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

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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 ± SD = 41.5 ± 56.4 visits mo^{-1} and 17.6 ± 30.5 h mo^{-1}) than inside the MPA (N = 218; 21.4 ± 28.1 visits mo^{-1} and 7.2 ± 15.2 h 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

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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, MacNeil 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

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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^2 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^2 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-

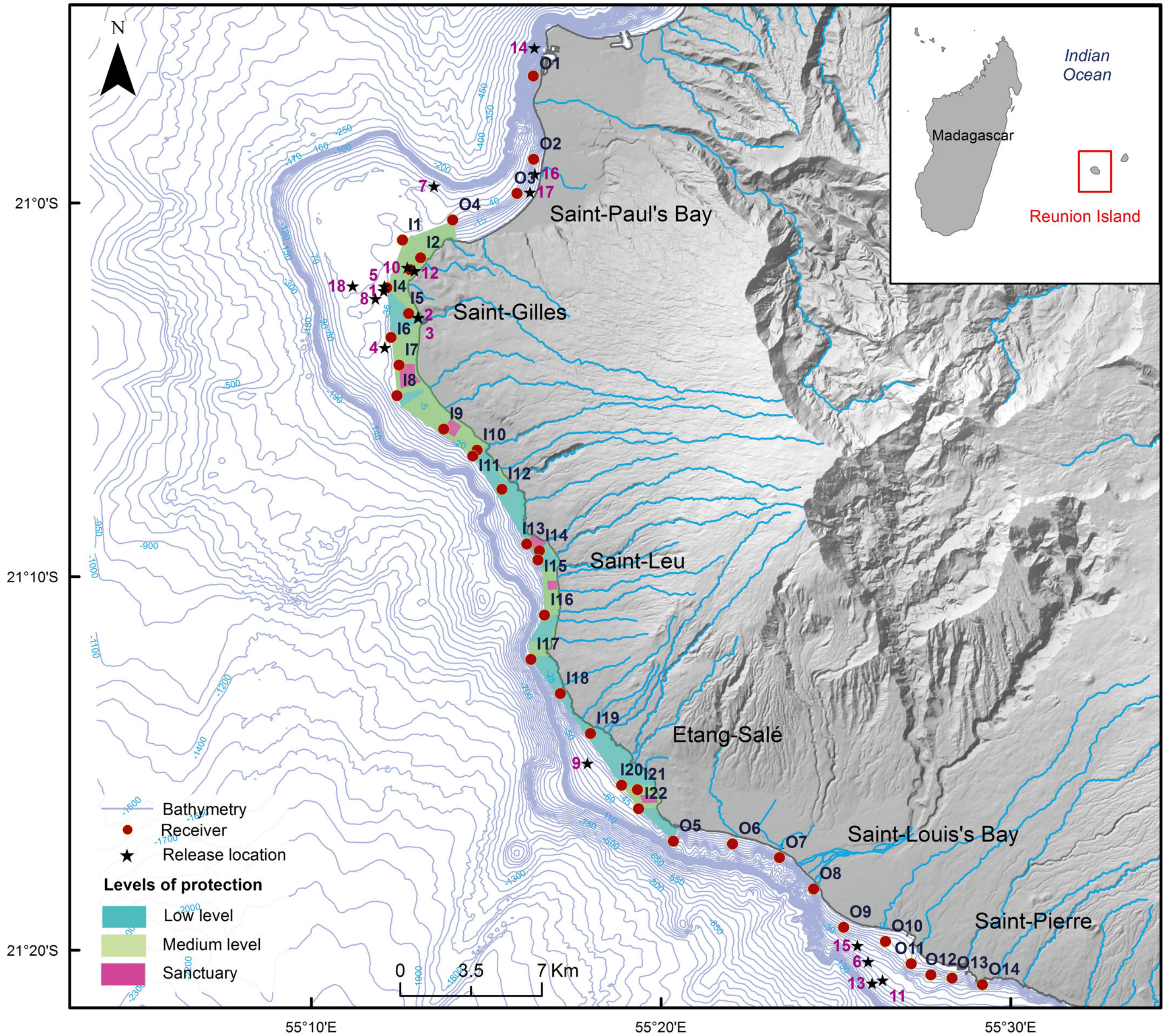

Fig. 1. Study site along the west coast of Reunion Island. The MPA is colored differently according to the different levels of protection. Shark release locations (shark code 1–18) are labeled with stars and the position of the receivers with closed circles. Receivers with I(O) in the receiver ID are 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 (±SD) 0.35 ± 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 ± 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 ± 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 ± 0.75 and 0.65 ± 1.50 h, respectively) and more than 100% when increasing MBP from 1 to 6 h (0.91 ± 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 ith 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 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: χ^2_{12} = 12.8, p = 0.38 and χ^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 ± 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 ± 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 h mo^{-1}) around receivers inside and outside the MPA (13.08 ± 21.07 h [0.05–109.95 h], N = 81 and 13.28 ± 20.91 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 ± 17.93 h [0.10–111.32 h], N = 87 and 8.00 ± 10.27 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 (±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

Inside MPA							Outside MPA						
Receiver	Distance		Presence (h)		Visits		Receiver	Distance		Presence (h)		Visits	
code	to coast (m)	N	Total	Monthly	Total	Monthly	code	to coast (m)	N	Total	Monthly	Total	Monthly
I1	1600	9	53.7	6 ± 7.6	122	13.6 ± 10.6	O1	400	7	15.3	2.2 ± 1.4	101	14.4 ± 8.3
I2	380	7	7.1	1 ± 0.7	30	4.3 ± 2.4	O2	460	12	438.5	36.5 ± 31.6	675	56.2 ± 38.5
I3	350	5	0.8	0.2 ± 0.1	6	1.2 ± 0.4	O3	800	9	205.6	22.8 ± 22.6	358	39.8 ± 28.9
I4	1050	6	95.6	15.9 ± 13.1	278	46.3 ± 34.6	O4	950	12	190.7	15.9 ± 15.2	434	36.2 ± 21.5
I5	470	11	195.6	17.8 ± 24.5	367	33.4 ± 37.8	O5	730	12	139.8	11.7 ± 13.3	652	54.4 ± 51.8
I6	1400	12	465.9	38.8 ± 43.3	698	58.2 ± 57.2	O6	400	12	517.9	43.2 ± 42.7	1373	114.5 ± 93
I7	850	12	22.1	1.8 ± 2.3	107	8.9 ± 8.3	O7	290	11	757.9	68.9 ± 61.5	1373	124.9 ± 95.8
I8	1450	9	14.0	1.6 ± 1.9	66	7.3 ± 4.1	O8	270	12	63.7	5.3 ± 5.5	329	27.4 ± 23.8
I9	810	12	34.3	2.9 ± 2.9	69	5.8 ± 4.1	O9	460	12	32.8	2.7 ± 4.2	144	12 ± 11.3
I10	430	10	42.9	4.3 ± 3.8	149	14.9 ± 10.2	O10	630	12	128.3	10.7 ± 14.4	363	30.2 ± 28.3
I11	720	12	48.1	4 ± 3.7	275	22.9 ± 17.3	O11	680	10	37.2	3.7 ± 3.5	73	7.3 ± 5.5
I12	540	9	42.7	4.7 ± 10.7	34	3.8 ± 2.9	O12	730	5	5.7	1.1 ± 1	43	8.7 ± 5.1
I13	540	11	10.7	1 ± 0.9	59	5.4 ± 3.2	O13	520	10	10.2	1 ± 0.7	34	3.4 ± 1.4
I14	560	12	104.2	8.7 ± 8.6	380	31.7 ± 17.1	O14	220	12	58.3	4.9 ± 3.6	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	17.6 ± 30.5	6137	41.5 ± 56.4

The amount of time sharks spent at receivers varied significantly with the interaction: area × 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 ± 14.2 h mo^{-1} $receiver^{-1}$ [0.05–55.34 h mo^{-1} $receiver^{-1}$], N = 55 and 0.7 ± 1.2 h mo^{-1} $receiver^{-1}$ [0.03–7.84 h mo^{-1} $receiver^{-1}$], 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

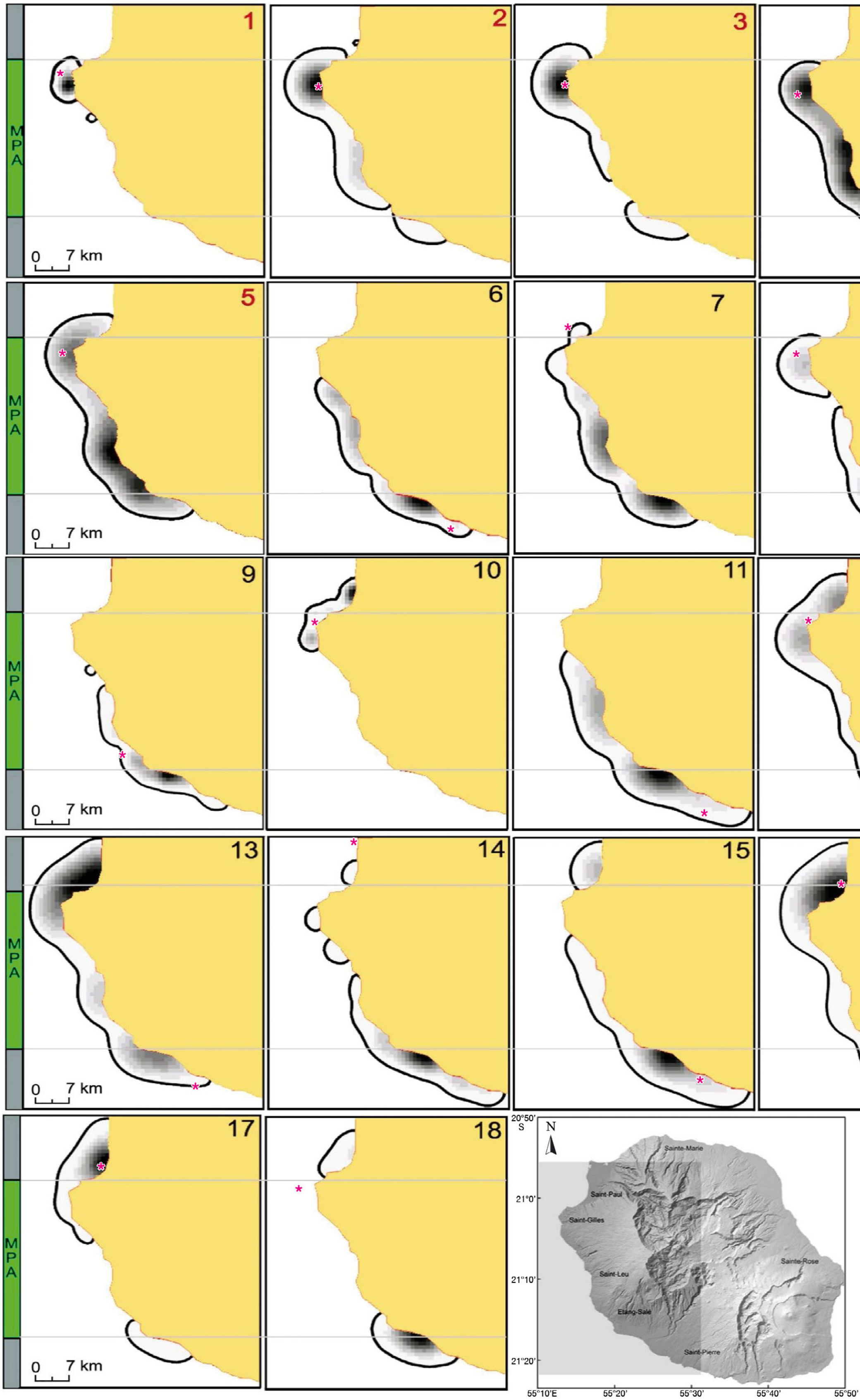

Fig. 2. 90% Kernel home-range densities of sharks that were detected in the array of acoustic receivers. Green boxes indicate the latitudinal extent of the MPA. Shark release locations are denoted by stars (*). Shark codes (1–18) indicated in each panel. Inset indicates the localization of the study 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

General information							Inside MPA				Outside MPA			
Shark code	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 ± SD presence time (h mo^{-1})	Mean ± SD visits (by month)	Total number of visits	Total presence time (h)	Mean ± SD presence time (h mo^{-1})	Mean ± SD visits (by month)	Total number of visits
1 ♀ *	300	I4	450	46	10.22	99.24	332.4	41.5 ± 37.8	66.4 ± 58.5	531	2.6	0.4 ± 0.4	4.2 ± 4.4	29.6
2 ♀	314	I5	200	20	10.00	90.20	127.7	42.6 ± 58.7	88 ± 89.4	264	13.9	4.6 ± 3.2	18.9 ± 14.2	56.8
3 ♀	308	I5	200	20	10.00	89.47	98.0	24.5 ± 23.6	67 ± 54	268	11.5	2.9 ± 1.3	11.2 ± 6.4	44.9
4 ♀ *	307	I6	424	54	12.74	74.43	121.7	12.2 ± 7.4	47.1 ± 28.8	471	41.8	4.2 ± 3.4	18.5 ± 11.6	184.5
5 ♀ *	300	I4	470	17	3.62	82.61	45.5	5.7 ± 5.7	22 ± 18.4	176	9.6	1.4 ± 1.2	5.4 ± 4.2	37.8
6 ♂	260	O10	456	135	29.61	40.80	241.3	16.1 ± 12.3	56.9 ± 40	854	350.1	23.3 ± 16.8	46.6 ± 22.7	699.7
7 ♀	300	O4	86	16	18.60	43.76	19.8	6.6 ± 5	43 ± 34	129	25.4	6.4 ± 3.9	19.4 ± 10.2	77.7
8 ♀	314	I4	507	24	4.73	33.09	25.1	8.4 ± 3.9	31 ± 6	93	50.8	16.9 ± 5.9	65.1 ± 10.3	195.3
9 ♂	269	I19	447	69	15.44	30.27	47.8	4.3 ± 3.3	21.9 ± 15	241	110.2	10 ± 9.1	36.9 ± 17.2	406.3
10 ♀	329	I3	507	51	10.06	29.19	131.5	13.2 ± 14.8	24.2 ± 23.5	242	319.1	29 ± 36.8	51.4 ± 47.2	565.6
11 ♂	290	O11	433	13	3.00	27.94	6.9	1.7 ± 2	10 ± 10.7	40	17.7	1.8 ± 1.5	7.8 ± 5.6	77.7
12 ♀ *	274	I3	507	92	18.15	27.47	124.1	7.3 ± 9.8	21.2 ± 21.7	361	327.8	19.3 ± 21.6	38.9 ± 28.5	661.2
13 ♂ *	294	O10	422	59	13.98	21.88	62.5	4.8 ± 5.3	22.2 ± 20.9	288	223.4	16 ± 14.4	38 ± 25.8	531.9
14 ♀ *	228	O1	501	99	19.76	21.80	120.3	10 ± 12.6	36 ± 41.6	432	431.6	25.4 ± 26.5	61.4 ± 42	1043.6
15 ♀ *	260	O9	456	60	13.16	18.81	53.6	4.1 ± 8.3	10.2 ± 18.5	132	231.4	16.5 ± 14.1	36 ± 25.4	503.6
16 ♂	298	O2	434	11	2.53	11.43	7.8	3.9 ± 2.5	29 ± 29.7	58	60.4	20.1 ± 26.8	59.2 ± 81.5	177.5
17 ♀ *	295	O3	501	12	2.40	7.04	8.0	2.7 ± 2.7	14.7 ± 14.6	44	105.9	10.6 ± 8.6	19 ± 10.6	189.9
18 ♂ *	260	I4	429	50	11.66	2.00	5.5	0.8 ± 0.8	6.1 ± 4	43	268.7	19.2 ± 24.7	46.7 ± 48.4	653.5
Total							1579.7	10.8 ± 17.3	32 ± 35.6	4667	2601.9	15 ± 19.5	35.3 ± 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 ± 14.2 h mo^{-1} $receiver^{-1}$ [0.03–82.28 h mo^{-1} $receiver^{-1}$], N = 477 and 1.0 ± 1.9 h mo^{-1} $receiver^{-1}$ [0.03–18.26 h mo^{-1} $receiver^{-1}$], 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^{-1}, 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^{-1}) 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

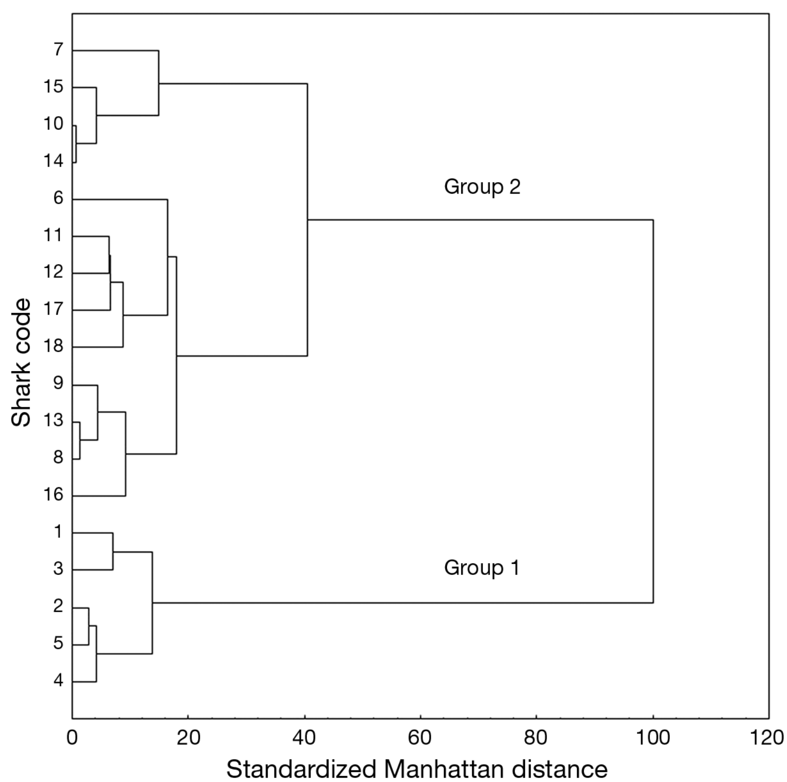

Fig. 3. Hierarchical clustering dendrogram of sharks (cf. shark codes in Table 2) based on the proportion of time spent in the MPA

Table 4. Total and mean (±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 ± 28.9	1710	51.8 ± 47.6	0.0001
	Outside	31	79.4	2.6 ± 2.7	354	11.4 ± 10.4	
2	Inside	113	854.4	7.6 ± 10	2957	26.2 ± 29	0.0001
	Outside	143	2522.5	17.6 ± 20.5	5784	40.4 ± 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).

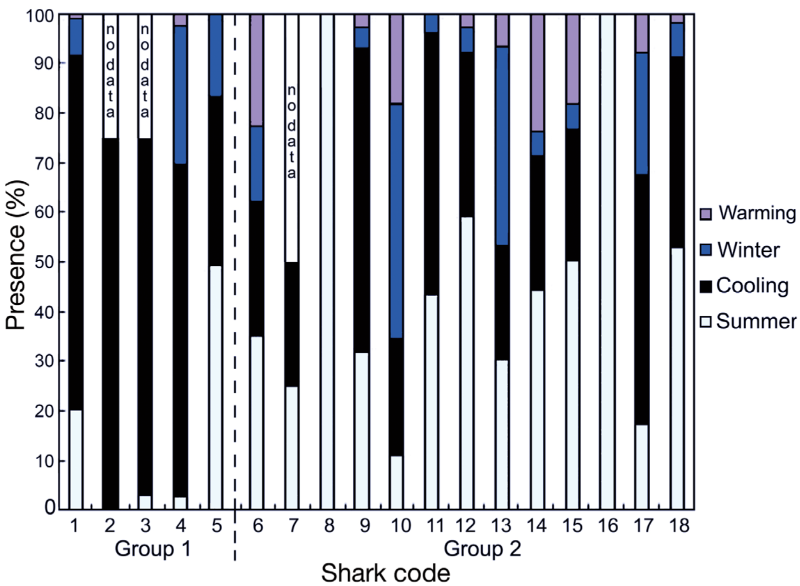

Fig. 4. Proportion of time individual sharks were detected across seasons (summer: January to March; cooling: April to June; winter: July to September; warming: October to December)

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 mating 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 considerable 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.

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