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Marc Soria, Yann Tremblay, A. Blaison, F. Forget, Estelle Crochelet, et al.. Large-scale movements and site fidelity of two bull sharks *Carcharhinus leucas* estimated from a double-tagging experiment at Reunion Island (southwest Indian Ocean). *African Journal of Marine Science*, 2021, 10.2989/1814232X.2021.1883736 . hal-03415690

HAL Id: hal-03415690

<https://hal.umontpellier.fr/hal-03415690>

Submitted on 17 Jan 2024

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

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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

39 Introduction

40

41 The bull shark *Carcharhinus leucas* occurs in warm tropical and subtropical waters, primarily on
42 continental shelves (Daly et al. 2014; Heupel et al. 2015). Bull sharks are reported to be largely
43 philopatric, with some seasonal migrations along the coast (Carlson et al. 2010; Espinoza et al. 2016).
44 Like other apex predators, bull sharks play a key role in the proper functioning of coastal tropical and
45 subtropical ecosystems (Ferretti et al. 2010). Globally, many shark populations have been under
46 intense fishing pressure throughout their ranges (Queiroz et al. 2019), resulting in substantial
47 population declines. According to the International Union for Conservation of Nature, *C. leucas* is
48 regarded as Near Threatened. However, bull sharks have also been considered to be responsible for
49 attacks on humans, particularly during the last decade at Reunion Island (Lagabrielle et al. 2018).
50 Since 2011, the mean number of shark bites per year has increased markedly from 1.1 to 3 for the
51 periods 1980–2010 and 2011–2019, respectively (Taglioni et al. 2018). Between 2011 and 2019, 27
52 attacks (of which 11 were fatal) occurred, which is considerable given the population of Reunion Island
53 (863 000 inhabitants in 2016).

54

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

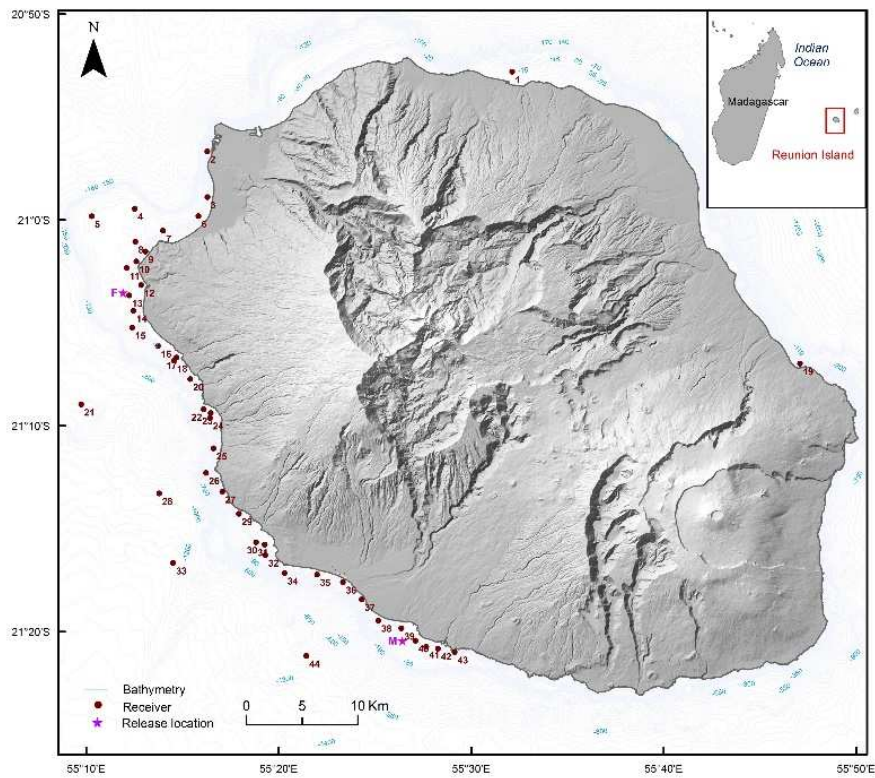
77 **Materials and methods**

78

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

83

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



89

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

92

93 Each PSAT tag was rigged with a heat-shrink-covered 20-cm monofilament tether and was attached
94 externally using a mono-filament line punctured through the first dorsal fin. Each PSAT tag was
95 programmed to detach itself after 192 days, float to the surface and transmit the archived data via the
96 Argos satellite constellation. The software WC-DAP Global Position Estimator 2.00.0027 (Wildlife
97 Computers) was used to process the raw light data (Wilson et al. 1992) and generated two location
98 estimates per day. We used the particle-filtering modelling approach described by Tremblay et al.
99 (2009), which is similar to the WC-GPE3 program of Wildlife Computers, to estimate the probable
100 locations of the sharks every eight hours. Constraints such as sea surface temperature and maximum

101 diving depth were not used to refine the position estimates due to the lack of a horizontal thermal
102 gradient and the relatively shallow occurrence of the sharks in the water column, which did not provide
103 useful information on the bathymetry of the area. The maximum swimming speed of 4.55 km h^{-1} was
104 used in the model and was based on the literature (Daly et al. 2014; Lea et al. 2015) and on speeds
105 estimated from movements between acoustic receivers. The known locations from acoustic
106 detections within the receiver array were used to refine the tracks generated by the geolocation model.
107 To reduce false acoustic detections, a shark was considered as present at a receiver when at least
108 two detections were recorded during one hour. The geolocation model was set to avoid the landmass
109 by using Dijkstra's algorithm (Singal and Chhillar, R.S. 2014) to find the path of least resistance (i.e.
110 shorter distance). Finally, given the limited accuracy of the geolocation estimates, we defined 'coastal
111 waters' as the waters within 20 km of the coast. As such, an 'excursion' was termed as a trip of at
112 least two days' duration outside coastal waters (i.e. $>20 \text{ km}$ from the coast).

113

114 **Results**

115

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

122

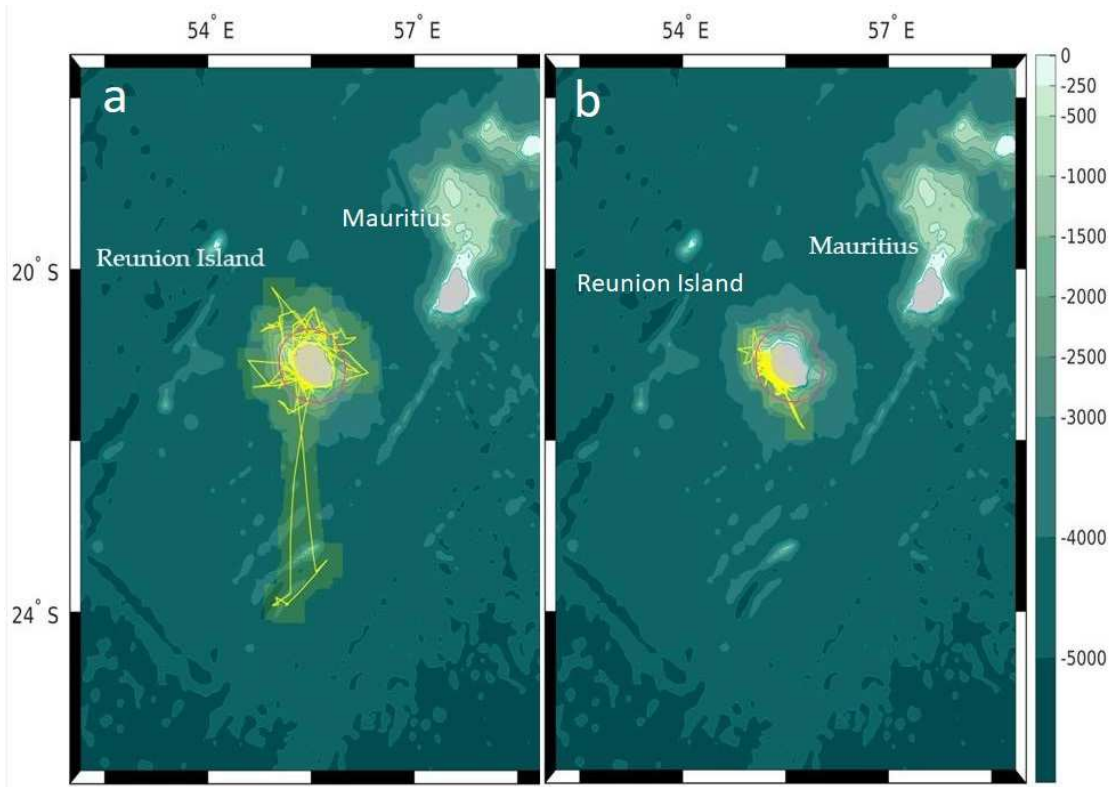
123 The proportion of time spent in coastal waters ($<20 \text{ km}$) was 58.1% and 89.9% for the male and
124 female, respectively. It appears that the female undertook a limited number of large-scale movements
125 and for most of the time remained in the coastal waters southwest of Reunion Island.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

128

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

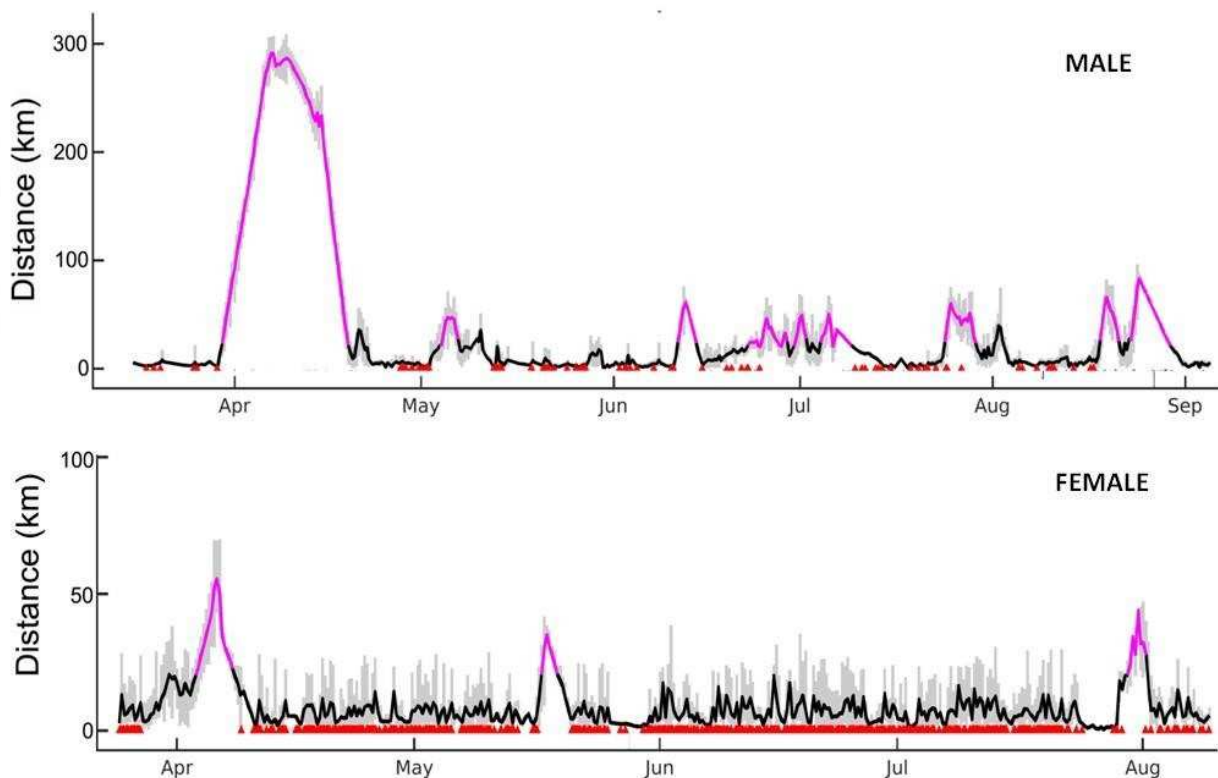
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137 **Figure 2:** Horizontal movements of (a) the tagged male bull shark from March to September 2013 and (b) the
 138 tagged female bull shark from March to August 2013. The intensity of the yellow pixels indicates the probability
 139 of occurrence. The pink circle indicates 20 km from the coast.
 140



141

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

147 **Discussion**

148

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

153

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

171

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

179

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

186

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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

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

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