

# Dynamic use of coastal areas by bull sharks and the conciliation of conservation and management of negative human–wildlife interactions

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## Abstract :

1. Knowledge about spatial and temporal variability in the distribution and abundance of predators is necessary to adapt measures to mitigate human–wildlife interactions.

2. Acoustic telemetry and network analyses were used to investigate the spatial ecology of bull sharks, the species responsible for most shark bites in Reunion Island, one of the world's shark bite hotspots.

3. The west coast of the island was not used uniformly by every individual, with size predicting the movements of sharks along the coast.

4. Node-based metrics – closeness, node strength, and cumulated continuous residency times – derived from up to 181 monthly movement networks from 20 individuals, revealed that smaller sharks (<250 cm total length) primarily used the south-west coast while larger individuals spent most of their time in the northern region with regular visits to multiple areas along the coast.

5. This study provides essential knowledge on bull shark behaviour and central areas used at different periods of the year, which correlates well with the dynamics of observed shark bites. Our approach provides a non-invasive alternative to help predicting and anticipating human–shark conflicts and avoid shark culling programmes detrimental to the conservation of large predators such as sharks.

**Keywords :** acoustic telemetry *Carcharhinus leucas*, Indian Ocean, network analysis, Reunion Island, shark bite management, shark risk

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3 36 **1. INTRODUCTION**  
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5 37 As the human population and associated infrastructure are rapidly developing along the coast,  
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7 38 wildlife habitats are being progressively reduced, leaving many species with little refuge  
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9 39 (Brierley & Kingsford, 2009). Conflict between humans and potentially dangerous wildlife is  
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11 40 becoming an important issue (Dickman, 2010; Pooley et al., 2017). Managing this conflict  
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13 41 demands a balance between the achievement of conservation goals and public safety. This  
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15 42 issue is highlighted in the management of human-shark conflicts. At a global scale, an  
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17 43 increase in the number of shark bites has been observed, yet the individual risk for beach  
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19 44 users is simultaneously decreasing due to the number of ocean users increasing even more  
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21 45 rapidly ( McPhee, 2014; Ferretti et al., 2015; Chapman & McPhee, 2016; Midway, Wagner &  
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23 46 Burgess, 2019). When compared with other types of human-wildlife interactions, the number  
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25 47 of shark bites is low, yet they receive massive media exposure (Muter et al., 2013) and  
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27 48 political attention (Neff, 2012). Consequently, many governments have introduced shark  
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29 49 mitigation strategies to increase public safety and awareness (Curtis et al., 2012).  
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38 51 According to the International Shark Attack File ([https://www.floridamuseum.ufl.edu/shark-](https://www.floridamuseum.ufl.edu/shark-attacks/)  
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40 52 [attacks/](https://www.floridamuseum.ufl.edu/shark-attacks/)), there was an average of 1.2 unprovoked shark bites per year in Reunion Island  
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42 53 between 1980 and 2011 but this rate increased to ~ 2.5 bites per year between 2011 and 2019  
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44 54 (10 fatal cases from 23 incidents). In the past decade this island has become a hotspot for  
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46 55 shark incidents (Lagabrielle et al., 2018; Midway, Wagner & Burgess, 2019; Taglioni et al.,  
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48 56 2019). There was, for example, a 23-fold increase in incidents between 2005 and 2016 when  
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50 57 the total number of surfing hours was taken into consideration (Lagabrielle et al., 2018). As  
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52 58 such, Reunion Island is an exception to other shark hotspot locations as it has an increased  
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54 59 rate in annual shark bites and an increase in individual risk. Two species were involved in  
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56 60 these incidents, the tiger shark *Galeocerdo cuvier* and the bull shark *Carcharhinus leucas*, the  
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latter being responsible for the majority of incidents (Taglioni et al., 2019). Human-shark incidents seem to peak in austral winter and are mostly concentrated on the island's west coast where most coastal water activities occur (Lemahieu et al., 2017; Soria et al., 2019); prior to 2010, such incidents were randomly distributed around the island.

Improving our understanding of individual shark space use dynamics as well as our ability to predict shark encounters requires much attention if we are to reduce the risk of bites from large sharks. Progress in these areas could allow for water-users to be better informed about areas and periods of increased risk, and potentially for the development of area-specific shark mitigation strategies. In this study acoustic telemetry was used to investigate the spatial ecology of bull sharks around Reunion Island. The specific objectives of this study were to examine: (i) whether bull shark movements are non-random, and if this is the case, (ii) whether shark movements can be classified into behavioural clusters, and (iii) how shifts between behavioural states occur through time. This study aims to provide insight into shark behaviour and central areas used through time which can then be compared with sites where shark bites occurred to help improve management and mitigation strategies in order to avoid culling programmes.

## 2. MATERIALS AND METHODS

### 2.1. Study species and site

The bull shark (*Carcharhinus leucas*) is a large Carcharhinidae with a cosmopolitan distribution along the continental coasts and around remote islands and archipelagos of all tropical and sub-tropical waters of the world. This species moves across a large range of habitats and environmental conditions (Daly et al., 2014; Heupel et al., 2015; Espinoza et al., 2016; Lee et al., 2019), including nearshore areas where it has more chance to interact with

water-users than many other species. Its behaviour varies across different spatial and temporal scales, and according to size and sex, with a high individual variability in its tendency to migrate or remain resident (Espinoza et al., 2016; Lee et al., 2019). Recent work reported that adults can migrate over large distances (Lea et al., 2015), but also display strong site fidelity on a seasonal or annual basis (Daly et al., 2014; Heupel et al., 2015).

Reunion Island (21°07'S / 55°32'E) is a volcanic island located 700 km east of Madagascar in the south-west Indian Ocean. The island is 2512 km<sup>2</sup> with 217 km of coastline and steep underwater slopes (*ca.* 10-20%) to a depth of 2,000 m. Fringing reefs stretch over 25 km along the west and south-west coast, from Saint-Gilles to Saint-Pierre (Figure 1).

## 2.2. Acoustic telemetry

Sharks were captured along the west coast of Reunion Island between September 2012 and March 2013 (Table S1), using horizontal bottom long-lines and drumlines (Blaison et al., 2015). Most fishing and captures occurred at dusk or overnight and longline set times were fixed at a maximum of 3 hours to minimize shark and bycatch mortality. The fishing effort was higher on the north west (80% in Saint-Paul's Bay and Saint-Gilles) and lower (20%) in the south offshore of Saint-Pierre (Blaison, 2017). Once captured, a shark was brought alongside the vessel and rolled onto its back to induce tonic immobility. Sex and total length (TL) were recorded and transmitters (Vemco V16, transmission interval 40-80 s, estimated battery life 845 days) were implanted into the peritoneal cavity through a mid-ventral incision. All the fieldwork and protocols of handling and tagging were approved by the Ethics Committee (n° 114) for the CYROI (Cyclotron Réunion Océan Indien) in Reunion Island.

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3 111 An array of 46 Vemco VR2W acoustic receivers was deployed along the coast with receivers  
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5 112 installed an average of approximately 2 km apart at depths of 10-60 m, comprising 33 (71%)  
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7 113 offshore receivers and 13 (29%) inshore receivers placed less than 300 m from shore (Figure  
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9 114 1). As detection ranges are known to vary with environmental characteristics (Huvaneers et  
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11 115 al., 2016), 13 range tests were conducted. Detection probability dropped by 50% at  $\sim 190 \pm 80$   
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13 116 m for six inshore receivers and at  $\sim 390 \pm 90$  m for seven offshore receivers. This slight  
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15 117 difference in detection range is unlikely to affect detection probabilities because nearshore  
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17 118 and offshore receivers were homogeneously distributed throughout the study area (Figure 1).  
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23 120 For each shark visit to a receiver, detection records were used to calculate a continuous  
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25 121 residency time (CRT) which was defined as the duration within which a tagged shark was  
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27 122 continuously monitored at a specific receiver without a one-hour ( $> 1$ h) absence (Capello et  
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29 123 al., 2015). Thus, all detections of the same shark at a given receiver that were separated by  
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31 124 less than a predefined period, referred to as the maximum blanking period (MBP=1 h), were  
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33 125 grouped into a single CRT and defined as a visit. Furthermore, detections of a tagged shark at  
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35 126 a different receiver resulted in a new visit. CRT values were not significantly different when  
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37 127 calculated with any MBPs  $< 12$  h.  
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### 44 129 2.3. Movement network and node-based metrics

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46 130 Network analyses are being used with increasing regularity to describe the spatial ecology  
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48 131 and movement patterns of aquatic animals, including sharks, obtained through acoustic  
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50 132 telemetry (Jacoby & Freeman, 2016; Mourier et al., 2018). Here, network analyses were used  
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52 133 to investigate the structure and dynamics of bull shark movements along the west coast of  
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54 134 Reunion Island in order to identify spatial hotspots and central areas in their spatial ecology.  
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56 135 First, monthly movement networks were built for individual sharks. This involved the linking  
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136 of acoustic receivers using shark movements. For each shark, monthly relative movement  
137 matrices were derived from movements between receivers based on visitation patterns  
138 deduced from CRTs. These were defined as the number of times individuals moved between  
139 two receivers divided by the total number of movements within its space use (i.e. total  
140 number of edges in the network). These matrices were used to create weighted directed  
141 networks for each individual that reflected the monthly extent of space use within the  
142 receiver array over the entire monitoring period.

143 Each network was tested for non-random associations between receivers, based on observed  
144 movements to determine whether sharks showed a non-random distribution of directed  
145 movements among sites. Null modelling and randomization of observed movements were  
146 conducted by considering spatial bias in the array design (i.e. a direct movement between one  
147 pair of nodes is more likely than another because nodes are closer to each other) using the  
148 function `rewire()` from R package `igraph` (Csardi & Nepusz, 2006). In order to preserve  
149 spatial structure in the data, observed individual movement events which contributed to  
150 overall edge weighting were permuted to create replicated (weighted) movements from the  
151 raw data. Reassignment of these individual directed movements during each permutation was  
152 constrained to only directional edges between pairs of locations which occurred in the  
153 empirical movement network (Jacoby et al., 2012a). Two metrics were calculated from the  
154 observed and random networks: diameter and average path length. The diameter measures the  
155 longest path between any pair of receivers in the network and is an indicator of the size of the  
156 network. Average path length provides a measure of the average ease/likelihood of a  
157 movement between two locations occurring. Then, p-value can be calculated by comparing  
158 the observed metric to the metric derived from randomized data. This randomization  
159 procedure was applied to individual monthly movement networks, by comparing each  
160 observed network with 10,000 permuted networks.

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162 Node-based metrics were then used to describe the influence that individual nodes had on the  
163 overall network structure and were determined from the level of interaction one node had  
164 with any other node, either directly or via intermediates. Two network centrality metrics were  
165 calculated: closeness and node strength. Closeness measures how central a receiver's position  
166 (visited by one individual) is in the network of monthly movements of each shark and is  
167 expressed as the smallest number of edges (pathways) linking receivers during the  
168 movements of the shark between receivers (i.e. the geodesic distance). This is the inverse of  
169 the average path lengths from a node to each of its neighbours. A low geodesic distance  
170 corresponds to a high closeness (Lédée et al., 2015). Node strength is a measure of the level  
171 of connectivity of a node and represents the total number of incoming/outgoing movements  
172 to/from a receiver. A receiver with a high node strength would suggest strong site fidelity. In  
173 addition to these centrality metrics, the monthly CRT (sum of CRTs for each month) was also  
174 calculated for each node. A receiver with a high monthly CRT suggests a site where the shark  
175 spent a large amount of time. These three node-based metrics were used to identify the  
176 receivers which corresponded to core use areas.

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## 178 2.4. Statistical analyses

179 In order to standardize the data, all receivers that were deployed for less than 20 days during  
180 the month were removed from monthly movement networks. Similarly, individuals that were  
181 not detected for at least 20 days during a month were also excluded. This empirical choice  
182 was made as a compromise between data loss and representativeness. All individual monthly  
183 networks that were found to show random patterns were also removed. Finally, only monthly  
184 individual networks containing more than five directed movements between receivers were  
185 kept, in an attempt to measure relevant network metrics.



186 To highlight the spatio-temporal patterns of space use related to individual life history traits,  
187 a principal component analyses (PCA) was performed on each matrix of network metrics, in  
188 which columns represent receivers and rows represent individuals in a given month. As such,  
189 receivers were considered as variables and individuals in a given month as observations in  
190 the PCAs. To display information on both receivers and sharks graphically, a biplot  
191 representation of the PCA results was used (Gabriel, 1971). This representation allows the  
192 visualization of similarities and differences in monthly movement patterns between sharks,  
193 and simultaneously reveals how each receiver contributes to each principal component.  
194 For each node-based metric, clustering of monthly shark movements was conducted on the  
195 ordination axes of the PCAs with k-means clustering. In order to find the main behavioural  
196 clusters, between 2 and 4 partitions were tested. Data from each cluster of monthly individual  
197 movements was extracted and interpreted according to spatial distribution, sex, size and time.  
198 To obtain a global understanding of the spatial distribution of node-metrics, closeness, node-  
199 strength and CRT were independently averaged across all months and individuals. Each  
200 metric was also averaged for each month of the year. In addition, to combine all three metrics  
201 within one score and determine the locations with high values across all metrics, the TOPSIS  
202 method (Technique for Order Preference by Similarity to an Ideal Solution; Huang, Keisler &  
203 Linkov, 2011) was used. This method is designed to solve multiple criteria decisions through  
204 evaluation of the alternatives by simultaneously measuring their distances to the Positive  
205 Ideal Solution (PIS) and to the Negative Ideal Solution (NIS). PIS is the most preferred  
206 solution (in our case the highest values for all metrics) and NIS is the least preferred solution  
207 (the lowest value for all metrics). The preference order from the TOPSIS method is then built  
208 according to the relative closeness of the alternatives to PIS, which is a scalar criterion that  
209 combines these three distance measures. In this case, the positive ideal solution  
210 corresponding to the condition where closeness, node-strength and CRT were greatest was



defined (note that in our case a 1:1:1 weight ratio of the three components was used so that each metric is given equal consideration). A resultant high TOPSIS score at one receiver means that it has high values for all three metrics (closeness, node-strength and CRT). Similar to the analysis of all node-metrics independently, clustering of monthly shark movements was also conducted on PCAs ordination axes of the TOPSIS score with k-means clustering. All analyses were performed in R 3.5.1 (R Development Core Team, 2020), using the ‘dudi.pca’ function from the R package ‘ade4’ (Dray & Dufour, 2007) for the PCAs, ‘cascadeKM’ function with the ‘calinski’ criterion (Caliński & Harabasz, 1974) from the R package ‘vegan’ for the clustering (Dixon, 2003) and R package ‘topsis’ (Yazdi, 2013).

### 3. RESULTS

From a total of 190 monthly networks only nine (5%) from seven sharks showed random movement patterns and were removed from subsequent analyses. After applying the thresholds (20 days per month of active receivers and tags and a minimum of five movements per month), 160 individual monthly networks for closeness and 164 networks for node-strength consisting of 20 sharks and 20 months from October 2012 to May 2014, were analysed. Differences in the number of networks is due to the removal of monthly networks where closeness was null for all receivers while node-strength was not. Similarly, 181 individual monthly CRT datasets were analysed from 23 sharks over 20 months from October 2012 to May 2014. The higher number of individuals used for the CRT analyses is due to the inclusion of three sharks that were present for at least a month but did not conduct more than five movements during their residence times. Some sharks were detected in the area for only a short period of time (< 3 months) while others were absent for only a few months during the entire study.

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3 235 Biplots of PCAs of the receivers for individual monthly network matrices containing the three  
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5 236 node-level metrics are presented in Figure 2. The first two axes of the PCAs ordinations,  
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7 237 obtained from closeness, node-strength and CRT values explained 46.2%, 30.5% and 26.8%  
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9 238 of the total variation in movement data respectively.  
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12 239 The distribution of projected principal scores of receivers revealed a clear geographic pattern,  
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14 240 with northern and southern receiver groups respectively showing strong negative and positive  
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16 241 correlation with the second axis. The first axis also showed a positive correlation with the  
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18 242 receivers located in the central region of the coast. These geographic gradients were observed  
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20 243 across all node-level metrics. The shark size distribution in the PCAs also showed a geographic  
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22 244 gradient. Smaller individuals corresponded to high values on axis 2 (i.e. receivers located in  
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24 245 the south) while larger individuals were associated with low values of axis 2 (i.e. receivers  
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26 246 located in the north). These patterns were only observed for closeness and node-strength. There  
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28 247 were no clear geographical patterns related to the sex of individuals.  
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31 248 Average closeness values were highest around Saint-Gilles in the north west and between  
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33 249 Etang-Salé and Saint-Pierre in the south west (Figure 3a). Average node-strength and CRT  
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35 250 values were highest at Saint-Gilles in the north west, and Saint-Leu and Etang-Salé in the south  
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37 251 west (Figure 3b,c). Combining all three node-metrics averaged across individuals using the  
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39 252 TOPSIS analysis and investigating resultant scores across months, the spatial distribution of  
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41 253 shark movement centrality was found to be highly dynamics. While activity remained high  
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45 255 year round, it spread between Saint-Gilles and Saint-Paul from July to December (Figure 3d).  
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47 256 Cluster analysis of TOPSIS scores (i.e. combining all three node-metrics) for each monthly  
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49 257 shark movement revealed three distinct clusters (Figure 4). Average shark size was  
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51 258 significantly different between clusters (one-way ANOVA:  $F = 40.41$ ;  $df$  factor = 2;  $df$   
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53 259 residuals = 154;  $P < 0.001$ ). Cluster 1, named “young residents”, comprised 62 individual  
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monthly networks, including mostly young female sharks (Chi<sup>2</sup> test: M:F = 19:43,  $\chi^2 = 9.290$ , df = 1, P = 0.0023), and characterized by high centrality scores in the south west of the island. Cluster 2, called “roamers”, consisted of 32 individual monthly networks from a set of large individuals with a relatively balanced sex ratio (Chi<sup>2</sup> test: M:F = 17:15,  $\chi^2 = 1.125$ , df = 1, P = 0.7237). This cluster had high centrality scores which were primarily located in the middle of the west coast. Cluster 3, called “large roamer females”, consisted of 66 individual monthly networks and included mostly large females (Chi<sup>2</sup> test: M:F = 16:50,  $\chi^2 = 17.515$ , df = 1, P < 0.001), for which centrality was higher in the northern portion of the west coast but was also spread along the coast. Movement network centrality was relatively stable but showed a clear ontogenetic shift from the south to the north of the island as individuals became larger. Results from cluster analyses conducted separately on each node-metric are available in the Supplementary Information (Figure S2-4).

#### 4. DISCUSSION

Understanding the spatio-temporal movement dynamics of potentially dangerous large predators helps in predicting and anticipating human-wildlife conflicts. Using acoustic telemetry and network analyses, the dynamics of the space use patterns of bull sharks around Reunion Island were revealed. Their spatial dynamics were found to be influenced strongly by size with some degree of size-segregation observed. Small individuals were typically restricted to the south of the island while larger sharks were mostly found in the north during the austral winter, which is also where most human-shark interactions have taken place (Figure 5).

The PCA demonstrated clear geographical patterns for all node-level metrics in relation to shark size. Smaller sharks (< 300 cm TL) used areas located on the south west coast while

larger individuals were mostly found in the northern areas. Closeness and node-strength centrality metrics described core use areas or centres of activity and revealed that spatial patterns are mainly explained by shark size (Figure S2-S3). This was further confirmed when all three metrics were combined (Figure 4). This result was less clear when only residency was considered (i.e. CRT), suggesting that most sharks were mobile and did not stay at specific receivers for long periods of time (Figure S4). In addition, no apparent geographic pattern related to sex was found for any metric. This geographic structure of the population indicates an ontogenetic segregation in habitat, where adult and young sharks use different habitats and their activity space rarely overlaps, a common pattern observed in many shark species (Speed et al., 2010). Shark populations can segregate into sub-units based on age and sex giving rise to complex patterns of spatial ecology at the population level. Juveniles will often remain within specific nursery areas for protection against predators and access to abundant prey, and will gradually increase their space use as they grow (Chapman et al., 2009). This behaviour corresponds to increasing physiological demands, increased individual variation in diet (Matich & Heithaus, 2015; Matich et al., 2019), a reduced threat of predation and the onset of maturity. It is not clear why, in Reunion Island, larger sharks display a preference for the northern coast, but it may be due to the presence of abundant food resources or a preference for the sandy bottom on a 50 m deep shelf between Saint-Gilles and Saint-Paul. Alternatively, this particular area could represent a resting area due to optimal current conditions, or sharks could be attracted by potential fish discards dropped by fishing vessels outside the port of Saint-Gilles. Individual bull sharks are known to have different foraging strategies as has been demonstrated through stable isotope analyses (Trystram et al., 2016). Foraging shifts also occur after reaching maturity with tendencies for individual foraging specialization to occur in adulthood (Matich, Heithaus & Layman, 2011). This pattern could also explain the various individual behavioural clusters found in our study, with

individual spatial dynamics possibly driven by specialized foraging strategies. In addition, immature sharks rely on coastal food sources whilst pelagic prey contributes more to the diet of adult sharks. This could explain why smaller sharks were more often continuously detected by coastal receivers while for larger sharks continuous presence spanning several months was less common. These absences may represent large scale offshore excursions leading sharks to leave the island for periods of weeks to months (Soria et al. 2021).

However, it was more surprising that no clear sexual segregation was found as this is common in many shark populations (Jacoby, Croft & Sims, 2012b) including bull sharks (Werry & Clua, 2013; Espinoza et al., 2016). Sexual segregation can emerge from females trying to avoid male harassment, especially during the mating period (Jacoby et al., 2010). Male harassment is possible in bull sharks as they have been found to show polyandry with multiple males siring juveniles from the same female (Pirog et al., 2019). The resolution of the current analysis may have been too coarse or the number of males too low to reveal such avoidance patterns.

High levels of individual variability in behaviour and space use were observed. While young sharks appeared to be present all year round, the detection of larger individuals increased during autumn and winter (Blaison et al., 2015; Soria et al., 2019), which is likely a result of increased mating activity. Soria et al. (2019) suggested that a pre-mating aggregation could occur in the north near the Saint-Gilles harbour from April. For example, ‘shark17’ shifted between four behavioural clusters, which corresponded to a higher closeness in movement patterns in the north at the end of 2012 and in the south at the end of 2013 (Figure S2). In addition, the largest female ‘shark01’ had a closeness centrality which was homogeneously spread along the coast between February and April 2013, and then slowly shifted to the north

from September 2013 (Figure S2). However, this individual also had a constant cluster for node-strength and all metrics combined suggesting that its main areas of centrality remained in the north near Saint-Paul (Figure 4, Figure S3).

The observed dynamics in movement patterns of bull sharks around Reunion Island could also be driven by parturition. Previous research suggested that female bull sharks use some areas as pupping and nursery grounds (Pirog et al., 2019), with parturition occurring in October–November. Immature sharks (<230 cm TL) restricted their core use to an area between Etang-Salé and Saint-Pierre suggesting the presence of nursery grounds where mature females may return to give birth (Tillett et al., 2012). In addition, large females displayed short-term shifts in centres of activity space between the north and the south; such as large female ‘shark 07’ moving south of Etang-Salé in October 2013 (Figures S2–S3).

Sharks can partition space use both within (Mourier, Vercelloni & Planes, 2012) and between (Papastamatiou et al., 2018) species. Spatial separation may arise via different foraging strategies (Matich, Heithaus & Layman, 2011) or competitive interactions (Brena et al., 2018). Spatial separation can also be the result of density-dependent competition in which some individuals leave an area once it becomes too congested. This size-based partitioning of space may prevent conflict over resources between size classes. Future work could investigate co-occurrence to determine whether bull sharks share space at the same time or whether they avoid each other.

The increased rate in human-shark incidents in Reunion Island since 2011 has resulted in conflicts between both sharks and human as well as among ocean user groups. It has also led to great interest in understanding the potential causes for this sudden increase in shark bites

and finding effective management solutions to mitigate the risk of these incidents. Since 2011, most shark bites (16 out of 26: 61%) have occurred between April and August in the north-west region of the island, between Saint-Paul and Saint-Leu (Figure 5). Only a few incidents (7 out of 26: 27%) occurred in the southern and eastern areas, and mostly during summer. The remainder (3 out of 26: 12%) were randomly distributed along the west coast and across the seasons. In addition, forensic analyses demonstrated that large sharks (2.5-3.5 m TL) were responsible for all the reported shark bites (Werbrouck et al., 2014). Centrality network metrics showed that larger sharks used larger core-use areas between February and August, and more spatially restricted areas in the north during other times of the year. In addition, the same large adult females tended to display high continuous residency times in the north between Saint-Paul and Saint-Gilles between February and August while for the remainder of the year they typically made longer visits in the south near Etang-Salé. These spatial dynamics are in accordance with the dynamics of observed human-shark bites (Figure 5). Other species of large sharks have also shown increased rates of movement and aggressiveness around mating periods, especially when social hierarchies are readjusted (Clua et al., 2010), which can result in increased bite risk. More than 50% of the bites in Reunion Island occurred during the mating period (between June and September), which is also the season when large swell attracts surfers. This suggests that increased aggressiveness may be related to mating activity, reinforced by the prevalence of polygyny in this species (Pirog et al., 2019) where males could compete for female mates. Evidence of multi-annual polygyny (Pirog et al., 2019) suggests that males may exhibit some mating-site fidelity, returning on a regular basis to specific places to mate. This also suggests that bull sharks may aggregate to mate. Although aggregative behaviour in sharks can be related to reproduction (Jacoby, Croft & Sims, 2012b), there are several other potential reasons, such as foraging on patchy or concentrated food resources (Schilds et al., 2019) or phenotypic assortment (e.g. a



385 preference to associate with individuals of similar size or sex; Mourier, Vercelloni & Planes,  
386 2012). Moreover, the dramatic increase in bite rates has only occurred from 2011, despite  
387 similar seasonal ocean-use before then. This suggests that mating may not be the only cause  
388 for shark bite incidents. Nonetheless, increased risk during the mating period in particular  
389 locations and the high variability in individual space use patterns should be taken into  
390 account in formulating management strategies to reduce shark bites that also have the  
391 minimum impact on shark populations (Clua & Linnell, 2019).

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393 Shark risk management is applied in areas with high probabilities of unprovoked shark bites  
394 with the aim to reduce the rate of incidents. A range of management and risk mitigation  
395 measures have been tested and employed including warning and education, lethal shark nets  
396 and drumlines that catch and kill sharks near shore to protect humans, SMART drumlines  
397 ('Shark Management Alert in Real Time') which is a system that alerts authorities when an  
398 animal is caught allowing the release of bycatch (i.e. species that are not targeted) as soon as  
399 possible, exclusion shark nets, *in situ* surveillance programmes and personal  
400 deterrents/protection (McPhee et al., 2021).

401 Shark hazard management varies between regions. Lethal strategies, which are common,  
402 have recently been criticized, based on their negative effects on marine life, unvalidated  
403 effectiveness for human safety and inconsistency with contemporary values that seek to  
404 improve both safety and conservation (Gibbs et al., 2020). Reunion Island authorities opted  
405 for a systematic culling strategy (Guyomard et al., 2020). While the combination of intensive  
406 shark culling representing the removal of about 150 individual bull sharks and 300 individual  
407 tiger sharks in eight years (since 2012; Source Centre Sécurité Requin : [http://www.info-](http://www.info-requin.re/)  
408 [requin.re/](http://www.info-requin.re/)) and a dramatic decline in recreational marine activities may have contributed to  
409 reduce the rate of shark bites, there is no evidence to suggest that the risk has been removed

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3 410 completely, since incidents have been recorded since the culling programme began in 2012  
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5 411 (although no bites were reported in 2020). Similarly, Hawaii historically culled tiger sharks to  
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7 412 alleviate public fear about shark bites but this strategy was obviously ineffective, with more  
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9 413 shark bites occurring after culling than before (Wetherbee, Lowe & Crow, 1994). Meyer et  
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11 414 al. (2018) recommended a more pragmatic approach, allowing the public to make informed  
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13 415 choices about ocean recreation by raising awareness of the natural presence of potentially  
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15 416 dangerous sharks at specific hotspots to prevent the risk of interactions.  
16  
17 417 Culling programmes, or the fishing of large sharks to reduce the risk of bites on human, can  
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19 418 result in serious alterations of shark populations, including declines in numbers and shifts in  
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21 419 species assemblages (Roff et al., 2018; Niella et al., 2021). A recent study highlighted that  
22  
23 420 the removal of bull sharks from coastal waters off Reunion may have contributed to an  
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25 421 increase in the presence of juvenile tiger sharks that utilized the vacated coastal habitats  
26  
27 422 (Niella et al., 2021), which may have future detrimental consequences in terms of shark bite  
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29 423 risk by giving space to another dangerous species. The same study also reported that the  
30  
31 424 culling programme of the targeted bull sharks also catches a significant number of bycatch  
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33 425 species, including two critically endangered elasmobranchs: the scalloped hammerhead shark  
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35 426 (*Sphyrna lewini*) and the giant guitarfish (*Rhynchobatus australiae*). Even if the mortality of  
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37 427 bycatch species in this programme is likely reduced by the use of SMART drumline  
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39 428 (Guyomard et al., 2019) as most bycatches are released alive in the water, further research is  
40  
41 429 needed to determine the survivorship of the released endangered species. Due to the potential  
42  
43 430 impact of the culling programme on species and the ecosystem, non-lethal approaches to  
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45 431 mitigating shark bites in Reunion Island should be prioritized to ensure the conservation of  
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47 432 the local elasmobranch species.  
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49 433 From a management perspective, individual behavioural differences and the random  
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51 434 character of the risk of shark bites makes spatial planning challenging. Yet the trend in size  
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segregated space use, coupled with the seasonal habitat preferences of large sharks, suggests that spatial management should be considered as a potential alternative to the lethal solutions adopted by culling programmes. Indeed, the predictability of shark activity and shark bites in space and time (Figure 3, Figure 5) can be utilized to delineate temporary closures of recreational activities at specific areas of high risk to reduce the probability of incidents thus removing the need for culling. Our data suggest that large sharks (> 2.5 m TL), which are responsible of most bites, are primarily utilizing northern areas of the island during the austral winter when the bite rate peaks (Figure 3, Figure 5). Based on our results on the distribution of sharks along the west coast of Reunion Island and the data on shark bite incidents, a temporary closure of marine recreational activities between April and September between Saint-Paul and Saint-Leu (Figures 1, 3, 5) is recommended. Such seasonal closure is probably the best way to reduce shark attacks while conserving marine wildlife. However, should such a recommendation not be implemented because of acceptance by the local population (restrictions of human access to the sea tend to trigger strong social protests in La Réunion island), a minimum measure would be the massive deployment of exclusion barriers at specific surfing spots in parts of the island during this period. Furthermore, public consultation and information-sharing in combination with other available mitigation tools such as surveillance programmes or personal protection devices, two tools that are now commonly employed in Reunion Island, are essential as they are likely to reduce the risk (Bradshaw et al., 2021). The need for consideration of dynamic spatial management measures has recently been suggested (Shabtay et al., 2020). Our study provides critical preliminary information on spatio-temporal use of the coast by large sharks. These findings can be integrated into a comprehensive management plan that not only considers a reduction of the risk of shark bites but also the conservation of sharks and of bycatch endangered species by offering an alternative to fishing control programmes.

460

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681 Figure legends

682 Figure 1: Study area along the west coast of Reunion Island and positions of acoustic  
 683 receivers (circles : ●). Names of main areas are indicated. Blue lines on land represents main  
 684 rivers while blue lines over the sea indicate bathymetry (5 m isobaths from 0 to 50 m, 10 m  
 685 from 50 to 100 m, 50 m from 100 to 1000 m and 100 m after 1000 m).

686

687 Figure 2: Biplots of Principal Component Analyses applied to matrices of individual monthly  
 688 values of receivers for the three node-level metrics. Receivers are represented by arrows  
 689 (middle panel) and sharks in a given month by dots (left panel). A three-dimensional standard  
 690 RGB (red, green, blue) colour space was used (red = high values in axis 1; green = high  
 691 values in axis 2 and blue = low values in axis 1). to assign colour to each observation (shark  
 692 in a given month) and variable (receiver), according to its position in the projected principal  
 693 components coordinates and scores. The same colours are used in the maps showing the  
 694 spatial distribution of receivers (right panel). Sex of individuals are represented by a symbol  
 695 which is proportional to shark's total length.

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697 Figure 3: Centres of activity of sharks. Maps of average node-based metrics for each receiver:  
 698 (a) closeness, (b) strength and (c) CRT. (d) Monthly TOPSIS scores for each receiver which  
 699 integrates the three node-based metrics mentioned above (a high TOPSIS score means that  
 700 the receiver has a high value for all three metrics)

701

702 Figure 4: Cluster analyses conducted on the overall centrality score (TOPSIS score) in  
 703 individual monthly movement networks: (a) Spatial distribution of mean activity score of  
 704 each receiver for each cluster; (b) Sex composition and mean total length of each cluster; (c)

705 Monthly cluster membership for each shark ordered according to total length. Males are  
706 indicated in italic and females in bold.

707

708 Figure 5: Spatiotemporal occurrence of shark bites in Reunion Island between 2011 and  
709 2020. Colours represent the site where shark bites occurred. Data source: [http://www.info-](http://www.info-requin.re/le-centre-securite-requin-r70.html)  
710 [requin.re/le-centre-securite-requin-r70.html](http://www.info-requin.re/le-centre-securite-requin-r70.html).

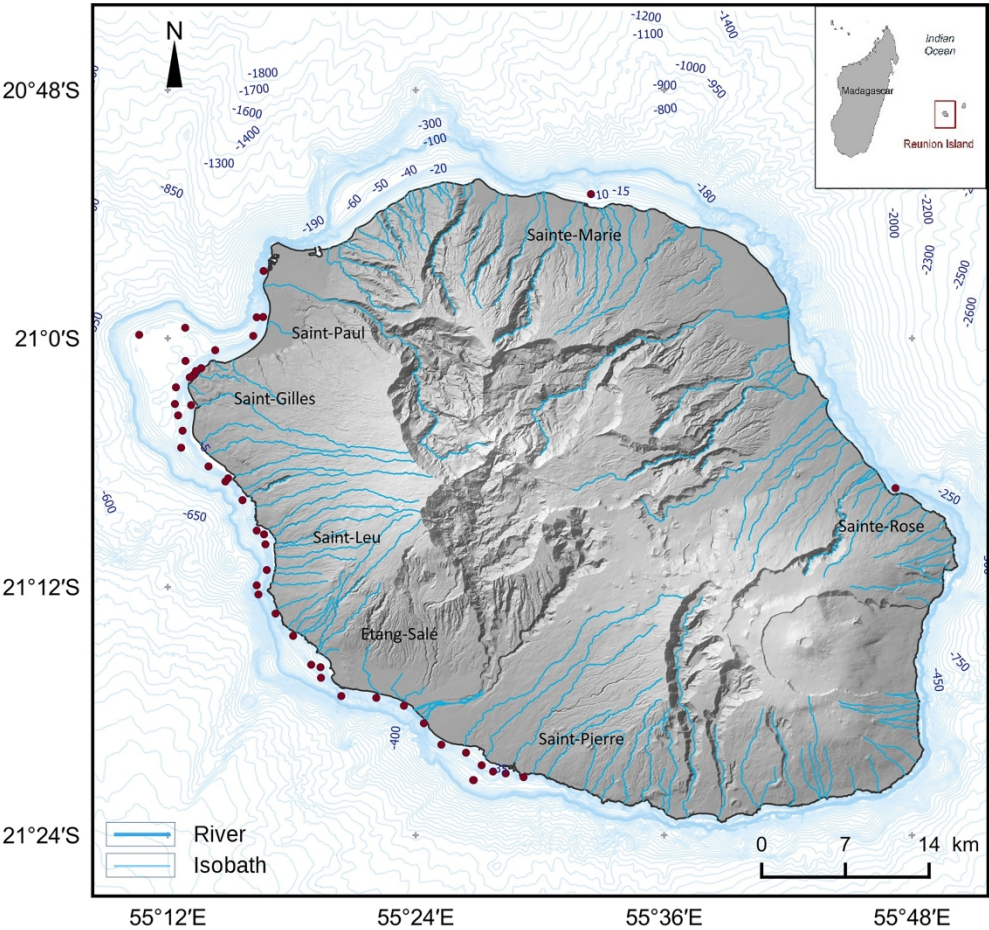
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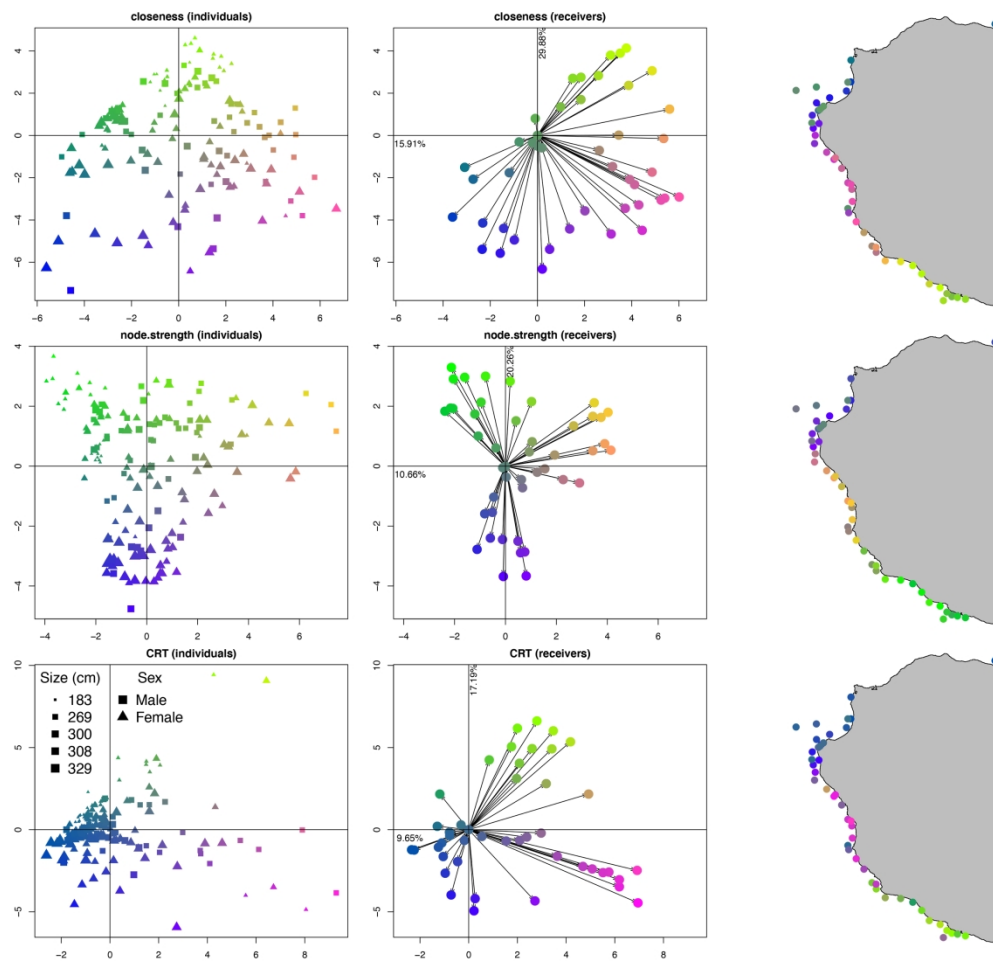


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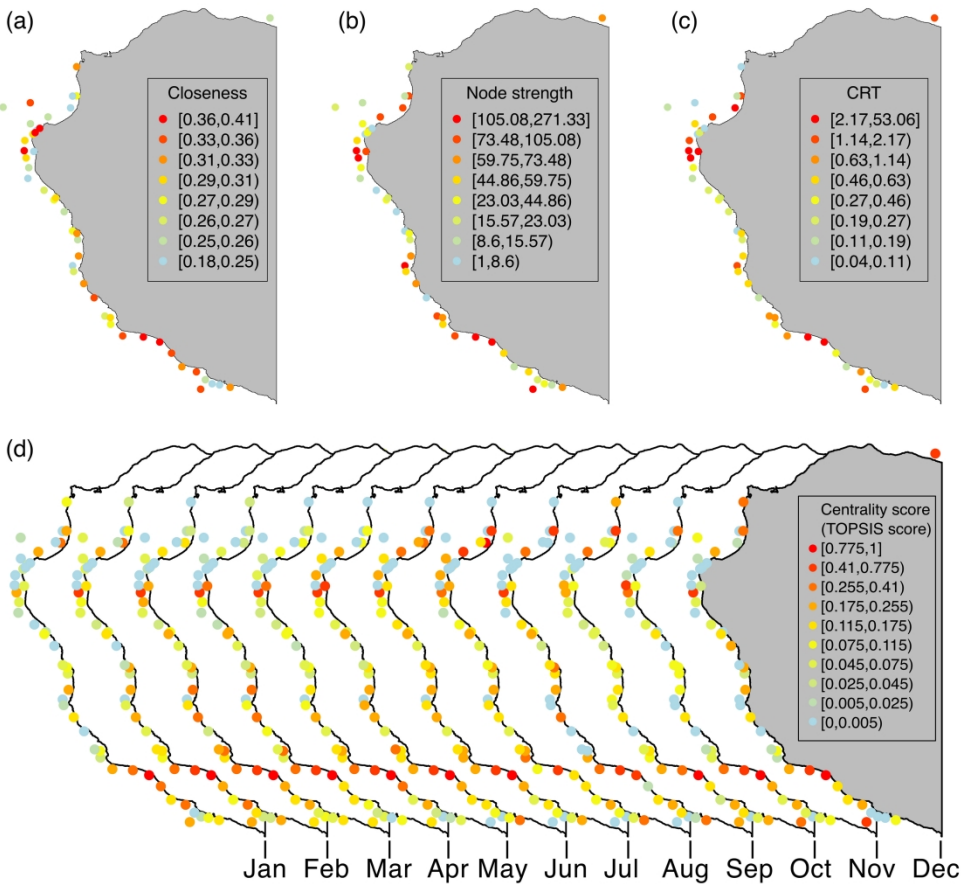


Study area along the west coast of Reunion Island and positions of acoustic receivers (circles : □). Names of main areas are indicated. Blue lines on land represents main rivers while blue lines over the sea indicate bathymetry (5 m isobaths from 0 to 50 m, 10 m from 50 to 100 m, 50 m from 100 to 1000 m and 100 m after 1000 m).

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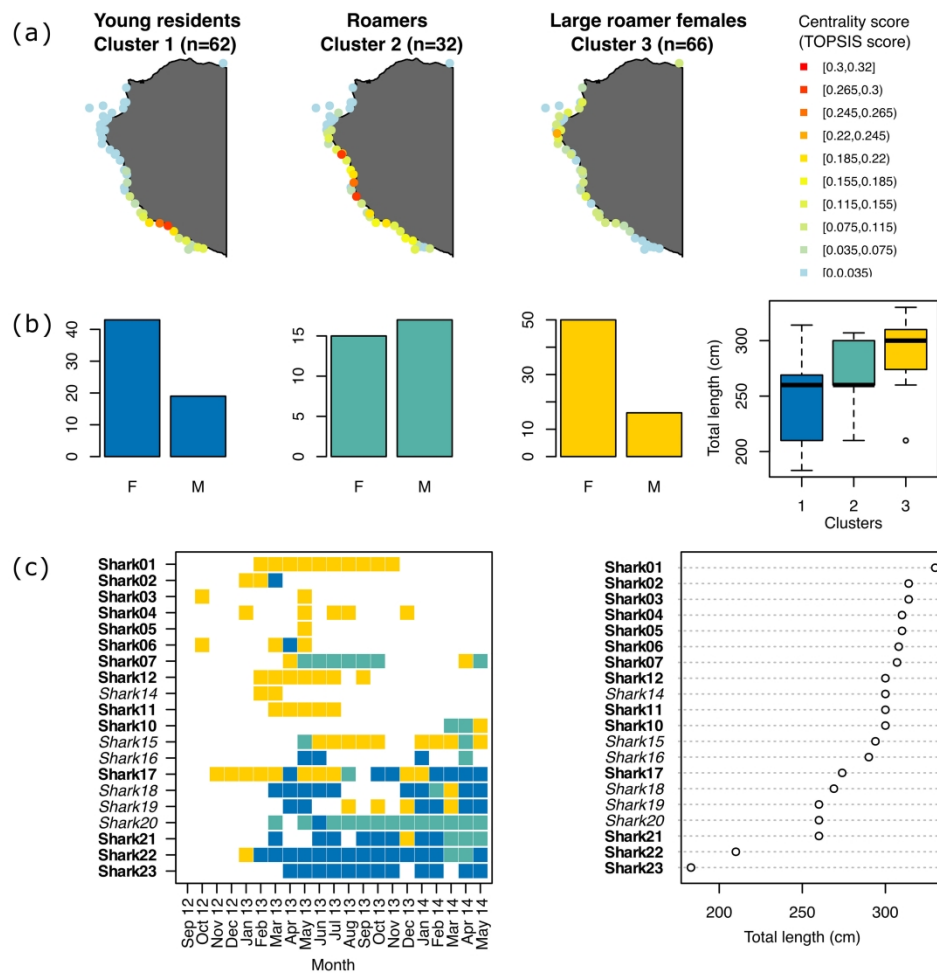


Biplots of Principal Component Analyses applied to matrices of individual monthly values of receivers for the three node-level metrics. Receivers are represented by arrows (middle panel) and sharks in a given month by dots (left panel). A three-dimensional standard RGB (red, green, blue) colour space was used (red = high values in axis 1 ; green = high values in axis 2 and blue = low values in axis 1). to assign colour to each observation (shark in a given month) and variable (receiver), according to its position in the projected principal components coordinates and scores. The same colours are used in the maps showing the spatial distribution of receivers (right panel). Sex of individuals are represented by a symbol which is proportional to shark's total length.



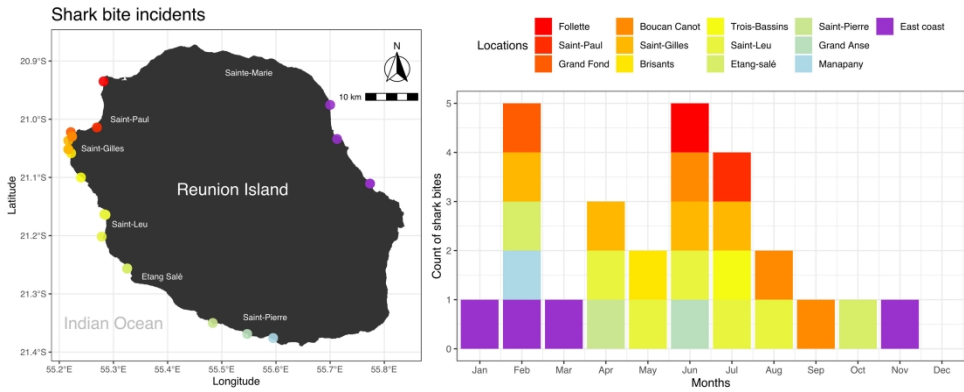
Centres of activity of sharks. Maps of average node-based metrics for each receiver: (a) closeness, (b) strength and (c) CRT. (d) Monthly TOPSIS scores for each receiver which integrates the three node-based metrics mentioned above (a high TOPSIS score means that the receiver has a high value for all three metrics)

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Cluster analyses conducted on the overall centrality score (TOPSIS score) in individual monthly movement networks: (a) Spatial distribution of mean activity score of each receiver for each cluster; (b) Sex composition and mean total length of each cluster ; (c) Monthly cluster membership for each shark ordered according to total length. Males are indicated in italic and females in bold.

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Spatiotemporal occurrence of shark bites in Reunion Island between 2011 and 2020. Colours represent the site where shark bites occurred. Data source: <http://www.info-requin.re/le-centre-securite-requin-r70.html>.

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