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

Mourier Johann ^{3,*}, Soria Marc ², Blaison Antonin ³, Simier Monique ², Certain Gregoire ¹, Demichelis Angélique ³, Hattab Tarek ¹

¹ MARBEC, Univ Montpellier, CNRS, IFREMER, IRD Sète, France

² MARBEC, Univ Montpellier, CNRS, IFREMER, IRD Sète, France

³ MARBEC, Univ Montpellier, CNRS, IFREMER, IRD Sète, France

* Corresponding author : Johann Mourier, email address : johann.mourier@gmail.com

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

1. INTRODUCTION

As the human population and associated infrastructure are rapidly developing along the coast, wildlife habitats are being progressively reduced, leaving many species with little refuge (Brierley & Kingsford, 2009). Conflict between humans and potentially dangerous wildlife is becoming an important issue (Dickman, 2010; Pooley et al., 2017). Managing this conflict demands a balance between the achievement of conservation goals and public safety. This issue is highlighted in the management of human-shark conflicts. At a global scale, an increase in the number of shark bites has been observed, yet the individual risk for beach users is simultaneously decreasing due to the number of ocean users increasing even more rapidly (McPhee, 2014; Ferretti et al., 2015; Chapman & MCPhee, 2016; Midway, Wagner & Burgess, 2019). When compared with other types of human-wildlife interactions, the number of shark bites is low, yet they receive massive media exposure (Muter et al., 2013) and political attention (Neff, 2012). Consequently, many governments have introduced shark mitigation strategies to increase public safety and awareness (Curtis et al., 2012).

According to the International Shark Attack File (<https://www.floridamuseum.ufl.edu/shark-attacks/>), there was an average of 1.2 unprovoked shark bites per year in Reunion Island between 1980 and 2011 but this rate increased to ~ 2.5 bites per year between 2011 and 2019 (10 fatal cases from 23 incidents). In the past decade this island has become a hotspot for shark incidents (Lagabrielle et al., 2018; Midway, Wagner & Burgess, 2019; Taglioni et al., 2019). There was, for example, a 23-fold increase in incidents between 2005 and 2016 when the total number of surfing hours was taken into consideration (Lagabrielle et al., 2018). As such, Reunion Island is an exception to other shark hotspot locations as it has an increased rate in annual shark bites and an increase in individual risk. Two species were involved in these incidents, the tiger shark *Galeocerdo cuvier* and the bull shark *Carcharhinus leucas*, the

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3 61 latter being responsible for the majority of incidents (Taglioni et al., 2019). Human-shark
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5 62 incidents seem to peak in austral winter and are mostly concentrated on the island's west
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8 63 coast where most coastal water activities occur (Lemahieu et al., 2017; Soria et al., 2019);
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10 64 prior to 2010, such incidents were randomly distributed around the island.
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14 66 Improving our understanding of individual shark space use dynamics as well as our ability to
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17 67 predict shark encounters requires much attention if we are to reduce the risk of bites from
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19 68 large sharks. Progress in these areas could allow for water-users to be better informed about
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21 69 areas and periods of increased risk, and potentially for the development of area-specific shark
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23 70 mitigation strategies. In this study acoustic telemetry was used to investigate the spatial
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26 71 ecology of bull sharks around Reunion Island. The specific objectives of this study were to
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28 72 examine: (i) whether bull shark movements are non-random, and if this is the case, (ii)
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30 73 whether shark movements can be classified into behavioural clusters, and (iii) how shifts
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33 74 between behavioural states occur through time. This study aims to provide insight into shark
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35 75 behaviour and central areas used through time which can then be compared with sites where
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37 76 shark bites occurred to help improve management and mitigation strategies in order to avoid
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40 77 culling programmes.
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44 79 **2. MATERIALS AND METHODS**

46 80 2.1. Study species and site

47
48
49 81 The bull shark (*Carcharhinus leucas*) is a large Carcharhinidae with a cosmopolitan
50
51 82 distribution along the continental coasts and around remote islands and archipelagos of all
52
53 83 tropical and sub-tropical waters of the world. This species moves across a large range of
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56 84 habitats and environmental conditions (Daly et al., 2014; Heupel et al., 2015; Espinoza et al.,
57
58 85 2016; Lee et al., 2019), including nearshore areas where it has more chance to interact with
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3 86 water-users than many other species. Its behaviour varies across different spatial and
4
5 87 temporal scales, and according to size and sex, with a high individual variability in its
6
7 88 tendency to migrate or remain resident (Espinoza et al., 2016; Lee et al., 2019). Recent work
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9 89 reported that adults can migrate over large distances (Lea et al., 2015), but also display strong
10
11 90 site fidelity on a seasonal or annual basis (Daly et al., 2014; Heupel et al., 2015).
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16
17 92 Reunion Island (21°07'S / 55°32'E) is a volcanic island located 700 km east of Madagascar
18
19 93 in the south-west Indian Ocean. The island is 2512 km² with 217 km of coastline and steep
20
21 94 underwater slopes (*ca.* 10-20%) to a depth of 2,000 m. Fringing reefs stretch over 25 km
22
23 95 along the west and south-west coast, from Saint-Gilles to Saint-Pierre (Figure 1).
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27 28 97 2.2. Acoustic telemetry

29
30 98 Sharks were captured along the west coast of Reunion Island between September 2012 and
31
32 99 March 2013 (Table S1), using horizontal bottom long-lines and drumlines (Blaison et al.,
33
34 100 2015). Most fishing and captures occurred at dusk or overnight and longline set times were
35
36 101 fixed at a maximum of 3 hours to minimize shark and bycatch mortality. The fishing effort
37
38 102 was higher on the north west (80% in Saint-Paul's Bay and Saint-Gilles) and lower (20%) in
39
40 103 the south offshore of Saint-Pierre (Blaison, 2017). Once captured, a shark was brought
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42 104 alongside the vessel and rolled onto its back to induce tonic immobility. Sex and total length
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44 105 (TL) were recorded and transmitters (Vemco V16, transmission interval 40-80 s, estimated
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46 106 battery life 845 days) were implanted into the peritoneal cavity through a mid-ventral
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48 107 incision. All the fieldwork and protocols of handling and tagging were approved by the
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50 108 Ethics Committee (n° 114) for the CYROI (Cyclotron Réunion Océan Indien) in Reunion
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52 109 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%)
6
7 113 offshore receivers and 13 (29%) inshore receivers placed less than 300 m from shore (Figure
8
9 114 1). As detection ranges are known to vary with environmental characteristics (Huveneers et
10
11 115 al., 2016), 13 range tests were conducted. Detection probability dropped by 50% at $\sim 190 \pm 80$
12
13 116 m for six inshore receivers and at $\sim 390 \pm 90$ m for seven offshore receivers. This slight
14
15 117 difference in detection range is unlikely to affect detection probabilities because nearshore
16
17 118 and offshore receivers were homogeneously distributed throughout the study area (Figure 1).
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19 119
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22
23 120 For each shark visit to a receiver, detection records were used to calculate a continuous
24
25 121 residency time (CRT) which was defined as the duration within which a tagged shark was
26
27 122 continuously monitored at a specific receiver without a one-hour (> 1 h) absence (Capello et
28
29 123 al., 2015). Thus, all detections of the same shark at a given receiver that were separated by
30
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

45
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
51
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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3 136 of acoustic receivers using shark movements. For each shark, monthly relative movement
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5 137 matrices were derived from movements between receivers based on visitation patterns
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8 138 deduced from CRTs. These were defined as the number of times individuals moved between
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10 139 two receivers divided by the total number of movements within its space use (i.e. total
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12 140 number of edges in the network). These matrices were used to create weighted directed
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14 141 networks for each individual that reflected the monthly extent of space use within the
15
16 142 receiver array over the entire monitoring period.
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19 143 Each network was tested for non-random associations between receivers, based on observed
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21 144 movements to determine whether sharks showed a non-random distribution of directed
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23 145 movements among sites. Null modelling and randomization of observed movements were
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25 146 conducted by considering spatial bias in the array design (i.e. a direct movement between one
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27 147 pair of nodes is more likely than another because nodes are closer to each other) using the
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29 148 function `rewire()` from R package `igraph` (Csardi & Nepusz, 2006). In order to preserve
30
31 149 spatial structure in the data, observed individual movement events which contributed to
32
33 150 overall edge weighting were permuted to create replicated (weighted) movements from the
34
35 151 raw data. Reassignment of these individual directed movements during each permutation was
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37 152 constrained to only directional edges between pairs of locations which occurred in the
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39 153 empirical movement network (Jacoby et al., 2012a). Two metrics were calculated from the
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41 154 observed and random networks: diameter and average path length. The diameter measures the
42
43 155 longest path between any pair of receivers in the network and is an indicator of the size of the
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45 156 network. Average path length provides a measure of the average ease/likelihood of a
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47 157 movement between two locations occurring. Then, p-value can be calculated by comparing
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49 158 the observed metric to the metric derived from randomized data. This randomization
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51 159 procedure was applied to individual monthly movement networks, by comparing each
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53 160 observed network with 10,000 permuted networks.
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6 162 Node-based metrics were then used to describe the influence that individual nodes had on the
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8 163 overall network structure and were determined from the level of interaction one node had
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10 164 with any other node, either directly or via intermediates. Two network centrality metrics were
11
12 165 calculated: closeness and node strength. Closeness measures how central a receiver's position
13
14 166 (visited by one individual) is in the network of monthly movements of each shark and is
15
16 167 expressed as the smallest number of edges (pathways) linking receivers during the
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18 168 movements of the shark between receivers (i.e. the geodesic distance). This is the inverse of
19
20 169 the average path lengths from a node to each of its neighbours. A low geodesic distance
21
22 170 corresponds to a high closeness (Lédée et al., 2015). Node strength is a measure of the level
23
24 171 of connectivity of a node and represents the total number of incoming/outgoing movements
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26 172 to/from a receiver. A receiver with a high node strength would suggest strong site fidelity. In
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28 173 addition to these centrality metrics, the monthly CRT (sum of CRTs for each month) was also
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30 174 calculated for each node. A receiver with a high monthly CRT suggests a site where the shark
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32 175 spent a large amount of time. These three node-based metrics were used to identify the
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34 176 receivers which corresponded to core use areas.
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42 178 2.4. Statistical analyses

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44 179 In order to standardize the data, all receivers that were deployed for less than 20 days during
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46 180 the month were removed from monthly movement networks. Similarly, individuals that were
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48 181 not detected for at least 20 days during a month were also excluded. This empirical choice
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50 182 was made as a compromise between data loss and representativeness. All individual monthly
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52 183 networks that were found to show random patterns were also removed. Finally, only monthly
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54 184 individual networks containing more than five directed movements between receivers were
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56 185 kept, in an attempt to measure relevant network metrics.
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3 186 To highlight the spatio-temporal patterns of space use related to individual life history traits,
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5 187 a principal component analyses (PCA) was performed on each matrix of network metrics, in
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7 188 which columns represent receivers and rows represent individuals in a given month. As such,
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9 189 receivers were considered as variables and individuals in a given month as observations in
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11 190 the PCAs. To display information on both receivers and sharks graphically, a biplot
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13 191 representation of the PCA results was used (Gabriel, 1971). This representation allows the
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15 192 visualization of similarities and differences in monthly movement patterns between sharks,
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17 193 and simultaneously reveals how each receiver contributes to each principal component.
18
19 194 For each node-based metric, clustering of monthly shark movements was conducted on the
20
21 195 ordination axes of the PCAs with k-means clustering. In order to find the main behavioural
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23 196 clusters, between 2 and 4 partitions were tested. Data from each cluster of monthly individual
24
25 197 movements was extracted and interpreted according to spatial distribution, sex, size and time.
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27 198 To obtain a global understanding of the spatial distribution of node-metrics, closeness, node-
28
29 199 strength and CRT were independently averaged across all months and individuals. Each
30
31 200 metric was also averaged for each month of the year. In addition, to combine all three metrics
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33 201 within one score and determine the locations with high values across all metrics, the TOPSIS
34
35 202 method (Technique for Order Preference by Similarity to an Ideal Solution; Huang, Keisler &
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37 203 Linkov, 2011) was used. This method is designed to solve multiple criteria decisions through
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39 204 evaluation of the alternatives by simultaneously measuring their distances to the Positive
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41 205 Ideal Solution (PIS) and to the Negative Ideal Solution (NIS). PIS is the most preferred
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43 206 solution (in our case the highest values for all metrics) and NIS is the least preferred solution
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45 207 (the lowest value for all metrics). The preference order from the TOPSIS method is then built
46
47 208 according to the relative closeness of the alternatives to PIS, which is a scalar criterion that
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49 209 combines these three distance measures. In this case, the positive ideal solution
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51 210 corresponding to the condition where closeness, node-strength and CRT were greatest was
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3 211 defined (note that in our case a 1:1:1 weight ratio of the three components was used so that
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5 212 each metric is given equal consideration). A resultant high TOPSIS score at one receiver
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7 213 means that it has high values for all three metrics (closeness, node-strength and CRT).
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10 214 Similar to the analysis of all node-metrics independently, clustering of monthly shark
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12 215 movements was also conducted on PCAs ordination axes of the TOPSIS score with k-means
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14 216 clustering.
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16
17 217 All analyses were performed in R 3.5.1 (R Development Core Team, 2020), using the
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19 218 ‘dudi.pca’ function from the R package ‘ade4’ (Dray & Dufour, 2007) for the PCAs,
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21 219 ‘cascadeKM’ function with the ‘calinski’ criterion (Caliński & Harabasz, 1974) from the R
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23
24 220 package ‘vegan’ for the clustering (Dixon, 2003) and R package ‘topsis’ (Yazdi, 2013).
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222 3. RESULTS

30 223 From a total of 190 monthly networks only nine (5%) from seven sharks showed random
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32 224 movement patterns and were removed from subsequent analyses. After applying the thresholds
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34 225 (20 days per month of active receivers and tags and a minimum of five movements per month),
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36 226 160 individual monthly networks for closeness and 164 networks for node-strength consisting
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38 227 of 20 sharks and 20 months from October 2012 to May 2014, were analysed. Differences in
39
40 228 the number of networks is due to the removal of monthly networks where closeness was null
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43 229 for all receivers while node-strength was not. Similarly, 181 individual monthly CRT datasets
44
45 230 were analysed from 23 sharks over 20 months from October 2012 to May 2014. The higher
46
47 231 number of individuals used for the CRT analyses is due to the inclusion of three sharks that
48
49 232 were present for at least a month but did not conduct more than five movements during their
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51 233 residence times. Some sharks were detected in the area for only a short period of time (< 3
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54 234 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
19
20 243 across all node-level metrics. The shark size distribution in the PCAs also showed a geographic
21
22 244 gradient. Smaller individuals corresponded to high values on axis 2 (i.e. receivers located in
23
24 245 the south) while larger individuals were associated with low values of axis 2 (i.e. receivers
25
26 246 located in the north). These patterns were only observed for closeness and node-strength. There
27
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
32
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
36
37 251 west (Figure 3b,c). Combining all three node-metrics averaged across individuals using the
38
39 252 TOPSIS analysis and investigating resultant scores across months, the spatial distribution of
40
41 253 shark movement centrality was found to be highly dynamics. While activity remained high
42
43 254 between Etang-Salé and Saint-Pierre in the south-west and at one receiver at Saint-Gilles all
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45 255 year round, it spread between Saint-Gilles and Saint-Paul from July to December (Figure 3d).
46
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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3 260 monthly networks, including mostly young female sharks (Chi² test: M:F = 19:43, $\chi^2 = 9.290$,
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5 261 $df = 1$, $P = 0.0023$), and characterized by high centrality scores in the south west of the island.
6
7 262 Cluster 2, called “roamers”, consisted of 32 individual monthly networks from a set of large
8
9 263 individuals with a relatively balanced sex ratio (Chi² test: M:F = 17:15, $\chi^2 = 1.125$, $df = 1$, $P =$
10
11 264 0.7237). This cluster had high centrality scores which were primarily located in the middle of
12
13 265 the west coast. Cluster 3, called “large roamer females”, consisted of 66 individual monthly
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15 266 networks and included mostly large females (Chi² test: M:F = 16:50, $\chi^2 = 17.515$, $df = 1$, $P <$
16
17 267 0.001), for which centrality was higher in the northern portion of the west coast but was also
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19 268 spread along the coast. Movement network centrality was relatively stable but showed a clear
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21 269 ontogenetic shift from the south to the north of the island as individuals became larger. Results
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23 270 from cluster analyses conducted separately on each node-metric are available in the
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25 271 Supplementary Information (Figure S2-4).
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33 273 4. DISCUSSION

34
35 274 Understanding the spatio-temporal movement dynamics of potentially dangerous large
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37 275 predators helps in predicting and anticipating human-wildlife conflicts. Using acoustic
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39 276 telemetry and network analyses, the dynamics of the space use patterns of bull sharks around
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41 277 Reunion Island were revealed. Their spatial dynamics were found to be influenced strongly
42
43 278 by size with some degree of size-segregation observed. Small individuals were typically
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45 279 restricted to the south of the island while larger sharks were mostly found in the north during
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47 280 the austral winter, which is also where most human-shark interactions have taken place
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49 281 (Figure 5).
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56 283 The PCA demonstrated clear geographical patterns for all node-level metrics in relation to
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58 284 shark size. Smaller sharks (< 300 cm TL) used areas located on the south west coast while
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3 285 larger individuals were mostly found in the northern areas. Closeness and node-strength
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5 286 centrality metrics described core use areas or centres of activity and revealed that spatial
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7 287 patterns are mainly explained by shark size (Figure S2-S3). This was further confirmed when
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9 288 all three metrics were combined (Figure 4). This result was less clear when only residency
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11 289 was considered (i.e. CRT), suggesting that most sharks were mobile and did not stay at
12
13 290 specific receivers for long periods of time (Figure S4). In addition, no apparent geographic
14
15 291 pattern related to sex was found for any metric. This geographic structure of the population
16
17 292 indicates an ontogenetic segregation in habitat, where adult and young sharks use different
18
19 293 habitats and their activity space rarely overlaps, a common pattern observed in many shark
20
21 294 species (Speed et al., 2010). Shark populations can segregate into sub-units based on age and
22
23 295 sex giving rise to complex patterns of spatial ecology at the population level. Juveniles will
24
25 296 often remain within specific nursery areas for protection against predators and access to
26
27 297 abundant prey, and will gradually increase their space use as they grow (Chapman et al.,
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29 298 2009). This behaviour corresponds to increasing physiological demands, increased individual
30
31 299 variation in diet (Matich & Heithaus, 2015; Matich et al., 2019), a reduced threat of predation
32
33 300 and the onset of maturity. It is not clear why, in Reunion Island, larger sharks display a
34
35 301 preference for the northern coast, but it may be due to the presence of abundant food
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37 302 resources or a preference for the sandy bottom on a 50 m deep shelf between Saint-Gilles and
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39 303 Saint-Paul. Alternatively, this particular area could represent a resting area due to optimal
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41 304 current conditions, or sharks could be attracted by potential fish discards dropped by fishing
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43 305 vessels outside the port of Saint-Gilles. Individual bull sharks are known to have different
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45 306 foraging strategies as has been demonstrated through stable isotope analyses (Trystram et al.,
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47 307 2016). Foraging shifts also occur after reaching maturity with tendencies for individual
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49 308 foraging specialization to occur in adulthood (Matich, Heithaus & Layman, 2011). This
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51 309 pattern could also explain the various individual behavioural clusters found in our study, with
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3 310 individual spatial dynamics possibly driven by specialized foraging strategies. In addition,
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5 311 immature sharks rely on coastal food sources whilst pelagic prey contributes more to the diet
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7 312 of adult sharks. This could explain why smaller sharks were more often continuously
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9 313 detected by coastal receivers while for larger sharks continuous presence spanning several
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11 314 months was less common. These absences may represent large scale offshore excursions
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13 315 leading sharks to leave the island for periods of weeks to months (Soria et al. 2021).
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18
19 317 However, it was more surprising that no clear sexual segregation was found as this is
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21 318 common in many shark populations (Jacoby, Croft & Sims, 2012b) including bull sharks
22
23 319 (Werry & Clua, 2013; Espinoza et al., 2016). Sexual segregation can emerge from females
24
25 320 trying to avoid male harassment, especially during the mating period (Jacoby et al., 2010).
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27 321 Male harassment is possible in bull sharks as they have been found to show polyandry with
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29 322 multiple males siring juveniles from the same female (Pirog et al., 2019). The resolution of
30
31 323 the current analysis may have been too coarse or the number of males too low to reveal such
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33 324 avoidance patterns.
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38
39 326 High levels of individual variability in behaviour and space use were observed. While young
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41 327 sharks appeared to be present all year round, the detection of larger individuals increased
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43 328 during autumn and winter (Blaison et al., 2015; Soria et al., 2019), which is likely a result of
44
45 329 increased mating activity. Soria et al. (2019) suggested that a pre-mating aggregation could
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47 330 occur in the north near the Saint-Gilles harbour from April. For example, 'shark17' shifted
48
49 331 between four behavioural clusters, which corresponded to a higher closeness in movement
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51 332 patterns in the north at the end of 2012 and in the south at the end of 2013 (Figure S2). In
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53 333 addition, the largest female 'shark01' had a closeness centrality which was homogeneously
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55 334 spread along the coast between February and April 2013, and then slowly shifted to the north
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3 335 from September 2013 (Figure S2). However, this individual also had a constant cluster for
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5 336 node-strength and all metrics combined suggesting that its main areas of centrality remained
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7 337 in the north near Saint-Paul (Figure 4, Figure S3).
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12 339 The observed dynamics in movement patterns of bull sharks around Reunion Island could
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14 340 also be driven by parturition. Previous research suggested that female bull sharks use some
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16 341 areas as pupping and nursery grounds (Pirog et al., 2019), with parturition occurring in
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18 342 October–November. Immature sharks (<230 cm TL) restricted their core use to an area
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20 343 between Etang-Salé and Saint-Pierre suggesting the presence of nursery grounds where
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22 344 mature females may return to give birth (Tillett et al., 2012). In addition, large females
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24 345 displayed short-term shifts in centres of activity space between the north and the south; such
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26 346 as large female ‘shark 07’ moving south of Etang-Salé in October 2013 (Figures S2-S3).
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33 348 Sharks can partition space use both within (Mourier, Vercelloni & Planes, 2012) and between
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35 349 (Papastamatiou et al., 2018) species. Spatial separation may arise via different foraging
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37 350 strategies (Matich, Heithaus & Layman, 2011) or competitive interactions (Brena et al.,
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39 351 2018). Spatial separation can also be the result of density-dependent competition in which
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41 352 some individuals leave an area once it becomes too congested. This size-based partitioning of
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43 353 space may prevent conflict over resources between size classes. Future work could
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45 354 investigate co-occurrence to determine whether bull sharks share space at the same time or
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47 355 whether they avoid each other.
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53 357 The increased rate in human-shark incidents in Reunion Island since 2011 has resulted in
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55 358 conflicts between both sharks and human as well as among ocean user groups. It has also led
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57 359 to great interest in understanding the potential causes for this sudden increase in shark bites
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3 360 and finding effective management solutions to mitigate the risk of these incidents. Since
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5 361 2011, most shark bites (16 out of 26: 61%) have occurred between April and August in the
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7 362 north-west region of the island, between Saint-Paul and Saint-Leu (Figure 5). Only a few
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9 363 incidents (7 out of 26: 27%) occurred in the southern and eastern areas, and mostly during
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11 364 summer. The remainder (3 out of 26: 12%) were randomly distributed along the west coast
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13 365 and across the seasons. In addition, forensic analyses demonstrated that large sharks (2.5-3.5
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15 366 m TL) were responsible for all the reported shark bites (Werbrouck et al., 2014). Centrality
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17 367 network metrics showed that larger sharks used larger core-use areas between February and
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19 368 August, and more spatially restricted areas in the north during other times of the year. In
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21 369 addition, the same large adult females tended to display high continuous residency times in
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23 370 the north between Saint-Paul and Saint-Gilles between February and August while for the
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25 371 remainder of the year they typically made longer visits in the south near Etang-Salé. These
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27 372 spatial dynamics are in accordance with the dynamics of observed human-shark bites (Figure
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29 373 5). Other species of large sharks have also shown increased rates of movement and
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31 374 aggressiveness around mating periods, especially when social hierarchies are readjusted
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33 375 (Clua et al., 2010), which can result in increased bite risk. More than 50% of the bites in
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35 376 Reunion Island occurred during the mating period (between June and September), which is
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37 377 also the season when large swell attracts surfers. This suggests that increased aggressiveness
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39 378 may be related to mating activity, reinforced by the prevalence of polygyny in this species
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41 379 (Pirog et al., 2019) where males could compete for female mates. Evidence of multi-annual
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43 380 polygyny (Pirog et al., 2019) suggests that males may exhibit some mating-site fidelity,
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45 381 returning on a regular basis to specific places to mate. This also suggests that bull sharks may
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47 382 aggregate to mate. Although aggregative behaviour in sharks can be related to reproduction
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49 383 (Jacoby, Croft & Sims, 2012b), there are several other potential reasons, such as foraging on
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51 384 patchy or concentrated food resources (Schilds et al., 2019) or phenotypic assortment (e.g. a
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3 385 preference to associate with individuals of similar size or sex; Mourier, Vercelloni & Planes,
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5 386 2012). Moreover, the dramatic increase in bite rates has only occurred from 2011, despite
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7 387 similar seasonal ocean-use before then. This suggests that mating may not be the only cause
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9 388 for shark bite incidents. Nonetheless, increased risk during the mating period in particular
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11 389 locations and the high variability in individual space use patterns should be taken into
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13 390 account in formulating management strategies to reduce shark bites that also have the
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15 391 minimum impact on shark populations (Clua & Linnell, 2019).
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21 392
22 393 Shark risk management is applied in areas with high probabilities of unprovoked shark bites
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24 394 with the aim to reduce the rate of incidents. A range of management and risk mitigation
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26 395 measures have been tested and employed including warning and education, lethal shark nets
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28 396 and drumlines that catch and kill sharks near shore to protect humans, SMART drumlines
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30 397 ('Shark Management Alert in Real Time') which is a system that alerts authorities when an
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32 398 animal is caught allowing the release of bycatch (i.e. species that are not targeted) as soon as
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34 399 possible, exclusion shark nets, *in situ* surveillance programmes and personal
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36 400 deterrents/protection (McPhee et al., 2021).
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40 401 Shark hazard management varies between regions. Lethal strategies, which are common,
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42 402 have recently been criticized, based on their negative effects on marine life, unvalidated
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44 403 effectiveness for human safety and inconsistency with contemporary values that seek to
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46 404 improve both safety and conservation (Gibbs et al., 2020). Reunion Island authorities opted
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48 405 for a systematic culling strategy (Guyomard et al., 2020). While the combination of intensive
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50 406 shark culling representing the removal of about 150 individual bull sharks and 300 individual
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52 407 tiger sharks in eight years (since 2012; Source Centre Sécurité Requin : [http://www.info-](http://www.info-requin.re/)
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54 408 [requin.re/](http://www.info-requin.re/)) and a dramatic decline in recreational marine activities may have contributed to
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56 409 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.
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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
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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
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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
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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
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41 429 needed to determine the survivorship of the released endangered species. Due to the potential
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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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3 435 segregated space use, coupled with the seasonal habitat preferences of large sharks, suggests
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5 436 that spatial management should be considered as a potential alternative to the lethal solutions
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7 437 adopted by culling programmes. Indeed, the predictability of shark activity and shark bites in
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9 438 space and time (Figure 3, Figure 5) can be utilized to delineate temporary closures of
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11 439 recreational activities at specific areas of high risk to reduce the probability of incidents thus
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13 440 removing the need for culling. Our data suggest that large sharks (> 2.5 m TL), which are
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15 441 responsible of most bites, are primarily utilizing northern areas of the island during the
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17 442 austral winter when the bite rate peaks (Figure 3, Figure 5). Based on our results on the
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19 443 distribution of sharks along the west coast of Reunion Island and the data on shark bite
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21 444 incidents, a temporary closure of marine recreational activities between April and September
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23 445 between Saint-Paul and Saint-Leu (Figures 1, 3, 5) is recommended. Such seasonal closure is
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25 446 probably the best way to reduce shark attacks while conserving marine wildlife. However,
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27 447 should such a recommendation not be implemented because of acceptance by the local
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29 448 population (restrictions of human access to the sea tend to trigger strong social protests in La
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31 449 Réunion island), a minimum measure would be the massive deployment of exclusion barriers
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33 450 at specific surfing spots in parts of the island during this period. Furthermore, public
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35 451 consultation and information-sharing in combination with other available mitigation tools
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37 452 such as surveillance programmes or personal protection devices, two tools that are now
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39 453 commonly employed in Reunion Island, are essential as they are likely to reduce the risk
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41 454 (Bradshaw et al., 2021). The need for consideration of dynamic spatial management measures
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43 455 has recently been suggested (Shabtay et al., 2020). Our study provides critical preliminary
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45 456 information on spatio-temporal use of the coast by large sharks. These findings can be
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47 457 integrated into a comprehensive management plan that not only considers a reduction of the
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49 458 risk of shark bites but also the conservation of sharks and of bycatch endangered species by
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51 459 offering an alternative to fishing control programmes.
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30 473 REFERENCES

- 31
32
33 474 Blaison, A. (2017). Écologie comportementale des requins bouledogue (*Carcharhinus*
34
35 475 *leucas*) sur les côtes de La Réunion : application à un modèle de gestion du « risque
36
37 476 requin ». PhD thesis, Université de la Réunion.
38
39
40 477 Blaison, A., Jaquemet, S., Guyomard, D., Vangrevelinghe, G., Gazzo, T., Cliff, G. et al.
41
42 478 (2015). Seasonal variability of bull and tiger shark presence on the west coast of
43
44 479 Reunion Island, western Indian Ocean. Seasonal variability of bull and tiger shark
45
46 480 presence on the west coast of Reunion Island, western Indian Ocean. *African Journal*
47
48 481 *of Marine Science*, 37(2), 199–208. <https://doi.org/10.2989/1814232X.2015.1050453>
49
50
51 482 Bradshaw, C. J., Meagher, P., Thiele, M. J., Harcourt, R. G. & Huveneers, C. (2021).
52
53 483 Predicting potential future reduction in shark bites on people. *Royal Society Open*
54
55 484 *Science*, 8(3), 201197. <https://doi.org/10.1098/rsos.201197>
56
57
58
59
60

- 1
2
3 485 Brena, P.F., Mourier, J., Planes, S. & Clua, E.E. (2018). Concede or clash? Solitary sharks
4
5 486 competing for food assess rivals to decide. Concede or clash? Solitary sharks
6
7 487 competing for food assess rivals to decide. *Proc. R. Soc. B*, 285(1875), 20180006.
8
9 488 <https://doi.org/10.1098/rspb.2018.0006>
10
11
12 489 Brierley, A.S. & Kingsford, M.J. (2009). Impacts of Climate Change on Marine Organisms
13
14 490 and Ecosystems. Impacts of Climate Change on Marine Organisms and Ecosystems.
15
16 491 *Current Biology*, 19(14), R602–R614. <https://doi.org/10.1016/j.cub.2009.05.046>
17
18
19 492 Caliński, T. & Harabasz, J. (1974). A dendrite method for cluster analysis. A dendrite method
20
21 493 for cluster analysis. *Communications in Statistics*, 3(1), 1–27.
22
23 494 <https://doi.org/10.1080/03610927408827101>
24
25
26 495 Capello, M., Robert, M., Soria, M., Potin, G., Itano, D., Holland, K. et al. (2015). A
27
28 496 methodological framework to estimate the site fidelity of tagged animals using
29
30 497 passive acoustic telemetry. *PLOS ONE*, 10(8), e0134002.
31
32 498 <https://doi.org/10.1371/journal.pone.0134002>
33
34
35 499 Chapman, D.D., Babcock, E.A., Gruber, S.H., Dibattista, J.D., Franks, B.R., Kessel, S.A. et
36
37 500 al. (2009). Long-term natal site-fidelity by immature lemon sharks (*Negaprion*
38
39 501 *brevirostris*) at a subtropical island. *Molecular Ecology*, 18(16), 3500–3507.
40
41 502 <https://doi.org/10.1111/j.1365-294X.2009.04289.x>
42
43
44 503 Chapman, B.K. & McPhee, D. (2016). Global shark attack hotspots: Identifying underlying
45
46 504 factors behind increased unprovoked shark bite incidence. *Ocean & Coastal*
47
48 505 *Management*, 133, 72–84. <https://doi.org/10.1016/j.ocecoaman.2016.09.010>
49
50
51 506 Clua, E., Buray, N., Legendre, P., Mourier, J. & Planes, S. (2010). Behavioural response of
52
53 507 sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism
54
55 508 purposes. *Marine Ecology Progress Series*, 414, 257–266.
56
57 509 <https://doi.org/10.3354/meps08746>
58
59
60

- 1
2
3 510 Clua, E.E. & Linnell, J.D.C. (2019). Individual shark profiling: An innovative and
4
5 511 environmentally responsible approach for selectively managing human fatalities.
6
7 512 *Conservation Letters*, 12(2), e12612. <https://doi.org/10.1111/conl.12612>
8
9
10 513 Csardi, G., & Nepusz, T. (2006). The Igraph software package for complex network research.
11
12 514 *InterJournal 2006, Complex Systems*, 1695.
13
14 515 Curtis, T.H., Bruce, B.D., Cliff, C., Dudley, S.F.J., Klimley, A.P., Kock, A.A. et al. (2012).
16
17 516 Responding to the risk of white shark attack: updated statistics, prevention, control
18
19 517 methods and recommendations. *Global perspectives on the biology and life history of*
20
21 518 *the white shark*. Boca Raton, FL: CRC Press, p. 477–510
22
23
24 519 Daly, R., Smale, M.J., Cowley, P.D. & Froneman, P.W. (2014). Residency patterns and
25
26 520 migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of
27
28 521 Southern Africa. *PLOS ONE*, 9(10), e109357.
29
30 522 <https://doi.org/10.1371/journal.pone.0109357>
31
32
33 523 Dickman, A.J. (2010). Complexities of conflict: the importance of considering social factors
34
35 524 for effectively resolving human–wildlife conflict. *Animal Conservation*, 13(5), 458–
36
37 525 466. <https://doi.org/10.1111/j.1469-1795.2010.00368.x>
38
39
40 526 Dixon, P. (2003). VEGAN, a package of R functions for community ecology. *Journal of*
41
42 527 *Vegetation Science*, 14(6), 927–930. <https://doi.org/10.1111/j.1654->
43
44 528 [1103.2003.tb02228.x](https://doi.org/10.1111/j.1654-1103.2003.tb02228.x)
45
46
47 529 Dray, S & Dufour, A-B. (2007). The ade4 Package: Implementing the duality diagram for
48
49 530 ecologists. *Journal of Statistical Software*, 022(i04).
50
51 531 Espinoza, M., Heupel, M.R., Tobin, A.J. & Simpfendorfer, C.A. (2016). Evidence of partial
52
53 532 migration in a large coastal predator: opportunistic foraging and reproduction as key
54
55 533 drivers? *PLOS ONE*, 11(2), e0147608. <https://doi.org/10.1371/journal.pone.0147608>
56
57
58
59
60

- 1
2
3 534 Ferretti, F., Salvador, J., Chapple, T.K., De Leo, G. & Micheli, F. (2015). Reconciling
4
5 535 predator conservation with public safety. *Frontiers in Ecology and the Environment*,
6
7 536 13(8), 412–417. <https://doi.org/10.1890/150109>
8
9
10 537 Gabriel, K.R. (1971). The biplot graphic display of matrices with application to principal
11
12 538 component analysis. *Biometrika*, 58(3), 453–467.
13
14 539 <https://doi.org/10.1093/biomet/58.3.453>
15
16
17 540 Gibbs, L., Fetterplace, L., Rees, M. & Hanich, Q. (2020). Effects and effectiveness of lethal
18
19 541 shark hazard management: The Shark Meshing (Bather Protection) Program, NSW,
20
21 542 Australia. *People and Nature*, 2(1), 189–203. <https://doi.org/10.1002/pan3.10063>
22
23
24 543 Guyomard, D., Lee, K.A., Perry, C., Jaquemet, S. & Cliff, G. (2020). SMART drumlines at
25
26 544 Réunion Island do not attract bull sharks *Carcharhinus leucas* into nearshore waters:
27
28 545 Evidence from acoustic monitoring. *Fisheries Research*, 225, 105480.
29
30 546 <https://doi.org/10.1016/j.fishres.2019.105480>
31
32
33 547 Heupel, M.R., Simpfendorfer, C.A., Espinoza, M., Smoothey, A.F., Tobin, A. & Peddemors,
34
35 548 V. (2015). Conservation challenges of sharks with continental scale migrations.
36
37 549 *Frontiers in Marine Science*, 2. <https://doi.org/10.3389/fmars.2015.00012>
38
39
40 550 Huang, I.B., Keisler, J. & Linkov, I. (2011). Multi-criteria decision analysis in environmental
41
42 551 sciences: Ten years of applications and trends. *Science of The Total Environment*,
43
44 552 409(19), 3578–3594. <https://doi.org/10.1016/j.scitotenv.2011.06.022>
45
46
47 553 Huvneers, C., Simpfendorfer, C.A., Kim, S., Semmens, J.M., Hobday, A.J., Pederson, H. et
48
49 554 al. (2016). The influence of environmental parameters on the performance and
50
51 555 detection range of acoustic receivers. *Methods in Ecology and Evolution*, 7(7), 825–
52
53 556 835. <https://doi.org/10.1111/2041-210X.12520>
54
55
56
57
58
59
60

- 1
2
3 557 Jacoby, D.M.P., Busawon, D.S., & Sims, D.W. (2010). Sex and social networking: the
4
5 558 influence of male presence on social structure of female shark groups. *Behavioral*
6
7 559 *Ecology*, 21(4). <https://doi.org/10.1093/beheco/arq061>
8
9
10 560 Jacoby, D.M.P., Brooks, E.J., Croft, D.P. & Sims, D.W. (2012a). Developing a deeper
11
12 561 understanding of animal movements and spatial dynamics through novel application
13
14 562 of network analyses. *Methods in Ecology and Evolution*, 3(3), 574–583.
15
16 563 <https://doi.org/10.1111/j.2041-210X.2012.00187.x>
17
18
19 564 Jacoby, D.M.P., Croft, D.P. & Sims, D.W. (2012b). Social behaviour in sharks and rays:
20
21 565 analysis, patterns and implications for conservation. *Fish and Fisheries*, 13(4), 399–
22
23 566 417. <https://doi.org/10.1111/j.1467-2979.2011.00436.x>
24
25
26 567 Jacoby, D.M.P. & Freeman, R. (2016). Emerging network-based tools in movement ecology.
27
28 568 *Trends in Ecology & Evolution*, 31(4), 301–314.
29
30 569 <https://doi.org/10.1016/j.tree.2016.01.011>
31
32
33 570 Lagabrielle, E., Allibert, A., Kiszka, J.J., Loiseau, N., Kilfoil, J.P. & Lemahieu, A. (2018).
34
35 571 Environmental and anthropogenic factors affecting the increasing occurrence of
36
37 572 shark-human interactions around a fast-developing Indian Ocean island. *Scientific*
38
39 573 *Reports*, 8(1), 3676. <https://doi.org/10.1038/s41598-018-21553-0>
40
41
42 574 Lea, J.S.E., Humphries, N.E., Clarke, C.R. & Sims, D.W. (2015). To Madagascar and back:
43
44 575 long-distance, return migration across open ocean by a pregnant female bull shark
45
46 576 *Carcharhinus leucas*. *Journal of Fish Biology*, 87(6), 1313–1321.
47
48 577 <https://doi.org/10.1111/jfb.12805>
49
50
51 578 Lédée, E.J.I., Heupel, M.R., Tobin, A.J., Knip, D.M. & Simpfendorfer, C.A. (2015). A
52
53 579 comparison between traditional kernel-based methods and network analysis: an
54
55 580 example from two nearshore shark species. *Animal Behaviour*, 103, 17–28.
56
57 581 <https://doi.org/10.1016/j.anbehav.2015.01.039>
58
59
60

- 1
2
3 582 Lee, K.A., Smoothey, A.F., Harcourt, R.G., Roughan, M., Butcher, P.A. & Peddemors, V.M.
4
5 583 (2019). Environmental drivers of abundance and residency of a large migratory shark,
6
7 584 *Carcharhinus leucas*, inshore of a dynamic western boundary current. *Marine*
8
9 585 *Ecology Progress Series*, 622, 121–137. <https://doi.org/10.3354/meps13052>
- 10
11
12 586 Lemahieu, A., Blaison, A., Crochelet, E., Bertrand, G., Pennober, G. & Soria, M. (2017).
13
14 587 Human-shark interactions: The case study of Reunion island in the south-west Indian
15
16 588 Ocean. *Ocean & Coastal Management*, 136, 73–82.
17
18 589 <https://doi.org/10.1016/j.ocecoaman.2016.11.020>
- 19
20
21 590 Matich, P., Heithaus, M.R. & Layman, C.A. (2011). Contrasting patterns of individual
22
23 591 specialization and trophic coupling in two marine apex predators. *Journal of Animal*
24
25 592 *Ecology*, 80(1), 294–305. <https://doi.org/10.1111/j.1365-2656.2010.01753.x>
- 26
27
28 593 Matich, P. & Heithaus, M.R. (2015). Individual variation in ontogenetic niche shifts in
29
30 594 habitat use and movement patterns of a large estuarine predator (*Carcharhinus*
31
32 595 *leucas*). *Oecologia*, 178(2), 347–359. <https://doi.org/10.1007/s00442-015-3253-2>
- 33
34
35 596 Matich, P., Kiszka, J.J., Heithaus, M.R., Le Bourg, B. & Mourier, J. (2019). Inter-individual
36
37 597 differences in ontogenetic trophic shifts among three marine predators. *Oecologia*,
38
39 598 189(3), 621–636. <https://doi.org/10.1007/s00442-019-04357-5>
- 40
41
42 599 McPhee, D. (2014). Unprovoked shark bites: Are they becoming more prevalent? *Coastal*
43
44 600 *Management*, 42(5), 478–492. <https://doi.org/10.1080/08920753.2014.942046>
- 45
46
47 601 McPhee, D. P., Blount, C., Smith, M. P. L. & Peddemors, V. M. (2021). A comparison of
48
49 602 alternative systems to catch and kill for mitigating unprovoked shark bite on bathers
50
51 603 or surfers at ocean beaches. *Ocean & Coastal Management*, 201, 105492.
52
53 604 <https://doi.org/10.1016/j.ocecoaman.2020.105492>
- 54
55
56 605 Meyer, C.G., Anderson, J.M., Coffey, D.M., Hutchinson, M.R., Royer, M.A. & Holland,
57
58 606 K.N. (2018). Habitat geography around Hawaii’s oceanic islands influences tiger
59
60

- 1
2
3 607 shark (*Galeocerdo cuvier*) spatial behaviour and shark bite risk at ocean recreation
4
5 608 sites. *Scientific Reports*, 8(1), 4945. <https://doi.org/10.1038/s41598-018-23006-0>
6
7
8 609 Midway, S.R., Wagner, T. & Burgess, G.H. (2019). Trends in global shark attacks. *PLOS*
9
10 610 *ONE*, 14(2), e0211049. <https://doi.org/10.1371/journal.pone.0211049>
11
12 611 Mourier, J., Vercelloni, J. & Planes, S. (2012). Evidence of social communities in a spatially
13
14 612 structured network of a free-ranging shark species. *Animal Behaviour*, 83(2), 389–
15
16 613 401. <https://doi.org/10.1016/j.anbehav.2011.11.008>
17
18
19 614 Mourier, J., Lédée, E.J.I., Guttridge, T.L. & Jacoby, D.M.P. (2018). Network analysis and
20
21 615 theory in shark ecology - methods and applications. *Shark Research: Emerging*
22
23 616 *Technologies and Application for the Study of Shark Biology*. CRC Press, pp. 337–
24
25 617 356
26
27
28 618 Muter, B.A., Gore, M.L., Gledhill, K.S., Lamont, C. & Huveneers, C. (2013). Australian and
29
30 619 U.S. news media portrayal of sharks and their conservation. *Conservation Biology*,
31
32 620 27(1), 187–196. <https://doi.org/10.1111/j.1523-1739.2012.01952.x>
33
34
35 621 Neff, C. (2012). Australian beach safety and the politics of shark attacks. *Coastal*
36
37 622 *Management*, 40(1), 88–106. <https://doi.org/10.1080/08920753.2011.639867>
38
39
40 623 Niella, Y., Wiefels, A., Almeida, U., Jaquemet, S., Lagabrielle, E., Harcourt, R. et al. (2021).
41
42 624 Dynamics of marine predators off an oceanic island and implications for management
43
44 625 of a preventative shark fishing program. *Marine Biology*, 168(4), 1-18.
45
46 626 <https://doi.org/10.1007/s00227-021-03852-9>
47
48
49 627 Papastamatiou, Y.P., Bodey, T.W., Friedlander, A.M., Lowe, C.G., Bradley, D., Weng, K. et
50
51 628 al. (2018). Spatial separation without territoriality in shark communities. *Oikos*,
52
53 629 127(6), 767–779. <https://doi.org/10.1111/oik.04289>
54
55
56
57
58
59
60

- 1
2
3 630 Pirog, A., Magalon, H., Poirout, T. & Jaquemet, S. (2019). Reproductive biology, multiple
4
5 631 paternity and polyandry of the bull shark *Carcharhinus leucas*. *Journal of Fish*
6
7 632 *Biology*, 95(5), 1195–1206. <https://doi.org/10.1111/jfb.14118>
8
9
10 633 Pooley, S., Barua, M., Beinart, W., Dickman, A., Holmes, G., Lorimer, J. et al. (2017). An
11
12 634 interdisciplinary review of current and future approaches to improving human–
13
14 635 predator relations. *Conservation Biology*, 31(3), 513–523.
15
16 636 <https://doi.org/10.1111/cobi.12859>
17
18
19 637 Roff, G., Brown, C. J., Priest, M. A. & Mumby, P. J. (2018). Decline of coastal apex shark
20
21 638 populations over the past half century. *Communications biology*, 1(1), 1-11.
22
23 639 <https://doi.org/10.1038/s42003-018-0233-1>
24
25
26 640 Schilds, A., Mourier, J., Huveneers, C., Nazimi, L., Fox, A. & Leu, S.T. (2019). Evidence for
27
28 641 non-random co-occurrences in a white shark aggregation. *Behavioral Ecology and*
29
30 642 *Sociobiology*, 73(10), 138. <https://doi.org/10.1007/s00265-019-2745-1>
31
32
33 643 Shabtay, A., Lagabriele, E., Plot, V., Potin, G. & Guyomard, D. (2020). Marine spatial
34
35 644 planning provides a comprehensive framework for building evidence-based shark risk
36
37 645 management policies with sea-users. *Environmental Science & Policy*, 111, 18–26.
38
39 646 <https://doi.org/10.1016/j.envsci.2020.05.014>
40
41
42 647 Soria, M., Heithaus, M.R., Blaison, A., Crochelet, E., Forget, F. & Chabanet, P. (2019).
43
44 648 Residency and spatial distribution of bull sharks *Carcharhinus leucas* in and around
45
46 649 Reunion Island marine protected area. *Marine Ecology Progress Series*, 630, 101–
47
48 650 113. <https://doi.org/10.3354/meps13139>
49
50
51 651 Soria, M., Tremblay, Y., Blaison, A., Forget, F., Crochelet, E. & Dagorn, L. (2021). Large-
52
53 652 scale movements and site fidelity of bull sharks (*Carcharhinus leucas*) at Reunion
54
55 653 Island (Indian ocean). *African Journal of Marine Science*, 43, 135-140.
56
57 654 <https://doi.org/10.2989/1814232X.2021.1883736>
58
59
60

- 1
2
3 655 Speed, C.W., Field, I.C., Meekan, M.G. & Bradshaw, C.J.A. (2010). Complexities of coastal
4
5 656 shark movements and their implications for management. *Marine Ecology Progress*
6
7 657 *Series*, 408, 275–293. <https://doi.org/10.3354/meps08581>
8
9
10 658 Taglioni, F., Guiltat, S., Teurlai, M., Delsaut, M. & Payet, D. (2019). A spatial and
11
12 659 environmental analysis of shark attacks on Reunion Island (1980–2017). *Marine*
13
14 660 *Policy*, 101, 51–62. <https://doi.org/10.1016/j.marpol.2018.12.010>
15
16
17 661 Tillett, B.J., Meekan, M.G., Field, I.C., Thorburn, D.C. & Ovenden, J.R. (2012). Evidence for
18
19 662 reproductive philopatry in the bull shark *Carcharhinus leucas*. *Journal of Fish*
20
21 663 *Biology*, 80(6), 2140–2158. <https://doi.org/10.1111/j.1095-8649.2012.03228.x>
22
23
24 664 Trystram, C., Rogers, K.M., Soria, M. & Jaquemet, S. (2016). Feeding patterns of two
25
26 665 sympatric shark predators in coastal ecosystems of an oceanic island. *Canadian*
27
28 666 *Journal of Fisheries and Aquatic Sciences*, 74(2), 216–227.
29
30 667 <https://doi.org/10.1139/cjfas-2016-0105>
31
32
33 668 Werbrouck, A., Van Grevelinghe, G., Landron, F., Charlier, P., Loire, C. & Gauthier, C.
34
35 669 (2014). Expertise médico-légale des victimes d’attaques et de morsures de requins à la
36
37 670 Réunion. *La Revue de Médecine Légale*, 5(3), 110–121.
38
39 671 <https://doi.org/10.1016/j.medleg.2014.07.003>
40
41
42 672 Werry, J.M. & Clua, E. (2013). Sex-based spatial segregation of adult bull sharks,
43
44 673 *Carcharhinus leucas*, in the New Caledonian great lagoon. *Aquatic Living Resources*,
45
46 674 26(4), 281–288. <https://doi.org/10.1051/alr/2013063>
47
48
49 675 Wetherbee, B., Lowe, C. & Crow, G. (1994). A review of shark control in Hawaii with
50
51 676 recommendations for future research. *Pacific Science*, 4, 95–115.
52
53
54 677 Yazdi, M. M. (2013): Package “topsis.” Available at: [https://cran.r-](https://cran.r-project.org/package=topsis)
55
56 678 [project.org/package=topsis](https://cran.r-project.org/package=topsis) [Assessed: 15 January 2021]
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Figure legends

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8 682 Figure 1: Study area along the west coast of Reunion Island and positions of acoustic
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10 683 receivers (circles : ●). Names of main areas are indicated. Blue lines on land represents main
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12 684 rivers while blue lines over the sea indicate bathymetry (5 m isobaths from 0 to 50 m, 10 m
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14 685 from 50 to 100 m, 50 m from 100 to 1000 m and 100 m after 1000 m).
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19 687 Figure 2: Biplots of Principal Component Analyses applied to matrices of individual monthly
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21 688 values of receivers for the three node-level metrics. Receivers are represented by arrows
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23 689 (middle panel) and sharks in a given month by dots (left panel). A three-dimensional standard
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25 690 RGB (red, green, blue) colour space was used (red = high values in axis 1; green = high
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27 691 values in axis 2 and blue = low values in axis 1). to assign colour to each observation (shark
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29 692 in a given month) and variable (receiver), according to its position in the projected principal
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31 693 components coordinates and scores. The same colours are used in the maps showing the
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33 694 spatial distribution of receivers (right panel). Sex of individuals are represented by a symbol
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35 695 which is proportional to shark's total length.
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42 697 Figure 3: Centres of activity of sharks. Maps of average node-based metrics for each receiver:
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44 698 (a) closeness, (b) strength and (c) CRT. (d) Monthly TOPSIS scores for each receiver which
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46 699 integrates the three node-based metrics mentioned above (a high TOPSIS score means that
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48 700 the receiver has a high value for all three metrics)
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52 702 Figure 4: Cluster analyses conducted on the overall centrality score (TOPSIS score) in
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54 703 individual monthly movement networks: (a) Spatial distribution of mean activity score of
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56 704 each receiver for each cluster; (b) Sex composition and mean total length of each cluster; (c)
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3 705 Monthly cluster membership for each shark ordered according to total length. Males are
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5 706 indicated in italic and females in bold.

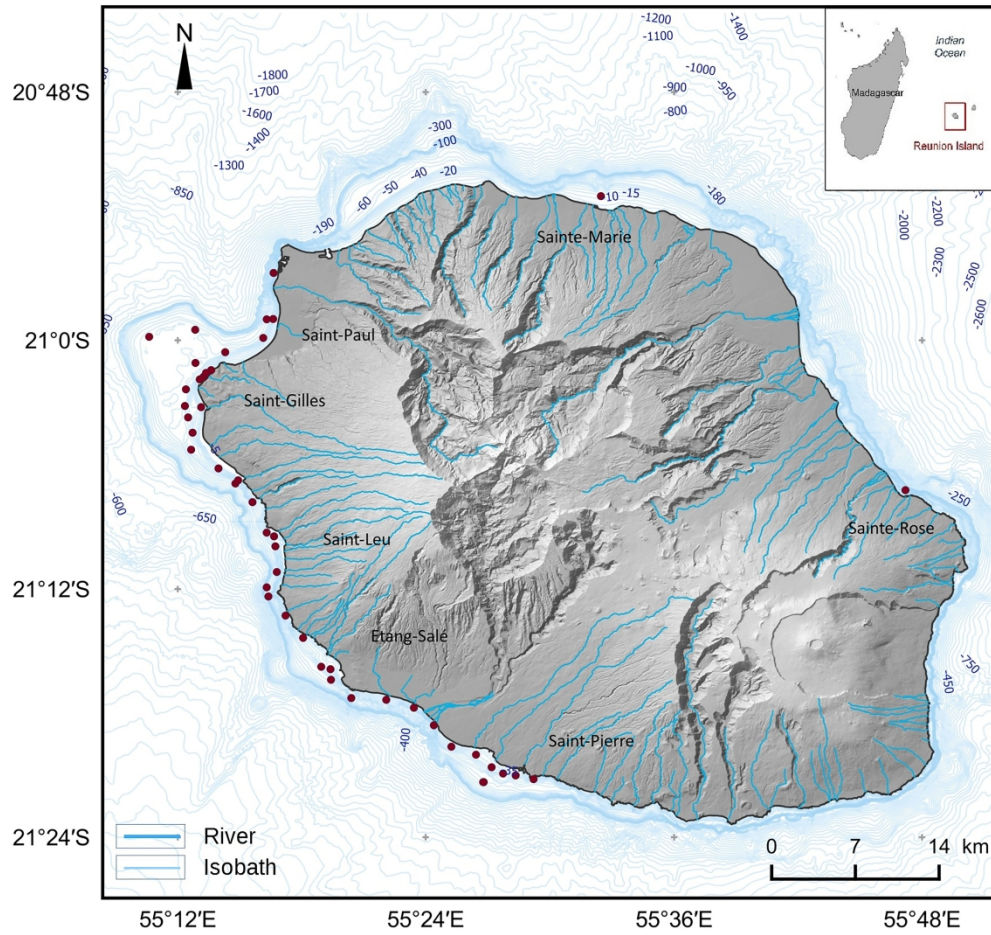
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10 708 Figure 5: Spatiotemporal occurrence of shark bites in Reunion Island between 2011 and
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12 709 2020. Colours represent the site where shark bites occurred. Data source: [http://www.info-](http://www.info-requin.re/le-centre-securite-requin-r70.html)
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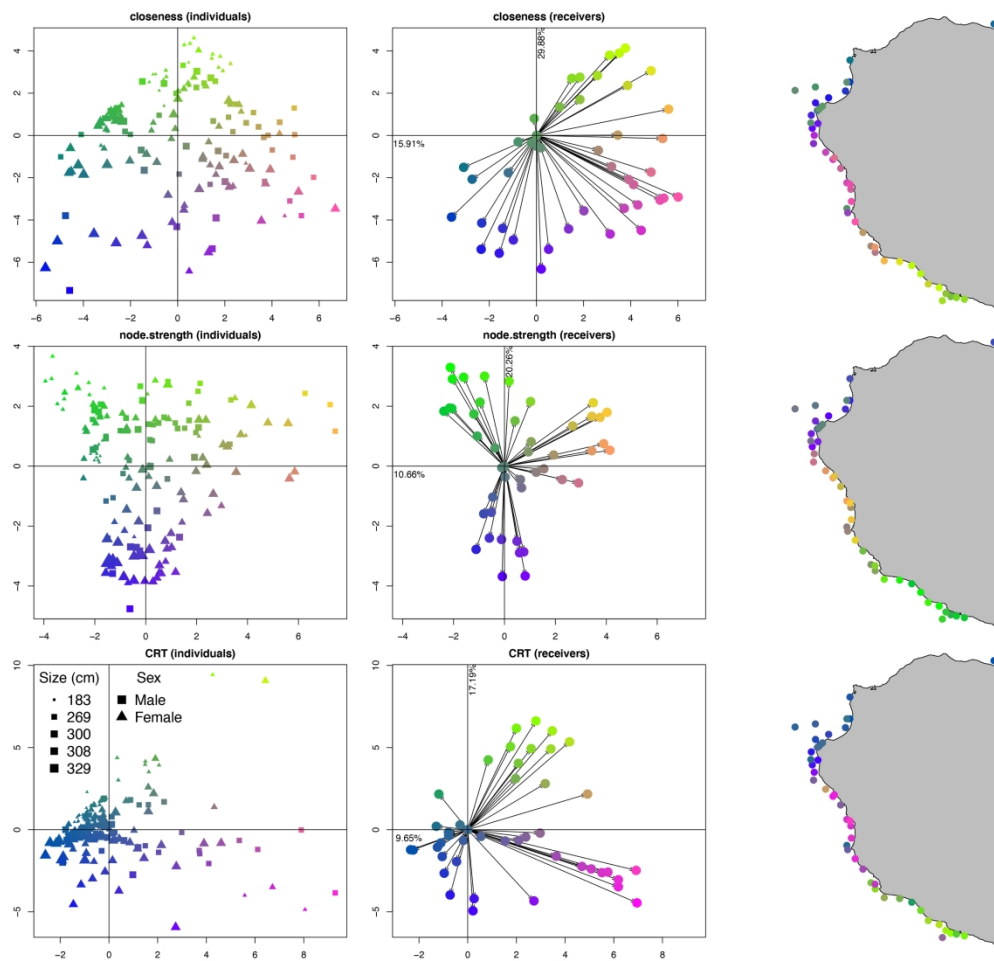
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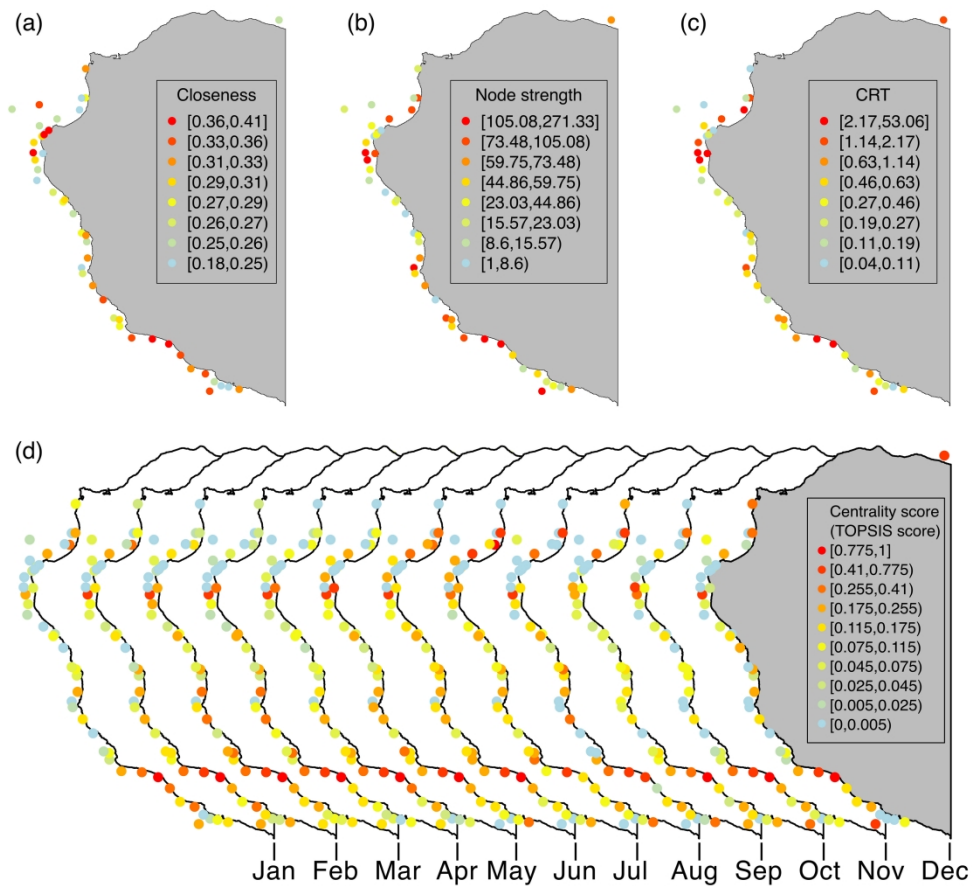


Study area along the west coast of Reunion Island and positions of acoustic receivers (circles : □). Names of main areas are indicated. Blue lines on land represents main rivers while blue lines over the sea indicate bathymetry (5 m isobaths from 0 to 50 m, 10 m from 50 to 100 m, 50 m from 100 to 1000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

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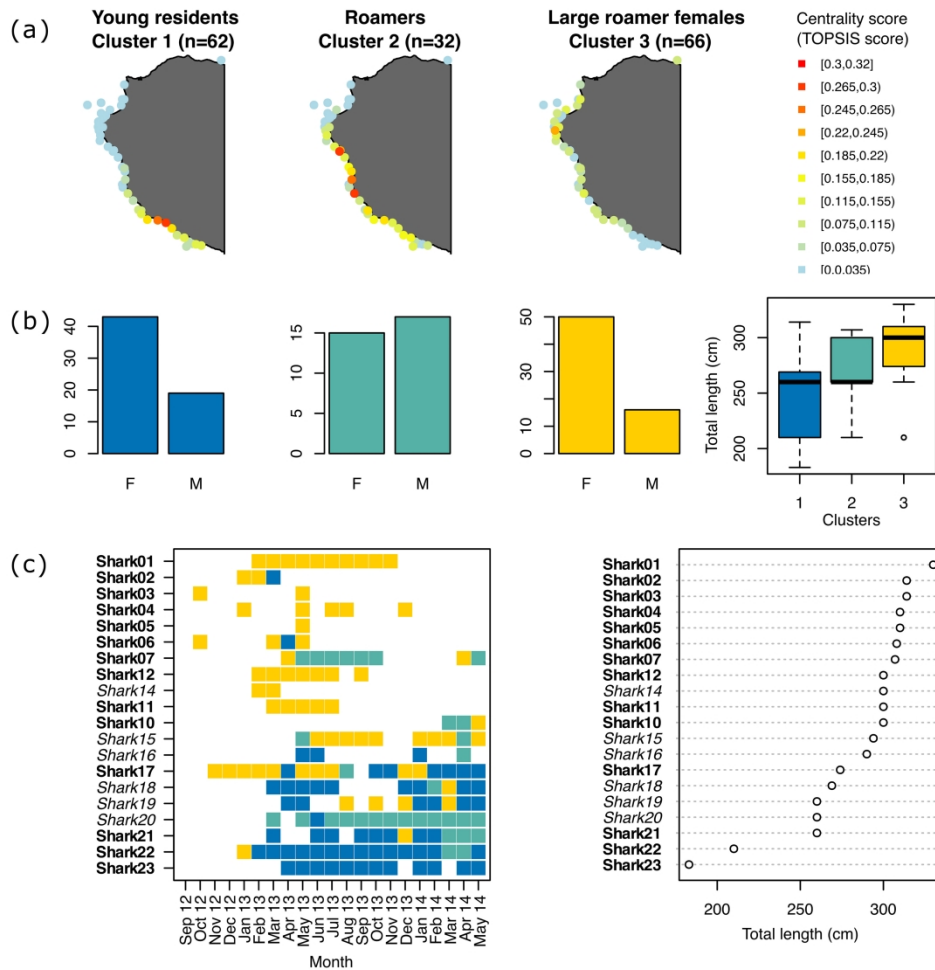


Biplots of Principal Component Analyses applied to matrices of individual monthly values of receivers for the three node-level metrics. Receivers are represented by arrows (middle panel) and sharks in a given month by dots (left panel). A three-dimensional standard RGB (red, green, blue) colour space 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)

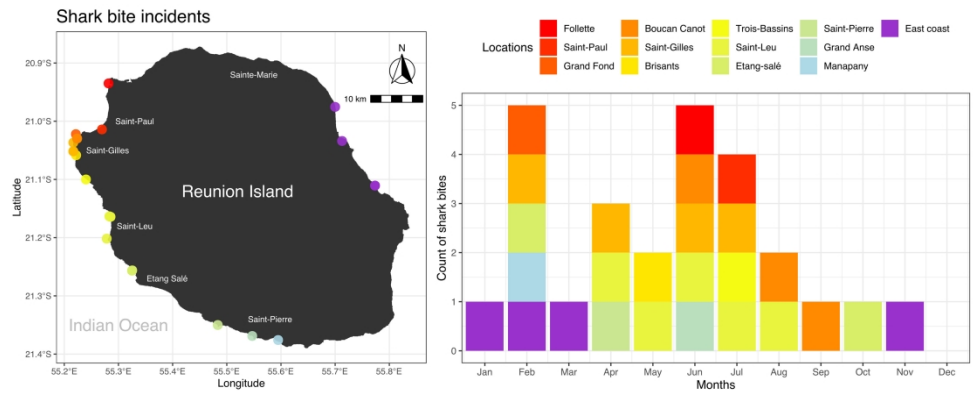
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Cluster analyses conducted on the overall centrality score (TOPSIS score) in individual monthly movement networks: (a) Spatial distribution of mean activity score of each receiver for each cluster; (b) Sex composition and mean total length of each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