Movements and habitat use of satellite-tagged whale sharks off western Madagascar

Running head: Whale shark movements off Madagascar

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ABSTRACT: Whale sharks *Rhincodon typus*, the world's largest fish, are routinely sighted off the northwest coast of Madagascar, particularly off the island of Nosy Be. Dedicated whale shark tourism has been developing in the area since 2011. During our first dedicated survey, from September-December 2016, we photo-identified 85 individual whale sharks, ranging from 3.5–8 m in total length (all juveniles). None had been previously identified from other known whale shark aggregations. We tagged eight sharks with tethered SPOT5 tags in October 2016, with tracking durations of 9–199 days. Kernel density plots showed that the main activity hotspot for tagged sharks was around the Nosy Be area. Three individuals were resighted back at Nosy Be in late 2017, after having lost their tags. A secondary hotspot was identified off Pointe d'Analalava, 180 km southeast of Nosy Be. Five sharks swam off the shelf into the north-eastern Mozambique Channel, between Madagascar and Mayotte, and one of these continued to near the Comoros islands. Two sharks swam to southern Madagascar, with minimum track distances of 3, 414 km and 4, 275 km. The species is presently unprotected in Madagascar, although a small proportion of the high-use area we identified in this study is encompassed within two marine protected areas adjacent to Nosy Be. Whale sharks are globally endangered, and valuable to the local economy, so there is a clear rationale to identify and mitigate impacts on the sharks within the two hotspots identified here.

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INTRODUCTION

Whale sharks (*Rhincodon typus*), the world's largest fish, aggregate seasonally in certain areas within their circumtropical distribution (Rowat and Brooks 2012). The western Indian Ocean (WIO) hosts several coastal whale shark aggregations, with high densities of sightings documented around Praia do Tofo in Mozambique (Cliff et al. 2007, Pierce et al. 2010, Rohner et al. 2013, 2015a), Mahé in the Seychelles (Rowat et al. 2009, 2011), and Mafia in Tanzania (Rohner et al. 2015a). Whale sharks are also widely distributed in the oceanic waters of the WIO, particularly within the Mozambique Channel (Sequeira et al. 2012). Their presence in the coastal areas is typically related to high prey abundance (Rohner et al. 2015b, 2018), while in offshore waters their movements are likely correlated with productive frontal zones (Ramírez-Macías et al. 2017, Ryan et al. 2017).

Limited data are available on whale shark movements within the WIO, although genetic data support a single subpopulation within the Indo-Pacific (Castro et al. 2007, Schmidt et al. 2009, Vignaud et al. 2014). However, international photo-identification comparisons have shown limited connectivity between the feeding aggregations in the region, which include Djibouti, the Maldives, Mozambique, the Seychelles, South Africa, and Tanzania (Brooks et al. 2010, Andrzejaczek et al. 2016, Norman et al. 2017), along with the Arabian Gulf and Gulf of Oman (Robinson et al. 2016). The few published satellite tracks from the WIO have not shown significant interchange between known aggregations (Gifford et al. 2007, Brunnschweiler et al.

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2009, Rowat et al. 2006, 2009, Rohner et al. 2018). However, interpretation of these results is complicated by the biased population structure at these aggregations, with all the aforementioned feeding areas dominated by male sharks, typically juveniles (Rohner et al. 2015a, Norman et al. 2017).

The predictable aggregative behaviour of whale sharks leaves them particularly vulnerable to human impacts. The species was downgraded to globally Endangered on the IUCN Red List of Threatened Species in 2016 as a result of overfishing, bycatch and ship strikes (Pierce and Norman 2016). The species remains unprotected in several WIO nations, although the 2017 listing of the whale shark on Appendix I of the Convention on Migratory Species (CMS) means signatory nations are now required to prohibit take. Significant declines in sightings have been noted in long-term hotspots in Mozambique (Rohner et al. 2013) and the Seychelles (D. Rowat pers. comm. 2017), as well as broadly within the northern Mozambique Channel (Sequeira et al. 2012). Further data are required to determine whether these local declines in whale shark sightings represent a spatial shift in distribution, or a genuine population-level decrease in abundance.

The distribution, status and abundance of whale sharks is poorly documented in Madagascar (Jonahson and Harding 2007, Kiszka and van der Elst 2015). Jonahson and Harding (2007) conducted an interview-based survey of whale shark sightings in Madagascar – known locally in Sakalava dialect under the name ‘*marokintana*’, meaning ‘many stars’ – and identified the island of Nosy Be in the northwest as the area with the most consistent sightings. Dedicated whale shark tourism started in 2011, although dive operators were searching for whale sharks

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opportunistically from prior to 2007 (Jonahson and Harding 2007). Operators perceive sightings off Nosy Be to be increasing to the present, although it is unclear whether these sightings may be correlated to rising search effort as tourism increases. Whale sharks are wide ranging, and local existing marine protected areas (MPAs) in NW Madagascar, including the community-managed Ankivonj (1, 394 km^2, located 50 km southeast of Nosy Be) and Ankarea (1, 356 km^2, 50 km northeast of Nosy Be) are unlikely to offer adequate protection for this species. In order to generate management measures for whale sharks in Madagascar and in the WIO, information on their movements and population structure is needed.

Here we used tethered satellite tags to provide the first data on the spatial habitat use of whale sharks in the Nosy Be area, and more broadly within the southwestern Indian Ocean. Our primary objective was to identify contemporary high-use areas by the sharks to determine whether enhanced management or protection of the sharks is likely to be required.

MATERIALS AND METHODS

Study area and boat surveys

Eighty-one whale shark surveys, both in conjunction with tourism operators and on a private vessel, were conducted between September and December 2016 off the island of Nosy Be (13.39°S, 48.20°E) in Antsiranana Province in northwest Madagascar (Fig. 1). Search efforts were focused on the southwest of Nosy Be, to about 10 km offshore, based on the experience of tourism professionals. Whale sharks were sighted when swimming close to the surface, often in

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association with mackerel tuna (*Euthynnus affinis*) and seabirds (particularly Laridae). Research was conducted with the approval of and in partnership with the Centre National de Recherches Océanographiques (CNRO) in Madagascar.

Photo-identification

Individual sharks were identified using standardized underwater photographs of each flank immediately posterior to the gills (Arzoumanian et al. 2005, Meekan et al. 2006). These images were uploaded to the online Wildbook for Whale Sharks (www.whaleshark.org) photo library, and a pattern matching algorithm was used to identify individuals (Arzoumanian et al. 2005, Holmberg et al. 2008). Individual whale shark encounters were defined as a sighting of an identified shark on a distinct day. Total length (TL) was estimated visually to the nearest metre, and sex was assessed based on the presence (males) or absence of claspers (Norman et al. 2007, Rohner et al. 2015a). Maturity status in whale sharks was established by visual observation of size in females, with the assumption that <9 m sharks were immature (Acuña-Marrero et al. 2014, Ramírez-Macías et al. 2012) and calcification of claspers for males (Norman et al. 2007, Rohner et al. 2015a).

Satellite tagging

Authorisation to deploy satellite tags on whale sharks was delivered by the Centre National de Recherches Océanographiques in July 2016 under the number N°16-12-CNRO-N. Tagging activities were carried out on snorkel from a dedicated 4 m private vessel. Smart Position or Temperature Transmitting (SPOT5) tags from Wildlife Computers (Oregon, USA) were connected to a small titanium dart (Wildlife Computers) via a ~150 cm tether of 240 kg

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Dyneema braided line. The dart was inserted into the skin using a pole spear so that the tag floated approximately above the 1st dorsal fin. Most sharks showed no obvious reaction to tagging, with the minority of sharks that increased their swimming speed immediately post-tagging resuming their previous behavior in 1–2 minutes.

Track analysis

Once detached, floating tags were identified by near-continuous transmissions to ARGOS in the first few hours over several consecutive days, coupled with no significant vertical movement inferred from time-at-temperature histograms (Hearn et al. 2013). We then applied the Douglas filter (Douglas et al. 2012) to remove unrealistic locations based on the error associated with the ARGOS location class (lc: 3, 2, 1, 0, A, B, Z in decreasing order of accuracy). We set the filter to include all locations with a lc ≥1 and used the maximum redundant distance (MRD) method set to 10 km. The filter removed 127 locations, or 6.3% of the total 2,029 locations, but kept some B and A locations that had a relatively large error radius. We also corrected the time stamp from tag-recorded UTC to local time during this step, meaning that the limit of 300 transmissions a day UTC were split between two days in local time. This meant that the number of transmissions received per day could be larger than expected, with transmissions in the late evening and early morning local time. We used the Douglas filter output for all subsequent analyses.

Tags did not transmit every day, and hence we report the overall tracking duration as well as transmitting days (Table 1). Horizontal track distance was calculated by summing the straight-line distance between consecutive locations, and therefore represents the minimum possible distance the shark swam horizontally. Analyses were conducted in R version 1.0.136 (R Core

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Team 2017). We created a density raster using the kernel density estimation tool “heatmap” in QGIS version 2.18.14 (QGIS Development Team 2017) to visualize hotspots of whale shark activity. Data input included all locations retained following application of the Douglas filter, and we used a kernel bandwidth of 10 km, a quartic kernel shape, a cell size of 0.5 km and a decay ratio of 0. Values of 0–24.9% were removed from the output.

Tags recorded temperatures in 12 predefined bins, <5°C, 5–10°C, then every 2.5°C to 32.5°C, and >32.5°C. Temperatures were measured every 10 seconds and integrated over three time periods per day (night = 18:00–6:00; morning = 6:00–12:00; afternoon = 12:00–18:00) to calculate time-at-temperature (TAT) histograms. There were large gaps in the TAT time-series because tags only transmitted data on 45% of tracking days overall. We did not plot these gaps, meaning that the x-axes of TAT plots are chronological but not continuous. We extracted bathymetric data using the *xtractomatic* package in R (Mendelssohn 2015) for those records in the TAT time-series that also had a simultaneous location transmitted. We divided depth data into (1) on the continental shelf (<200 m deep) and (2) off the shelf (>200 m) for graphical output.

RESULTS

Photo-identification

Eighty-eight individual whale sharks were recorded from 169 separate encounters between September and December 2016, comprised of 18 females (size range 5–7.5 m TL), 69 males

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(size range 3.5–8 m TL), and one shark of unknown sex. All were immature, based on a lack of clasper calcification in males and the estimated TL of females. None of these sharks had been previously identified in surrounding countries.

Tag performance and horizontal movements

Eight juvenile whale sharks, six males and two females ranging from 4–7 m TL, were tracked between October 2016 and May 2017 (Table 1). The SPOT5 tags stayed attached for 9–199 days (mean ±SD = 110 ±78.3d). Data were transmitted on 7–87 days (mean ±SD = 49 ±24.7d). The four tags that stayed on for >100 days transmitted on <50% days (range = 23–46%), while the four tags with shorter retention times transmitted on most days (mean ±SD = 93 ±10.1%, range = 78–100%). Tags transmitted a mean of 4.8 locations per transmitting day. Straight-line horizontal track distances ranged from 191–4,275 km, with 6 of the 8 tracks longer than 1,000 km. Sharks travelled at a mean horizontal speed of 21 km day^{-1}.

Tagged whale sharks spent a substantial time near the tagging area around Nosy Be, but some broader movements to the west into the Mozambique Channel, and to the south along the west coast of Madagascar were also recorded (Fig. 1a). Two whale sharks swam to the southern end of Madagascar, with MD-196 moving offshore in the southern Mozambique Channel before returning to the Nosy Be area, and MD-169 following the continental shelf break south before losing its tag southeast of Madagascar. One of these (MD-196), and four other sharks swam off the shelf into the north-eastern Mozambique Channel, between Madagascar and Mayotte, and one (MD-154) continued to near the Comoros islands (Fig. 1b). Two sharks (MD-153 and MD-201) stayed on the shelf, albeit over relatively short tracking durations (9 and 36 days,

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respectively). Kernel density estimates displayed two whale shark activity hotspots (Fig. 2) on the continental shelf, one close to the tagging locations near Nosy Be and a secondary hotspot ~180 km to the southeast near Pointe d' Analalava.

Following the conclusion of the study, three sharks were resighted in the Nosy Be area after tag detachment: MD-201 was sighted on 3 November 2017, MD-151 was identified on multiple days in September and October 2017, and MD-177 was sighted on 23 July 2017.

Time-at-temperature

There were 218 time-at-temperature (TAT) records available for all tags combined. Sharks moved through the entire temperature range of temperature bins, <5°C to >32.5°C. Based on the transmitted data, whale sharks spent most of their time in the 27.5–30°C (59.4%) and 25–27.5°C (29.5%) bins (Fig. 3a). Only 3.1% of time was spent in <20°C. There were some apparent diel differences observed among TAT data from the morning (6:00–12:00), afternoon (12:00–18:00) and night (18:00–06:00). Sharks spent 0.9% of the afternoon in cool water <20°C, increasing to 3.3% in the morning and 5.1% at night (Fig. 3).

Vertical movements, as inferred from the available TAT time-series, varied among individuals (Supp. Fig. 1 for all plots). Broadly, sharks spent more time at cooler temperatures when they were off the shelf, and during the night and morning. As an example, shark MD-177 (Fig. 4) spent the first 12 days of its track on the continental shelf, where it recorded no vertical excursions into deep (cool) water. This shark then moved off the shelf to the open ocean, over

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deep water. The recorded temperature range then increased, with the shark spending more time in cooler waters, especially at night and during the morning (Fig. 4).

DISCUSSION

The Nosy Be area appears to host a globally-significant whale shark aggregation, with 88 individual sharks identified during the three-month whale shark season (as identified by local tourist operators) in 2016. By way of comparison, 33 individual whale sharks were identified in Mozambique during 2016, and 70 in Tanzania (CAR & SJP, unpublished data). Two clear hotspots of whale shark activity were identified in NW Madagascar, the first around the tagging site off Nosy Be, and the second 180 km south, close to Pointe d'Analalava. While the Nosy Be hotspot is close, relative to the observed shark movement capability, to previously-identified whale shark feeding areas in Inhambane, Mozambique (1,760 km, Cliff et al. 2007, Pierce et al. 2010), Mahe in the Seychelles (1,250 km, Rowat et al. 2009, 2011), and Mafia Island in Tanzania (1,120 km, Rohner et al. 2015b, we found no evidence of movements to or from these known aggregations through our tracking or photo-ID datasets. However, the sharks were tracked moving close to the islands of Comoros and Mayotte (France) in the Mozambique Channel, showing that international movement does occur.

NW Madagascar is a significant whale shark hotspot

Quantitative hotspot analysis determined that most satellite tag transmissions occurred off the island of Nosy Be, with a secondary hotspot used by four sharks at Pointe d'Analalava, slightly

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to the south. These two areas were both identified as whale shark hotspots by Jonahson and Harding (2007) through interview surveys of fishers and dive operators, suggesting that these areas are consistently used by whale sharks across years. The relatively high density of whale sharks documented in the Nosy Be area, and the inter-annual site fidelity demonstrated by some tagged sharks, indicates that this is an important seasonal habitat for juvenile sharks.

The biased population structure of whale sharks present, with the majority being juvenile male sharks, is common within their coastal feeding aggregations (Rohner et al. 2015a). While we inferred no specific behaviours from tracking data, Nosy Be is also likely to be a feeding area for these whale sharks. Most whale sharks sighted, including all tagged sharks, were associated with surface schools of mackerel tuna feeding on small pelagic fishes (Clupeidae), which were presumably also being targeted by the whale sharks. Omura's whales (*Balaenoptera omurai*) also feed in the same area on zooplankton, occasionally in association with whale sharks (Cerchio et al. 2015a). Giant manta rays (*Mobula birostris*) and devil rays, *M. mobular* and *M. thurstoni*, which feed on zooplankton and small fishes (Rohner et al. 2017), also co-occur in this area (Jonahson and Harding 2007; pers. obs.), indicating a high level of prey availability. No adult sharks were recorded during field surveys, so it is unlikely to be a reproductive aggregation. The temperature range (27.5–30°C) recorded for locations on the shelf were similar to surface water temperatures, indicating that little diving behavior took place, which is further supported by the high number of daily surface transmissions in this area.

Broad-scale movements through the SW Indian Ocean

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The five sharks tracked into January 2017 all moved away from the Nosy Be area. January is typically the start of cyclone season in northwest Madagascar (Brenier and Vogel 2017) and, related to this, dedicated whale shark tourism ceases. Fewer transmissions from tags were received after this time, suggestive of diminished surface activity and more time spent on directed travel. Four of the eight tagged sharks moved west of Nosy Be, towards the islands of Mayotte and the Comoros, a region with seasonally high densities of whale sharks (Sequeira et al. 2012). Two sharks, MD-169 and MD-196, travelled to the south of Madagascar, although MD-196 subsequently returned to Nosy Be (a 4,275 km horizontal distance in total). Both sharks dived to cold temperatures of between 5.1–10°C while in oceanic waters. MD-169 moved to the southeast of Madagascar, where an important upwelling system that can be highly productive in the late austral summer has been previously identified (Uz 2007, Huhn et al. 2012). A tagged whale shark from southern Mozambique also moved to this area in autumn 2006 (Brunnschweiler et al. 2009). It appears that the Indian Ocean tuna fishing fleet do not routinely use the waters off southern Madagascar (Sequeira et al. 2012). Therefore, while it is possible that this is an additional whale shark foraging area, we are not aware of additional data to support this hypothesis.

Management and conservation implications

Northwest Madagascar is a significant, long-term hotspot for a number of threatened marine megafauna species, including whale sharks (Jonahson and Harding 2007, this study), cetaceans (Cerchio et al. 2015a, 2015b), and sea turtles (Bourjea et al. 2006). The area is also a global hotspot of coral biodiversity (Brenier and Vogel 2017). The presence of whale sharks, a diversity of cetacean species, and sea turtles in this region is already a major tourism attraction for Nosy

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Be, presenting both a biological and economic rationale to manage the area for long-term sustainability. Local interest in the species is high, and most tourism operators have already implemented best-practice voluntary guidelines for whale shark interactions off Nosy Be.

It appears that whale sharks are at a low risk of fishing-related injury or mortality within the Ankivonjy and Ankarea MPAs, located to the southwest and northeast of Nosy Be, respectively, based on the gear restrictions in place (Brenier and Vogel 2017). They are currently afforded no official protection outside these areas, and there is no legislation in place specifically pertaining to elasmobranchs in the country (Humber et al. 2015). The recent listing of whale shark on CMS Appendix I (October 2017) does compel Madagascar to prohibit take of the species, with limited exceptions possible for traditional subsistence use (http://www.cms.int/en/node/3916). Dolphin bycatch in gillnets has been documented in the Nosy Be area, particularly from Nosy Faly to the east of Nosy Be (Cerchio et al. 2015b). Whale sharks have occasionally been caught or entangled in gillnets in Madagascar (Jonahson and Harding 2007, Everett et al. 2015). Therefore, a restriction of gillnet use throughout the identified whale shark activity centres to minimize the risk of accidental bycatch or directed fishing is recommended. Management of tuna fisheries in the area may also require attention, given the strong association between whale sharks and mackerel tuna schools we observed.

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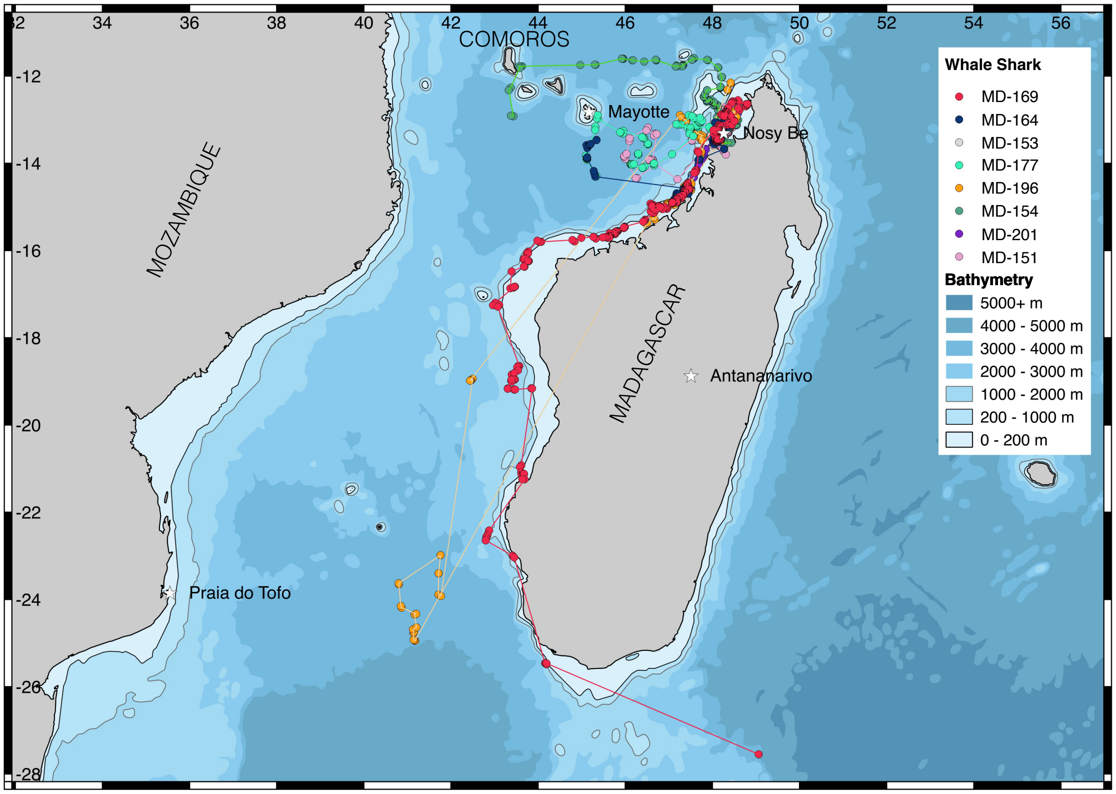

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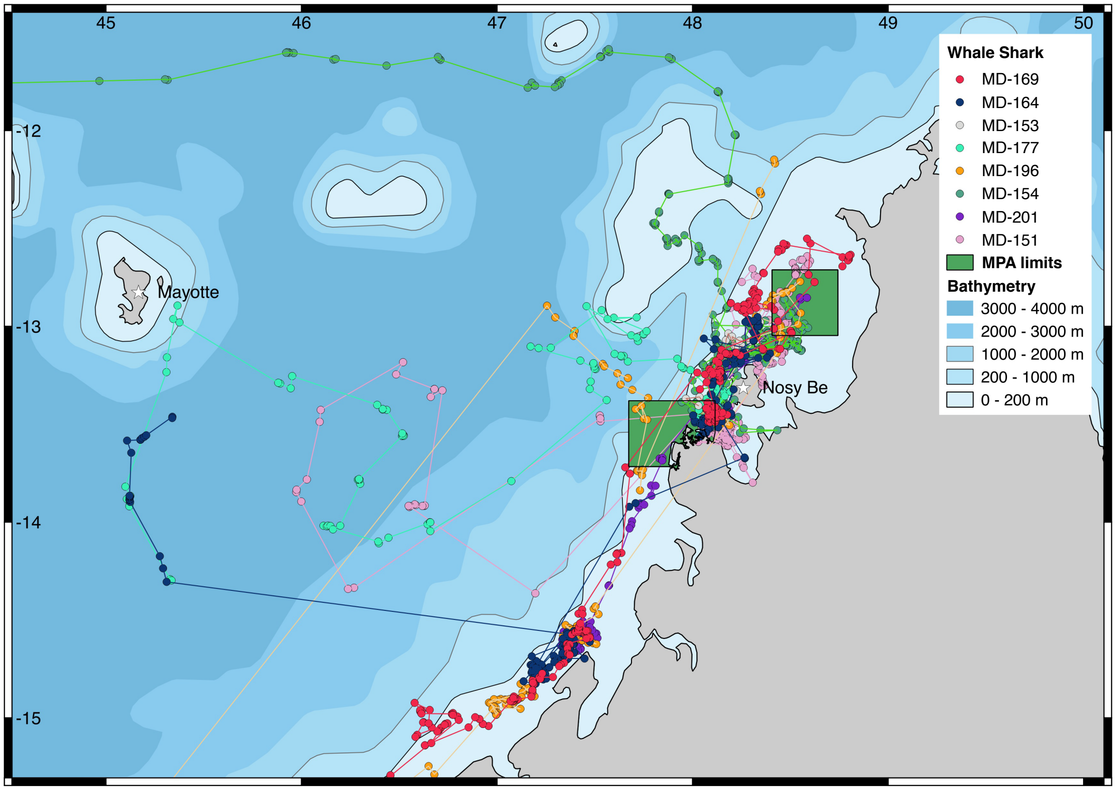

Fig. 1. Horizontal movements of whale sharks tagged with SPOT5 tags in Madagascar. (a) The eight individual shark tracks, all originating from Nosy Be; (b) Transmission sites from within the NW Madagascar area.

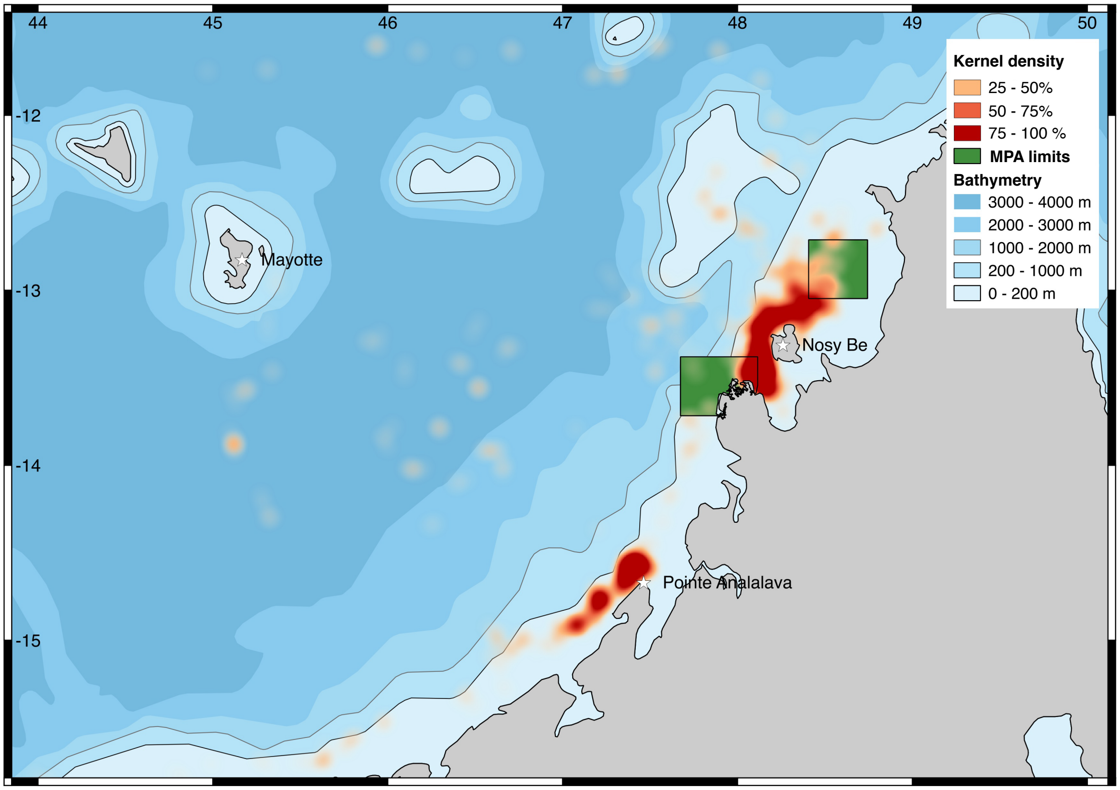

Fig. 2. Kernel density estimation of whale shark distribution based on transmissions of the satellite-tagged sharks (n = 8).

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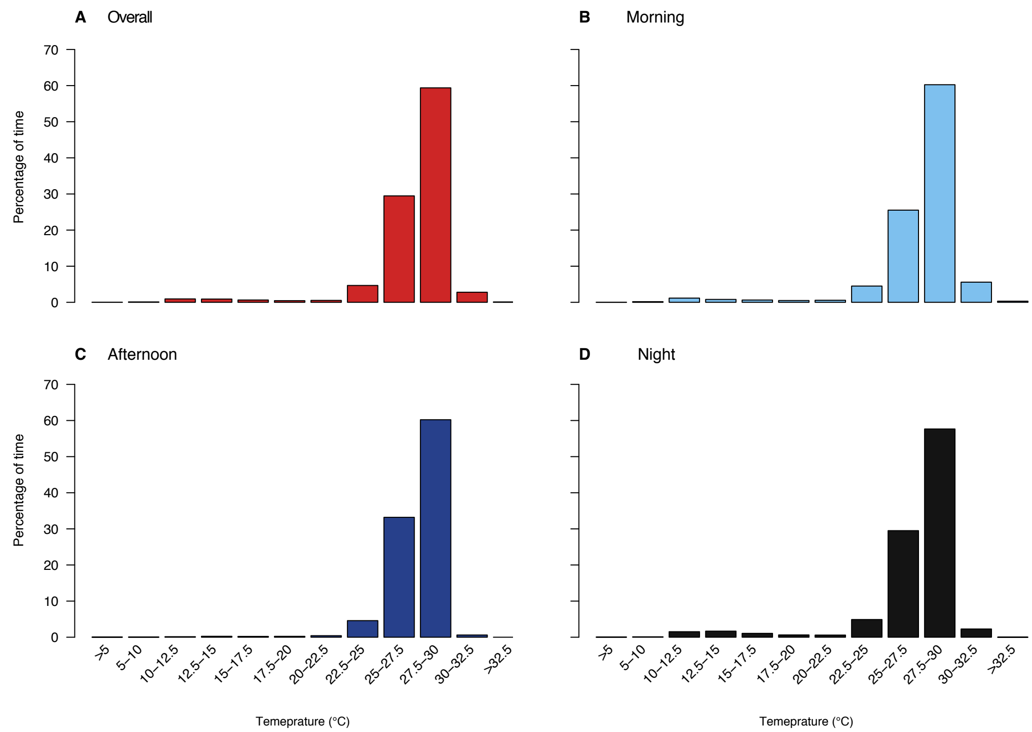

Fig. 3. Time-at-temperature (TAT) histograms for all tags combined, showing the overall distribution and the histograms for the morning (6-12h), afternoon (12-18h) and night (18-6h) separately.

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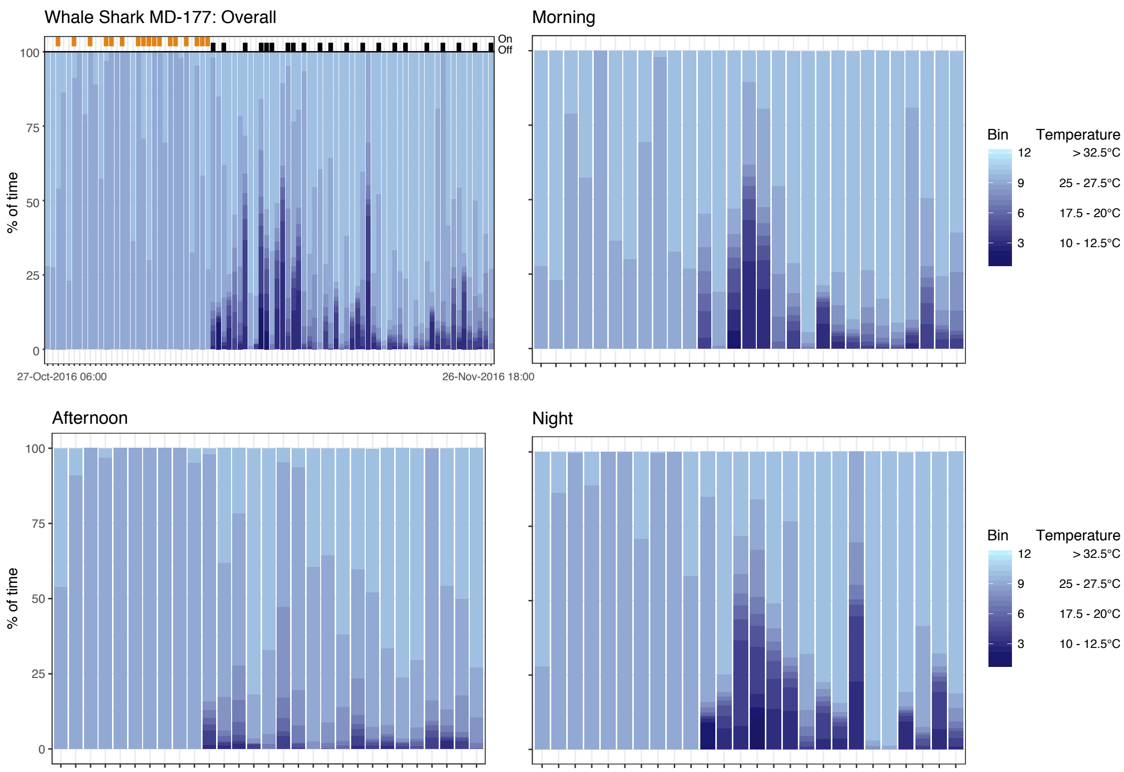

Fig. 4. Time-at-temperature (TAT) data for whale shark MD-177 showing the percentage of time it spent in each temperature bin overall and during the three temporal bins: “morning” (6-12h), “afternoon” (12-18h), and “night” (18-6h). Note that the x-axis is chronological but not continuous due to gaps in data transmission.

Table 1: Satellite track details of whale sharks tagged in Madagascar, with the tag number, shark ID on www.whaleshark.org, sex, estimated total length (TL), deployment and last transmission dates, tracking duration, number of transmitting days, overall track distance, mean speed and the number of positions per (transmitting) day.

Tag	Shark ID	Sex	TL (m)	Deployment	Last location	Tracking duration	Transmitting days	Track distance (km)	Speed (km day^{-1})	Positions per day
142221	MD-151	M	4	27-Oct-16	22-Mar-17	147	68	2295	15.6	5.7 +2.85 (1-12)
142222	MD-201	M	4	31-Oct-16	05-Dec-16	36	35	765	21.3	5.4 +2.28 (1-9)
142223	MD-154	M	5.5	26-Oct-16	22-Jan-17	89	85	2160	24.3	4.7 +2.15 (1-12)
142224	MD-196	F	7	29-Oct-16	14-May-17	198	50	4275	21.6	4.2 +2.23 (1-11)
142226	MD-177	F	5	26-Oct-16	27-Nov-16	33	33	1126	34.1	4.5 +2.32 (1-10)
142227	MD-153	M	6.5	28-Oct-16	05-Nov-16	9	7	191	21.2	4.7 +1.70 (2-7)
142230	MD-164	M	7	27-Oct-16	13-May-17	199	46	1439	7.2	4.3 +2.38 (1-9)
142234	MD-169	M	5	28-Oct-16	17-Apr-17	172	69	3414	19.8	4.9 +2.29 (1-13)