

# Residency and spatial distribution of bull sharks *Carcharhinus leucas* in and around Reunion Island marine protected area

Marc Soria<sup>1,\*</sup>, Michael R. Heithaus<sup>2</sup>, Antonin Blaison<sup>1</sup>, Estelle Crochelet<sup>3</sup>,  
Fabien Forget<sup>1</sup>, Pascale Chabanet<sup>4</sup>

<sup>1</sup>MARBEC, University Montpellier, CNRS, Ifremer, IRD, 34200 Sète, France

<sup>2</sup>Center for Coastal Oceans Research, Marine Sciences Program, Florida International University, North Miami, FL 33181, USA

<sup>3</sup>ARBRE - Agence de Recherche pour la Biodiversité à la Réunion, 18 rue des Seychelles, Lotissement Horizon, 97436 Saint-Leu, La Réunion, France

<sup>4</sup>UMR 9220 ENTROPIE, IRD, 97400 La Réunion, France

**ABSTRACT:** A sudden increase in the rates of shark attacks on humans at Reunion Island has been blamed by some on the implementation of a marine protected area (MPA) along the island's west coast, where attacks, primarily by bull sharks *Carcharhinus leucas*, were concentrated. We used passive acoustic telemetry to investigate the spatial distribution of bull sharks (N = 36) by quantifying their residency and their frequentation of the MPA and compared it to outside of the MPA. Over the study duration of 17 mo, 18 sharks were detected in the acoustic receiver array, most of which were detected more frequently outside the MPA (N = 148; mean  $\pm$  SD =  $41.5 \pm 56.4$  visits  $\text{mo}^{-1}$  and  $17.6 \pm 30.5$  h  $\text{mo}^{-1}$ ) than inside the MPA (N = 218;  $21.4 \pm 28.1$  visits  $\text{mo}^{-1}$  and  $7.2 \pm 15.2$  h  $\text{mo}^{-1}$ ). However, we found individual variation in the sharks' use of the MPA. Thirteen sharks spent more time outside the MPA than inside, while 5 sharks (all females) spent significantly more time inside the MPA. These results suggest that the spatial distribution of bull sharks is not primarily centered in the MPA along the west coast of Reunion Island, although we identified specific locations where bull shark encounter probabilities are relatively high during particular times of the year. Such higher-risk areas could be targeted as part of the risk management strategy for changes in human uses in order to reduce the risks of negative shark–human interactions observed during the past decade.

**KEY WORDS:** Bull shark · Marine protected area · Human–shark conflict · Acoustic telemetry

Resale or republication not permitted without written consent of the publisher

## 1. INTRODUCTION

Despite the substantial decline in global shark populations (e.g. Ferretti et al. 2010), with approximately 25% of shark and ray populations threatened by extinction (Dulvy et al. 2014), some areas around the world have seen shark populations stabilize or even begin to increase (e.g. Carlson et al. 2012). This has raised concerns about the potential for negative shark–human interactions, including increased rates of depredation of fisheries (Gilman et al. 2008, Mac-

Neil et al. 2009) or even shark attacks on humans (Taglioni & Guiltat 2015). Despite the low probability of shark bites on ocean users at a global scale (<https://www.floridamuseum.ufl.edu/shark-attacks/>), the rate of shark–human interactions offshore of Reunion Island in the Southwest Indian Ocean has increased considerably over the past decade (Lagabrielle et al. 2018). Off Reunion Island, the incidence of shark bites rose from 1.2 bites yearly between 1980 and 2010 to an average of 3.7 bites yearly between 2011 and 2015 (Taglioni & Guiltat 2015). According to

\*Corresponding author: marc.soria@ird.fr

Taglioni & Guiltat (2015), the majority of incidents involved bull sharks *Carcharhinus leucas* and people practicing board sports (e.g. surfing). When correcting for the total number of surfing hours, the increase in incidents represents a 23-fold increase from 2005 to 2016 (Lagabrielle et al. 2018). Shark–human incidents peak in winter and appear to have shifted from being distributed randomly around the island before 2010 to the island's west coast, the hub of Reunion's coastal water activities (Lemahieu et al. 2017).

Increasing shark–human incident rates, concentrated on one part of the island, has exacerbated conflicts among ocean users and has led to great interest in understanding potential causes for these patterns. Previous analyses have suggested that seasonal patterns of shark abundance and the total numbers of ocean users may drive some of observed patterns of shark–human incidents (Ferretti et al. 2015, Chapman & McPhee 2016). Another factor that could potentially contribute to the increased incident rates could be the rapid tourism development of the west coast over the past 20 yr. Such developments may have increased freshwater runoff to the coast, expanding habitat for juvenile bull sharks. It is also possible that increased fishing pressure on reef sharks has reduced their populations. Because reef sharks are potential predators of young bull sharks, bull sharks may have experienced relaxed predation pressure at a key life history stage. But there are no convincing data on this activity of predation. Tourism development has resulted in eutrophication of the reef waters and over-exploitation of resources, leading to declines in living coral cover and fish biomass (McClanahan et al. 2007, Hughes et al. 2010, Naim et al. 2013) as well as erosion of coral beaches (Mahabot 2016). Recognizing this, a marine protected area (MPA) was established in 2007 to restore and protect reef zones.

The creation of the MPA has been controversial with some ocean users. They consider that reduced human uses combined with increased fish biomass in the MPA have attracted sharks towards the coastal waters where ocean activities, especially surfing, occur. To address these concerns associated with increasing shark–human incidents (Yemane et al. 2009), the 'Connaissance de l'Habitat des requins côtiers de la Réunion' (CHARC) program was launched in October 2011 (FEDER convention of 28 June 2012; French State convention Bop 113 no. 2012/03 and Region Reunion convention ref. POLENV no. 20120257). The aim of this broader project was to use acoustic telemetry to investigate spatiotemporal patterns in the occurrence and residence times of bull and tiger (*Galeocerdo cuvier*) sharks, both species having

been implicated in incidents (Blaison 2017). In this study, we investigated the degree of residency and spatial distribution of bull sharks in and out of the Reunion Island MPA.

## 2. MATERIALS AND METHODS

### 2.1. Study species

Bulls sharks are large carcharhinids that frequent warm coastal waters worldwide. Bull sharks in the Indian Ocean are larger than those in the Atlantic Ocean and can reach total lengths exceeding 400 cm (McCord & Lamberth 2009). Bull sharks are viviparous, with neonates generally occupying coastal rivers, mangroves and estuaries for the first several years of life before moving to coastal waters (Cruz-Martínez et al. 2004, Simpfendorfer et al. 2005). Large bull sharks are capable of taking large-bodied prey and have broad diets that include cephalopods, crustaceans, teleosts, elasmobranchs and marine mammals (Daly et al. 2013, Trystram et al. 2017). Larger individuals generally restrict their movements to particular areas along coasts (Yeiser et al. 2008, Carlson et al. 2010), although some individuals undertake long-distance movements or seasonal migrations depending on location (Daly et al. 2014, Lea et al. 2015, Espinoza et al. 2016).

### 2.2. Study site

Reunion Island is a relatively young volcanic island (ca. 3 million years old) in the southern hemisphere (21° 07' S, 55° 32' E), located 700 km east of Madagascar in the southwest Indian Ocean (Fig. 1). The island is 2512 km<sup>2</sup> and has 217 km of coastline. Like most volcanic islands, Reunion is characterized by its lack of insular plateau (except in the north at Saint-Paul and in the south at Saint-Pierre). Beyond this plateau, the underwater slopes are very steep (ca. 10–20%) to a depth of 2000 m (Piton & Taquet 1992). The coastal ecosystems of Reunion include sandy and rocky bottoms as well as coral reefs. Fringing reefs stretch over 25 km along the west and south-west coast, from Saint-Gilles to Saint-Pierre (Montaggioni & Faure 1980). They form a natural coral barrier that bounds the reef flats and back-reef depressions and lie no further than 500 m from the beach. In February 2007, a 35 km<sup>2</sup> MPA was established that extends ca. 36 km from Cap La Houssaye (Saint-Paul) to La Pointe aux Oiseaux (Etang-Salé). Much of the existing reef habi-

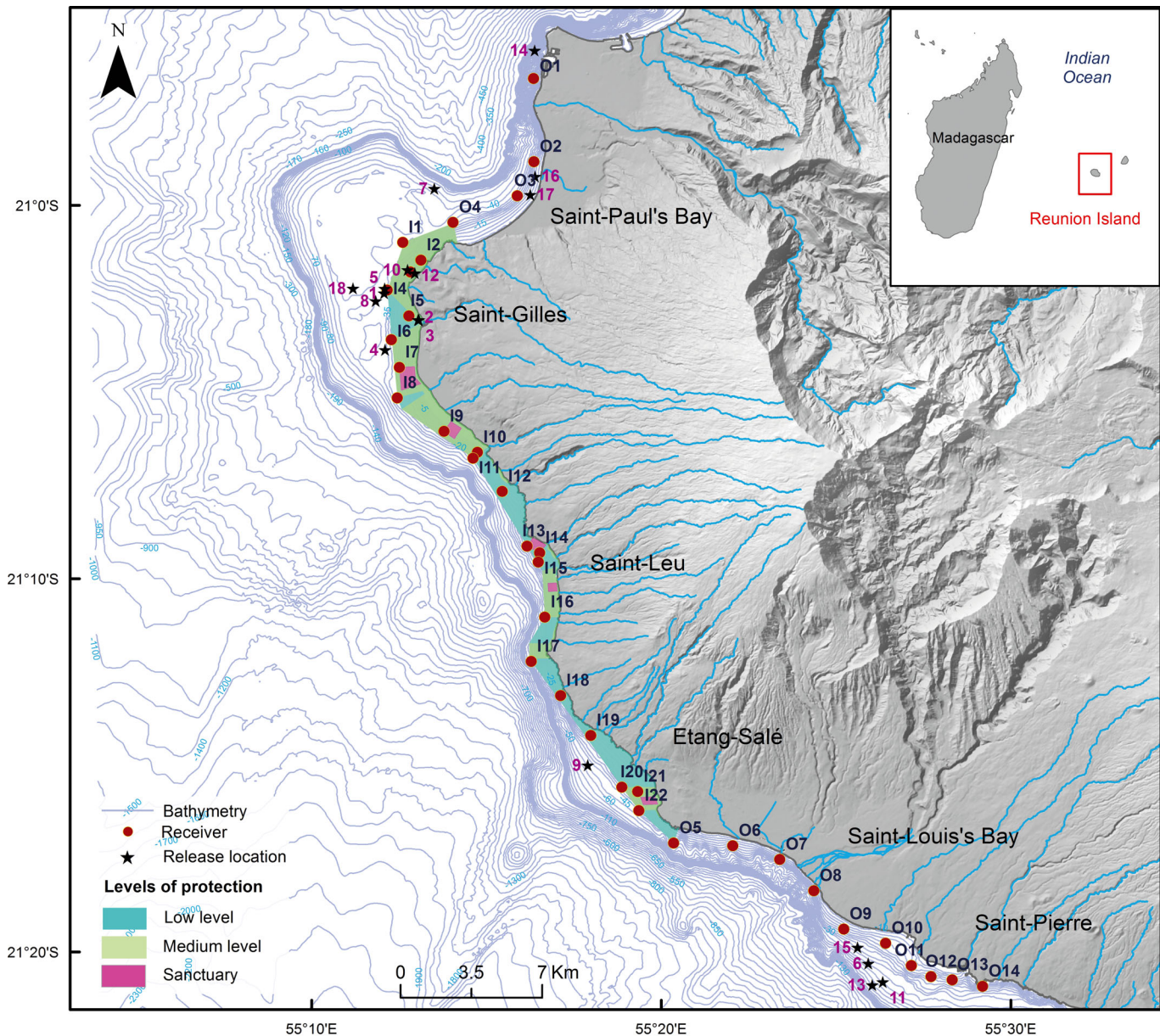


Fig. 1. Study site along the west coast of Reunion Island. The MPA is colored differently according to the different levels of protection. Shark release locations (shark code 1–18) are labeled with stars and the position of the receivers with closed circles. Receivers with I(O) in the receiver ID are inside (outside) the MPA

tat is included in the MPA (Letourneur et al. 2004; Fig. 1). Our study was focused primarily along the western (leeward) coast, from Saint-Paul's Bay to Saint-Pierre, and was centered around the MPA (Fig. 1).

### 2.3. Field methods

Occurrence and residence times of bull sharks were assessed using passive acoustic telemetry (Heupel et al. 2018). Sharks were captured along the west coast

of Reunion Island between September 2012 and March 2013 using horizontal drifting long-lines 0.2 to 1 km in length and equipped with 20 to 200 baited 16/0 circle hooks (Blaison 2017). Most fishing occurred at dusk or overnight, and soak times were fixed at 3 h to minimize mortality. The catch per unit effort (CPUE), expressed as the number of sharks per 100 hooks per hour, averaged ( $\pm$ SD)  $0.35 \pm 1.07$  (range 0–6.25,  $N = 115$  settings; Blaison et al. 2015). The fishing effort was higher on the north-west coast (70% of the fishing effort was done in Saint-Paul's



Bay and offshore from the harbor of Saint-Gilles and 30 % in the south offshore from the harbor of Saint-Pierre). CPUEs were not significantly different between the different sites ( $N = 115$ ; Kruskal-Wallis test,  $H = 11.8$ ,  $p = 0.07$ ; Blaison et al. 2015).

Once captured, sharks were brought alongside a tagging vessel, where they were measured and the sex was recorded. Sharks were then inverted and, once they entered a state of tonic immobility (Henningsen 1994), transmitters (Vemco V16TP-4H, transmission interval 40–80 s, power output 158 db, estimated battery life 845 d,  $N = 13$ , or V16-5H, 40–80 s, 162 db, 482 d,  $N = 5$ ) were implanted through a mid-ventral incision. Two independent absorbable sutures were made to close the wound. All fieldwork and protocols of handling and tagging the sharks were approved by the Ethics Committee (no. 114) of the Cyclotron Réunion Océan Indien (CYROI) in Reunion Island.

The array of acoustic receivers consisted of 36 Vemco VR2W receivers, deployed on average ca. 2 km apart and 700 m from shore at depths of 10–60 m (Fig. 1). Detection ranges are known to vary with environmental characteristics such as depth, sea conditions, surrounding noise and the presence of thermoclines (Mathies et al. 2014). Therefore, 13 range tests were conducted in the study site. The range to 50 % detection probability was on average  $190 \pm 80$  m ( $N = 6$ ) for the receivers placed less than 400 m from the shore (22 % of the acoustic network and evenly distributed inside and outside the MPA) and  $390 \pm 90$  m ( $N = 7$ ) for the receivers further offshore (78 % of the acoustic network). We can therefore presume that the detection ranges are comparable throughout the network, inside and outside the MPA.

#### 2.4. Data analysis

Data analysis was restricted to the period between 1 January 2013 and 25 May 2014. During this period, all receivers were operational; 14 receivers were deployed along roughly 27 km of coastline outside of the MPA, and 22 receivers were deployed along the 36 km of coastline of the MPA (Fig. 1). During the analysis period, 36 sharks were detected in the receiver array. We calculated the proportion of time within the study zone by dividing the proportion of time a shark was within the monitoring array (defined as having been detected on any receiver during a 60 min window) divided by the total number of monitored hours (the time between tagging and either the end of the study period or the estimated

tag lifetime). The proportion of detection time inside the MPA was calculated by dividing the number of hours inside the MPA by the number of hours in the study zone.

To determine whether sharks used the MPA differently than areas outside of the MPA, we calculated the number of visits each shark made to individual receivers as well as the duration of these visits. The duration of a visit to a receiver was defined as the time between first being detected and when it was last detected on that receiver before an absence (maximum blanking period; MBP) of more than 1 h (Ohta & Kakuma 2005, Capello et al. 2015). This period of absence from a receiver overestimates the amount of time spent within the detection range of the receiver. Moreover, sharks that return within this interval of 1 h would have remained within the MPA or outside the MPA during this relatively short absence. To ensure that results were not biased by the selection of a 60 min MBP, we analyzed the effect of the MBP duration on the presence estimated inside and outside the MPA. This effect was tested for MBPs of 1, 3 and 6 h. The number of times sharks returned to specific receivers (i.e. the number of distinct visits) decreased by 50 % (2326 to 1161) for a 3 h MBP and by 68 % (2326 to 727) for a 6 h MBP. The duration of presence per visit increased by 72 % when increasing the MBP from 1 to 3 h ( $0.38 \pm 0.75$  and  $0.65 \pm 1.50$  h, respectively) and more than 100 % when increasing MBP from 1 to 6 h ( $0.91 \pm 2.22$  h). While MBP affected the number and duration of visits, there was no difference in the increase between receivers inside and outside the MPA (Kruskal-Wallis test:  $H_2 = 0.045$ ,  $p = 0.977$ ,  $N = 441$ ; Siegel post hoc test:  $Z_{1h,3h} = 0.148$ ,  $Z_{1h,6h} = 0.205$ ,  $Z_{3h,6h} = 0.0567$ ). Therefore, MBP does not affect the nature of our results. Here we present results based on an MBP of 1 h.

The home range of bull sharks inside the study zone was estimated by using the 'adehabitatHR' R package v0.4.15 (Calenge 2006). The home range for each shark was computed in order to visualize its activity area within the receiver array and to determine the importance of the MPA in the spatial distribution of sharks. If the MPA is attractive to sharks, it can be expected that it plays an important role in their spatial distribution. The function 'kernelUD' estimates the utilization distribution (UD) of each shark by considering that the animal's use of space can be described by a bivariate probability density function. The 90 % home range was calculated from the UD estimates. The UD gives the probability density to relocate the sharks at any place according to the coordinates ( $x, y$ ) of the 36 receivers deployed in

the study zone. The kernel estimation of the UD at a given point coordinate is obtained by:

$$f(x) = \frac{1}{2\pi nh^2} \sum_{i=1}^n \exp\left(-\frac{d_i^2}{2h^2}\right) \quad (1)$$

where  $h$  is a smoothing parameter,  $n$  is the number of relocations, and  $d_i$  is the distance of the  $i$ th observation from the  $x, y$  coordinate. We determined kernel bandwidth  $h$ , by numerical optimization using the optimal  $h$  for a standard multivariate normal distribution (Horne & Garton 2006).

Since the number of receivers was not the same inside and outside the MPA, the duration of presence and the number of visits per month, per shark and per receiver were weighted by the densities of receivers in each area (with a factor of 1 inside the MPA, 1.32 outside the MPA in the north [4 receivers along 9.8 km of coastline], and 1.05 outside the MPA in the south [10 receivers along 17.6 km of coastline]). The sums and means of the duration of presence and of the number of visits inside or outside MPA were then calculated per month, for each shark or for each receiver. Only adult sharks detected during more than 2 mo were included in the analyses (with the exception of 2 sharks that were detected during 4 mo but with less than 2 detections  $\text{mo}^{-1}$  and were excluded from the analysis).

Presence times were log and Box-Cox transformed, and visits were Box-Cox transformed. These transformations were appropriate (chi-squared test:  $\chi^2_{12} = 12.8$ ,  $p = 0.38$  and  $\chi^2_8 = 11.03$ ,  $p = 0.20$ , respectively). We also did not detect differences in variances between data inside and outside the reserve (Levene tests:  $F_{1,318} = 0.67$ ,  $p = 0.41$ , and  $F_{1,318} = 3.10$ ,  $p = 0.08$ , respectively). Therefore, our data met the assumptions of parametric tests.

We used mixed ANOVA models, firstly, to determine whether the release sites (i.e. whether sharks were captured inside or outside the MPA) could affect the proportion of detection time and number of visits inside the MPA, and secondly, whether the monthly presence of sharks varied between areas (i.e. inside or outside the MPA). Area, month and interactions were fixed-effect factors, and we included the individual identity of sharks as a random factor.

To group the sharks relative to their MPA use, we conducted a hierarchical cluster analysis (HCA) on the monthly proportions of time spent in the MPA using Ward's minimum variance method and Manhattan distance, which has the advantage of both having triangular inequality and offering better data contrast than Euclidean distance. Tukey's HSD was

used to correct for multiple comparisons. Seasonality of presence by group was described following the marine seasons in Reunion Island (Conand et al. 2008). All statistical tests were carried out in Statistica 12.0 (StatSoft) or using specific R packages. Results are presented as mean  $\pm$  SD (min.–max.), unless otherwise indicated.

### 3. RESULTS

Of the 36 tagged sharks, 24 were caught and tagged inside the MPA and 12 outside the MPA. Only 18 were detected frequently enough to be included in analyses (i.e. during more than 2 mo). Of the 18 sharks that were not included in the analysis, 8 sharks were never detected and 10 were detected too rarely and sporadically (i.e. during only a few months).

The final database contains 10 804 visits from 103 170 detections. The 18 individuals monitored on the west coast of Reunion Island included 6 males and 12 females, with 2 individuals detected in all 17 mo, 4 detected during 14–16 mo, 7 detected during 9–12 mo and 5 detected during 3–6 mo. These sharks spent between 2.3 and 29.3 % of their time in range of at least 1 receiver (mean =  $11.5 \pm 7.0\%$ ,  $N = 18$ ). Overall, sharks made more visits and spent longer times within the range of receivers found outside the MPA than inside (Table 1).

Based on Kernel home range estimates, 12 of 18 sharks that entered the array moved over extensive areas of the coast, and ranges extended over the entire study zone (Fig. 2). Two sharks had a restricted occupancy: 1 individual (Shark 1) in the northern part of the MPA, the other north of the MPA (Shark 10). Two other individuals (Sharks 17 and 18) occupied 2 areas outside the MPA (north and south of the study zone) but did not stay in (Shark 17) or even enter (Shark 18) coastal waters of the MPA (Figs. 1 & 2, Table 2).

Sharks released within the MPA spent approximately equal amounts of time (in  $\text{h mo}^{-1}$ ) around receivers inside and outside the MPA ( $13.08 \pm 21.07 \text{ h}$  [0.05–109.95 h],  $N = 81$  and  $13.28 \pm 20.91 \text{ h}$  [0.04–103.90 h],  $N = 87$ , respectively; ANOVA  $F_{1,166} = 0.02$ ,  $p = 0.89$ ), while those that were tagged outside the MPA spent considerably more time at receivers outside the reserve than inside ( $16.62 \pm 17.93 \text{ h}$  [0.10–111.32 h],  $N = 87$  and  $8.00 \pm 10.27 \text{ h}$  [0.05–42.27 h],  $N = 65$ , respectively; ANOVA  $F_{1,150} = 19.05$ ,  $p = 0.001$ ). Sharks in the latter category also were detected for longer overall proportions of time as well.

Table 1. Total and mean ( $\pm$ SD) monthly bull shark presence time and number of visits at receivers inside and outside the Reunion Island marine protected area (MPA) between January 2013 and May 2014. Monthly mean presence time was estimated from the sum of time of presence by month

Receiver code	Distance to coast (m)	N	Inside MPA		N	Outside MPA		Visits		
			Presence (h)			Presence (h)				
			Total	Monthly		Total	Monthly			
I1	1600	9	53.7	6 ± 7.6	122	13.6 ± 10.6	101	14.4 ± 8.3		
I2	380	7	7.1	1 ± 0.7	30	4.3 ± 2.4	675	56.2 ± 38.5		
I3	350	5	0.8	0.2 ± 0.1	6	1.2 ± 0.4	358	39.8 ± 28.9		
I4	1050	6	95.6	15.9 ± 13.1	278	46.3 ± 34.6	434	36.2 ± 21.5		
I5	470	11	195.6	17.8 ± 24.5	367	33.4 ± 37.8	652	54.4 ± 51.8		
I6	1400	12	465.9	38.8 ± 43.3	698	58.2 ± 57.2	1373	114.5 ± 93		
I7	850	12	22.1	1.8 ± 2.3	107	8.9 ± 8.3	1373	124.9 ± 95.8		
I8	1450	9	14.0	1.6 ± 1.9	66	7.3 ± 4.1	329	27.4 ± 23.8		
I9	810	12	34.3	2.9 ± 2.9	69	5.8 ± 4.1	144	12 ± 11.3		
I10	430	10	42.9	4.3 ± 3.8	149	14.9 ± 10.2	363	30.2 ± 28.3		
I11	720	12	48.1	4 ± 3.7	275	22.9 ± 17.3	73	7.3 ± 5.5		
I12	540	9	42.7	4.7 ± 10.7	34	3.8 ± 2.9	43	8.7 ± 5.1		
I13	540	11	10.7	1 ± 0.9	59	5.4 ± 3.2	34	3.4 ± 1.4		
I14	560	12	104.2	8.7 ± 8.6	380	31.7 ± 17.1	185	15.4 ± 9.1		
I15	910	12	7.4	0.6 ± 0.4	44	3.7 ± 1.8				
I16	700	12	106.8	8.9 ± 9.3	521	43.4 ± 33.8				
I17	900	9	31.7	3.5 ± 4	125	13.9 ± 9.8				
I18	300	12	85.9	7.2 ± 6	568	47.3 ± 39				
I19	340	7	34.9	5 ± 5.5	76	10.9 ± 9.9				
I20	1250	9	35.7	4 ± 3.4	158	17.6 ± 13.1				
I21	850	11	87.3	7.9 ± 12.1	302	27.5 ± 35.1				
I22	900	9	52.1	5.8 ± 3.3	233	25.9 ± 13.3				
Total		218	1579.7	7.2 ± 15.2	4667	21.4 ± 28.1	148	2601.9	6137	41.5 ± 56.4
								17.6 ± 30.5		

The amount of time sharks spent at receivers varied significantly with the interaction: area  $\times$  shark ID and the main effects of area, month and shark ID (Table 3). In general, sharks spent more time outside the MPA, with small but significant variation across months. Individual sharks varied in the duration of time they spent in the study zone and inside versus outside the reserve (Table 3).

HCA revealed 2 groups. Group 1 (Fig. 3, Table 2) was composed of 5 individuals (Sharks 1–5), all females, which spent more time ( $>70\%$  of the total presence time) in the MPA and visited it more often (Table 4). However, the difference between areas was significant for only 3 sharks (Sharks 1, 4 and 5; Table 2). Except for Shark 1, these sharks ranged widely (see home ranges, Fig. 2). Four of the 5 sharks in Group 1 (Sharks 1, 2, 3 and 5, Table 2) spent more time at the 3 receivers offshore of Saint-Gilles harbor (receivers I4, I5 and I6, Fig. 1) than at the other receivers inside the MPA ( $9.7 \pm 14.2 \text{ h mo}^{-1} \text{ receiver}^{-1}$  [ $0.05\text{--}55.34 \text{ h mo}^{-1} \text{ receiver}^{-1}$ ],  $N = 55$  and  $0.7 \pm 1.2 \text{ h mo}^{-1} \text{ receiver}^{-1}$  [ $0.03\text{--}7.84 \text{ h mo}^{-1} \text{ receiver}^{-1}$ ],  $N = 257$ , respectively; ANOVA,  $F_{1,310} = 94.34$ ,  $p = 0.001$ ). In addition, these sharks were observed mainly between April and June when water temperatures are dropping (Fig. 4).

Group 2 (Fig. 3, Table 2) was composed of 13 individuals (Sharks 6–18) which spent more time outside the MPA than inside and made more visits to receivers outside the MPA (Table 4). Post hoc analyses indicated that presence times were significantly different inside and outside the MPA for 6 of the 13 individuals (Table 2). In general, these sharks were widely dispersed in the study zone, with the exception of 2 individuals (Sharks 10 and 18) that were detected mostly outside the

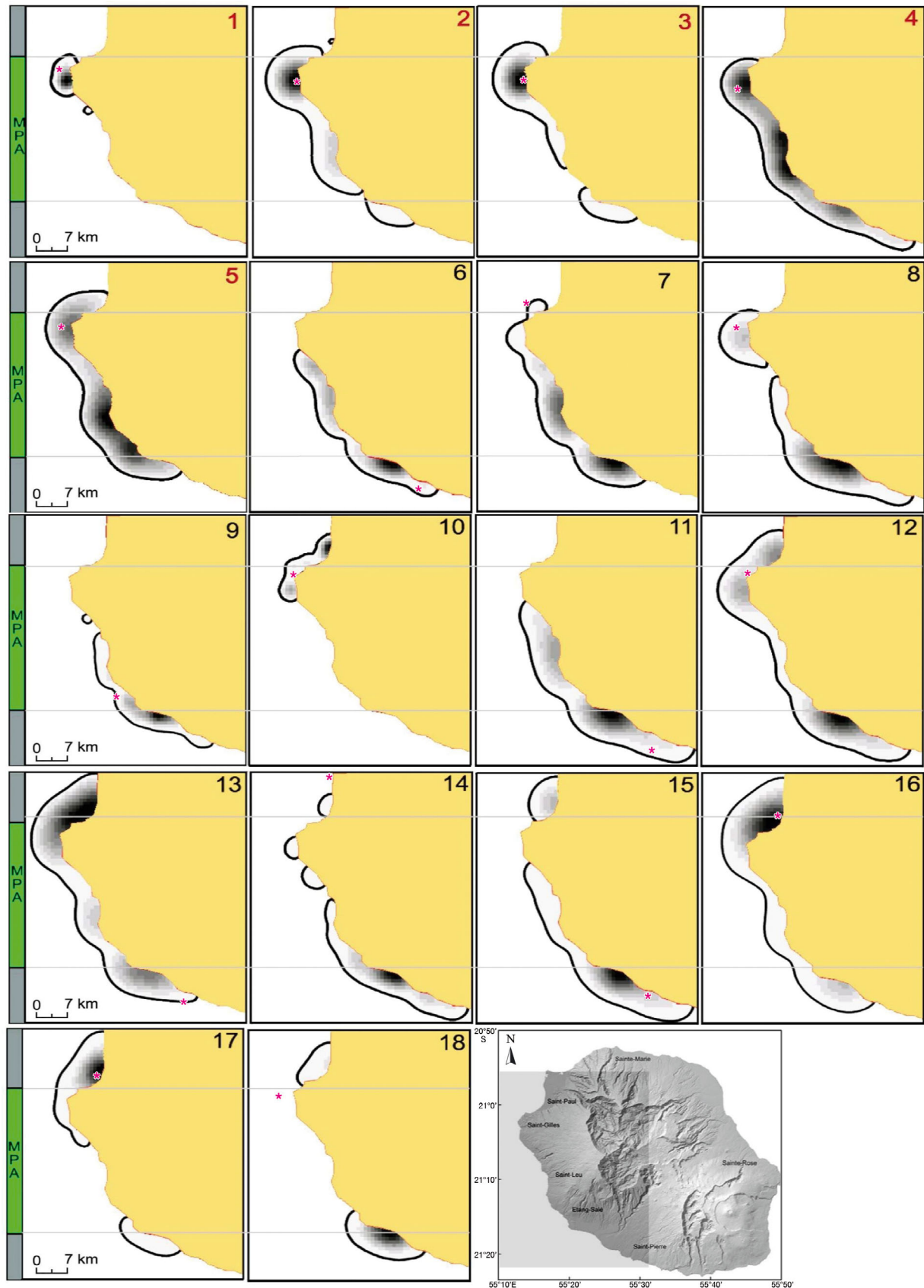


Fig. 2. 90 % Kernel home-range densities of sharks that were detected in the array of acoustic receivers. Green boxes indicate the latitudinal extent of the MPA. Shark release locations are denoted by stars (\*). Shark codes (1–18) indicated in each panel. Inset indicates the localization of the study zone (shaded rectangle) relative to Reunion Island. Red shark codes denote sharks that spent more time within the MPA (Group 1, see Table 2 and Fig. 3)

Table 2. Summary statistics of 18 bull sharks from January 2013 to May 2014. Asterisks denote sharks whose presences inside and outside the Reunion Island marine protected area (MPA) are significantly different (Tukey's HSD test). I(O): receiver inside (outside) MPA

Shark code	General information				Inside MPA				Outside MPA					
	Total length (cm)	Closest receiver to release location	Monitoring time (d)	Detection time (d)	Proportion of time detected (%)	Proportion of detection time inside MPA (%)	Total presence time (h)	Mean $\pm$ SD presence time (h mo <sup>-1</sup> )	Mean $\pm$ SD visits (by month)	Total number of visits	Total presence time (h)	Mean $\pm$ SD presence time (h mo <sup>-1</sup> )	Mean $\pm$ SD visits (by month)	Total number of visits
1 ♀ *	300	I4	450	46	10.22	99.24	332.4	41.5 $\pm$ 37.8	66.4 $\pm$ 58.5	531	2.6	0.4 $\pm$ 0.4	4.2 $\pm$ 4.4	29.6
2 ♀	314	I5	200	20	10.00	90.20	127.7	42.6 $\pm$ 58.7	88 $\pm$ 89.4	264	13.9	4.6 $\pm$ 3.2	18.9 $\pm$ 14.2	56.8
3 ♀	308	I5	200	20	10.00	89.47	98.0	24.5 $\pm$ 23.6	67 $\pm$ 54	268	11.5	2.9 $\pm$ 1.3	11.2 $\pm$ 6.4	44.9
4 ♀ *	307	I6	424	54	12.74	74.43	121.7	12.2 $\pm$ 7.4	47.1 $\pm$ 28.8	471	41.8	4.2 $\pm$ 3.4	18.5 $\pm$ 11.6	184.5
5 ♀ *	300	I4	470	17	3.62	82.61	45.5	5.7 $\pm$ 5.7	22 $\pm$ 18.4	176	9.6	1.4 $\pm$ 1.2	5.4 $\pm$ 4.2	37.8
6 ♂	260	O10	456	135	29.61	40.80	241.3	16.1 $\pm$ 12.3	56.9 $\pm$ 40	854	350.1	23.3 $\pm$ 16.8	46.6 $\pm$ 22.7	699.7
7 ♀	300	O4	86	16	18.60	43.76	19.8	6.6 $\pm$ 5	43 $\pm$ 34	129	25.4	6.4 $\pm$ 3.9	19.4 $\pm$ 10.2	77.7
8 ♀	314	I4	507	24	4.73	33.09	25.1	8.4 $\pm$ 3.9	31 $\pm$ 6	93	50.8	16.9 $\pm$ 5.9	65.1 $\pm$ 10.3	195.3
9 ♂	269	I19	447	69	15.44	30.27	47.8	4.3 $\pm$ 3.3	21.9 $\pm$ 15	241	110.2	10 $\pm$ 9.1	36.9 $\pm$ 17.2	406.3
10 ♀	329	I3	507	51	10.06	29.19	131.5	13.2 $\pm$ 14.8	24.2 $\pm$ 23.5	242	319.1	29 $\pm$ 36.8	51.4 $\pm$ 47.2	565.6
11 ♂	290	O11	433	13	3.00	27.94	6.9	1.7 $\pm$ 2	10 $\pm$ 10.7	40	17.7	1.8 $\pm$ 1.5	7.8 $\pm$ 5.6	77.7
12 ♀ *	274	I3	507	92	18.15	27.47	124.1	7.3 $\pm$ 9.8	21.2 $\pm$ 21.7	361	327.8	19.3 $\pm$ 21.6	38.9 $\pm$ 28.5	661.2
13 ♂ *	294	O10	422	59	13.98	21.88	62.5	4.8 $\pm$ 5.3	22.2 $\pm$ 20.9	288	223.4	16 $\pm$ 14.4	38 $\pm$ 25.8	531.9
14 ♀ *	228	O1	501	99	19.76	21.80	120.3	10 $\pm$ 12.6	36 $\pm$ 41.6	432	431.6	25.4 $\pm$ 26.5	61.4 $\pm$ 42	1043.6
15 ♀ *	260	O9	456	60	13.16	18.81	53.6	4.1 $\pm$ 8.3	10.2 $\pm$ 18.5	132	231.4	16.5 $\pm$ 14.1	36 $\pm$ 25.4	503.6
16 ♂	298	O2	434	11	2.53	11.43	7.8	3.9 $\pm$ 2.5	29 $\pm$ 29.7	58	60.4	20.1 $\pm$ 26.8	59.2 $\pm$ 81.5	177.5
17 ♀ *	295	O3	501	12	2.40	7.04	8.0	2.7 $\pm$ 2.7	14.7 $\pm$ 14.6	44	105.9	10.6 $\pm$ 8.6	19 $\pm$ 10.6	189.9
18 ♂ *	260	I4	429	50	11.66	2.00	5.5	0.8 $\pm$ 0.8	6.1 $\pm$ 4	43	268.7	19.2 $\pm$ 24.7	46.7 $\pm$ 48.4	653.5
Total							1579.7	10.8 $\pm$ 17.3	32 $\pm$ 35.6	4667	2601.9	15 $\pm$ 19.5	35.3 $\pm$ 33.2	6137.0

MPA (Fig. 2). Outside the MPA, they occupied mostly receivers on either side of the MPA (receivers O2, O3 and O4 in Saint-Paul's Bay and O5, O6 and O7 in Saint-Louis's Bay; see Fig. 1) than the other receivers outside the MPA ( $4.6 \pm 14.2$  h mo<sup>-1</sup> receiver<sup>-1</sup> [0.03–82.28 h mo<sup>-1</sup> receiver<sup>-1</sup>], N = 477 and  $1.0 \pm 1.9$  h mo<sup>-1</sup> receiver<sup>-1</sup> [0.03–18.26 h mo<sup>-1</sup> receiver<sup>-1</sup>], N = 327, respectively; ANOVA,  $F_{1,802} = 153.04$ ,  $p = 0.001$ ). Except for 2 sharks that were exclusively observed in summer (Sharks 8 and 16), these sharks were present throughout the year and did not display marked seasonality (Fig. 4).

#### 4. DISCUSSION

Given the high rate of bull shark–human incidents and the increasing public concern, it is important to understand whether the Reunion Island MPA affects the spatial distribution of bull sharks. In the absence of movement data prior to the implementation of the MPA and in the absence of knowledge on the habitat quality for bull sharks inside and outside the MPA, it is impossible to pinpoint whether MPA implementation modified the movements and residency of bull sharks along the west coast of Reunion Island. Regardless, we found that 50% of the tagged sharks (18 individuals) were never detected in the coastal network and most of the 18 sharks that remained within the acoustic array spent more time outside than inside the MPA. Generally, their home ranges appear to extend along the coast of the study area. Finally, only 5 (21%) of the 24 individuals tagged inside the MPA regularly frequented this area. This suggests that tagging location did not have an effect on the sharks' movements and that bull sharks were not using the MPA more heavily than surrounding areas.

Reunion Island's MPA was created in 2007 in order to restore coral reef biodiversity and augment fish stocks by managing the human activities taking place within it. For coastal sharks, such as bull sharks, this could provide an opportunity to find feeding sites if prey resources recovered (Garla



Table 3. Results of the ANOVA mixed model for effects of MPA, month and shark on the presence time of tagged bull sharks in the study area of Reunion Island

Factors	Effect	df	MS effect	df error	MS error	F	p
Area	Fixed	1	26.32	51	1.93	13.62	0.001
Month	Fixed	11	4.87	51	1.93	2.52	0.013
Shark	Random	17	7.47	51	1.93	3.87	0.000
Area × Month	Fixed	11	2.64	51	1.93	1.37	0.218
Area × Shark	Fixed	17	9.25	51	1.93	4.79	<0.001
Month × Shark	Fixed	118	1.77	51	1.93	0.91	0.660
Area × Month × Shark	Fixed	93	1.25	51	1.93	0.65	0.964

et al. 2006, Knip et al. 2012a). While MPAs in other areas have been shown to result in rebounds in shark numbers fairly quickly (Knip et al. 2012b, Edgar et al. 2014), this pattern has not been verified for bull sharks off Reunion. Indeed, our tracking data do not suggest that bull sharks preferentially select areas within the MPA. This difference could be due to the continued presence of extractive fishing in the Reunion MPA and relatively low biomass of potential prey within the MPA. Indeed, from 2008 to 2014, fish biomass in the reserve increased from ca. 400 to 500 kg ha<sup>-1</sup>, but only in the full sanctuary zones of the MPA (Bigot et al. 2016) that represent ca. 5% of the reserve's area (see Fig. 1). This small increase in biomass is unlikely to be sufficient to drive shifts in shark numbers. Moreover, biomass on Reunion's reefs is generally low (~500 kg ha<sup>-1</sup>) compared to biomass levels observed on other Indian Ocean coral reefs (McClanahan et al. 2011, Chabanet et al. 2016) and may represent only a modest attraction for large-bodied predators like bull sharks. Shark use of the MPA was spatially heterogeneous. The one location where shark activity was concentrated inside the MPA was offshore of Saint-Gilles, where professional and recreational fishing are authorized. From the perspective of implementing an efficient strategy of warning and prevention in Reunion island, this result further suggests the need to focus more on the habitat use, movements and site fidelity of sharks than on the impact of the MPA, which is unlikely a cause of increased incidents.

Sharks often exhibit inter-individual variation in behaviors (e.g. Heithaus et al.

2002, Matich et al. 2011). Here, we found that individuals varied considerably in their use of the MPA and temporal patterns of occurrence. Broadly, sharks could be grouped into those that were present virtually year-round and used waters outside or at the boundaries of the MPA more than those inside, and another smaller group of female sharks that occurred primarily from April to June, when water temperatures are dropping, and used waters off Saint-Gilles more often than other individuals.

Variation in the abundance and behavior of bull sharks has been attributed to several factors, including temperature (Brunnschweiler et al. 2010, Carlson et al. 2010, Matich & Heithaus 2012, Drymon et al. 2014), dissolved oxygen levels (Heithaus et al. 2009), salinity (Simpfendorfer et al. 2005, Curtis 2008) and water turbidity (Cliff & Dudley 1991, Taylor 2007, Froeschke et al. 2010).

At Reunion Island, several factors could be responsible for the increase in shark–human interactions, including benthic substrate, sea temperature and

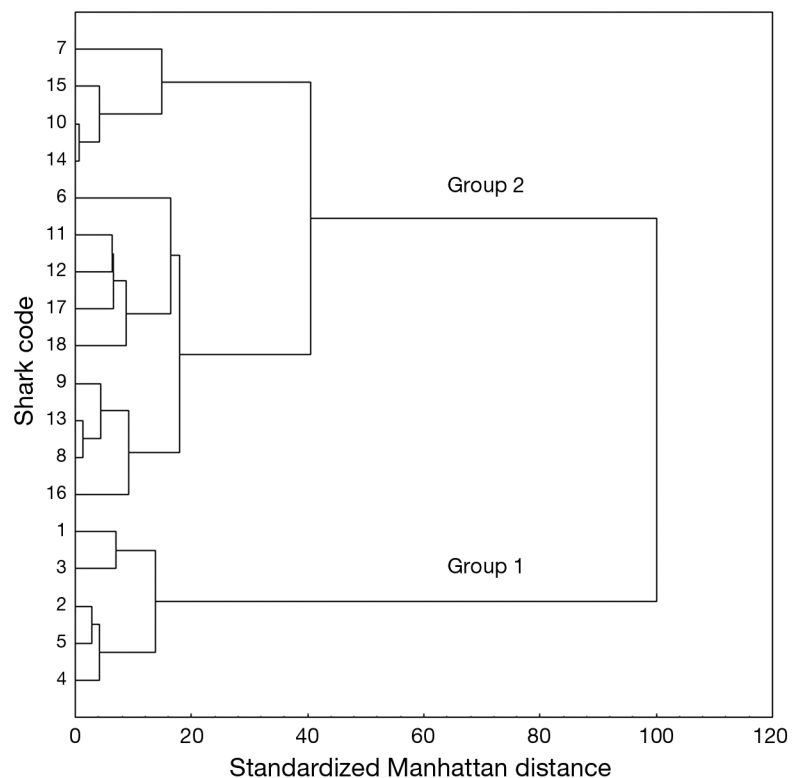


Fig. 3. Hierarchical clustering dendrogram of sharks (cf. shark codes in Table 2) based on the proportion of time spent in the MPA

Table 4. Total and mean ( $\pm$ SD) monthly bull shark presence time and number of visits at receivers inside and outside the Reunion Island MPA for 2 behavior types resolved by hierarchical cluster analysis (see Fig. 3); p-values are based on ANOVA

Group	MPA	N	— Presence time (h) —		—— Visits ——		p
			Total	Monthly	Total	Monthly	
1	Inside	33	725.4	22.0 $\pm$ 28.9	1710	51.8 $\pm$ 47.6	0.0001
	Outside	31	79.4	2.6 $\pm$ 2.7	354	11.4 $\pm$ 10.4	
2	Inside	113	854.4	7.6 $\pm$ 10	2957	26.2 $\pm$ 29	0.0001
	Outside	143	2522.5	17.6 $\pm$ 20.5	5784	40.4 $\pm$ 34.2	

period of day (Lagabrielle et al. 2018), turbidity and swell height (Taglioni et al. 2019). Multiple rivers and ravines provide freshwater inputs to the coastal waters. During rainfall events, turbid outflow waters rich in organic matter (Piper & Normark 2009) would not only reduce visibility in coastal waters but also reduce water salinity, conditions that might be attractive to bull sharks (Werry et al. 2018). Over recent decades, the fast expansion of urban zones on the west coast of the island might have increased the soil sealing and consequently the rate and quantity of stormwater runoff flowing to the sea (Shuster et al. 2014). Consistent with this hypothesis is the finding that the highest occurrence of sharks outside the MPA was in the 2 bays located at the mouths of the 2 largest rivers of the west coast (Fig. 1), on both sides of the MPA (receivers O2, O3 and O4 in Saint-Paul's Bay and O5, O6 and O7 in Saint-Louis's Bay).

Overexploitation of stocks of coastal and deep-sea demersal fish in Reunion observed since the early 2000s (Le Manach et al. 2015) may have reduced the availability of potential prey for bull sharks, inducing them to forage over wider areas and nearer to the coast irrespective of the presence of the MPA. Anthropogenic changes to the environment could also influence shark behavior and habitat use (Wong & Candolin 2015, Hays et al. 2016). For example, the presence of the harbor of Saint-Gilles, where fish carcasses are discarded regularly (N. Loiseau pers. comm.) would offer feeding opportunities and could attract sharks (Hazin et al. 2008, Papastamatiou et al. 2011). Consistent with this hypothesis is the finding that the 3 receivers in the MPA with the greatest presence were offshore of Saint-Gilles harbor (I4, I5 and I6, see Fig. 1). Another hypothesis is that the preferred use of the Saint-Gilles site by 4 adult females during April to June is linked to reproduction. Indeed, this period overlaps with the apparent mating period of bull sharks in the intertropical zone (March to June; Stevens & McLoughlin 1991, Espinoza et al. 2016). Recently, Pirog et al. (2019) reported that the mating period in Reunion Island should occur during the cold season (June to September). The hypothesis stated above suggests that a pre-spawning shark aggregation could occur near Saint-Gilles harbor before the mat-

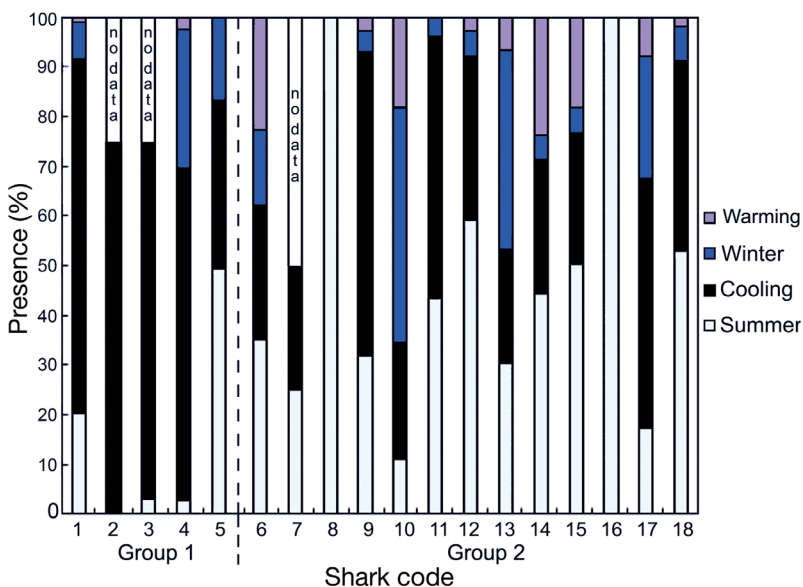


Fig. 4. Proportion of time individual sharks were detected across seasons (summer: January to March; cooling: April to June; winter: July to September; warming: October to December)

ing period. In addition to external factors like turbidity, swell height and human activity (Taglioni et al. 2019), localized movements might influence the occurrence of attacks. For example, the site of Saint-Gilles, where 4 of the 5 sharks observed in the MPA were mainly present, is one of the most popular surfing sites of Reunion island. Therefore, a high level of shark-human interactions could be expected at this site. Specific analysis on fine-scale movements along the coast related to biotic and abiotic factors could help to test this hypothesis.

While passive acoustic telemetry is an important tool in studies of elasmobranch habitat use, it has limitations (e.g. Kessel et al. 2014, Heupel et al. 2018). The first challenge is detection area within the network of receivers. For example, sharks can spend a con-

siderable portion of their time outside of a monitoring array, as was the case for most of the sharks tagged in this study. In our study at Reunion Island, the receivers only covered ca. 40 % of the coastal zone of the study area and did not extend far into offshore waters where sharks likely spend considerable time. It also did not extend along the coast further away from the MPA. However, the array was optimized to determine whether individuals were spending extended periods of time nearshore where shark–human interactions might occur both inside and outside the MPA.

With highly mobile species like bull sharks, and relatively large detection ranges, movements along the coastline have a high probability of being detected by receivers. Importantly, this design is unlikely to bias results towards greater use of waters inside or outside the reserve. The weighting factors used to take into account the difference in the densities of receivers inside and outside the MPA should not have influenced the results. A second challenge is the number of tagged sharks that could be analyzed in our study. Of the 36 sharks tagged, only 18 were detected often enough to warrant inclusion in the analyses. However, this sample is large enough to gain insights into general patterns of visitation and residence times for individuals using coastal waters and provides evidence that sharks are not using MPA waters more often than those outside the MPA. Finally, spatial or temporal variations in detection ranges of the receivers might confound data analysis. While the potential impact of such variation is difficult to fully quantify, the design of the array and range testing suggest that patterns were unlikely to have been driven by variation in detection ranges of receivers. Indeed, receivers were deployed in acoustically similar environments inside and outside the MPA, and only 8 receivers of 36 (22 %) were situated near the coastline and the coral reefs where background noise could reduce detection ranges. Nevertheless, these nearshore receivers were evenly distributed inside and outside the MPA. Lastly, receiver recoveries were performed every 4–5 mo to reduce the potential effects of biofouling (Heupel et al. 2008).

In summary, our results indicated that although some sharks may use specific areas inside the MPA during limited time periods, they do not seem to use the habitat inside the MPA more than the area around the MPA. Indeed, sharks generally were not detected in coastal waters after release, or they spent more time in waters outside the MPA than inside the MPA. Concerning the influence of release positions on residence time in or out of the MPA, we are currently

studying the relationship between fine-scale individual movements and potential social interactions amongst sharks. Further studies that employ additional field and analytical methods, increase the sample sizes, extend the temporal period of observation and integrate data on environmental and biotic factors will provide further insights into the factors driving bull shark habitat use along the coast of Reunion Island. Together with biological and ecological studies, social science studies on the perception by different ocean users of wildlife as both damaging and fascinating (Dickman 2010) are also necessary to develop policies that could reduce shark–human incidents.

**Acknowledgements.** We are grateful to all members of the institutions and associations involved in the shark program (IRD, CRPMEM, University of Reunion Island, Globice, Kélonia, ARVAM, Squal'Idées, RNMR, Ifremer), as well as the fishermen, the members of the CRESSM and all volunteers who assisted with shark fishing and tagging and made our work possible. Finally, we thank the anonymous reviewers and the Guest Editor for their comments and advice, which helped to improve this paper. This study received financial support from the European Union (convention FEDER ref. 2012-dossier Presage no. 33021), the French government (BOP 113 no. 2012/03) and the Regional Council of Reunion Island (POLENV no. 20120257). Research grants were provided to M.R.H. by the Regional Council of Reunion Island. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

#### LITERATURE CITED

- Bigot L, Bruggemann H, Cadet C, Cauvin B and others (2016) Point I du suivi de "l'effet réserve" sur les communautés ichthyologiques et benthiques récifales - Secteurs de St Gilles/ La Saline et de Saint-Leu - Etat des lieux à 7 ans après la création de la réserve naturelle nationale marine de La Réunion. Rapport final. ECOMAR, IRD, MNHN, Saint-Denis
- Blaison A (2017) Écologie comportementale des requins bouledogue (*Carcharhinus leucas*) sur les côtes de La Réunion: application à un modèle de gestion du 'risque requin'. PhD thesis, Université de la Réunion, Saint-Denis
- ✦ Blaison A, Jaquemet S, Guyomard D, Vangrevelinghe G and others (2015) Seasonal variability of bull and tiger shark presence on the west coast of Reunion Island, western Indian Ocean. *Afr J Mar Sci* 37:199–208
- ✦ Brunnenschweiler JM, Queiroz N, Sims DW (2010) Oceans apart? Short-term movements and behaviour of adult bull sharks *Carcharhinus leucas* in Atlantic and Pacific Oceans determined from pop-off satellite archival tagging. *J Fish Biol* 77:1343–1358
- ✦ Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519
- ✦ Capello M, Robert M, Soria M, Potin G and others (2015) A methodological framework to estimate the site fidelity of

- tagged animals using passive acoustic telemetry. PLOS ONE 10:e0134002
- ✦ Carlson JK, Ribera MM, Conrath CL, Heupel MR, Burgess GH (2010) Habitat use and movement patterns of bull sharks *Carcharhinus leucas* determined using pop-up satellite archival tags. J Fish Biol 77:661–675
- ✦ Carlson JK, Hale LF, Morgan A, Burgess G (2012) Relative abundance and size of coastal sharks derived from commercial shark longline catch and effort data. J Fish Biol 80:1749–1764
- ✦ Chabanet P, Bigot L, Nicet JB, Durville P and others (2016) Coral reef monitoring in the Iles Eparses, Mozambique Channel (2011–2013). Acta Oecol 72:62–71
- ✦ Chapman BK, McPhee D (2016) Global shark attack hotspots: identifying underlying factors behind increased unprovoked shark bite incidence. Ocean Coast Manag 133: 72–84
- ✦ Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. S Afr J Mar Sci 10:253–270
- ✦ Conand F, Marsac F, Tessier E, Conand C (2008) A ten-year period of daily sea surface temperature at a coastal station in Reunion Island, Indian Ocean (July 1993–April 2004): patterns of variability and biological responses. West Ind Ocean J Mar Sci 6:1–16
- ✦ Cruz-Martínez A, Chiappa-Carrara X, Arenas-Fuentes V (2004) Age and growth of the bull shark, *Carcharhinus leucas*, from southern Gulf of Mexico. J Northwest Atl Fish Sci 35:367–374
- Curtis TH (2008) Distribution, movements, and habitat use of bull sharks (*Carcharhinus leucas*, Müller and Henle 1839) in the Indian River Lagoon system, Florida. PhD dissertation, University of Florida, Gainesville, FL
- ✦ Daly R, Froneman PW, Smale MJ (2013) Comparative feeding ecology of bull sharks (*Carcharhinus leucas*) in the coastal waters of the southwest Indian Ocean inferred from stable isotope analysis. PLOS ONE 8:e78229
- ✦ Daly R, Smale MJ, Cowley PD, Froneman PW (2014) Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of Southern Africa. PLOS ONE 9:e109357
- ✦ Dickman AJ (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Anim Conserv 13:458–466
- ✦ Drymon JM, Ajemian MJ, Powers SP (2014) Distribution and dynamic habitat use of young bull sharks *Carcharhinus leucas* in a highly stratified northern Gulf of Mexico estuary. PLOS ONE 9:e97124
- ✦ Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. eLife 3:e00590
- ✦ Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S and others (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506: 216–220
- ✦ Espinoza M, Heupel MR, Tobin AJ, Simpfendorfer CA (2016) Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? PLOS ONE 11:e0147608
- ✦ Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071
- ✦ Ferretti F, Jorgensen S, Chapple TK, De Leo G, Micheli F (2015) Reconciling predator conservation with public safety. Front Ecol Environ 13:412–417
- ✦ Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279–292
- ✦ Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Mar Biol 149:189–199
- ✦ Gilman E, Clarke S, Brothers N, Alfaro-Shigueto J and others (2008) Shark interactions in pelagic longline fisheries. Mar Policy 32:1–18
- ✦ Hays GC, Ferreira LC, Sequeira AMM, Meekan MG and others (2016) Key questions in marine megafauna movement ecology. Trends Ecol Evol 31:463–475
- Hazin FHV, Burgess GH, Carvalho FC (2008) A shark attack outbreak off Recife, Pernambuco, Brazil: 1992–2006. Bull Mar Sci 82:199–212
- ✦ Heithaus MR, Dill L, Marshall G, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Mar Biol 140:237–248
- ✦ Heithaus MR, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. Limnol Oceanogr 54:472–482
- ✦ Henningsen AD (1994) Tonic immobility in 12 elasmobranchs: use as an aid in captive husbandry. Zoo Biol 13: 325–332
- ✦ Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA (2008) Effects of biofouling on performance of moored data logging acoustic receivers. Limnol Oceanogr Methods 6: 327–335
- Heupel MR, Kessel ST, Matley JK, Simpfendorfer CA (2018) Acoustic telemetry. In: Carrier JC, Heithaus MR, Simpfendorfer CA (eds) Shark research: emerging technologies and applications for the field and laboratory. CRC Press, Taylor & Francis Group, Boca Raton, FL, p 133–156
- ✦ Horne JS, Garton EO (2006) Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in Kernel home-range analysis. J Wildl Manag 70:641–648
- ✦ Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633–642
- ✦ Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218
- ✦ Knip DM, Heupel MR, Simpfendorfer CA (2012a) To roam or to home: site fidelity in a tropical coastal shark. Mar Biol 159:1647–1657
- ✦ Knip DM, Heupel MR, Simpfendorfer CA (2012b) Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol Conserv 148:200–209
- ✦ Lagabriele E, Allibert A, Kiszka JJ, Loiseau N, Kilfoil JP, Lemahieu A (2018) Environmental and anthropogenic factors affecting the increasing occurrence of shark–human interactions around a fast-developing Indian Ocean island. Sci Rep 8:3676
- Le Manach F, Bach P, Boistol L, Robinson J, Pauly D (2015) Artisanal fisheries in the world's second largest tuna fishing ground—reconstruction of the Seychelles' marine fisheries catch, 1950–2010. In: Le Manach F, Pauly D (eds) Fisheries catch reconstructions in the Western Indian Ocean, 1950–2010. Fisheries Centre Research Report. University of British Columbia, Vancouver, p 99–110



- ✦ Lea JSE, Humphries NE, Clarke CR, Sims DW (2015) To Madagascar and back: long-distance, return migration across open ocean by a pregnant female bull shark *Carcharhinus leucas*. *J Fish Biol* 87:1313–1321
- ✦ Lemahieu A, Blaison A, Crochelet E, Bertrand G, Pennober G, Soria M (2017) Human-shark interactions: the case study of Reunion island in the south-west Indian ocean. *Ocean Coast Manag* 136:73–82
- Letourneur Y, Chabanet P, Durville P, Taquet M and others (2004) An updated checklist of the marine fish fauna of Reunion Island, South-Western Indian Ocean. *Cybio* 28:199–216
- ✦ MacNeil MA, Carlson JK, Beerkircher LR (2009) Shark depredation rates in pelagic longline fisheries: a case study from the Northwest Atlantic. *ICES J Mar Sci* 66:708–719
- Mahabot MM (2016) Suivi morphodynamique des plages récifales de La Réunion en contexte d'observatoire. PhD thesis, Université de La Réunion, Saint-Denis
- ✦ Mathies NH, Ogburn MB, McFall G, Fangman S (2014) Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Mar Ecol Prog Ser* 495:27–38
- ✦ Matich P, Heithaus MR (2012) Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. *Mar Ecol Prog Ser* 447:165–178
- ✦ Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *J Anim Ecol* 80:294–305
- ✦ McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastián CR, Guillaume MMM, Bruggemann JH (2007) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Mar Ecol Prog Ser* 337:1–13
- ✦ McClanahan TR, Graham NAJ, MacNeil MA, Muthiga NA, Cinner JE, Bruggemann JH, Wilson SK (2011) Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc Natl Acad Sci USA* 108:17230–17233
- ✦ McCord ME, Lamberth SJ (2009) Catching and tracking the world's largest Zambezi (bull) shark *Carcharhinus leucas* in the Breede estuary, South Africa: the first 43 hours. *Afr J Mar Sci* 31:107–111
- Montaggioni LF, Faure G (1980) Récifs coralliens des Mascareignes (Océan Indien). Collection des Travaux du Centre Universitaire. Université de La Réunion, Saint-Denis
- ✦ Naim O, Tourrand O, Faure G, Bigot L, Cauvin B, Semple S, Montaggioni LF (2013) Fringing reefs of Reunion Island and eutrophication effects — Part 3: long-term monitoring of living coral. *Atoll Res Bull* 598:1–32
- ✦ Ohta I, Kakuma S (2005) Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. *Mar Biol* 146: 581–594
- ✦ Papastamatiou YP, Cartamil DP, Lowe CG, Meyer CG, Wetherbee BM, Holland KN (2011) Scales of orientation, directed walks and movement path structure in sharks. *J Anim Ecol* 80:864–874
- ✦ Piper DJW, Normark WR (2009) Processes that initiate turbidity currents and their influence on turbidites: a marine geology perspective. *J Sediment Res* 79:347–362
- ✦ Pirog A, Magalon H, Poirout T, Jaquemet S (2019) Reproductive biology, multiple paternity and polyandry of the bull shark *Carcharhinus leucas*. *J Fish Biol*, doi:10.1111/jfb.14118
- ✦ Piton B, Taquet M (1992) Océanographie physique des parages de l'île de la Réunion (Océan Indien). Rapport Scientifique Orstom Le Port. [http://horizon.documentation.ird.fr/exl-doc/pleins\\_textes/divers10-06/010025163.pdf](http://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers10-06/010025163.pdf)
- ✦ Shuster WD, Dadio S, Drohan P, Losco R, Shaffer J (2014) Residential demolition and its impact on vacant lot hydrology: implications for the management of stormwater and sewer system overflows. *Landsc Urban Plan* 125:48–56
- ✦ Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida estuary. *Estuaries* 28:78–85
- ✦ Stevens JD, McLoughlin KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. *Mar Freshw Res* 42:151–199
- ✦ Taglioni F, Guiltat S (2015) Le risque d'attaques de requins à La Réunion. Éléments d'analyse des attaques et contextualisation d'une gestion contestée. *EchoGéo online*: <http://journals.openedition.org/echogeo/14205>
- ✦ Taglioni F, Guiltat S, Teurlai M, Delsaut M, Payet D (2019) A spatial and environmental analysis of shark attacks on Reunion Island (1980–2017). *Mar Policy* 101:51–62
- Taylor S (2007) Population structure and resource partitioning among carcharhiniform sharks in Moreton Bay, Southeast Queensland, Australia. PhD thesis, University of Queensland, St Lucia
- ✦ Trystram C, Rogers KM, Soria M, Jaquemet S (2017) Feeding patterns of two sympatric shark predators in coastal ecosystems of an oceanic island. *Can J Fish Aquat Sci* 74: 216–227
- ✦ Werry JM, Sumpton W, Otway NM, Lee SY, Haig JA, Mayer DG (2018) Rainfall and sea surface temperature: key drivers for occurrence of bull shark, *Carcharhinus leucas*, in beach areas. *Glob Ecol Conserv* 15:e00430
- ✦ Wong BBM, Candolin U (2015) Behavioral responses to changing environments. *Behav Ecol* 26:665–673
- ✦ Yeiser BG, Heupel MR, Simpfendorfer CA (2008) Occurrence, home range and movement patterns of juvenile bull (*Carcharhinus leucas*) and lemon (*Negaprion brevirostris*) sharks within a Florida estuary. *Mar Freshw Res* 59:489–501
- ✦ Yemane D, Shin YJ, Field JG (2009) Exploring the effect of marine protected areas on the dynamics of fish communities in the southern Benguela: an individual-based modelling approach. *ICES J Mar Sci* 66:378–387