

Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia

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Abstract Tiger sharks are important predators in the seagrass ecosystem of Shark Bay, Australia. Although sharks appear to return to a long-term study site within the Eastern Gulf periodically, the extent of their long-term movements is not known. Five sharks fitted with satellite transmitters showed variable movement patterns. Three sharks remained within the Shark Bay region and another made a 500 km round-trip excursion to oceanic waters northwest of the bay. These four sharks showed relatively low displacement rates relative to sharks tracked over shorter time periods, suggesting that sharks move through large home ranges that include Shark Bay. Although no reliable position fixes were obtained for the fifth shark, we were able to use the timing of satellite uplinks and the position of the satellite to determine that it had moved at least 8,000 km to the coastal waters of southeast Africa in 99 days—the longest recorded movement by a tiger shark. This movement and previously documented trans-Atlantic movements suggest that tiger shark

populations may mix across ocean basins and that tiger sharks are subject to anthropogenic effects at great distances from protected waters. Finally, our method for using single satellite uplinks may be useful in estimating movements for wide-ranging species that rarely provide high quality location estimates.

Introduction

Top predators are widely assumed to play important roles in marine ecosystems through top-down effects on the distribution and abundance of their prey. Sharks are apex predators in many marine ecosystems, and may be important in structuring marine communities (see Heithaus 2004). Shark populations, however, appear to be declining due to overfishing (e.g. Baum et al. 2003, 2004), making studies of their movements and role in marine ecosystems a high priority.

We have used the relatively pristine seagrass ecosystem of Shark Bay, Western Australia as a model system for elucidating the effects of tiger sharks (*Galeocerdo cuvier*) on multiple prey species. For example, pied cormorants (*Phalacrocorax varius*), bottlenose dolphins (*Tursiops aduncus*) and dugongs (*Dugong dugon*) give up foraging opportunities in shallow seagrass habitats where tiger sharks are most common (Heithaus and Dill 2002; Heithaus et al. 2002; Heithaus 2005; Wirsing 2005). At smaller spatial scales, dolphins and dugongs reduce their use of the more dangerous interior portions of shallow banks relative to edge microhabitats to reduce their probability of being captured by tiger sharks (Heithaus et al. 2006; Heithaus and Dill 2006; Wirsing et al. 2007). These interactions between sharks and their prey may

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cascade through the community (e.g. to the prey of cormorants and dolphins and possibly the seagrass upon which dugongs graze; Dill et al. 2003) and, ultimately, play a crucial role in structuring the Shark Bay ecosystem.

An interesting aspect of the Shark Bay ecosystem is marked seasonal variation in tiger shark abundance, which is elevated between September and May and reduced from June to August (Heithaus 2001; Wirsing et al. 2006). While few (<5%) of the 523 sharks tagged in the bay from 1997 to 2005 have been recaptured, acoustic monitoring suggests that sharks regularly return to the location where they were tagged (Heithaus 2001; Wirsing et al. 2006). However, the nature and extent of tiger shark movements when they leave the ~150 km² study area in the Eastern Gulf of Shark Bay are poorly understood. The long-term movements of tiger sharks that use Shark Bay are of great interest because they are linked to the tiger shark's potential effects on its prey and the possibility that these apex predators may encounter fisheries outside of the protected waters of the Shark Bay World Heritage Area.

Satellite telemetry has been used to determine the movements of many species of marine species including marine mammals, sea turtles, sea birds, and several species of large sharks (e.g. white sharks *Carcharodon carcharias*, Bonfil et al. 2005; salmon sharks, *Lamna ditropis*, Weng et al. 2005). For species that spend a considerable amount of time at the surface, position-only tags, which must be out of the water to obtain a position estimate, may be useful for determining movements over periods of weeks to months. For example, salmon sharks and blue sharks (*Prionace glauca*) fitted with position-only tags transmitted locations for weeks to over a year (Weng et al. 2005). Tiger sharks tracked with acoustic telemetry in Shark Bay spend considerable time in surface waters (Heithaus et al. 2002), suggesting that position-only tags may provide important data on the movements of this species.

Position-only tags link through the Argos system, and depending on the timing and number of messages received by a satellite during an overflight provide fixes of variable accuracy that are labeled with a "location class" that provides an estimate of position error (see Table 1). The most accurate position estimates—location class 3—usually fall within approximately 300 m of the actual tag location, while the poorest location class that can calculate a position, "B", is only accurate to around 10 km (Hays et al. 2001a). Argos also provides data on the time at which tags are detected by satellites, and the identity of the satellite making the detection, when no position can

be calculated (location class Z). While advances in data analysis systems helped to provide sufficient data for air-breathing species tracked with early satellite tags (e.g. Hays et al 1991), advances in tag technology have limited the need for such techniques. However, many species that spend brief periods at the surface or remain largely submerged (e.g. large fishes) may provide few high-quality positions and many location class "Z" uplinks, necessitating the development of methods to make use of these traditionally discarded data.

The objectives of this study were to assess the utility of position-only satellite telemetry for studies of large coastal sharks, like tiger sharks, and to gain preliminary insights into the movements of tiger sharks that use Shark Bay over time periods of days to months. Also, we developed a technique for using Argos location class Z data to enhance datasets for species that rarely surface.

Methods

During March 2002 and April–May 2004, we deployed position-only tags (Wildlife Computers SPOT4, Telonics ST-10) on the first dorsal fin of five tiger sharks captured in the Eastern Gulf of Shark Bay (Table 1). SPOT4 tags with semi-rigid antennas were attached to neoprene-lined plexiglass fin-mounts. These mounts were affixed to the sharks so that the saltwater switch, which activates the tag when it breaks the surface of the water, and the base of the antenna were above the top of the dorsal fin (Fig. 1). This configuration maximized the probability that the tag would transmit when the shark was near the surface. Mounts were designed so the drag from the tag was borne primarily by the leading edge of the fin rather than by the corrodible bolts that held the mount to the fin. The ST-10, with a semi-rigid antenna, was attached to the leading edge of a syntactic foam fin mount that slid over the leading edge of the dorsal fin and was held in place by two corrodible bolts. The tag protruded above the mount so that the saltwater switch and base of the antenna were near the top of the dorsal fin.

Minimum travel speeds were calculated by (1) dividing the sum of all straight-line distances traveled between successive points by the time between the deployment of the transmitter and the last reliable position estimate or (2) by calculating the speed for individual moves between successive points over 90 km apart which allows reasonable accuracy given the error in tag locations provided by the ARGOS system (see

Table 1 Details of satellite tag deployments on five tiger sharks in Shark Bay, Australia

	Model	Date	S	TL	D	T	DP	ARGOS location class					A	B	Z
								3	2	1	0	0			
Uplinks for fix								≥4	≥4	≥4	≥4	≥4	3	2	1
Published accuracy (km) ^a								<0.15	0.15–0.35	0.35–1.0	>1.0	>1.0	N/A	N/A	–
Field accuracy (km; Mean±SD) ^b								0.27 ± 0.20	0.54 ± 0.40	1.33 ± 1.35	10.10 ± 12.31	0.99 ± 1.36	0.99 ± 1.36	7.00 ± 6.92	–
Shark 0201	ST-10 ^c	19 Mar 02	M	345	12	628	132	0	0	0	1	1	1	1	0
Shark 0401	SPOT4 ^d	26 Apr 04	F	270	21	136	69	0	0	1	0	0	0	2	4
Shark 0402	SPOT4 ^d	1 May 04	F	332	67(83)	505	89	0	1	1	0	0	2	2	26
Shark 0403	SPOT4 ^d	1 May 04	F	362	0(99)	–	8000 ^e	0	0	0	0	0	0	0	2
Shark 0404	SPOT4 ^d	1 May 04	F	291	14(24)	402	137	0	1	3	2	4	7	7	15

S sex, TL total length, T total distance (km) along track, DP distance (km) between release point and last position fix (displacement), D days between release and final position fix (Argos location class 0, 1, 2, 3, A, B); Number in parentheses is days between release and final transmission of Argos location class Z uplink;

^a Argos (1996)

^b Hays et al. (2001a)

^c Telonics (Mesa, AZ)

^d Wildlife Computers (Redmond, WA)

^e Estimated based on shortest distance that could have been traveled based on satellite locations at the time of uplinks (see text)



Fig. 1 SPOT4 tag attached to a tiger shark in Shark Bay. Note that the saltwater switch and antenna are positioned above the dorsal fin to maximize the probability that the tag will transmit when the shark is near the surface

Hays et al. 2001a). When multiple position fixes of ARGOS location classes worse than “1” were received within a 12 h time period, we calculated and plotted a single average position for the time block.

For every position estimate, ARGOS provides two potential positions. Often, one position is easily eliminated because the distance between successive points would require unrealistic swimming speeds or it is on land. However, in some instances it is not possible to eliminate widely separated points because both are equally plausible based on known swimming speeds of tiger sharks (e.g. Holland et al. 1999; Heithaus et al. 2002). In 43 of 44 cases (97.7%) where one position could be definitively eliminated, the correct position was the primary location estimate, suggesting that in ambiguous cases, the primary location was likely to be correct. Location class “Z” hits that occurred close to the time a reliable position was recorded (including hits when the transmitters were onboard research boats before deployment) also were used to help discriminate between widely spaced possible locations. We used Satscape 2.0.2 (<http://www.satscape.co.uk>) to determine the area being monitored by particular satellites (i.e. “footprints”) when they received a signal from a tag. The footprint of all satellites estimated by Satscape when location class “Z” uplinks occurred was consistent with the known position of the tag in all cases where the tag’s position was known with a reasonable degree of certainty ($n = 51$). Therefore, we used Satscape to determine the area in which one shark for which there were no reliable position estimates (0403) was located at the time of two location class Z uplinks. Due to the huge error (1,000 s of km) in these positions, we did not use data from this individual in further analyses.

Results and discussion

All tags reported, but they varied greatly in the number and quality of location estimates (Table 1). Tags provided reliable position fixes for 0–67 days, and in general the number of reliable fixes declined over time. The duration of useful tag life on tiger sharks was shorter than that on more pelagic salmon and blue sharks (Weng et al. 2005). The declining quality and frequency of location fixes could be due to several factors. Battery failure is unlikely because of the low number of transmissions. Also, a change in the amount of time that sharks spent at the surface seems unlikely over the time scales at which signals were lost, but may account for variability among individuals. Most likely, tags experienced fouling of salt water switches. Four of five wildlife computers SPOT3 transmitters deployed on loggerhead turtles (*Caretta caretta*) in Shark Bay ceased transmitting long before battery failure (unpublished data). Three of these were observed after tag failure and were covered in fouling organisms; one also had lost its antenna. Two of these turtle tags resumed transmitting after the removal of fouling organisms (unpublished data). It is unlikely that the antennas of transmitters on tiger sharks were lost by rubbing because no sharks ($n = 44$) fitted with animal-borne video cameras attempted to remove these much larger devices (Heithaus et al. 2001, 2002).

Three tiger sharks remained within the Shark Bay region throughout the transmission period of their tags (Fig. 2). A fourth individual remained in Western Australian waters, moving ca. 400 km north before returning toward the Shark Bay region (Fig. 3), although the distance may have been somewhat shorter given that the furthest point north is a location class “B” position. This resulted in a round-trip of ca. 500 km in 5 days by this 343 cm shark. Swimming speeds during individual moves (ca. 4 km/h) were similar to those reported for a slightly larger (ca. 380 cm TL) white shark (4.7 km/h) making a transoceanic migration (Bonfil et al. 2005) and average speeds of six tiger sharks tracked in open waters off Hawaii (3.85 km/h \pm 0.45 SD; Holland et al. 1999).

Swimming speeds and displacement rates of tiger sharks tracked with acoustic telemetry (Heithaus et al. 2002) were significantly greater than those calculated by satellite telemetry ($t_{47} = 7.9$, $P < 0.0001$ and $t_{47} = 7.6$, $P < 0.0001$, respectively; Fig. 4). This disparity suggests that while sharks manifest directional movement over periods of hours (Heithaus et al. 2002), they may restrict their movements and remain in large home ranges (at least 1,000 s of km²) over periods of days to weeks, resulting in less straight-line movement.

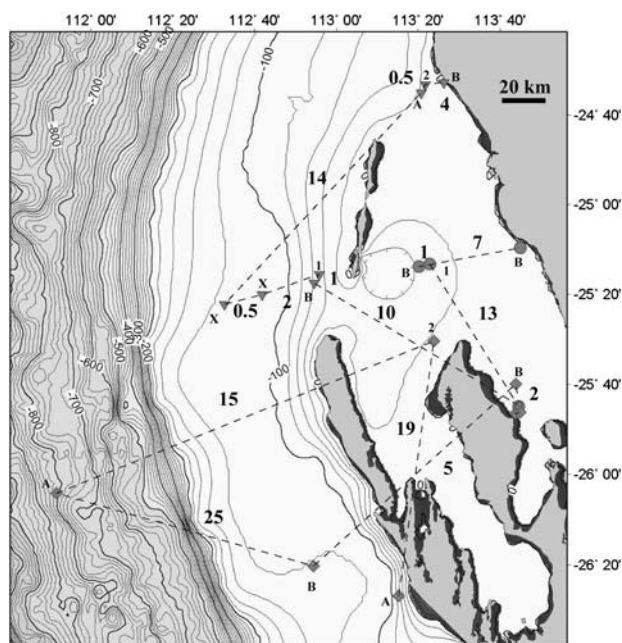


Fig. 2 Tracks of tiger sharks 0401 (circles), 0402 (diamonds), and 0404 (triangles). Multiple locations within a 12 h period with location qualities between B-1 were averaged into a single position. Numbers next to lines are the number of days between position fixes and smaller letters and numbers next to estimated positions are location classes (X = average of two positions)

Although the need to use low-quality position fixes may increase estimates of home range size due to position errors (e.g. Hays et al. 2001b), the low rate of reliable position fixes may have led to an underestimate of the area over which tiger sharks moved over a period of weeks as well as their sustained swimming speeds. When many days passed between reliable position estimates, sharks may have traveled hundreds of kilometers outside of the Shark Bay region, only to return. For example, missing one position fix from 0201 would have greatly reduced the estimated range size, distance traveled, and swimming speed. Our technique, using low-quality uplinks, could be used to gain further insights into home range size of species where good-quality uplinks are rare but movements occur over large distances. If single uplinks are obtained over relatively short time periods, or by multiple satellites, plotting the footprints of satellites and determining their overlap could allow reasonable position estimates in some instances. This technique may be of particular use for sharks and marine mammals that surface only briefly.

It is interesting to note that several sharks traveled into deep pelagic waters of the Indian Ocean before moving back into shallow coastal waters. Four of five individuals moved into waters over 100 m depth and two moved into waters over 800 m depth. Relatively

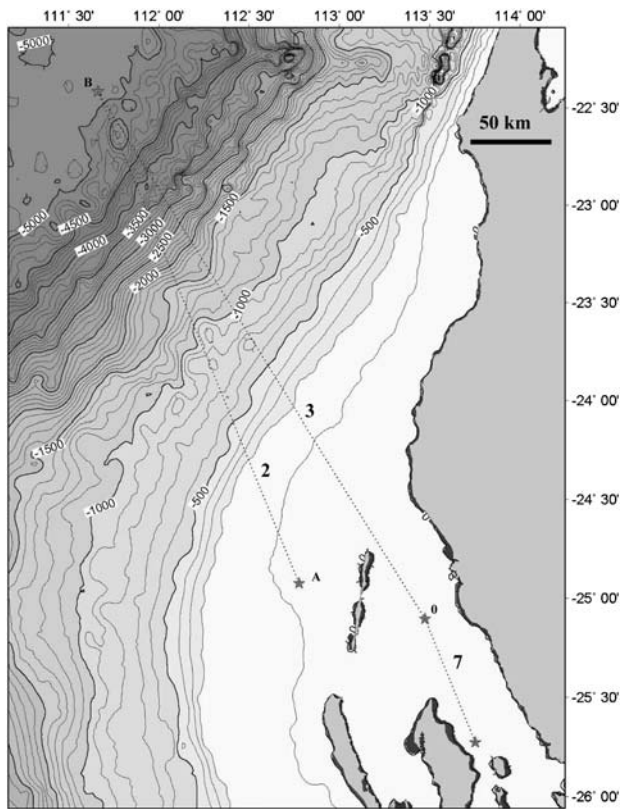


Fig. 3 Track of tiger shark 0201. Argos location classes of each fix are given by *numbers* and *letters* next to each point and the numbers next to movement lines indicate the number of days between position fixes. The extent of the northward movement may be overestimated slightly due to the relatively poor quality of the point furthest to the north (see Table 1)

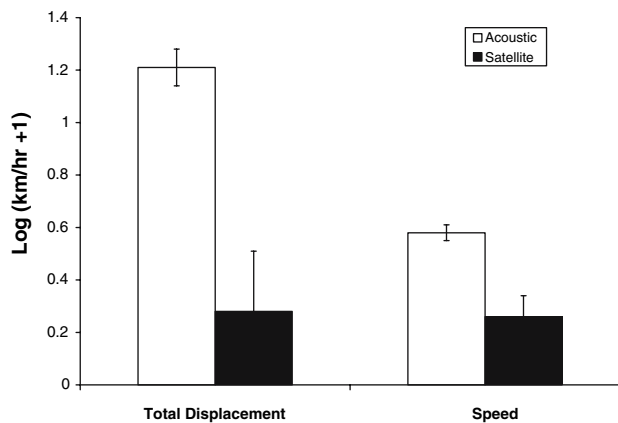


Fig. 4 Average swimming speed and displacement rates (straight-line distance between initial tagging and final position divided by total deployment time) for tiger sharks fitted with satellite tags compared to short-term acoustic tracks (Heithaus et al. 2002). Note that at the longer time scale of satellite position fixes average swimming speeds and total displacement per hour were lower than at shorter time scales. *Error bars* represent 95% confidence intervals

straight-line movements from coastal to offshore habitats have been observed for tiger sharks captured off Oahu, HI which transited deep waters to reach offshore banks (Holland et al. 1999). The tiger sharks in this study, however, did not use offshore banks, and most quickly returned to shallower coastal waters.

Previous studies have hypothesized that tiger shark movements over large temporal scales in Shark Bay may mirror those made by dugongs, which appear to be an important prey item for tiger sharks in the study area (Heithaus 2001). The results of the present study do not allow us to test this hypothesis, but we would not expect sharks to move into pelagic waters if they were following dugong movements because dugongs remain largely in coastal waters during their migrations (Gales et al. 2004). Instead tiger sharks may simply rove over large areas at long temporal scales, with restricted movements over small temporal scales in areas of high prey density. For example, tiger sharks inside the primary Shark Bay study area select habitat patches (1,000 s of m) and microhabitats within patches (100 s of m) that have high prey density, but quickly transit out of the study area (Heithaus et al. 2002, 2006), often returning to the general location at a later date (Heithaus 2001).

Shark 0403 showed a remarkably different pattern of movement than the other individuals. No reliable position estimates were obtained, possibly due to the shark spending little time near the surface, which has been reported for tiger sharks in other locations (e.g. Hawaii, Holland et al. 1999). However, two uplinks from the tag after 37 and 99 days show that the shark moved from Shark Bay to at least waters off the southeastern coast of South Africa (Fig. 5). The minimum travel distance for this 362 cm female was 8,000 km, requiring a swimming speed of ca. 3.5 km/h. Although this is the longest movement recorded for a tiger shark, tiger sharks also have been recorded crossing the Atlantic Ocean. Several tiger sharks tagged off the northeastern USA have traveled more than 6,500 km to the western coast of Africa (Kohler et al. 1999, N. Kohler, personal communication). Similarly, a satellite-tagged white shark traveled from South Africa to waters off the coast of Western Australia and then returned to South Africa (Bonfil et al. 2005). The long-distance east–west movements of these large sharks contrast with movements of many other oceanic migratory species, including many species of sharks, marine mammals, and leatherback sea turtles (*Dermochelys coriacea*; McMahon and Hays 2006), which tend to move north and south seasonally. The reasons for, and relative frequency of, long-distance east–west movements of tiger and white sharks remain unclear.

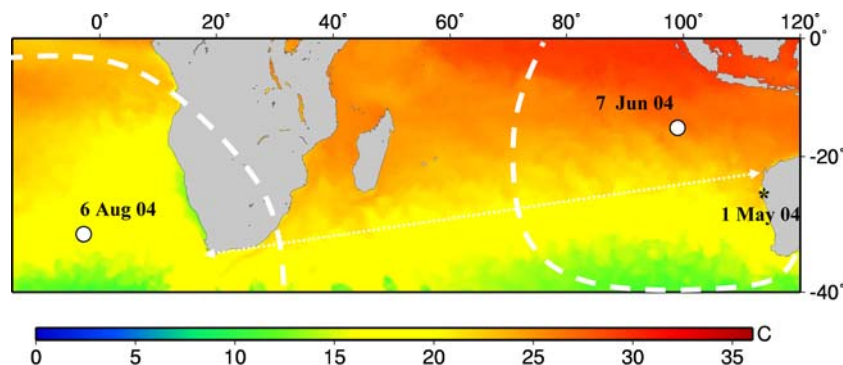


Fig. 5 Position on the earth directly below satellites (white dots) and the approximate outer boundary of their detection range (dashed lines) at the time of location class “Z” satellite uplinks with tag 0403. Despite the enormous potential area over which the shark could have been located at the time of uplinks, the shark traveled at least to the waters of eastern South Africa. The release

point (Shark Bay) is indicated with an asterisk. The dashed arrow indicates the starting and ending points (South Africa) and turnaround point (Western Australia) for the trans-oceanic migration of a white shark (see Bonfil et al. 2005 for actual track). Shading indicates average SST for July 2004

Long-distance movements of tiger sharks across open ocean habitats have important implications for the management of tiger sharks and possibly their population dynamics. First, because female tiger sharks may move across ocean basins, population subdivision may be low. However, genetic studies are required to investigate this possibility. Second, tiger sharks moving over such great distances could potentially be exposed to commercial fisheries at a great distance from the areas where they are captured or protected. For example, while tiger and other large sharks are protected from commercial fishing in Western Australian waters from 26°30'S latitude north the North West Cape, they may rove far from these areas into unprotected open-ocean waters and limited-entry fisheries north and east of the exclusion zone. Thus, even the World Heritage area of Shark Bay could be detrimentally impacted by pelagic fishing operations, and the implications of reported, and ongoing, declines in large shark populations, (e.g. Baum et al. 2003, 2004) for ecosystems far removed from areas where sharks are taken should be considered.

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