Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean

J. M. Brunnschweiler*†, H. Baensch‡, S. J. Pierce§ and D. W. Sims¶

*Institute of Zoology, University of Zurich, Winterthurerstrasse 190, CH–8057 Zurich, Switzerland, ‡The Open University, Walton Hall, Milton Keynes MK7 6AA, U.K., §Manta Ray & Whale Shark Research Centre, Tofo Beach, Mozambique, ¶Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, U.K. and ||Marine Biology and Ecology Research Centre, School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, U.K.

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A whale shark *Rhincodon typus* satellite tagged off the coast of Mozambique showed a highly directional movement across the Mozambique Channel and around the southern tip of Madagascar, a minimum distance of 1200 km in 87 days. Dives to depths well into the mesopelagic and bathypelagic zones (1286 m maximum depth) were recorded in a bathymetrically non-constraining habitat. The water temperature range recorded during the fish’s movement was 3.4–29.9°C.

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Whale sharks *Rhincodon typus* Smith play an important role in socio-economic activities in many parts of the world because they are both harvested by fisheries and the subject of major marine tourism industries (Davis et al., 1997; Clarke et al., 2005; Stewart & Wilson, 2005). Although detailed knowledge of the biology and ecology of *R. typus* remains limited, the discovery of several predictable aggregations in highly productive areas has enabled much to be learnt since Colman (1997) (Martin, 2007; Stevens, 2007). In terms of their movements, *R. typus* satellite tagged in the Sea of Cortez, in South-east Asia and off Western Australia, seemingly travel distances of thousands of kilometres, moving through multiple political jurisdictions (Eckert & Stewart, 2001; Eckert et al., 2002; Wilson et al., 2006). A detailed understanding of

†Author to whom correspondence should be addressed at present address. Swiss Federal Institute of Technology, Raemistrasse 101, CH-8092 Zurich, Switzerland. Tel.: +41 44 632 2071; fax: +41 44 362 5085; email: juerg@gluecklich.net

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the vertical and horizontal movement patterns contributes to a better understanding of the still little-known habitat of this planktivorous species, and which is important for sustainable management of socio-economic activities.

Despite an increasing amount of data on large-scale movement patterns in *R. typus*, information on habitat use away from shallow-water feeding grounds is generally lacking, especially in poorly studied, remote geographic regions. The Indian Ocean is one of the most productive areas for *R. typus* sightings and the species occurs all along the east African coast from the Red Sea to South Africa (Compagno, 2001). A focal point for *R. typus* aggregation is the coastline around Tofo in southern Mozambique (Cliff *et al.*, 2007). Here, a high density of fish gathers year-round in a narrow (c. 20 km²) corridor close to shore and the high sighting rates and accessibility of the fish has led to the development of a burgeoning marine tourism industry. Although the broader-scale movement patterns and behaviour of these fish are unknown, the local population structure (81% males) suggests that these fish constitute a sub-set of a larger population (unpubl. data). Satellite tags were deployed from this site to gain a better understanding of both regional population linkages and also the vertical habitat use of this planktivorous species.

On 18 February 2006, a male (shark 1; tag 1) and female (shark 2; tag 2) *R. typus* were equipped with pop-up satellite archival tags (PTT-100; Microwave Telemetry, Inc.; www.microwave-telemetry.com) at 24°106′ S; 35°504′ E, southeast of Tofo, Mozambique. The sizes of the fish were visually estimated to be 8 m (shark 1) and 6–7 m (shark 2), respectively, using the length of the research vessel as reference. The fish were approached by a snorkeller, and the tags were embedded into the dorsal musculature between the first and the second dorsal fins using a spear gun. The full set-up consisted of the pop-up satellite archival tag unit, a monofilament line (c. 100 mm) marked with an individually coloured plastic tube and a double barbed stainless steel anchor (modified Floy FH-69 dart; Floy Tag & Mfg Inc.; www.floytag.com). The tags archived ambient light measurements (every 2 min), temperature and pressure readings (every 15 min) and recorded time of sunrise and sunset for subsequent calculation of latitude and longitude. Error ranges for the temperature and pressure sensors were ±0.2°C and ±2.7 m, respectively. In both tags, a constant pressure release mechanism was enabled. This release feature is standard on Microwave Telemetry pop-up satellite archival tags and automatically releases the tag and begins to transmit to the Argos satellite if it senses that it has been at a constant depth for 4 days. Depth variations <20 m were regarded as constant depth by the tag model used in this study. The tags were programmed to pop-up on 30 November 2006. All times reported here (unless noted) are local times.

Both tags popped up prematurely after 7 (tag 1) and 87 (tag 2) days, respectively. Tag attachment duration was similar to other studies that satellite-tagged *R. typus* using similar attachment methods (Graham *et al.*, 2006; Wilson *et al.*, 2006). Tag 1 popped up on 25 February 2006 before 0900 hours at 24°214′ S; 35°431′ E (location class 3 on 26 February at GMT 0045 hours) due to activation of the constant pressure release mechanism. This location was 14 km south-west of the tagging site. The light-based geolocation longitude estimates indicate that the fish stayed within a 100 km area off coast for the duration of this short track. Argos positions received and temperature readings
recorded after pop-up on 25 February strongly indicated that the tag had washed ashore. All (100%) archived depth and seawater temperature data \((n = 653)\) were retrieved from tag 1. The maximum diving depth of shark 1 was 48 m and the male shark spent >90% of its time at depths between 0 and 20 m in isothermic water. The distribution of time at depth between day and night was not different \((\chi^2 \text{ test, d.f. } 4, P > 0.05)\). Mean ± s.D. and median depths were 7-4 ± 7-1 m and 5-4 m, respectively. Mean ± s.D. ambient seawater temperature experienced was 27-2 ± 1-5 °C, median = 27-7 °C and range = 20-9–29-3 °C.

Tag 2 popped up on 16 May 2006, 87 days after attachment. The tag detached for unknown reasons (last depth reading was 107-6 m) and floated on the surface for 4 days (depth readings constantly 0 m) until it 'uplinked' to the Argos satellite receiving system. The first Argos location \((24-224° S; 47-639° E; \text{location class } 2)\) was received on 20 May at GMT 1952 hours from off the south-east coast of Madagascar [Fig. 1(a)]. Raw estimates of locations between attachment and tag pop-up were calculated from recovered light-level data by Microwave Telemetry, Inc. using a proprietary algorithm derived from standard celestial algorithms (Wilson et al., 2007). A total of 38-7% of daily latitude estimates and 75% of daily longitude estimates, respectively, were available for analysis. Light-level longitude estimates are typically accurate and robust (Teo et al., 2004), and therefore, only longitude values were used to describe the horizontal west to east movement of shark 2.

The minimum point-to-point distance covered by the \(R. \text{typus}\) in 87 days was c. 1200 km between Mozambique and the east coast of Madagascar. Combining light-level longitude estimates with archived depth readings indicate
a strongly directional movement by shark 2. Minimum mean ± s.d. movement rate calculated as the minimum straight distance between two consecutive daily longitude estimates was 1.3 ± 1.3 km h^{-1} (median = 0.8 km h^{-1}; range = 0.0–6.1 km h^{-1}). These estimated mean minimum movement rates are well within previously published estimates of daily movement rates in this species (Eckert & Stewart, 2001; Wilson et al., 2006). The data showing the animal crossing the Mozambique Channel from coastal Mozambique to south-eastern Madagascar waters provides the first track of an individual connecting mainland Africa to Malagasy waters, where occasional *R. typus* shark aggregations are also known to occur (Jonahson & Harding, 2007).

Vertical movements and diel patterns in behaviour were analysed using 87.1% \((n = 7262)\) of the archived depth readings and 87.8% \((n = 7321)\) of the archived seawater temperature readings available from tag 2. Mean ± s.d. depth and temperature during the entire track were 66.1 ± 118.4 m (median = 10.8 m; range = 0–1286 m) and 23.9 ± 4.3°C (median = 25.1°C; range = 3.4–29.9°C), respectively. The fish showed a broad depth distribution, spending 79.6% of the time shallower than 100 m [Fig. 2(a)]. Within the first 100 m of the water column, the majority of the fish’s time was spent close to the surface, with 60% of the time spent between 0–10 m depths [Fig. 2(b)]. It spent 64% of its time in water >24°C [Fig. 2(c)]. No thermocline could be detected, indicating the fish dived in well-mixed layers. This result agrees with previous satellite tagging studies for this species (Graham et al., 2006; Wilson et al., 2006).

Light-based geolocation longitude estimates from tag 2 indicate that the female fish initially moved south along the Mozambique coast in shallow coastal water reaching the minimum longitude of 34.382°E on 7 March

![Fig. 2. Histograms of percentage time spent at depth for (a) 100 m intervals, (b) 0–100 m and (c) percentage time spent in different water temperatures (■, day; □, night) for *Rhincodon typus* 2.](image_url)
Between the date of tagging and 7 March, the fish stayed in shallow coastal habitats, spending 64% of its time in water <10 m deep, with only occasional deeper dives to a maximum depth of 108 m [Table I and Fig. 1(b)]. The mean ambient seawater temperature experienced in coastal habitat was 27.5°C (Table I). Temperature records from both sharks 1 and 2 indicated that the upper 0–40 m of the water column close to the coast was isothermal with little vertical stratification. Shark 2 stayed significantly deeper during the night while in shallow coastal waters (Mann–Whitney U-test, d.f. = 1, P < 0.001). No difference was detected between night and day ambient seawater temperatures in this coastal habitat (Mann–Whitney U-test, d.f. = 1, P > 0.05).

Compared to the coastal habitat, an opposite diel pattern was found in oceanic waters (Table I). While in the oceanic habitat, mean depths were significantly shallower at night than during the day (Mann–Whitney U-test, d.f. = 1, P < 0.001), which was linked to the mean ambient seawater temperature experienced being significantly warmer at night than during the day (Mann–Whitney U-test, d.f. = 1, P < 0.001).

After moving into oceanic waters in the Mozambique Channel, the vertical movements of the fish changed dramatically to regular epipelagic diving punctuated by periodic deep dives, experiencing a wide range of ambient water temperatures (Table I). The first dive of *R. typus* below 100 m was recorded on 6 March and regular deep diving to well below 100 m was observed from 12 March onwards [Fig. 1(b)]. After leaving shelf waters on 7 March, the fish entered deeper coastal waters heading east towards the Mozambique Basin [Fig. 1(a)]. Crossing the deep waters (c. 5000 m maximum depth) of the southern Mozambique Channel into the Madagascar Basin was characterized by increased diving activity compared to the shallow coastal habitat including dives to depths well into the mesopelagic and bathypelagic zones [Fig. 1(b)]. On 20 March, one dive profile included descents to 1264 and 1092 m, respectively. Seawater temperatures recorded at these depths were 4.2 and 9.2°C, respectively. A third deep dive to 1087 m with ambient seawater temperature of 5.5°C was recorded on 23 March. Between the beginning of April and 19 April, the *R. typus* crossed the Madagascar Ridge entering the Madagascar Basin [Fig. 1(a)]. On 18 April, the fish dived to at least 1286 m. Previous studies have found that *R. typus* dive

| Table I. Summary statistics for dive data from shark 2 in coastal and oceanic habitats. All depth and temperature variables show range (median) and mean ± S.D. |
|---|---|---|
| **Depth** | **Coastal** | **Oceanic** |
| Readings | 1395 | 5867 |
| Overall (m) | 0–108 (5.4) 8.2 ± 12.9 | 0–1286 (21.5) 79.9 ± 127.7 |
| Day (m) | 0–54 (0) 6.1 ± 8.5 | 0–1087 (32.3) 118.2 ± 147 |
| Night (m) | 0–108 (5.4) 10.3 ± 15.8 | 0–1286 (10.8) 41.5 ± 89.9 |
| **Temperature** | | |
| Readings | 1469 | 5852 |
| Overall (°C) | 18.3–29.9 (27.8) 27.5 ± 1.5 | 3.4–29.5 (24.4) 23 ± 4.3 |
| Day (°C) | 22.4–29.9 (27.8) 27.6 ± 1.3 | 5.2–29.5 (23) 21.5 ± 5 |
| Night (°C) | 18.3–29.7 (27.8) 27.4 ± 1.7 | 3.4–29 (24.8) 24.5 ± 2.6 |
to at least 980 m (Graham et al., 2006; Wilson et al., 2006). The maximum depth of 1286 m, some 22 m deeper than the maximum diving depth recorded for a basking shark *Cetorhinus maximus* (Gunnerus) in the North Atlantic Ocean (Gore et al., 2008), shark 2 obtained in this study is, as far as is known, the deepest dive depth ever directly recorded for any elasmobranch species. Deeper dives are possible but cannot be recorded by this tag type since the maximum possible recordable depth is 1286 m, triggering an immediate tag release and pop-up if this depth is maintained for >15 min (Microwave Telemetry, pers. comm.). The seawater temperature of 3-4°C recorded at this depth was the lowest temperature measured during the entire track (Table I). Bathypelagic dive profiles were similar and showed the fish diving straight down from the epipelagic zone to the deepest recorded depth of each individual profile. This was followed by an ascent through the water column by undertaking very regular oscillations, with each subsequent oscillatory dive during the ascent descending less deep than the previous one by a similar depth.

The function of deep dives in *R. typus* and other shark species remains unknown. One possible explanation for dives through vertical depth strata is the acquisition of navigational cues. Although little is known about how animals navigate over long distances (Alerstam, 2006), it has been suggested that sharks might explore the water column to gain directional information from, for example, magnetic gradients or depth strata with different chemical properties (Klimley et al., 2002). A more likely explanation, however, is that these dives represent search behaviour for feeding opportunities. The use of a broad vertical habitat, extending from the surface across both epipelagic and mesopelagic zones over a time scale of hours, has also been found in plankton-feeding *C. maximus* in which deep dives were suggested to relate to search patterns for deep-water zooplankton (Sims et al., 2003). Large-amplitude changes in depth in response to concomitant depth changes in prey concentrations have been suggested for a wide range of marine vertebrates including all three planktivorous shark species: *C. maximus* (Sims et al., 2005), *Megachasma pelagios* Taylor, Compagno & Struhsaker (Nelson et al., 1997) and *R. typus* (Gunn et al., 1999; Graham et al., 2006; Wilson et al., 2006). The observed diel changes in preferred depth are consistent with a response to food patches that occupy deeper depth strata during the day in vertically thermally stratified habitats (Sims et al., 2005). In the absence of data on deep-water plankton from this region, a related explanation may be that the recorded deep dives in the Mozambique and Madagascar Basin represent searches through the fish’s entire vertical niche (0–1286 m), a strategy that would enable any food layers at shallower depths to be encountered more readily.

The archived record of shark 2’s long-distance movement across the Mozambique Channel represents the most detailed data set available on the vertical behaviour of a *R. typus* in the western Indian Ocean, a key area for this species. The long-term horizontal and vertical movements of *R. typus* are among the best studied of any elasmobranch species. Some published tracks obtained from satellite-linked transmitters have shown large geographic displacements, such as Eckert & Stewart’s (2001) report of a *R. typus* swimming 13 000 km from the Sea of Cortez to the western north Pacific Ocean and a fish tagged in the Seychelles apparently moving as far east as south of Sri Lanka (Rowat & Gore,
2007). Unfortunately, these large-scale displacements are based on very few Ar- 
gos position estimates, with few or no intermediate positions, and similar re-
sults could potentially be obtained from a detached tag drifting on the 
surface. Tracks, including the above mentioned, lacking associated depth data 
make it impossible to verify that the tag remained attached. The 1200 km long-
distance movement reported for shark 2 in this study is one of the longest re-
corded where the geographic movement of the fish can be validated with a high 
degree of certainty.

The tagged female *R. typus* crossed the Mozambique Channel, passed the 
southern tip of Madagascar and into the Madagascar Basin as far east as 
50°494′ E reaching the maximum value on 5 May [Fig. 1(c)]. From there, 
the fish apparently turned in a north-westward direction swimming towards 
the east coast of Madagascar where the tag eventually popped up on 16 
May [Fig. 1(a)]. The trigger for large-scale geographic movement in *R. typus* re-
mains largely unknown. A plausible explanation for planktivorous shark spe-
cies is that individuals move between locations with high concentrations of 
planktonic organisms (Sims & Quayle, 1998; Heyman et al., 2001; Sims 
et al., 2003, 2006). Although data on plankton densities from the southern 
coast of Mozambique are lacking, *R. typus* are regularly observed feeding in 
surface waters near Tofo. The *R. typus* in this study was tagged in February 
and initially remained in these warm and shallow coastal waters. After 20 days, 
shark 2 left the coastal waters and crossed the southern part of the Mozambi-
que Channel, an area with little primary production (Machu et al., 2005), 
within 30 days before reaching the Madagascar Ridge at the beginning of April 
and continuing to move eastwards into the Madagascar Basin. This area south-
west of Madagascar is known to support a vast phytoplankton bloom in late 
austral summer (Longhurst, 2001). Such an abundant food source might attract 
planktivorous species seasonally and could explain the large-scale directed 
movement of this female *R. typus*. This location, identified by shark 2, may rep-
resent a place where large numbers of *R. typus* seasonally aggregate.

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