African Journal Of Marine Science
January 2021, Volume 43 Issue 1 Pages 135-140
https://doi.org/10.2989/1814232X.2021.1883736
https://archimer.ifremer.fr/doc/00682/79404/

Large-scale movements and site fidelity of two bull sharks *Carcharhinus leucas* estimated from a double-tagging experiment at Réunion Island (southwest Indian Ocean)

Soria Marc [1,*] , Tremblay Yann [1], Blaison A [1], Forget Fabien [1], Crochelet E [2], Dagorn Laurent [1]

[1] Marine Biodiversity Exploitation and Conservation (MARBEC), University of Montpellier, Centre National de la Recherche Scientifique (CNRS), l'Institut Français de Recherche pour l'Exploitation de la Mer (Ifremer), Institut de Recherche pour le Developpement (IRD), Sète, France
[2] Agence de Recherche pour la Biodiversité à la Réunion (ARBRE), Saint Gilles, Réunion

* Corresponding author : Marc Soria, email address : marc.soria@ird.fr

Abstract :

Since 2011, the mean number of bites per year by bull sharks Carcharhinus leucas has increased markedly at Réunion Island. To predict areas and periods of increased risk, we need to better understand the space-use dynamics of individual sharks. In coastal waters off Réunion Island, two bull sharks, one of each sex, were double-tagged and tracked for 174 days (male) and 139 days (female) using pop-up satellite archival tags (PSATs) and acoustic transmitters. Both sharks spent most of their time inshore (58.1% for the male and 89.9% for the female). The female performed short excursions but typically remained inshore. The male alternated between spending residence time along the coast and undertaking wide-ranging movements, including one extensive open-ocean excursion to the vicinity of a seamount situated about 210 km from the island. Differences in the residency and home range between the two sharks probably reflect different patterns of foraging and mating behaviours. Our results highlight the advantages of double-tagging in telemetry studies that attempt to estimate the degree of habitat fidelity of a species and illustrate the need to consider the movement patterns of sharks at different scales when developing efficient risk-mitigation management.

Keywords : philopatry, pop-up satellite archival tags, residence time, shark-bite management, telemetry, western Indian Ocean

Introduction

The bull shark *Carcharhinus leucas* occurs in warm tropical and subtropical waters, primarily on continental shelves (Daly et al. 2014; Heupel et al. 2015). Bull sharks are reported to be largely philopatric, with some seasonal migrations along the coast (Carlson et al. 2010; Espinoza et al. 2016). Like other apex predators, bull sharks play a key role in the proper functioning of coastal tropical and subtropical ecosystems (Ferretti et al. 2010). Globally, many shark populations have been under intense fishing pressure throughout their ranges (Queiroz et al. 2019), resulting in substantial population declines. According to the International Union for Conservation of Nature, *C. leucas* is regarded as Near Threatened. However, bull sharks have also been considered to be responsible for attacks on humans, particularly during the last decade at Reunion Island (Lagabrielle et al. 2018). Since 2011, the mean number of shark bites per year has increased markedly from 1.1 to 3 for the periods 1980–2010 and 2011–2019, respectively (Taglioni et al. 2018). Between 2011 and 2019, 27 attacks (of which 11 were fatal) occurred, which is considerable given the population of Reunion Island (863 000 inhabitants in 2016).

To date, little is known about the large-scale movements of bull sharks, particularly around small oceanic islands (Brunnschweiler et al. 2010). Therefore, there is a critical need to improve our understanding of the habitat use of bull sharks, particularly their site fidelity and movements, to mitigate the negative interactions between humans and sharks (Ferretti et al. 2015; Meyer et al. 2018). However, classic tracking technologies used on terrestrial animals, such as GPS and radio, cannot be used to track aquatic animals as radio waves and GPS signals cannot travel efficiently through water (Grothues 2009). For fishes that do not regularly surface, a good alternative is to use archival tags or pop-up satellite archival tags (PSAT) that can provide geolocation estimates through the measurement of light. However, raw geolocations derived from light-based algorithms have a large uncertainty, often hundreds of kilometers, and may have limited potential for addressing specific questions in fine-scale spatial ecology. To improve the precision of geolocation estimates, different environmental data, such as sea surface temperature (Teo et al. 2004), have been used to restrict geolocation uncertainty (Nielsen et al. 2006). However, these methods are limited to estimates that occur more than once or a few times a day (Patterson et al. 2010). In this study, we utilised a double-tagging method consisting of two independent tracking technologies used simultaneously on the same individual: PSAT and acoustic telemetry (Cochran et al. 2019). Acoustic telemetry uses a combination of transmitters deployed on tagged individuals with a network of fixed acoustic receivers that provide presence/absence data with a relatively good level of precision (site dependent: 100–800 m). PSAT tags are not spatially restricted to stationary acoustic-monitoring receivers for location estimates, and provide time-series data on ambient light (used for geolocation), temperature and depth of the tagged individual. By using these two biologging tools, we investigated the degree of site fidelity and the extent of movements of bull sharks when they leave the coastal waters of Reunion Island.

Materials and methods

In March 2013 two adult bull sharks were each equipped with two electronic tags: a pop-up archival transmitting tag (MiniPAT-247A PSAT tag, Wildlife Computers, Chicago, USA) and a coded acoustic transmitter (V16TP-4x; delay range: 40–80 s, power output 158 dB, battery life of 845 days, Vemco, INNOVA SEA, Nova Scotia, Canada).

Each acoustic transmitter was implanted into the peritoneal cavity through a mid-ventral incision. The acoustic network consisted of 44 receivers deployed around Reunion Island (Figure 1). Each time an acoustic tag enters the detection radius (maximum range ~400 m) of a receiver, its ID and a time stamp are recorded (Blaison et al. 2015). The acoustic telemetry dataset was used to assert the locations of the sharks in the coastal waters of the island throughout the study duration.

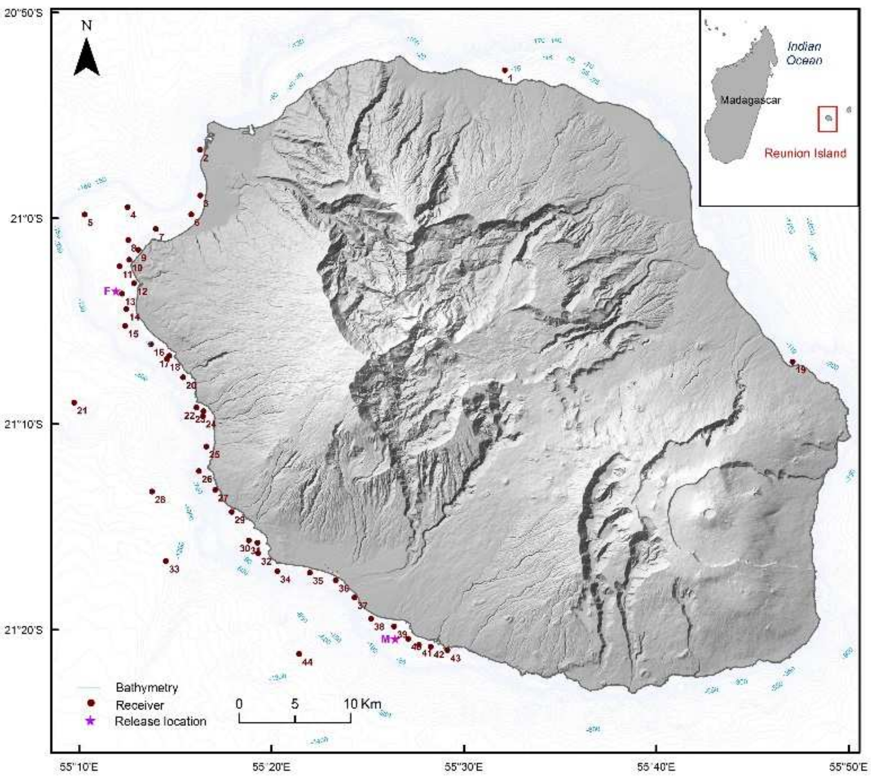

Figure 1: Positions of 44 acoustic receivers around Reunion Island and tagging locations of the male (M) and the female (F) bull sharks *Carcharhinus leucas*

Each PSAT tag was rigged with a heat-shrink-covered 20-cm monofilament tether and was attached externally using a mono-filament line punctured through the first dorsal fin. Each PSAT tag was programmed to detach itself after 192 days, float to the surface and transmit the archived data via the Argos satellite constellation. The software WC-DAP Global Position Estimator 2.00.0027 (Wildlife Computers) was used to process the raw light data (Wilson et al. 1992) and generated two location estimates per day. We used the particle-filtering modelling approach described by Tremblay et al. (2009), which is similar to the WC-GPE3 program of Wildlife Computers, to estimate the probable locations of the sharks every eight hours. Constraints such as sea surface temperature and maximum diving depth were not used to refine the position estimates due to the lack of a horizontal thermal gradient and the relatively shallow occurrence of the sharks in the water column, which did not provide useful information on the bathymetry of the area. The maximum swimming speed of 4.55 km h^{-1} was used in the model and was based on the literature (Daly et al. 2014; Lea et al. 2015) and on speeds estimated from movements between acoustic receivers. The known locations from acoustic detections within the receiver array were used to refine the tracks generated by the geolocation model. To reduce false acoustic detections, a shark was considered as present at a receiver when at least two detections were recorded during one hour. The geolocation model was set to avoid the landmass by using Dijkstra's algorithm (Singal and Chhillar, R.S. 2014) to find the path of least resistance (i.e. shorter distance). Finally, given the limited accuracy of the geolocation estimates, we defined 'coastal waters' as the waters within 20 km of the coast. As such, an 'excursion' was termed as a trip of at least two days' duration outside coastal waters (i.e. >20 km from the coast).

Results

The details of the tagging and tracking data are summarised in Table 1. The tag on the male detached prematurely. Using a backward-drift model (P Sabarros, IRD, pers. comm.), the pop-up location was estimated to be southeast of the island, approximately 10 km offshore (21°30' S, 55°45' E). For the tag on the female, the pressure sensor indicated a fixed depth of 100 meters from 9 August 2013 until the tag surfaced on the 192nd day. Consequently, we used only the data collected prior to that date. The pop-up location was 36 km south of the tagging site and 2 km offshore (21°19' S, 55°23' E).

The proportion of time spent in coastal waters (<20 km) was 58.1% and 89.9% for the male and female, respectively. It appears that the female undertook a limited number of large-scale movements and for most of the time remained in the coastal waters southwest of Reunion Island. This individual performed only three excursions off the coast of the island, each lasting a few days (less than a week), with a maximum distance from the island of about 60 km (Figures 2, 3, Table 2).

The male exhibited a broader spatial pattern all around the island (Figures 2, 3) and performed a single long excursion south of the island to the vicinity of a submarine ridge that culminated at a seamount situated 210 km from Reunion Island (23°.17' S, 55°.30' E). This excursion was performed in April over 20 d and covered approximately 1 260 km (Table 2). This large-scale movement was followed by six other short excursions of between 40 and 90 km from the coast.

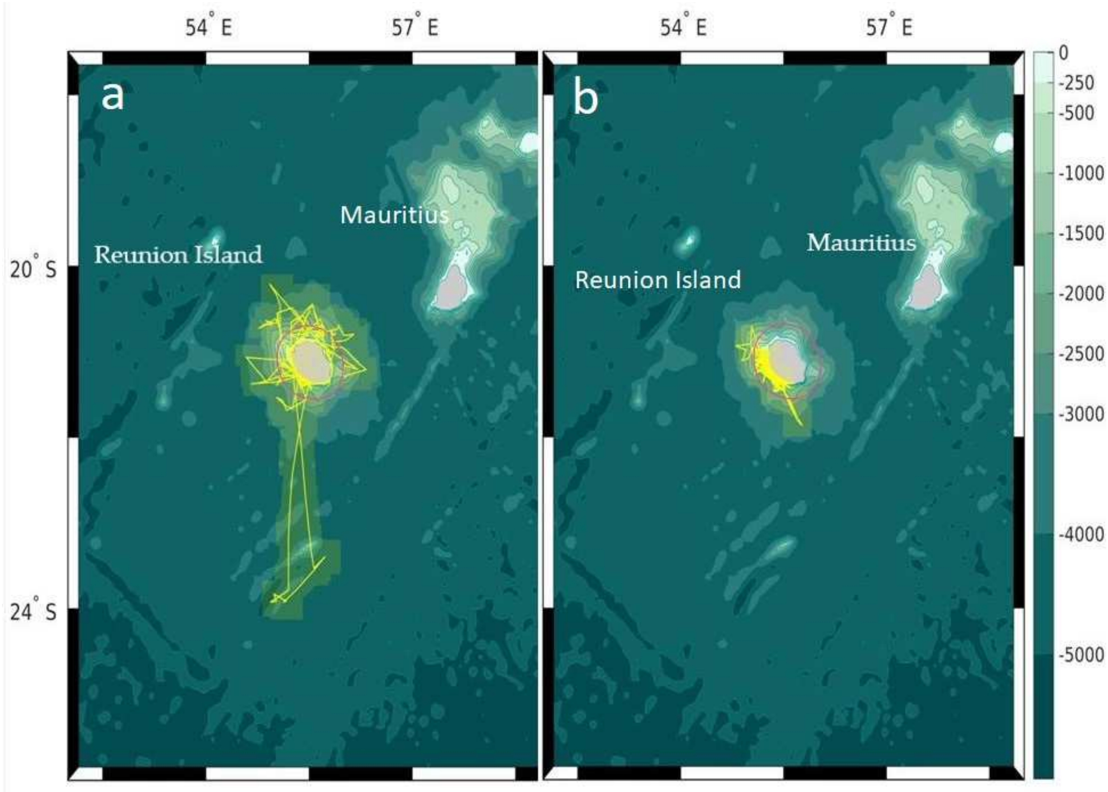

Figure 2: Horizontal movements of (a) the tagged male bull shark from March to September 2013 and (b) the tagged female bull shark from March to August 2013. The intensity of the yellow pixels indicates the probability of occurrence. The pink circle indicates 20 km from the coast.

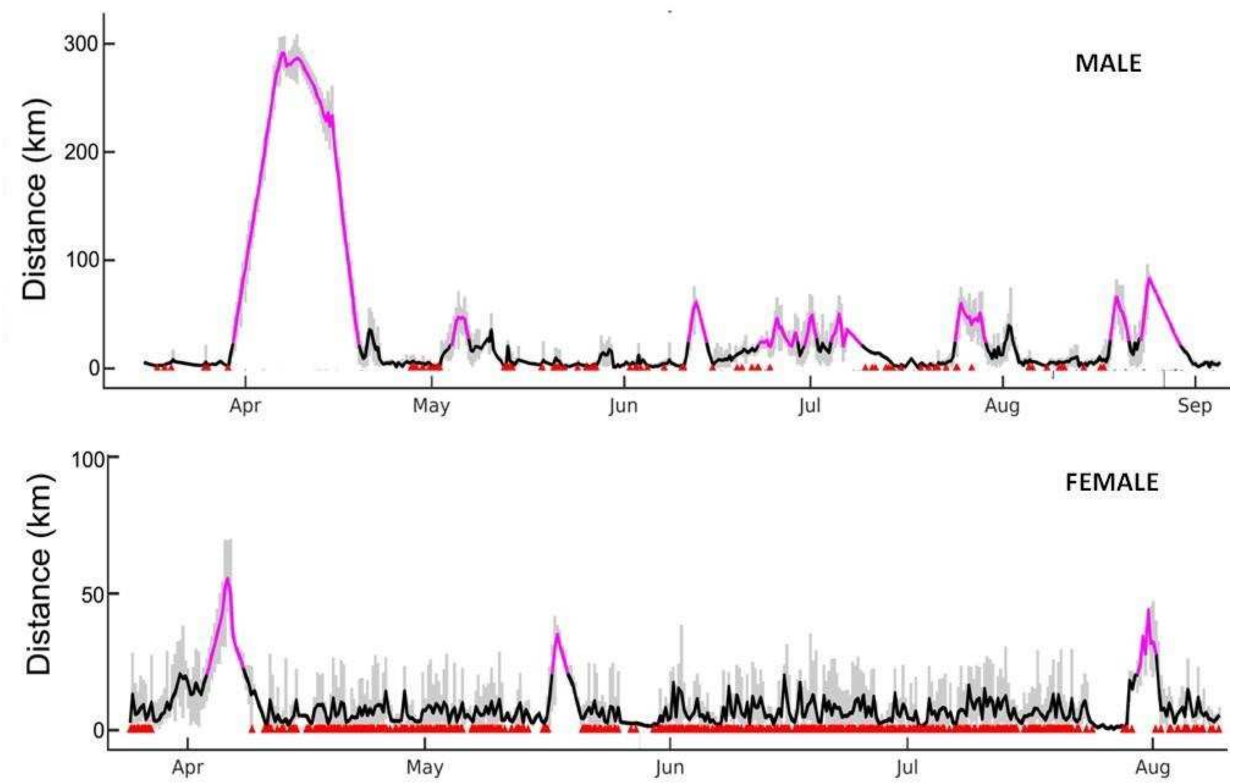

Figure 3: Timeline displaying estimations of the distance from the coast (solid line) and acoustic detections in the coastal waters (red triangles) of (a) a male and (b) a female bull shark tagged off Reunion Island. The pink line indicates excursions of over 20 km and a minimum of two days duration. Pale grey line represents the error (standard deviation) of a location estimated from the positions generated by the model using a combination of speeds drawn at random below the maximum speed threshold set.

Discussion

Using a double-tagging approach with acoustic telemetry and pop-up archival tags, we were able to substantially improve the accuracy of the tracks by adding more-precise locations. This approach is particularly useful for marine animals that rarely surface, like the bullshark, and which cannot be tracked using GPS technology (Winship et al. 2012).

The results showed that both bull sharks were regularly found inshore, suggesting a possible fidelity to the west coast of Reunion Island. This insular fidelity is similar to that described in previous studies on adult bull sharks (Brunnschweiler et al. 2010; Werry and Clua 2013). At Reunion Island, coastal fidelity of adult female bull sharks could be related to the mating activities thought to occur between May and August (Pirog et al. 2019). The observed offshore excursions, particularly those undertaken by the male, differed from the large-scale movements of several months and thousands of kilometers previously reported for this species (Lea et al. 2015; Espinoza et al. 2016) or for other shark species (Chapman et al. 2015; Meyer et al. 2018). It seems unlikely that these offshore movements resemble large scale, seasonal and philopatric migrations as previously recorded for this species. Extensive movements punctuated by repeated offshore excursions have already been observed in sharks. This behaviour was observed in great white sharks (Jorgensen et al. 2010) where several individuals simultaneously occurred in an offshore area, and it was hypothesised that these potential meeting points, or ‘cafés’, were motivated by feeding or mating. The offshore excursion of the male bull shark observed in our study was oriented toward a ridge situated more than 250 km from the island. Such oceanic features are known to increase productivity via water enrichment associated with localised upwelling (Morato et al. 2010); hence it can be hypothesised that this seamount serves as an offshore feeding area.

Considering the limitations of the PSAT technology (Hays et al. 2007), the small sample size (two individuals) and the limited study duration, great care has to be taken when trying to generalise the observed patterns of movement behaviour and residency to the entire bull shark population frequenting Reunion Island. However, the offshore excursions observed in our study confirm the ability of bull sharks to leave coastal waters for the open ocean and potentially highlight the important role of the oceanic habitat in the ecology of this species. The motive driving these repetitive offshore excursions displayed by bull sharks remains unclear and should be examined in future studies.

Acknowledgements — We are grateful to all the members of the institutions and associations involved in the CHARC program (Connaissance de l’HAbitat des Requins Côtiers de la Réunion) and to IRD, CRPMEM, University of Reunion Island, Globice, Kélonia, ARVAM, Squal’Idées, RNMR and Ifremer, as well as the fishers and volunteers who assisted with the shark tagging and made our work possible. This study received financial support from the European Union (convention FEDER ref. 2012-dossier Presage n°33021), the French government (BOP 113 n°2012/03) and the Regional Council of Reunion Island (POLENV n°20120257).

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Table 1: Tagging and tracking metadata for a male and a female bull shark *Carcharhinus leucas* double-tagged at Reunion Island in March 2013

Parameter	Male	Female
Size (total length, cm)	290	310
Life stage	Adult	Adult
Deployment date range	15 Mar 2013–6 Sept 2013	24 Mar 2013–9 Aug 2013
Release position	21°20' S, 55°26' E	21°04' S, 55°12' E
Track duration (days)	174	139
Numbers of light-based geolocations	320	261
Numbers of acoustic detections	400	2 429

Table 2: Summary of the offshore excursions of a male and a female bull shark *Carcharhinus leucas* double-tagged at Reunion Island in March 2013

Individual	Orientation	Departure date	Return date	Excursion duration (days)	Distance travelled (km) **± SD**	Max distance (km) **± SD**
Male	South	29 Mar	19 Apr	20	1 259 ± 98	290 ± 39
Male	South	3 May	11 May	9	428 ± 44	54 ± 09
Male	West	11 Jun	14 Jun	4	160 ± 16	65 ± 10
Male	North	19 Jun	12 Jul	22	974 ± 82	62 ± 11
Male	South	23 Jul	29 Jul	6	341 ± 34	69 ± 10
Male	West	17 Aug	21 Aug	4	283 ± 37	76 ± 11
Male	North	22 Aug	30 Aug	8	327 ± 41	88 ± 12
Female	Southeast	3 Apr	9 Apr	7	179 ± 31	59 ± 14
Female	Southeast	17 May	19 May	3	90 ± 20	35 ± 09
Female	Northwest	29 Jul	2 Aug	4	192 ± 33	50 ± 11