWS-09's track overlapped all other conspecifics as it covered the entire bay, but its IOSS was lower than those from Hartenbos (0.240) because its home range covered such a large area. Dorsal fin identification revealed five of the eight sharks tagged in 2008 and one from 2007 were present in Mossel Bay during October 2008 (GWS's 05, 06, 09, 10, 12 and 13). Comparing MCP over time displayed the rate of change in activity area as more tracking occurs (Fig. 6a). Activity area plateaus once a shark remains in the same area, or areas for prolonged periods of time. Steep rises in activity area are an indication of either high level of linearity or as a result of a shark being detected in a new area between different tracking shifts. Observation-area curve (Fig. 6b) showed that the optimum tracking duration in Mossel Bay was 72 h, a duration of which we surpassed three times in this investigation.

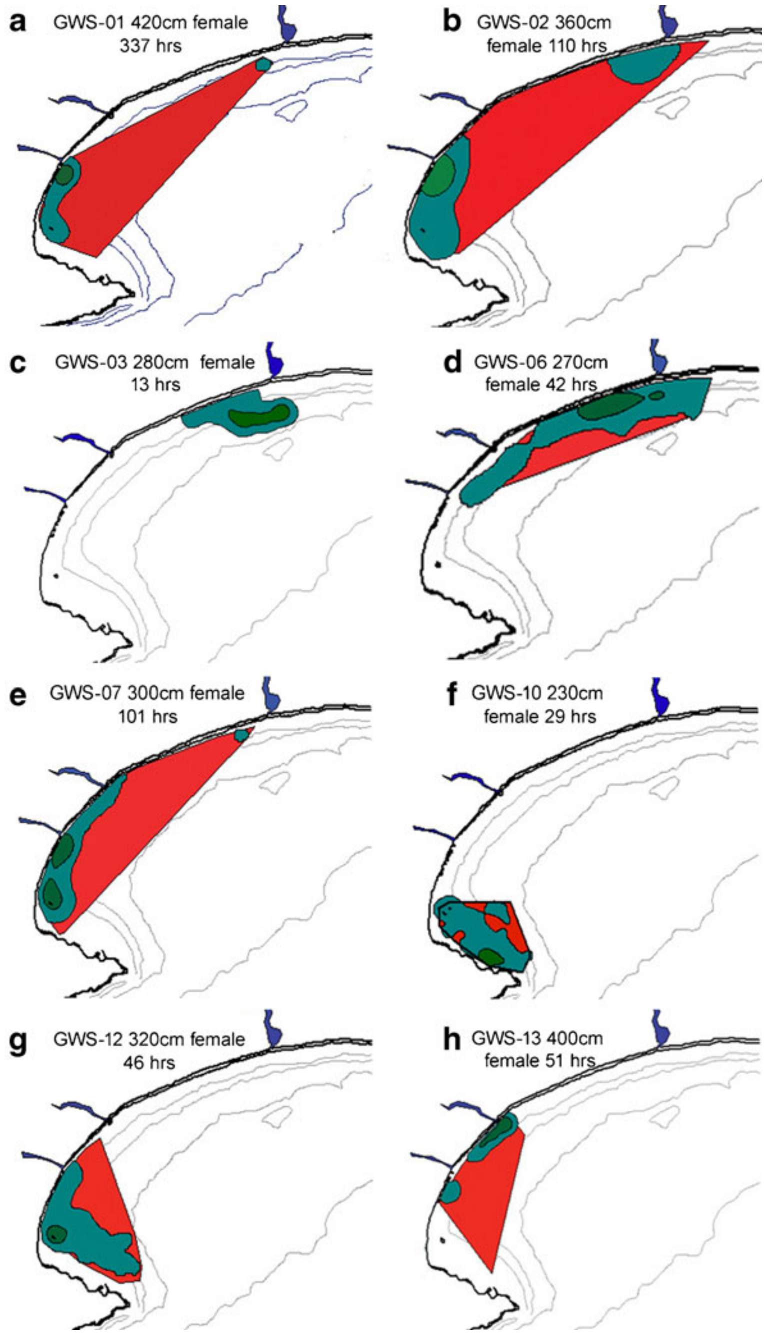


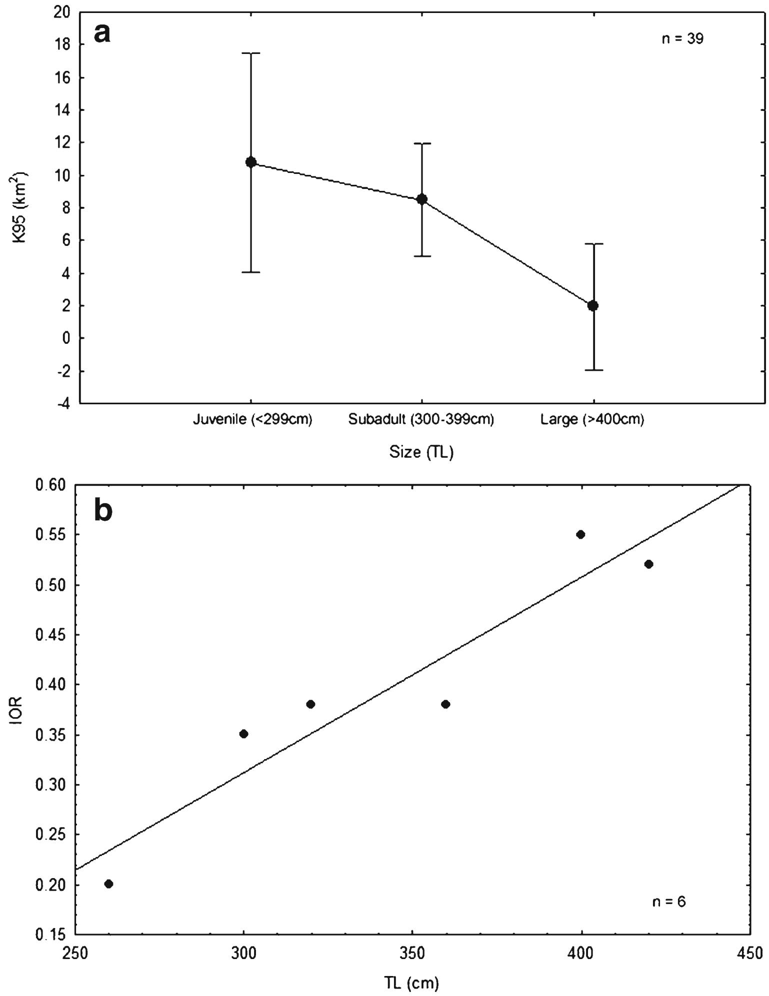
Fig. 3 Activity area, home range and core habitat use of 8 individual white sharks tracked at Mossel Bay as determined by MCP, K95 and K50 calculations. **a**. GWS-01 420 cm female, **b**. GWS-02 360 cm female, **c**. GWS03 280 cm female, **d**. GWS-06 270 cm female, **e**. GWS-07 300 cm female, **f**. GWS-10 230 cm female, **g**. GWS-12 330 cm female, **h**. GWS-13 400 cm female

Discussion

The total range (MCP) of sharks tracked encompassed most of Mossel Bay; however 95 % and 50 % kernel analysis revealed a spatial pattern of highly utilised core habitats that fell within this range. Some of these core habitats have been previously identified, such as Seal Island, Hartenbos and Grootbrak (Johnson and Kock 2006; Johnson et al. 2009), whilst others, such as Kleinbrak and Mossel Bay Harbor represent newly identified areas.

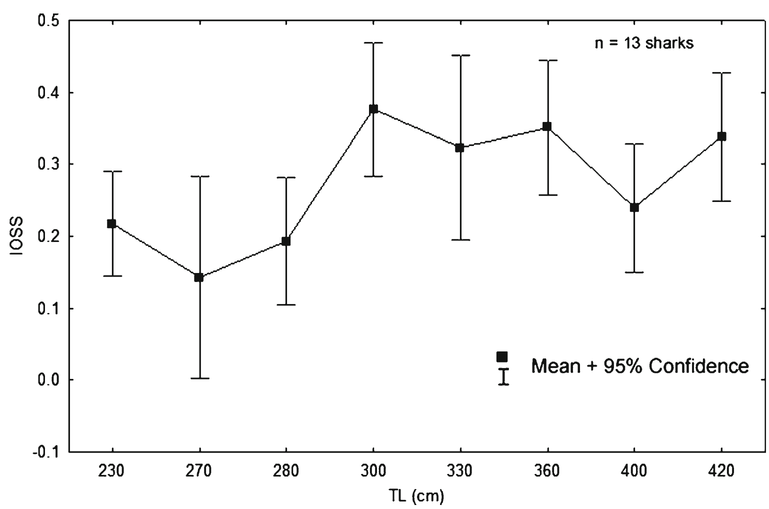
Hartenbos was the most frequently used core habitat identified during this study. Johnson et al. (2009) found this site to be frequented by white sharks during

Fig. 4 **a** Test for variance between home range size (K95) of white sharks tracks in relation to shark total length (TL). ANOVA, $F_{(2,36)}=4.315$, $P<0.05$, $n=39$ and **b** the effect of total length (TL) on Index of Reuse (IOR) measured with Linear Regression; $r^2=0.896$, $P<0.01$, $n=6$



a hiatus between morning and evening patrolling bouts at Seal Island. Lower levels of movement and linearity were observed and it was suggested this could be a site for resting or social purposes. This

Fig. 5 Index of shared space (IOSS) to total length (TL) Kruskal-Wallis$_{(7,156)}=21.65$, $P>0.005$, $n=13$



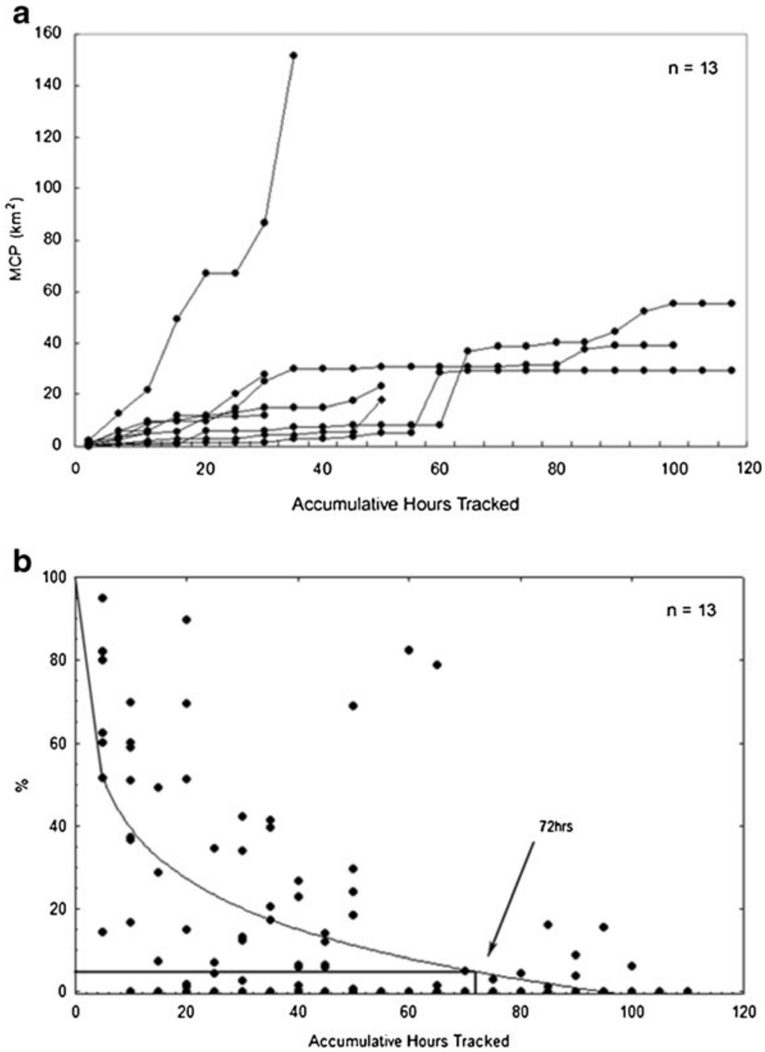


Fig. 6 **a** Effect of tracking duration on activity area (MCP) and **b** Observation-area curve derived from activity area (MCP) change over time

may explain why Hartenbos displayed higher levels of white shark home range use than Seal Island, contradicting earlier studies that suggest waters directly adjacent to Cape fur seal colonies would have the most dense aggregations of white sharks in the Western Cape (Compagno 1997). Johnson (in prep.) went on to suggest that when not foraging for seals, sharks in Mossel Bay fulfil other life history requirements, such as resting to digest food and conserve energy for the next Seal Island patrol or patrolling for other prey items in areas away from Seal Island.

Seal Island was frequented by the majority of tracked sharks, but did not fall in the core habitat of as many sharks as Hartenbos. This parallels the findings of Johnson et al. (2009) who found a daily effort of 8.9 to 10.7 % spent patrolling at Seal Island which was much lower than that observed in California (Klimely et al. 2001). Our results show that whilst waters adjacent to pinniped colonies may represent a primary hunting ground for white sharks, they do not necessarily represent the most commonly used areas of an aggregation site. The Grootbrak river mouth was highly frequented by four sharks in this study and has the potential to support a feeding ground for white sharks due to the extensive reef areas harboring prominent teleost and elasmobranch populations (Johnson et al. 2009). The area adjacent to the Kleinbrak river mouth presents a new core habitat. GWS-13 spent the majority of its tracked time in this area following initial tracking at Hartenbos. Two other sharks (GWS-6 and GWS-7) also utilised Kleinbrak area in a similar way to GWS-13, but with lower levels of overall fidelity. The final core habitat was adjacent to Mossel Bay Harbor. This area was frequented by two sharks; one juvenile (GWS-10) and one subadult (GWS-12). The harbor is an active commercial fishery and the potential overspill of fish being unloaded or discarded could produce a chum slick similar to those used to attract white sharks for viewing purposes. The repeated presence of olfactory stimulus, and potential food, may motivate a number of white sharks to actively forage in this area.

Our data suggests that home range size is dependent on shark total length and that larger sharks show higher levels of reuse within Mossel Bay. Goldman and Anderson (1999) also found that larger sharks utilised a smaller activity area compared to smaller conspecifics. These findings differ from lemon shark acoustic telemetry studies that found positive correlations between length and home range of individuals (Gruber et al. 1988). Goldman and Anderson (1999) suggested that larger white sharks were experienced hunters within South Farallon Islands and that experience could lead them to utilise certain areas efficiently whereas smaller, less experienced, individuals roamed greater areas in search of prey. On the other hand, Gruber et al. (1988) suggested that as juvenile lemon sharks in Bimini Lagoon grew they were able to expand their home range and venture away from nursery areas. We suggest that smaller white sharks need to fulfil life history requirements in spatially separate areas to larger sharks. As such, Grootbrak may provide a high abundance of teleost and cartilaginous prey, which smaller white sharks are considered more adept at hunting (Bruce 1992; Ferrara et al. 2011; Smale and Cliff 2012). Larger and medium sharks are more adept at hunting marine mammals, and therefore utilise the food resources of Seal Island. Medium sharks which have switched to marine mammal prey more recently (Bruce 1992; Estrada et al. 2006; Ferrara et al. 2011), need to learn the best areas and methods in which to hunt these prey and therefore may utilise these areas less efficiently than the larger individuals. The predictable occurrence of Cape fur seals in waters adjacent to Seal Island may enable large white sharks to gain sufficient food resources without the need for extensive horizontal searching.

Conservation implications

Our study suggests that white sharks in Mossel Bay have limited home ranges, focused core areas, and that their individual home ranges overlap significantly with one another. The results could be used to provide guidance to management authorities in the implementation of a marine protective area in Mossel Bay as an effective means for the protection of the species. Costal developments at these sites have the potential to impact the life histories of the white sharks which seasonally inhabit them. The protection of these coastal areas will benefit the recovery of white sharks in South Africa which has begun to stabilise post protection in 1991, but still remains a fraction of the numbers 50 years ago (Dudley and Simpfendorfer 2006; Kock and Johnson 2006).

This study provides a further demonstration that active tracking can aid conservation efforts for endangered marine species. These methods are applicable to white sharks across the Western Cape of South Africa and beyond and could also be used where similar partially residential species are threatened. An increase in the knowledge of the species movements can only increase the effectiveness of conservation efforts for the species, improving survival rates and aiding recovery.

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