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Migration and habitat use of formerly captive and wild raggedtooth sharks (Carcharias taurus) on the southeast coast of South Africa

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ORIGINAL ARTICLE

Migration and habitat use of formerly captive and wild raggedtooth sharks (*Carcharias taurus*) on the southeast coast of South Africa

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Abstract

Releasing aquarium-held sharks when no longer needed by the holding institution may help mitigate the impacts that aquaria have on declining wild populations. To investigate the viability of releasing display specimens, four raggedtooth sharks (*Carcharias taurus*) that had been held at Two Oceans Aquarium, Cape Town were released back to the wild between 2004 and 2008. To test the hypothesis that they survived and that their movement patterns were similar to wild conspecifics, wild-caught sharks were also tagged and released at the same time and locality. Aquarium- and wild-caught sharks were equipped with pop-up archival (PAT) tags, VEMCO ultrasonic tags, and numbered spaghetti dart tags. With the exception of one individual, all the aquarium-released sharks survived. Both aquarium-released and wild-captured sharks displayed eastward movements and travelled hundreds of kilometres after release. Data from the PAT tags indicated that individuals from both groups swam mainly in shallow waters, but dived as deep as 80 m to mid-shelf waters. A wide temperature tolerance was exhibited as they travelled though temperatures ranging from 10 to 22°C. Movement tracks of the sharks revealed 'station keeping' and an autumn migration between April and May. Rates of movement between individuals were variable. The depth range recorded in this study supports published information on habitat and prey choice. This study illustrates that this species can survive aquarium release after years of captivity and that they appear to behave similarly to wild-caught conspecifics.

Key words: *Raggedtooth sharks, pop-up archival tags, shark behaviour, aquarium release*

Introduction

The role that public aquaria have in conservation, captive breeding, education and entertainment is widely acknowledged (Taylor 1993; Koob 2004). Although captive breeding is widely practiced in zoos (Balmford et al. 1996), it is poorly developed in aquaria (Maitland & Evans 1986), with few institutions implementing fish captive breeding programmes. Captive breeding is generally restricted to small species as large fish, such as sharks, are logistically difficult. This is of particular concern from a conservation perspective, as many shark populations are declining rapidly (Baum et al. 2003). Sharks held in aquaria are normally caught from wild stocks and may either remain within the aquarium for the rest of their lives or may be released back to the wild. Release of aquarium sharks is a contentious issue and there have been few attempts to investigate its success.

Carcharias taurus Rafinesque, 1810 (raggedtooth, grey nurse or sand tiger shark) is a large species that readily adapts to aquaria and is a popular display animal (Dehart 2004). Despite these favourable husbandry characteristics, there can be multi-species compatibility issues because they may attack and feed on other high-value species on display. *Carcharias taurus* is a widely distributed lamniform

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shark inhabiting warm–temperate and tropical coastal waters (Compagno 2001). Off southern Africa it is found mainly along the east coast as far north as Mozambique (Bass et al. 1975; Smale 2002; Dicken et al. 2006a). Reproduction involves intrauterine cannibalism (or adelphophagy) which results in the birth of two young after a 9–12-month gestation period (Bass et al. 1975; Gilmore et al. 1983). It is a late-maturing species (Goldman et al. 2006) and reproduction is biennial (Branstetter & Musick 1994; Lucifora et al. 2002; Dicken et al. 2007). These life-history characteristics and unsustainable levels of exploitation have resulted in population declines from several parts of its range (Musick et al. 1993, 2000; Lucifora et al. 2002; Otway et al. 2004). Fortunately, off southern Africa the population appears to be relatively stable (Dudley & Simpfendorfer 2006; Dicken et al. 2008). Off South Africa, nursery areas are located on the Eastern and Western Cape coasts. Pregnant females inhabit subtropical waters in northern KwaZulu-Natal and southern Mozambique, in austral summer, and then migrate south during autumn and winter to pup in the Eastern and Western Cape in spring and summer (Bass et al. 1975; Smale 2002; Dicken et al. 2007). Northward movements from the southwestern parts of the range are thought to occur in summer and autumn, but details are sketchy (Bass et al. 1975; Smale 2002; Dicken et al. 2007).

Two Oceans Aquarium, Cape Town (TOA) has maintained *C. taurus* in its Predator Exhibit display tank since 1995. As older sharks had not successfully bred within the exhibit, the TOA wanted to develop a policy of releasing large display animals and replacing them with younger individuals for public education purposes. The release of captive animals is controversial and guidelines are needed to optimize release and survival and to minimize negative impacts on wild stocks (Hall 2003). This study was initiated to investigate the survival and behaviour of *C. taurus* released after several years of captivity and to test the hypothesis that once released, these formerly captive sharks would use similar habitats and behave similarly to wild sharks that had never been held in captivity. The experimental approach was to release the aquarium-held sharks with archival and ultrasonic tags and then capture and release wild individuals (0–3 days subsequently) which were similarly tagged. This study therefore aimed to obtain a better understanding of movement behaviour by comparing aquarium-released sharks and their wild conspecifics. We focused on three research questions. (1) Would captive animals survive release? (2) Would released animals migrate eastwards in autumn as appears to be the pattern with wild individuals? (3) Would aquarium-released animals display similar patterns of use of the water column as wild sharks? We hypothesize that if these three behavioural aspects of released animals are congruent with wild sharks, aquarium-released sharks would survive in the wild successfully, and that aquarium release of *C. taurus* is feasible.

Material and methods

Study site

The southeast Atlantic and southwest Indian Oceans meet off South Africa with the cool Benguela system on the west coast and the warm Agulhas current on the east coast (Lutjeharms 2006). As a consequence of the physical geography and oceanographic influences, the structure of the water column varies both seasonally and latitudinally along the east coast (Schumann 1999; Roberts 2005; Lutjeharms 2006). River inflows along the south coast are minimal. North of Algoa Bay, riverine inflows and fine sediments result in low-visibility water almost throughout the year. Coastal waters are highly dynamic and experience upwelling following strong easterly winds, and in summer inshore water temperatures may be as high as 23°C but can drop as low as 10°C after sustained easterly gales. This pattern is reversed with westerly winds that may result in increased swell height but clearer, warmer water (Schumann 1999; Roberts 2005).

Capture and tagging

Raggedtooth sharks used in this study were all captured along the southeast coast of South Africa and had been in captivity for periods ranging between 3 and 11 years (see Appendix 1 for details of capture origin and history of each shark where known).

Aquarium-held sharks were sedated by injection of either Valium/Diazepam (between 2004 and 2006) or Domitor/Medetomidine (in 2007) by SCUBA divers. When sedated, sharks were directed by nets into a large drum that was raised from the water onto the top deck of the aquarium. Sharks were immediately examined by a consulting veterinary specialist for disease, then measured and weighed, and then isolated for at least two weeks. Isolation allowed for closer monitoring of the sharks prior to their release and the animals were not fed for at least 10 days prior to transport to the release site. This period was long enough to allow the sharks to purge their alimentary canals and thus prevent polluting the limited volume of water in the transport tank during the 5-h transit to the release site at Struis Bay near Cape Agulhas. Sharks were transported on a flat-bed truck fitted with a 4900-l seawater tank and life-support system using optimal transport procedures recommended by Smith et al. (2004). Sharks were allowed time to recover overnight from the road journey prior to being transported in a large tank aboard a semi-rigid inflatable boat to the release site early the following morning during optimal sea conditions. A surface support team and divers monitored the release of the sharks and ensured that they had adjusted to sea conditions.

Wild sharks were captured with baited barbless hooks at known aggregation sites close to the release point of the captive sharks, usually within a day of the aquarium release. An exception was in 2004 when no wild animals were tagged and in 2007 when no aquarium releases were made (Table I). Sharks were brought aboard the boat and sedated in a fibreglass tank with 2-phenoxyethanol in the seawater (0.2 ml l^{-1}).

Pop-up satellite archival tags (PAT 4.0 and PAT 10, Wildlife Computers, Redmond, Washington, USA) were painted with antifouling over paint the body of the tag (but not the sensors, float or aerial) to minimize biofouling (Dicken et al. 2006b, 2011). PAT tags were then attached to the four aquarium-held and five wild-caught ragged tooth sharks. PAT tags were inserted with a stainless steel dart head to the base of the first dorsal fin (2004) or attached to a saddle on the first dorsal fin (2005–2008). Saddle attachment was achieved by drilling two cores out of the dorsal fin and then attaching the saddle and bolting it on with Delrin bolts and brass washers held by mild steel nuts. The attachment to the saddle was designed with galvanic corroding nuts to ensure that the saddle and tether dropped off the animal approximately 6 months after deployment. In addition, a numbered stainless steel dart head spaghetti tag (Hallprint Pty Ltd 15 Victoria Rd, Victor Harbor, South Australia) was attached at the base of the first dorsal for longer-term marking. The sharks also had a VEMCO V16 coded ultrasonic tag (VEMCO, 211 Horseshoe Lake Drive, Halifax, Canada) that was either attached externally with stainless steel trace covered with shrink-wrap to a stainless steel dart head (2004–2005) or inserted into the abdominal cavity after surgery (2006–2008). The 2-cm incision was closed with two to three sutures.

Wild sharks were injected with oxytetracycline into the body cavity at concentrations of approximately 50 mg kg^{-1} (Tanaka 1990) to mark vertebrae for later age validation. Weights were estimated for wild sharks using a length–weight regression relationship (Dicken et al. 2006a).

Sharks were ultrasonically detected throughout the duration of the study by an array of VR2 listening stations along the length of the coastline. The listening stations were deployed in Mossel Bay, Algoa Bay, Port Alfred and East London.

Data capture and analysis

Pop-up archival satellite tags were user-programmed to pop-up after a predetermined period post-release (Table I) and prior to the corrosion and release of the attachment saddle. The tags were programmed to archive data on light levels, depth and water temperature at 10 s intervals and archival data were summarized into bins of 1 h (2004) or 6 h (2005–2008) for transmission to Argos satellites on release. For each data bin, mean depth and temperature was calculated together with depth–temperature profiles and a dawn-to-dusk curve. Premature release dates may be programmed into the tag to ensure release should the shark stay at constant depths (≤ 3 m) for extended periods. As *Carcharias taurus* remains in caves for prolonged periods, we programmed the constant depth period to span multiple days as either 5 days (2004, 2007), 3 days (2005–2006), or 8 days (2008).

Geolocation during tracking was estimated using the manufacturer's proprietary software. Longitude was estimated using an algorithm based on time calculated from light levels as described by both Hill (1994) and Hill & Braun (2001). Standard astronomical formulae are used to calculate the difference between local solar noon and Greenwich solar noon. Errors associated with these methods of calculating longitude have been estimated at 0.15–0.25° (Musyl et al. 2001) and 54 ± 36 km (mean $\pm$ SD, Weng et al. 2007). Estimates of latitude are calculated from day length. These were found to be less accurate, as a result of environmental influences such as cloud cover, water turbidity and swimming depth. Estimated latitudinal errors range from 0.78–3.5° (Musyl et al. 2001) to 17–434 km (Weng et al. 2007), which averages 231 ± 159 km. At dates near the equinox, it is not possible to derive meaningful latitude estimates based on day length (Hill & Braun 2001). We applied a Kalman filter to refine positions but this had little improvement, partly because of low numbers of positions obtained. As a consequence, we used an alternative approach advocated by West & Stevens (2001) and Bruce et al. (2006). The depth contours of the south coast of Africa are approximately parallel with the coastline, as is also found off south Australia. Knowing that these sharks are generally found near reefs or in gullies by day, we used the nearest possible maximum depth on the same day as a longitude position was obtained for the mid-day time bin. If these data were absent (had not been received in the data transmission stream

Table I. Summary data of aquarium-released and wild-caught *Carcharias taurus* tagged with different tag configurations during this study. Daily rate of movement is calculated for only the release to pop-up date. Premature release was set at 5 days at constant depth within 2.5 m except AR1, which was constant depth within 5 m. VEMCO tag (ext) denotes external dart head attachment, and (int) for surgically implanted within abdominal cavity. Two tags were attached to AR1. AR2 reported only corrupted data. W5 had a refurbished redeployed tag which did not release or report data. Time (in days) is the time interval between release and pop-up.

Shark (sex)	TL (cm)	Mass (kg)	Release date	VEMCO acoustic tag number	Hallprint tag number	Programmed pop-up date	Actual pop-up date	Pop-up locality	Distance travelled (km)	Time (days)	Rate of movement (km day^{-1})
						Aquarium-released sharks					
AR1 (F*)	278	192	2004/03/18	769(ext)	2303	2004/09/15	2004/07/11	Plettenberg Bay	298	115	2.6
AR1 (F*)						2004/06/15	2005/02/03	Algoa Bay	419	322	1.3
AR2 (F)	295	210	2005/04/04	782 (ext)	2901	2005/08/04	2005/08/05	Unknown	–	–	–
AR3 (F)	280	196	2006/03/15	805 (int)	3541	2006/07/10	2006/07/11	Near Port Alfred	700	117	6.0
AR4 (F)	280	165	2008/03/12	8691 (int)	–	2008/08/17	2008/03/24	SSE Cape Agulhas	11	12	0.9
						Wild-caught sharks					
W1 (F)	308	243	2005/04/05	783 (ext)	2902	2005/08/08	2005/08/09	Port St Johns	993	126	7.9
W2 (F)	261	138	2006/03/15	826 (int)	3537	2006/07/12	2006/07/15	Coffee Bay	970	122	8.0
W3 (M)	203	52	2007/03/28	818 (int)	–	2007/07/26	2007/05/17	Near Port Alfred	684	50	13.7
W4 (F)	252	122	2007/03/28	817 (int)	–	2007/08/07	2007/05/10	Algoa Bay	562	43	13.1
W5 (F)	273	160	2008/03/13	8692 (int)	–	2008/09/07		Unknown	–		–

from the tag to ARGOS satellite), then the next nearest time bin was chosen. Since these are largely demersal sharks, which generally shelter in caves and gullies by day, we assumed that these depths were equivalent to bottom depth and combined them with the light-derived estimate of longitude to make the best estimate of position. These positions were captured into *ArcGIS 9* and plotted. Distances travelled were calculated using the distances between positions and the most likely track distance (i.e. not crossing headlands). A speed filter was used to reject points that provided unreasonable swim speed rates between points. While there are several reports for white shark speed of movement, there are limited data for other species. The approach used in this study was to use species with similar anatomy and physiology to provide maximum speed parameters. To filter the positions, a combination of maximum allowable distance per day (60 km, approximately 0.7 m s^{-1}) and 0.3 body lengths s^{-1} were used as maxima. These criteria were obtained from speed estimates of Klimley et al. (2002) for blue sharks and Tricas et al. (1981) for tiger sharks. These criteria are less than those estimated for endothermic white (1.1–3.8 km h^{-1} approximately 26.4–91 km day^{-1}) (Bruce et al. 2006) and mako (0.5–1.2 m s^{-1} approximately 43–104 km day^{-1} found for 60% of time tracked) (Klimley et al. 2002) sharks.

Directionality of movement was investigated using circular statistics. The mean resultant vector of each shark was calculated using the methods described by Batschelet (1981) and its variability estimated using non-parametric bootstrapping with 1000 iterations. Pairwise Watson U^2 tests (Zar 1984) were used to test the null hypothesis that mean angle of the bearing of the shark pairs was equal.

Vertical movements

Use of the water column was investigated using the summary data transmitted via the ARGOS satellites and analysed with the Wildlife Computer proprietary software. Depth use was plotted as proportion of time at depth as contours where sufficient data were available. Temperature range encountered by each shark was plotted using the overall mean of the 6-hourly bins encountered by each shark. Raw data archived aboard the only PAT tag recovered (W4, Table I) were downloaded and analysed. Preliminary examination of the raw data suggested that the diurnal pattern of behaviour was autocorrelated by the previous position and photoperiod. Data were subsequently subsampled at a rate ranging between every 2 and 30 min to reduce the level of autocorrelation. To investigate whether there was any change in activity through the water column, the mean and variance of depths per time period (dawn, day, dusk and night) each day was calculated and compared. The dawn and dusk photoperiods were defined as one hour whose mid-point was during the mid-point of the crepuscular light level change provided by the tag, with day spanning the highest light level and night the low level of the light record. Differences in variability between photoperiods were assessed by removing the day trend in the data with a multiple linear regression and conducting a Bartlett's test (Zar 1984) on the resulting residuals to test the null hypothesis that movement variability was equal across photoperiods.

Results

Survival

Aquarium-released sharks survived for periods of at least months. The only exception was one individual (AR4) that may have died approximately 4 days after release. All the wild-caught animals survived capture and tagging and were detected at least a month after release.

Overall movement patterns

A total of four female sharks, measuring 278–295 cm total length, were released from the TOA between 2004 and 2008 (Table I). Two additional sharks, a male and a female, intended for release died at the aquarium in 2007 following anaesthesia and surgery. Consequently, no sharks were released in 2007.

Aquarium-released (AR) sharks showed considerable northeastward movements from the point of release off Struis Bay (Figure 1a). Because the first shark (AR1) released was double PAT tagged, two pop-up positions were detected by ARGOS off Plettenberg Bay 115 days post-release, and Algoa Bay eight months after the programmed release date. She moved from Cape Agulhas eastward as far east as 28.9°E then returned westward in August, moving towards Algoa Bay (Figure 1a). AR2 only provided corrupted data through the ARGOS system, but this shark was detected from VR2 listening stations in Mossel Bay 220 km east of the release point, on 22 April 2005, some 18 days after release – a movement rate of 12 km day^{-1}. The PAT tag from AR3 was detected on 11 July off the Eastern Cape, halfway between Port Alfred and East London. Although washed ashore, it was not recovered. She had travelled 700 km in 118 days. She was subsequently acoustically detected in Algoa Bay in August and December 2006 and in January and February 2007 by the VR2 listening stations (Figure 1a). The PAT estimated position data showed that AR3 remained on the western part of the Agulhas Bank until about 18 April. She then moved rapidly eastwards and by 15 May had moved 824 km eastwards at a speed of 31 km day^{-1} (Figure 1a). The track indicated that she moved from Cape Agulhas through to Algoa Bay (26.119°E) then further northeast (28.556°E) before returning westward just prior to the tag's release (Figure 1a). The PAT tag of AR4 was detected at a position some 11 km SSE (147° true) of her release point 12 days after she had been released. The tag drifted westwards into the Atlantic Ocean. The premature release was caused by her moving from waters of $<$ 10–40m on 12–15 March and then descending to 56 m where the water temperature was a little more than 10°C on the 16 March. She remained at this depth and temperature until at least 24 March when her tag released due to the pre-programmed release limit. It is assumed that she died.

A total of four female and one male wild sharks (W3) were caught in the same vicinity and same time (0–3 days) as the aquarium-held animals were released each year. The first, W1, a 308-cm TL female, was caught and equipped with three types of tag in April 2005 (Table I). Her PAT tag was detected by ARGOS after 126 days near Port St Johns and only logged and transmitted reliable data from June 2005, possibly explaining the interrupted data stream between her release date and 2 June 2005. She moved past Algoa Bay, and beyond Coffee Bay to 30.234°E then moved up and down along the northern portion of the Eastern Cape coast (Figure 1b). W2's PAT tag was detected just north of Coffee Bay. She had travelled at least 970 km in 120 days. The PAT positioning software showed that she had remained between Struis Bay and Mossel Bay for about a month, but by 15 May she had moved 540 km in 24 days, at a rate of 22.5 km day^{-1}. The track revealed movement north of Port St Johns to 30.112°E (Figure 1b). This shark was caught thee years later by an angler at Struis Bay on 28 February 2009 and re-released. W3, an adolescent male, was equipped with an internal VEMCO coded tag (818) and a PAT tag. The PAT tag was detected on 17 May 2007 approximately 36 km northeast of Port Alfred. It beached but transmitted limited data. The tag was not recovered. The tag surfaced more than 10 weeks prematurely because the shark remained at constant depth (within 2.5 m) for more than 5 days – the time set for premature release. The surfacing position was approximately 684 km east of the shark release. A rate of movement of 13.7 km day^{-1} was estimated over the 50-day tracking period. W4 was caught on 28 March 2007 just east of Cape Agulhas, equipped with a PAT10 and an internal VEMCO coded tag (817) and released. Her PAT tag surfaced in Algoa Bay on 10 May 2007, a distance of approximately 562 km from the point of initial release near Cape Agulhas (Figure 1b). She moved at a speed of approximately 13 km day^{-1} over the 43 days. The premature pop-up was caused by her spending extensive time with little depth variation. The tag beached at Sundays River mouth in Algoa Bay, was retrieved and data downloaded by Wildlife Computers. The PAT positioning software showed that she had remained on the western side of the Agulhas Bank until about 10 April. She moved rapidly in the next 7 days covering approximately 238 km (34 km day^{-1}) then the next 5.5 days moving 164 km eastwards at 30 km day^{-1}. She was subsequently detected by listening stations at Port Alfred on 21 June 2007 and repeatedly recorded in Algoa Bay between October 2007 and January 2008 at six different VR2 listening station localities, suggesting that she was holding her position in the area during the austral summer of 2007/2008. W5, a female of 273 cm TL, was equipped with an internal VEMCO tag and a refurbished PAT tag. The PAT tag (apparently) failed to release, as neither position nor data were obtained from this tag. W5 was recorded by a VR2 listening station at Cape Recife, Algoa Bay on 4 July 2008, 4 months (113 days) after tagging (Figure 1b).

Comparison of horizontal movement patterns

All sharks, both aquarium-released and wild-caught, moved in an easterly direction. Mean bearings were estimated as 14.32° (95% CI = 2.57–25.19°) for AR1, 21.02° (9.22–28.96°) for AR3, 18.86° (10.22–26.59°) for W1, 36.42° (34.29–38.51°) for W2, and 12.80° (2.88–24.45°) for W4. The only statistically significant ($p < 0.05$) pairwise differences between bearings were noted for W2 and all other sharks as W2 was observed to move further eastwards up the coast that follows a northeast bearing.

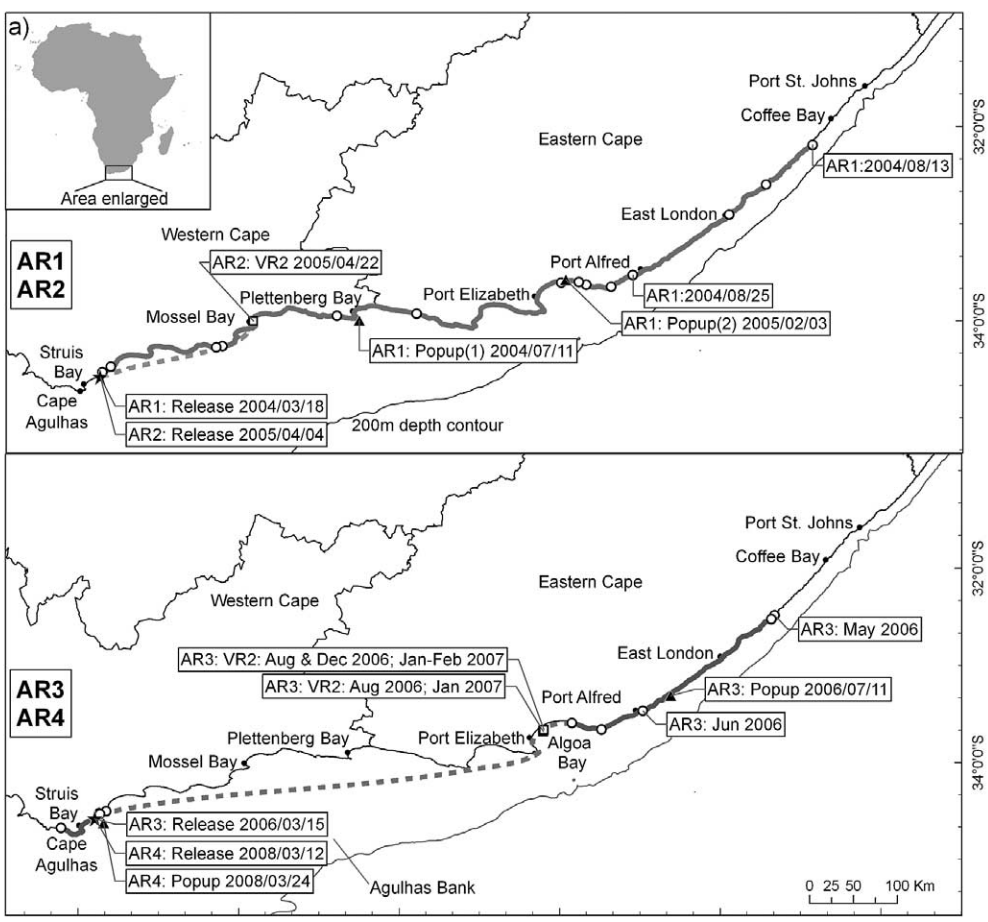

Figure 1a. Positions of PAT tag release (*), pop-up (▲) and intermediate localities (○) for four aquarium-released *Carcharias taurus* denoted as AR1, AR2, AR3 and AR4, together with both the most likely tracks (—) and the tracks with more than 550 km between positions (- - -). VR2 listening stations are denoted as □.

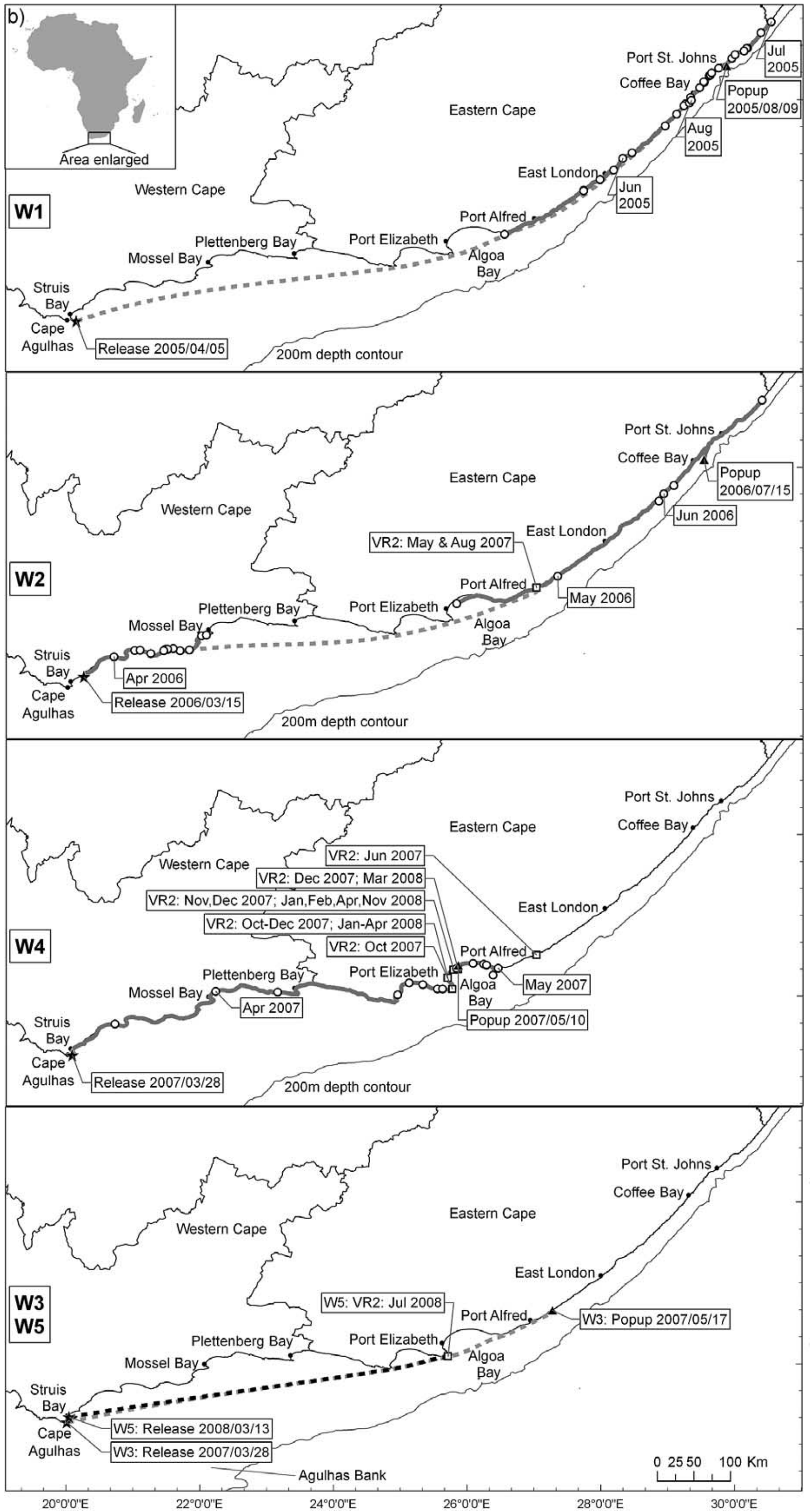

Figure 1b. Positions of PAT tag release (⋆), pop-up (▲) and intermediate localities (○) for five wild-caught *Carcharias taurus* denoted as W1, W2, W3, W4 and W5, together with both the most likely tracks (—) and the tracks with more than 550 km between positions (- - -). VR2 listening stations are denoted as □.

Comparison of vertical movement patterns

Both aquarium-released and wild-caught sharks showed a similar pattern of movement through the water column (Figure 2). Initially, while they were on the western part of the Agulhas Bank, most sharks remained in waters shallower than 20 m. Later, they penetrated into water as deep as 80 m. Deeper swimming often coincided with their arrival on the eastern part of the Agulhas Bank (Figure 1). Water temperature may have been influential in constraining their movements and the temperature ranges they experienced were generally similar with means of 15.3–18.4°C (Figure 3) and ranges of approximately 10–22°C. The temperature data from AR4 were the most varied and apparently bimodal. This was caused by her initially spending days above the thermocline then penetrating deep waters off Cape Agulhas and she remained at 10°C for more than 5 days. Because these data do not reflect normal movement patterns, they are not illustrated in Figure 3. She had probably died and sank to the sea floor and the tag popped off as programmed for extended period of time at one depth.

The detailed track from the raw data of the recovered PAT tag from W4 was analysed to better understand the summarized satellite data obtained from the other tags. It showed that she initially swam into waters of nearly 30 m then moved into shallower water at the end of March (Figure 4a). The pattern indicated the alternating depth use between shallow and deeper waters. During April, she spent time in very shallow water (< 10 m) to a maximum depth of 84 m around 28 April, when in the vicinity of Cape

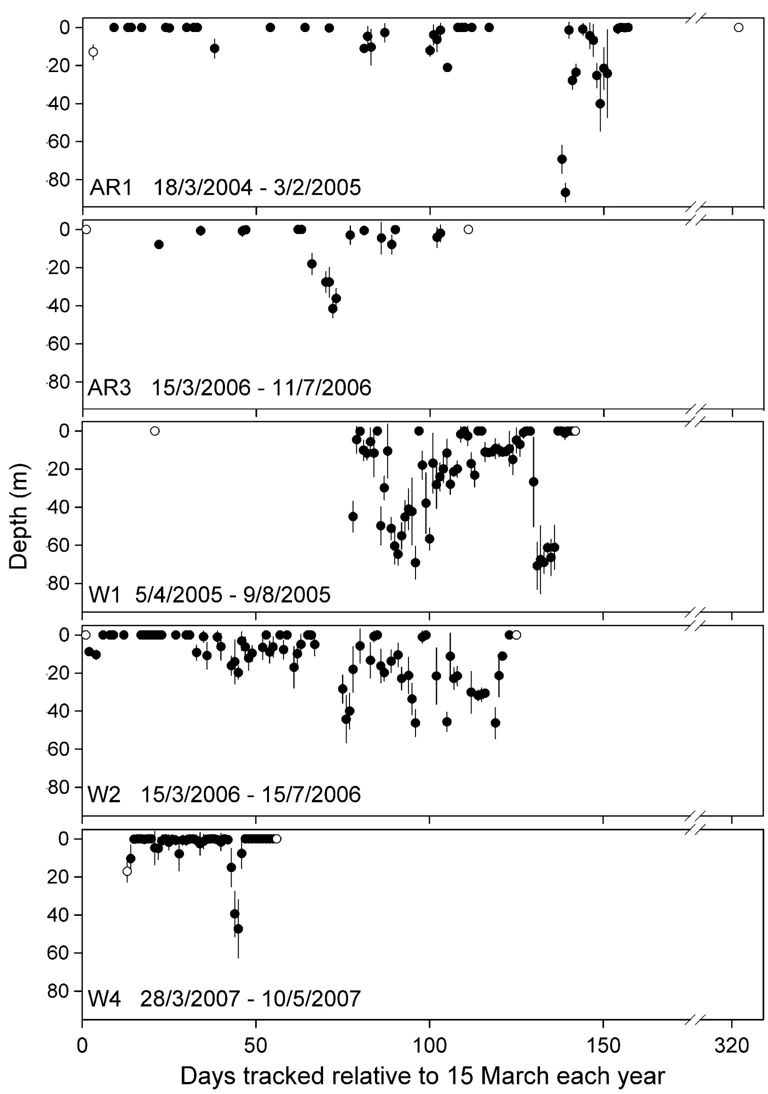

Figure 2. Mean daily depth (±SD) usage over time for five *Carcharias taurus* obtained from ARGOS satellite transmissions. For each shark, data are plotted from the date when the PATs were deployed to when they popped up. Deployment and pop-up dates are shown using open symbols. The AR1 pop-up date shown is that reported by ARGOS. The actual release from the shark was most likely to have occurred earlier.

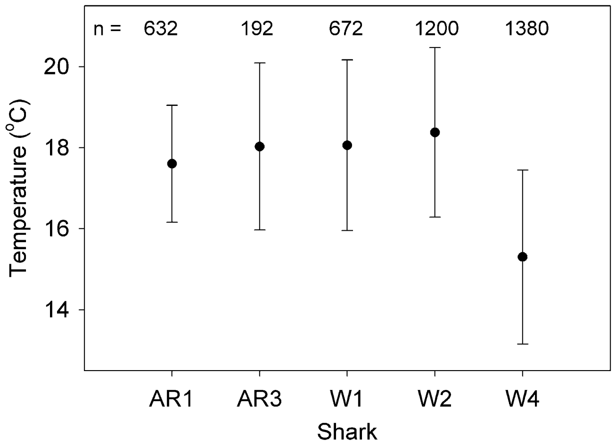

Figure 3. Mean (±SD) ambient water temperatures from two aquarium-released (AR) and three wild-caught (W) *Carcharias taurus* collected every 6 h.

Recife, Algoa Bay. In May, she moved into shallow water inside Algoa Bay where she remained at approximately constant depth for more than 5 days. Her ultrasonic tag was subsequently detected by a VR2 listening station at Port Alfred on 21 June 2007. She later moved back to Algoa Bay where she was detected in November and December 2007 and January to March, and in November 2008 (Figure 2b).

Vertical ascents (or rises) of W4 to the surface occurred throughout the track, but were more obvious when moving from deep waters to the surface and then down again. Three rises to the surface were recorded on 26 April 2007 (Figure 4b). The number of rises between her release and tag pop-off totalled 41 by night, 16 by day, 5 during dawn twilight and 3 during sunset twilight during the 42 days between release and pop-off, an average of 1.5 rises day^{-1}.

Vertical swimming activity in the water column (shown in the depth record of the tag) varied considerably, but was most commonly recorded at night. The tracks could be indicative of movements around pinnacles of reefs, or chasing midwater prey. Although higher vertical activity patterns were more frequent at night, they were not confined to night

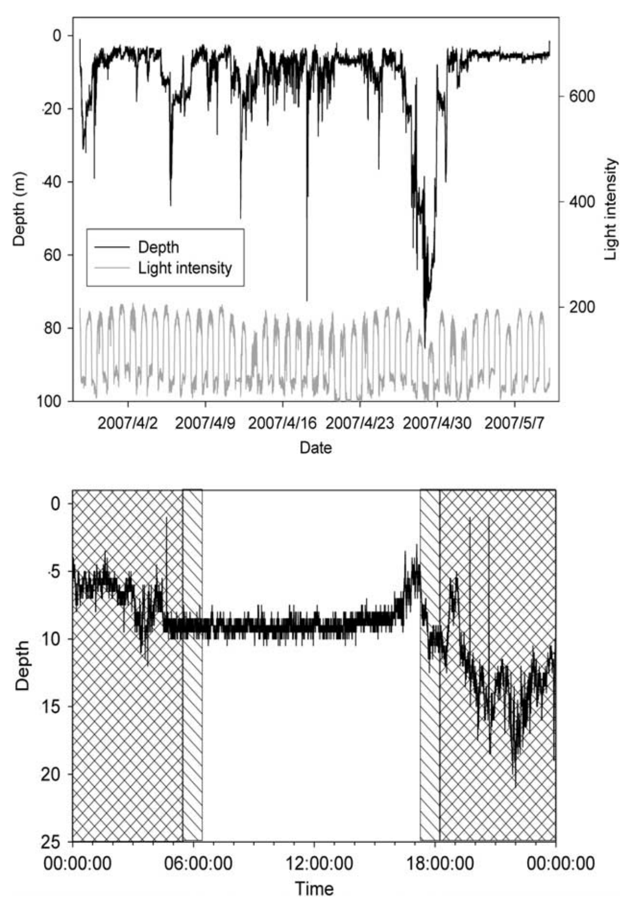

Figure 4. Depth track of a wild-caught *Carcharias taurus*, W4, from release to pop-up (upper panel) including light level reading to indicate diurnal changes. The lower panel illustrates the depth record on 26 April. The single-hatched areas denotes dawn and dusk, the white area day, and the cross-hatched area night.

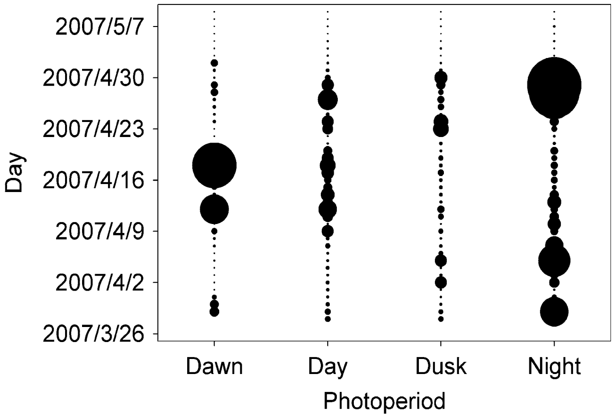

Figure 5. Bubble plot of the standard deviations per time of day over the entire track of a wild-caught *Carcharias taurus*, W4, indicating periods of vertical displacement from the mean depth of that period.

time. Significant differences were found in the variability in depth use with photoperiod ($p < 0.01$) for all subsampled data sets, with variability the highest at night (Figure 5).

Analysis of the raw depth and temperature data from W4's tag provided 367,173 data points with the mean depth of 11.33 m (range = 1–86, SD = 11.57) and mean temperature of 15.7°C (range = 9.7–20.55, SD = 1.97).

Differences in tag reporting

Of the nine sharks tagged, there were considerable differences in tag reporting with the number of complete days of reported data ranging between 4 and 74 days despite the length time between deployment and pop-up ranging between 10 and 315 days, although the latter was probably the first detection of the tag from a beach following a storm, rather than release from the shark. For those tags where sufficient data were collected, tag reporting was 44 days for AR1, 19 days for AR3, 65 days for W1, 74 days for W2, and 44 days for W4 (Figure 1). Data reporting rates ranged between 18 and 90%.

Discussion

Excluding the two animals that died at the aquarium prior to release because of inadequate supply of aerated water during surgery, only one shark died post-release. The other three aquarium-released sharks tagged and released in this study survived in the wild. Both the surviving aquarium-released and wild-captured sharks swam distances of hundreds of kilometres all in an eastward direction after release. While the PAT tag data showed that both release groups spent the majority of time in shallow waters there was evidence for deep-water (80 m) forays to mid-shelf water. One wild-caught shark also exhibited rapid ascents, possibly to gulp air. Both wild-caught and aquarium-released sharks were eurythermic inhabiting a wide range of temperatures that ranged between 10 and 22°C.

All the aquarium-released and all the wild-caught sharks survived for periods of up at least a month. The one exception was AR4, which probably died and sank to the bottom in cold (10°C) waters. While the cause of death is unknown, anthropogenic causes unrelated to this study cannot be ruled out, as boat-based commercial fishermen often kill sharks that attack prized teleosts (Dicken et al. 2007). Predation is also possible, as the area of release is also inhabited by white sharks (*Carcharodon carcharias*) that are known to predate on *C. taurus* (Cliff et al. 1989; Compagno 2001). Without additional data, however, the cause of death can only be speculated.

Both the aquarium-released and wild-caught sharks showed similar eastward movement patterns that were in agreement with published data. Eastward movement from the Agulhas Bank was described by both Bass et al. (1975) and Dicken et al. (2007). Our study showed that *C. taurus* also exhibits 'station keeping' behaviour (*sensu* Dingle 1996) from the time of tagging in March and April to then rapidly moving eastwards. The rate of movement was variable between individuals. Whether this movement may be described as a migration (*sensu stricto*) is moot because there may also be temporary delays and deep active diving activity (possibly feeding activity) over the period of moving east. Dingle (1996) suggested that migration typically is not interrupted by feeding or other events, so this movement pattern may not fit that definition. Nevertheless, there are phases of movement that are rapid, followed by either station keeping or less directed movements. Dicken et al. (2007) described the most rapid rate of movement for juveniles to be 5.6 km day^{-1}. Two other individuals in that study moved at 2.7 and 1.4 km day^{-1}, but most sharks were slower than 1 km day^{-1}. Adults generally moved faster and further. While the highest rate of movement recorded by Dicken et al. (2007) was 29.5 km day^{-1} the rates of movement recorded from release to tag pop-up in this study were slightly lower with a maximum of 13.7 km day^{-1} in wild-caught individuals. The highest rates of movement were recorded 43–50 days post-release in April and May, during their movement from Cape Agulhas eastward towards the Eastern Cape. The beached tag from AR1 unsurprisingly showed the slowest rate of movement between release and first transmission from a beach during a storm event (1.3 km day^{-1}). The positions calculated from the positioning software were considerably faster at the beginning of migration up to 36.7 km day^{-1} in the case of AR3 and 34 km day^{-1} for W3. Data from spaghetti dart tags returns include both the movement phase and prolonged station keeping and are consequently not accurate for estimating speed of movement. For returns over a longer duration, the spaghetti-tagged sharks may have moved in any direction and the speeds calculated are consequently underestimates. AR1's southward movement after release from bather protection shark nets (prior to her capture and placement in TOA – see Appendix 1) of 1369 km in 91 days is 15 km day^{-1} and was likely to have been a rapid southwestward migration, possibly as a pregnant female moving to the nursery areas (Smale 2002; Dicken et al. 2007).

The geographic location using the longitude position and depth record of the day technique of West & Stevens (2001) and Bruce et al. (2006) suggested that the sharks follow inshore contours of the coast. This assumption is supported threefold. First, these sharks were recorded on inshore VR2 listening stations; second the pop-up localities were often close to shore, causing the tags to strand; and third, this species is frequently caught by shore-based fishers (Smale 2005; Dicken et al. 2006c). Although slightly shorter distances could have been swum had sharks missed inner bay localities, this would imply that they had swum in upper layers of the water column over deep water, which would have made them more vulnerable to predation by other shark species. Nevertheless, this hypothesis could be tested using a wider spread of acoustic listening stations positioned across the continental shelf.

This study provided new insights into the behaviour of *C. taurus* in the wild. Both aquarium released and wild-caught sharks covered a wide range of depths, but often stayed for moderately long periods (days) at specific depths either in the shallows or in mid-shelf waters. They did not exhibit oscillatory, or yo-yo, swimming commonly recorded for pelagic sharks when they regularly change depths from the surface to deeper waters. This has been reported for mako *Isurus oxyrinchus* (Carey & Scharold 1990), blue *Prionace glauca* (Klimley et al. 2002), and white *Carcharodon carcharias* (Bruce et al. 2006) sharks. This suggests that they acclimate to a particular depth and temperature range and this may be related to choosing caves and suitable reefs for extended stays. One shark did exhibit periodic up-and-down swimming behaviour over periods of hours. Although vertical swimming was noticed during the day and night, it was more commonly recorded at night.

The temperature regimes through which the sharks travelled were from 9.8 to 22.4°C and reflect, in part, the depth range encountered ranging from surface waters to depths of 108 m. The thermal tolerance may influence the behaviour and movement of this species and in the study area, coastal temperatures vary considerably seasonally and inter-annually (Schumann 1999; Roberts 2005). Although raggedtooth sharks were previously known to move into mid-continental shelf depth waters (Bass et al. 1975; Smale 2002), the pattern of this movement and the time spent at depths beyond normal encounters by SCUBA divers presents a different perspective of habitat of this shark. It also provides an alternative perspective to earlier findings of mid- to outer continental shelf prey (e.g. Merluciidae and Ophidiidae) in their stomach contents (Smale 2005). Knowledge of its habitat use will further assist designing research surveys to assess the stock size of this species.

The rapid ascent to the surface described in this study might be the first time this behaviour has been described for this shark naturally beyond the influence of humans as Bruce et al. (2005) recorded surface rises during manual tracking *C. taurus* off the east coast of Australia. This is attributable to their unique behaviour of air swallowing that was originally described by Bass & Ballard (1972) as a form of buoyancy control. Not frequently observed at sea, this is the first support of this behaviour using this technology. Furthermore, it was noted that rises may happen repeatedly in a single day and that the sharks may swim from depths of tens of metres, then return to those depths where buoyancy derived from swallowing air would be considerably reduced because of the higher ambient pressure at depth. The alternative interpretation that it may be in pursuit of prey seems less likely given that these rises were done at rates of about 0.3 m s^{-1} and on reaching the surface they immediately returned to the bottom. Feeding on surface prey is usually related to associating with schooling prey prior to and following attack (Smale, unpublished data).

Although a large proportion of the vertical movements in the water column were recorded at night, this activity was also found by day. This probably reflects the behavioural plasticity of this apex predator to different prey that become available at different times. Direct observation of hunting in this region has been made by day and night (Smale et al. 2001; Smale, unpublished data).

The PATs and acoustic tags used in this study facilitated the comparison of movements between wild-caught and aquarium-released individuals. The inclusion of ultrasonic tags augmented the information obtained, and in some cases provided the only data, when the PAT tags failed to report. The reason for the differences in tag reporting was most likely because the sharks were inshore and the tags were stranded and unable to transmit. An alternative explanation could have been grooming behaviour that these sharks demonstrate whereby sharks rub their backs and flanks on sandy areas (Smale, personal observation), possibly damaging the aerials and preventing data transmission (Braun, Wildlife Computers, personal communication).

To conclude, this study has shown that aquarium-released sharks reintroduced into the same population from which they originated after varying periods of captivity use the habitat in a similar way to wild-caught sharks. Released captive animals generally survived well after release. It is noteworthy that one individual (AR3) held in two different aquaria after initial capture as a 0-year-old also behaved similarly to other sharks, suggesting that this is an innate behaviour. The eastward movement pattern was observed in both wild-caught and aquarium-released animals and it is likely that these sharks had successfully integrated back into the wild population in that they went to well-known raggedtooth shark aggregation sites. The main caveat to the possible practice of releasing aquarium-held sharks is that care has to be taken that disease is not introduced by aquarium-released specimens, as has already been discussed by the IUCN recommendations (Hall 2003). Although Hall (2003) suggests that aquarium releases should be at the site of capture, this study suggests that provided release is within the normal range of movement of the particular population from which it was removed, it will immediately return to apparently normal behaviour and movement patterns.

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Appendix 1: Additional information pertaining to *Carcharias taurus* released from Two Oceans Aquarium

AR1, or 'Maxine', was first captured in the KwaZulu-Natal Sharks Board bather protection nets off Durban on 4 August 1995, tagged with a spaghetti tag and released. She was recaptured in a tag-and-release fishing competition on October 1995 off Struis Bay. She had travelled 1369 km in 91 days at a rate of 15 km day^{-1}. She was trucked to Cape Town and was on display in the predator tank for 9 years until 18 March 2004.

AR2, or 'Val', was originally caught at Arniston near Struis Bay in 1998. She was on display at the TOA for seven years.

AR3, or 'Dee', was originally caught on 4 March 1992 at Dynamite Jetty, Algoa Bay where she measured 105 cm TL (72 cm PCL) and weighed 6.4 kg. She was a young of the year shark that had likely been pupped between October and December 1991. She was injected with 2 cc of oxytetracycline and a passive internal transponder (PIT) tag numbered 0021 3E28 and placed on display at the Bayworld Aquarium. On 28 October 1995 she was donated to TOA and transported to Cape Town. At this time she measured 216 cm TL and weighed 72 kg. She remained in the TOA display for 11 years until March 2006.

AR4, or 'Elle', was caught at Struis Bay and displayed at the TOA for three years between April 2005 and March 2008.