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1 **Human-induced shifts in habitat use and behaviour of a marine**  
2 **predator: the effects of bait provisioning in the blacktip reef shark**

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23 Headings: Provisioning modifies habitat use of sharks

24

25 **Abstract**

26 While the negative effects of consumptive pressures on marine predators are well established, the  
27 effects of increasing non-consumptive activities wildlife tourism are still understudied. As such, the  
28 long-term effects of the provision of bait on shark behaviour are still unclear. Here, we assessed the  
29 effects of provisioning using a Control-Impact design on the spatial use and level of residency of the  
30 blacktip reef shark (*Carcharhinus melanopterus*) over a two-year period. We used effect sizes to  
31 model the differences relative changes in residency between provisioning and non-provisioning sites.  
32 Sharks showed a high degree of residency and significant changes in their habitat use which persisted  
33 overnight while the activity ceased. We suggest that provisioning activities can affect species with  
34 high level of residency such as the blacktip reef shark. Further research is needed to better understand  
35 how these changes behavioural modifications can alter the fitness of this species. It is important to  
36 adapt shark provisioning activities to limit the induced changes in habitat.

37

38 **Keywords:** wildlife provisioning; shark; coral reef; habitat use; sexual segregation

## 39 Introduction

40 Wildlife watching is often presented as a win-win scenario for both people and nature as it can  
41 provide new sources of jobs and income to local economies and can enhance environmental awareness  
42 (Orams, 2002; Knight, 2009). However, the economic viability of commercial wildlife watching  
43 depends on the predictable and constant sightings of wild animals (Whittaker, 1997), which can be  
44 enhanced by attracting them with food. These practices have rapidly developed worldwide in different  
45 terrestrial and marine ecosystems but have also raised concerns regarding possible negative  
46 consequences to the targeted animals and their ecosystems. A number of studies have now  
47 demonstrated potential alterations of behavioural and physiological parameters in terrestrial  
48 vertebrates, cetaceans and fish, including changes in overall health and increased aggression toward  
49 humans (see Brena *et al.*, 2015; Gallagher *et al.*, 2015; Orams, 2002 for reviews). These can act as  
50 additional stressors on populations of megafauna that are frequently already endangered or threatened.

51 For sharks, one of the two taxonomic groups most concerned by marine wildlife watching  
52 together with cetaceans (Christiansen *et al.*, 2016), the use of bait is common practice as these species  
53 are often sparse or elusive (Brena *et al.*, 2015; Gallagher *et al.*, 2015). An increasing number of studies  
54 over the last decade show that provisioning can have a number of impacts on individuals, including on  
55 their abundance and residency (Eric Clua *et al.*, 2010; Juerg M. Brunnschweiler, Abrantes, & Barnett,  
56 2014; Kiszka *et al.*, 2016), movement patterns and activity space (Fitzpatrick *et al.*, 2011; Huveneers  
57 *et al.*, 2013) or physiology (Barnett *et al.*, 2016; Huveneers *et al.*, 2018). In their review, Brena *et al.*  
58 (2015) further highlighted that these most commonly described alterations of individual behaviour can  
59 have cascading effects at the group and community scales (Drew & McKeon, 2019; Meyer *et al.*,  
60 2020).

61 Alteration of the size of individual home range is one of the changes most commonly observed  
62 after provisioning sharks or rays in the same location for long periods of time (several years)  
63 (Huveneers *et al.*, 2013). Sharks and rays tend to increase their time residency and decrease their  
64 activity space following provisioning activities, at least for subsets of the populations (Clua *et al.*,  
65 2010; Fitzpatrick *et al.*, 2011; Corcoran *et al.*, 2013; Kiszka *et al.*, 2016). These modifications in space

66 utilization question whether they promote substantive trade-offs in activity budgets and in turn alter  
67 energy budget (Barnett *et al.*, 2016), individual fitness and overall the structuring role these top  
68 predators play in their ecosystem. While most studies have shown that provisioning unlikely affects  
69 the long-term and overall population behaviour of large species of sharks (Hammerschlag *et al.*, 2012;  
70 Meyer *et al.*, 2019), less evidence is available on smaller species (< 3 m total length) that are  
71 potentially more vulnerable to such activities due to restricted movements (Maljković & Côté, 2011;  
72 Kiszka *et al.*, 2016).

73 Here, using a Control-Impact design, we investigated potential changes induced by provisioning  
74 in behaviour at the individual and population levels of a common reef shark species. In particular,  
75 using acoustic telemetry, we assessed how shark provisioning activities restricted to specific locations  
76 for the last two decades can affect habitat use of both females and males for a period of more than two  
77 years.

78

## 79 Materials and methods

### 80 *Study site and species*

81 The study was conducted at Moorea Island (17°30'S; 149°51'W), French Polynesia. The  
82 tourism industry has grown rapidly in Moorea (Clua *et al.*, 2011; Leenhardt *et al.*, 2017), and has  
83 offered activities including interaction with sharks and rays in the lagoon since the 1980's (Gaspar,  
84 Chateau, & Galzin, 2008; Kiszka *et al.*, 2016) as well as shark-feeding dives on the outer reef of the  
85 North coast (Clua *et al.*, 2010). In 2004, Moorea authorities implemented a Management Plan for the  
86 Marine Environment (*Plan de Gestion de l'Espace Maritime*) that restricted these shark provisioning  
87 activities to two sites on the outer reef in the North (Fig. 1) which primarily sought to attract sicklefin  
88 lemon sharks (*Negaprion acutidens*) and which banned shark provisioning in the lagoon but  
89 authorized ray-feeding (*Himantura fai*) that also ended up attracting large numbers of blacktip reef  
90 sharks (*C. melanopterus*)(site A2 in Fig. 1; Kiszka *et al.*, 2016). Despite local regulations, another  
91 former provisioning site is also used, but on a more sporadic basis (site A1 in Fig. 1). Provisioning  
92 location A2 is used during the day by both professional operators who can bring up to 50 tourists per

93 boat and individual users who feed pink whiplays and blacktip reef sharks with fish discards and  
94 frozen squid in less than 1.5 m depth on sandy banks. Provisioning has been present along the entire  
95 northern coast of Moorea since the 1980's and here we considered it as representative of an area  
96 potentially impacted by provisioning.

97 The blacktip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard, 1824), the target species  
98 for the artificial feeding, is one of the most abundant and a common shark species in the coral reefs of  
99 the Western Indo-Pacific (Vignaud *et al.*, 2014), inhabiting shallow reefs and sand-flats of both atolls  
100 and high islands (Papastamatiou *et al.*, 2009; Speed *et al.*, 2011; Mourier, Mills, & Planes, 2013; Chin  
101 *et al.*, 2016). Blacktip reef sharks demonstrate a high degree of site attachment and individual spatial  
102 overlap (Papastamatiou *et al.*, 2009; Mourier, Vercelloni, & Planes, 2012), with individuals displaying  
103 larger range of movements only during the reproductive period (Mourier & Planes, 2013; Speed *et al.*,  
104 2016). These sharks have limited home ranges and are resident to specific reefs for periods of at least  
105 several years (up to 10 years or more in Moorea; Mourier *et al.*, 2012). Genetic studies demonstrated  
106 low connectivity at global (Vignaud *et al.*, 2014) and even local (Vignaud *et al.*, 2013) scales,  
107 highlighting limited and likely very rare large-scale migrations. Blacktip reef sharks have recently  
108 been found to demonstrate complex social interactions and assortment by sex at the group level  
109 (Mourier, Vercelloni, & Planes, 2012) as well as some patterns of spatial sexual segregation (Mourier,  
110 Mills, & Planes, 2013).

111

#### 112 *Control-Impact design*

113 We used an array of 6 VR2W acoustic receivers (VEMCO Ltd., Halifax, Canada) deployed  
114 from June 2008 to November 2010 to build a Control-Impact design; for each of the three coasts, a  
115 pair of receivers was selected at a pass with one receiver in the lagoon and the other on the fore reef  
116 (Fig. 1). Receivers were anchored to the substratum using cement-filled car tires with a single metal  
117 bar (150 cm tall) through the centre, to which the receiver was attached. This design included two  
118 'Impact' sites on the north coast (i.e., receivers A1 and A2) where provisioning was developed, and  
119 two groups of 'Control' sites where no provisioning was developed (i.e., Control 1 on the west coast  
120 with receivers B1 and B2; and Control 2 on the east coast with receivers C1 and C2) (Fig. 1). This

121 design allowed us to compare the movements of sharks between the lagoon and the outer-reef for sites  
122 affected by provisioning activities and control sites where feeding does not occur. Two controls were  
123 chosen to account for influence of spatial effects in individual variability of movements. Range testing  
124 of the acoustic receiver array was conducted to determine the distance by which most tag emissions  
125 were detected by the receivers. Detection probabilities were found to drop at 400 meters from the  
126 receiver. For each detection, the receiver recorded the time, date and transmitter number. We retrieved  
127 and downloaded receivers every 6 months, from June 2008 to November 2010, in order to back-up the  
128 data, clean them from biofouling and change batteries.

129

### 130 *Sampling and tagging*

131 Blacktip reef sharks were caught from a boat using a fishing rod with barbless hooks at multiple  
132 locations within and outside the lagoon in each area where acoustic receivers were deployed (Fig. 1;  
133 TableS1; Mourier *et al.*, 2013). They were brought alongside the boat where they were inverted and  
134 controlled in tonic immobility. Each individual was sexed and total length (TL) was measured from  
135 the snout tip to the end of the upper caudal lobe. Sharks were then equipped with VEMCO V16-4H  
136 transmitters (68 mm length x 13 mm width; VEMCO, Halifax, Nova Scotia, Canada). These tags  
137 continually transmitted an individual coded pulse, randomly within 40 and 80s intervals, producing a  
138 nominal transmission around 60 s apart at a frequency of 69 kHz, with an expected battery life of more  
139 than 800 days. The tags were externally attached and secured to the dorsal fins. We analysed data from  
140 the 35 blacktip reef sharks equipped with acoustic transmitters, ranging from 102 to 157 cm TL (mean  
141  $\pm$  SD = 132.7  $\pm$  13.0) including 21 males and 14 females (Table S1).

142

### 143 *Data analysis*

144 To determine the amount of connectivity between provisioning sites and control sites and to  
145 confirm independency of “impact” and “control” sites, we inferred individual daily rate of movements  
146 between receivers defined as the number of total movements between each receiver divided by the  
147 total number of days of monitoring. Mean daily movement was used to examine the level of  
148 connectivity between sites and coasts. A connectivity plot was therefore constructed based on average

149 daily movements between paired receivers indicating the magnitude of incoming and outgoing  
150 movements at receivers from the different coasts (Heupel *et al.*, 2015). The connectivity map was  
151 constructed using R package "circlize" package (Gu *et al.*, 2014) in R v.3.3.0 (R Development Core  
152 Team, 2019).

153 We then assessed the degree of residency of sharks by calculating the proportion of hours each  
154 shark spent within the detection range of each receiver. For this, the number of monitoring days was  
155 inferred for each shark (i.e., the number of days a shark spent at liberty from tagging date to last  
156 recorded detection, with both extreme dates excluded). The degree of residency was calculated for  
157 each individual shark where diurnal and nocturnal periods were separated for each day at each  
158 receiver. Daily sunrise and sunset hours were used to determine the number of hours of diurnal and  
159 nocturnal periods for each day (Source - U.S. Naval Observatory:  
160 <http://aa.usno.navy.mil/data/index.php>).

161 We then used this measure of residency as the response variable in our Control-Impact analysis.  
162 For this, the residency of sharks from impacted sites represented by a receiver on the ocean side and  
163 one on the inside of the lagoon (A1 and A2, respectively; Fig. 1) on the north coast was compared  
164 with the residency of sharks from inside and outside the lagoon at two sets of control sites on the west  
165 and east coasts (Control 1: B1 on the ocean side and B2 in the lagoon; Control 2: C1 in the lagoon and  
166 C2 on the ocean side; Fig. 1).

167 We used effect sizes to model the differences between impacted and control sites. This approach  
168 has proven to be powerful in Control-Impact frameworks (see Claudet *et al.*, 2010, 2008 as examples).  
169 As we were interested in relative changes in residency between provisioning and non-provisioning  
170 sites, we used  $R_{ijk}$  log-ratios as effect size (Hedges, Gurevitch, & Curtis, 1999), calculated as follows:

171 
$$R_{ijk} = \ln\left(\frac{\bar{X}_{I,ijk}}{\bar{X}_{C,ijk}}\right)$$

172 where  $\bar{X}_{I,ijk}$  and  $\bar{X}_{C,ijk}$  are the mean shark residency indices in habitat  $i$  (i.e., lagoon or ocean), sex  $j$   
173 (i.e., male or female) and diel phase  $k$  (i.e., day or night), in impact ( $I$ ) or control ( $C$ ) sites,  
174 respectively.

175 The variance  $v_{ijk}$  associated to each effect size was calculated as follows;



176 
$$v_{ijk} = \frac{sd_{I,ijk}^2}{n_{I,ijk}\bar{X}_{I,ijk}} + \frac{sd_{C,ijk}^2}{n_{C,ijk}\bar{X}_{C,ijk}}$$

177 where  $sd_{I,ijk}$  and  $sd_{C,ijk}$ , and  $n_{I,ijk}$  and  $n_{C,ijk}$  are the standard deviations and sample sizes (i.e.,  
178 number of sharks detected by the receivers in habitat  $i$ , of sex  $j$ , during diel phase  $k$ ), associated to  
179  $\bar{X}_{I,ijk}$  and  $\bar{X}_{C,ijk}$ , respectively.

180 We then weighted the effect sizes in our analyses by the inverse of their variance, as follows:

181 
$$w_{ijk} = 1/v_{ijk}$$

182 Weighted analyses increase the precision of the combined estimates and increase the power of  
183 tests (Gurevitch & Hedges, 1999; Osenberg *et al.*, 1999).

184 For each moderator of interest (i.e., habitat, sex and diurnal phase), we calculated weighted averaged  
185 effect sizes. All analyses were done using R v.3.3.0 (R Development Core Team, 2019).

186

## 187 Results

188 The maximum hourly residency, corresponding to the proportion of hours present at the receiver  
189 where the individual had the highest detection rate, ranged from 0.05 to 83.45% of hours for a single  
190 receiver, with a mean of 15.73 (Table S1). Inter-coast connectivity (i.e., from one side of the island to  
191 the other) was low compared to intra-coast connectivity (i.e., from lagoon to open ocean) (Fig. 2) as  
192 shown by the rate of movements between receivers (maximum of 0.015 movements per day). There  
193 was no connection between the east and north coasts and only limited North-West and West-East  
194 connections (31 recorded N-W movements and only 1 W-E movement).

195 When considering both habitats together (lagoon or open ocean), time of the day (day or night),  
196 and sex (male and female), on average, there was no significant effect of provisioning on mean  
197 residency (i.e., the proportion of hour spent at a site) ( $R = -0.05 \pm 0.44$ , 95% CI). However, there was  
198 some heterogeneity and effect of provisioning varied by habitat, time of the day, or sex.

199 On provisioning sites, both male and female sharks were disproportionately more resident on  
200 the fore reef than in the lagoon, when compared to control sites. There were significant 5 to 13-fold  
201 increases in residency in the fore reef, in comparison to control sites, not only during the day ( $R = 2.32$

202  $\pm 1.78$ , 95% CI for females;  $R = 2.29 \pm 1.04$ , 95% CI for males; Fig. 3) but also at night ( $R = 2.62 \pm$   
203  $2.42$ , 95% CI for females;  $R = 1.60 \pm 1.10$ , 95% CI for males; Fig. 3).

204 Impact of provisioning varied between day and night. For females, loss of lagoon use in  
205 provisioning sites, when compared to control sites, was greater at night ( $R = -4.04 \pm 2.12$ , 95% CI;  
206 Fig. 3) than during the day ( $R = -2.73 \pm 1.90$ , 95% CI; Fig. 3). A decrease in lagoon use by males at  
207 provisioning sites followed a similar pattern during the night ( $R = -2.79 \pm 1.04$ , 95% CI; Fig. 3) but no  
208 differences in habitat use was observed between provisioning and control sites during the day ( $R =$   
209  $0.34 \pm 0.98$ , 95% CI; Fig. 3).

210

## 211 Discussion

212 Here, we showed that blacktip reef sharks have high levels of attachment to small areas and low  
213 extent of movements at an island scale, and that this pattern of habitat use can be significantly  
214 modified by provisioning.

215 Effects of provisioning were materialized by a shift in habitat use and spatio-temporal dynamics  
216 of the monitored sharks. Overall, shark residency was higher during the day at provisioning sites than  
217 at control sites, but was lower at night. This is not surprising as provisioning is believed to increase  
218 residency of sharks when the activity is conducted (Brena *et al.*, 2015). More importantly, we show  
219 that in those provisioning sites, sharks' habitat use was modified, with higher residency on the fore  
220 reef than in the lagoon, when compared to control sites. [The presence of three main provisioning sites](#)  
221 [may have increase rate of movement between them and therefore between fore reef and lagoon \(Figure](#)  
222 [2\). Even if one of the provisioning sites is located in the lagoon, the other site outside the lagoon may](#)  
223 [have attracted to the fore reef at least a portion of the population that would have remained in the](#)  
224 [lagoon under natural conditions.](#)

225 Changes in habitat use induced by provisioning were different for males and females. Females  
226 lost some residency time in the lagoon at provisioning sites when compared to control sites, not only  
227 during the day (when provisioning occurs) but also at night. These patterns likely reflect a shift in  
228 habitat use via a translocation of their activity space from lagoon to fore reef habitats when under

229 provisioning influence. While previous studies on the effects of provisioning on sharks have shown an  
230 increased residency at provisioning sites (Clua *et al.*, 2010), reduced activity space (Huveneers *et al.*,  
231 2013) or change in depth niche during provisioning (Fitzpatrick *et al.*, 2011), no studies have shown  
232 evidence of a clear long-term shift in habitat use in any shark species. The presence of three official  
233 provisioning sites within a ~10km portion of reef both in the lagoon and fore reef in Moorea may  
234 partially explain the increase in time spent by sharks on the fore reef and a decrease in the level of  
235 residency in the lagoon. In fact, sharks likely increased movements and exchanges between these sites,  
236 simultaneously dividing their spatial use between different habitats.

237         On the north coast of Moorea, the effects of provisioning on habitat use may induce even larger  
238 impacts on natural population dynamics and social structure. Catch-data previously revealed that sex  
239 ratio was in favor of males in the fore reef and in favor of females in the lagoon at the island scale.  
240 While the use of the lagoon by males is only weakly affected by provisioning, female habitat  
241 preferences shifted from lagoon to fore reef in the north as a consequence of the presence of  
242 provisioning sites on the fore reef. These changes may cause patterns of competition between the  
243 sexes with a potential increase in sexual harassment by males as previously documented (Jacoby,  
244 Busawon, & Sims, 2010), or may affect natural patterns of spatial sexual segregation found at the  
245 island scale (Mourier, Mills, & Planes, 2013). In addition, data from northern locations did not show  
246 any significant differences in sex-ratios. On the north coast, this lack of spatial sexual segregation was  
247 confirmed at the group scale with mixed-sex communities, although there were some assortment  
248 preferences for same sex at the level of associations (Mourier, Vercelloni, & Planes, 2012). Increase in  
249 use of the fore reef by females may favor a stronger pattern of spatial overlap between the sexes on the  
250 north coast.

251         A high level of male harassment can drive spatial segregation of the sexes. In many species of  
252 elasmobranch, sexual dimorphism in body size or differential activity budget between the sexes may  
253 be sufficient to cause very different behavioural strategies and movement patterns (Jacoby, Croft, &  
254 Sims, 2012). These differences may select for male sharks to invest more time in pursuit of mates than  
255 female sharks that may themselves allocate a higher percentage of time in search of suitable  
256 environmental conditions to aid gestation (Speed *et al.*, 2012). As a consequence of mating, females

257 often sustain bite marks and serious abrasions to the body and pectoral fins (Chin, Mourier, &  
258 Rummer, 2015) which may in turn favour sexual segregation. Females need to avoid energetically  
259 expensive and potentially damaging multiple mating events, a mechanism which leads to sexual  
260 segregation. More research is needed to understand whether this change in sexual segregation patterns  
261 due to provisioning negatively affects reproduction in blacktip reef shark, and in turn fitness and  
262 population dynamics.

263 Female mobility seems to be increased by provisioning as demonstrated by the observed  
264 decrease in residency. Despite increased shark densities during provisioning (Mourier, Vercelloni, &  
265 Planes, 2012; Kiszka *et al.*, 2016), female sharks appear to spend shorter amount of time at  
266 provisioning sites in the lagoon, potentially moving across the seascape at higher rates. Previous  
267 findings have demonstrated that provisioning can modify activity rate and mobility of sharks  
268 (Fitzpatrick *et al.*, 2011; Barnett *et al.*, 2016; Huvneers *et al.*, 2018) and can enhance competitive  
269 exclusion with increase intra- and interspecific densities (Juerg M. Brunnschweiler, Abrantes, &  
270 Barnett, 2014), but these changes tend to persist at night even if the provisioning activity has ended.  
271 This is surprising and difficult to explain, although it can have important consequences for female  
272 sharks. In fact, female reef sharks use shallow warm waters of the lagoons to optimize their gestation  
273 (Speed *et al.*, 2012). If they are reducing the amount of time spent in the lagoon or increasing their  
274 activity, it can affect the time and energy allocated to gestation and could in turn have some  
275 implications for the fitness and survival of their pups, especially for a species with a relatively high  
276 turnover (1-year reproductive cycle; 10-11 year gestation period; Mourier & Planes, 2013). Moreover,  
277 food from provisioning activities can induce trophic shifts in fed individuals and, in certain cases, can  
278 impact the health and the condition of an animal's body (Semeniuk, Speers-Roesch, & Rothley, 2007;  
279 Semeniuk *et al.*, 2009; Maljković & Côté, 2011; J. M. Brunnschweiler, Payne, & Barnett, 2018). Yet,  
280 no negative effects have been reported so far on the reproduction of females using provisioning areas  
281 (Mourier & Planes, 2013), although further detailed investigations are needed.

282 Sharks from provisioning sites may allocate less time and energy in search of food and food  
283 should therefore be easier to acquire than under natural conditions. While food quantity delivered at  
284 the provisioning site in the lagoon is non-negligible (Gaspar, Chateau, & Galzin, 2008), the quantity of

285 food that blacktip reef sharks may acquire at the fore reef provisioning locations may be much lower  
286 as blacktip reef sharks also have to compete for food with larger sharks such as the sicklefin lemon  
287 shark (Clua *et al.*, 2010) and with higher numbers of conspecifics due to increased female's residency.  
288 Nothing is currently known about the quantity of food that sharks may acquire from provisioning  
289 activities and what proportion of their diet it represents. Previous work on bull sharks in Fiji found that  
290 the amount of provisioned food was unlikely a significant contributor to the daily food budget  
291 (Abrantes, Brunnschweiler, & Barnett, 2018), although it can depend on the individual degree of  
292 residency (J. M. Brunnschweiler, Payne, & Barnett, 2018). Still, the observed changes in activity  
293 space may explain observed intraspecific variation in trophic interactions documented in blacktip reef  
294 sharks in Moorea (Matich *et al.*, 2019). Therefore, future research is required to better understand the  
295 influence of provisioning activities on diet, trophic ecology, metabolism and the health of sharks in  
296 Moorea. In particular, it may help us to understand whether food acquired easily from provisioning  
297 can offset the loss of energy allocation for reproduction, specifically in females.

298         The blacktip reef shark is a highly resident shark, like most reef-associated shark species  
299 (Papastamatiou *et al.*, 2010; Barnett *et al.*, 2012; Bond *et al.*, 2012; Mourier *et al.*, 2016). Degree of  
300 residency may be exacerbated in remote, isolated islands such as those of the Pacific due to low  
301 connectivity and low habitat availability in small islands and atolls (Vignaud *et al.*, 2014; Mourier *et*  
302 *al.*, 2016). Sharks can remain within small 'sub-habitats' with very limited movements of individuals  
303 between sub-habitats, possibly as a result of intra-specific competition (Brena *et al.*, 2018;  
304 Papastamatiou *et al.*, 2018). The rare movements from one coast to another mostly occurred during the  
305 mating period, likely representing reproductive migrations (Mourier & Planes, 2013). The  
306 independence between impact and control sites also reinforces the robustness of inferences we made  
307 about the influence of provisioning on the degree of residency. All together, these findings also  
308 suggest that blacktip reef sharks can be highly susceptible to local changes, including provisioning, as  
309 they tend to have restricted movements and hence low abilities to avoid these external pressures.

310         Wildlife tourism, including shark provisioning, has the potential to contribute significantly to  
311 the conservation of animals. However, both tourists and management agencies have the obligation to  
312 carefully consider the potential negative effects on health, fitness and long-term behaviour of targeted

313 species and to ensure a sustainable activity by guaranteeing best practice/least impact tourism. If  
314 mobility and habitat use is modified for one sex (in our case for female sharks), this activity could  
315 have cryptic long-term detrimental impact on the local population, potentially affecting reproduction  
316 and population dynamics of resident, long-living fish like reef sharks. Further research is required to  
317 determine whether the results of the present study represent an isolated case and to what extent they  
318 apply to other localities for blacktip reef sharks and other taxa, as shark and ray provisioning is a  
319 popular activity throughout French Polynesia involving many species. In particular, it will be  
320 important to address provisioning management from an ecosystem perspective (Vignon et al., 2010;  
321 Drew & McKeon, 2019; Meyer et al., 2020) as non-targeted species can also be affected, potentially  
322 leading to cascading effects within the ecosystem.

323

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330

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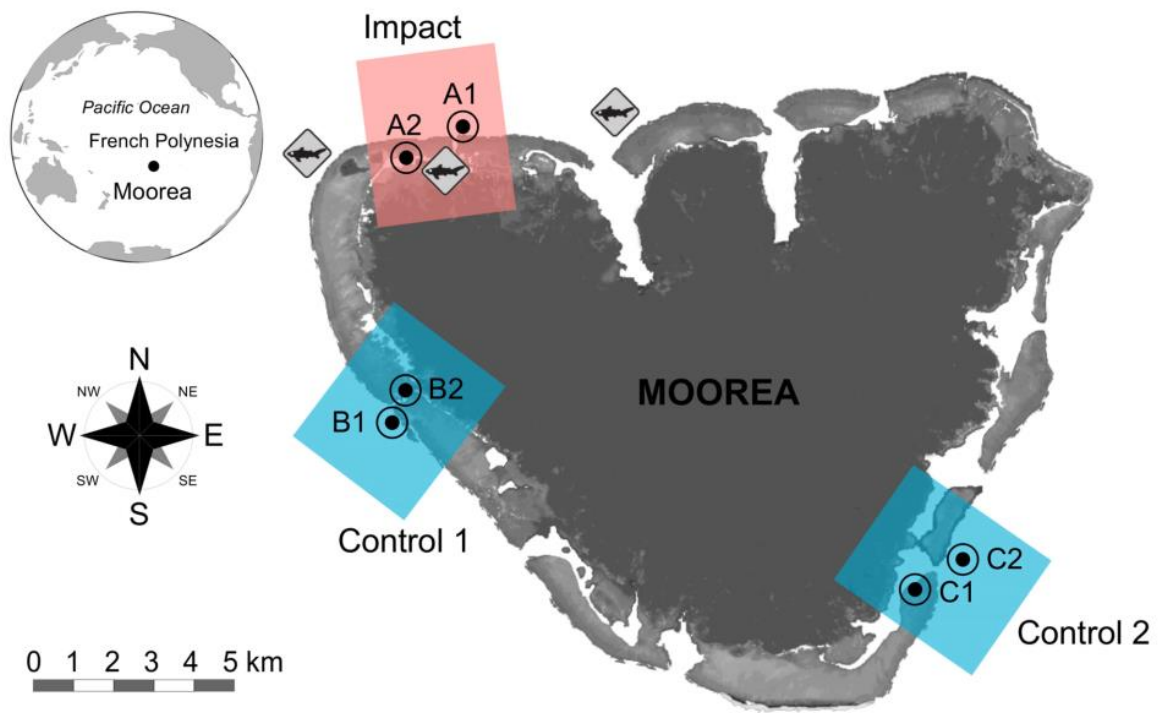
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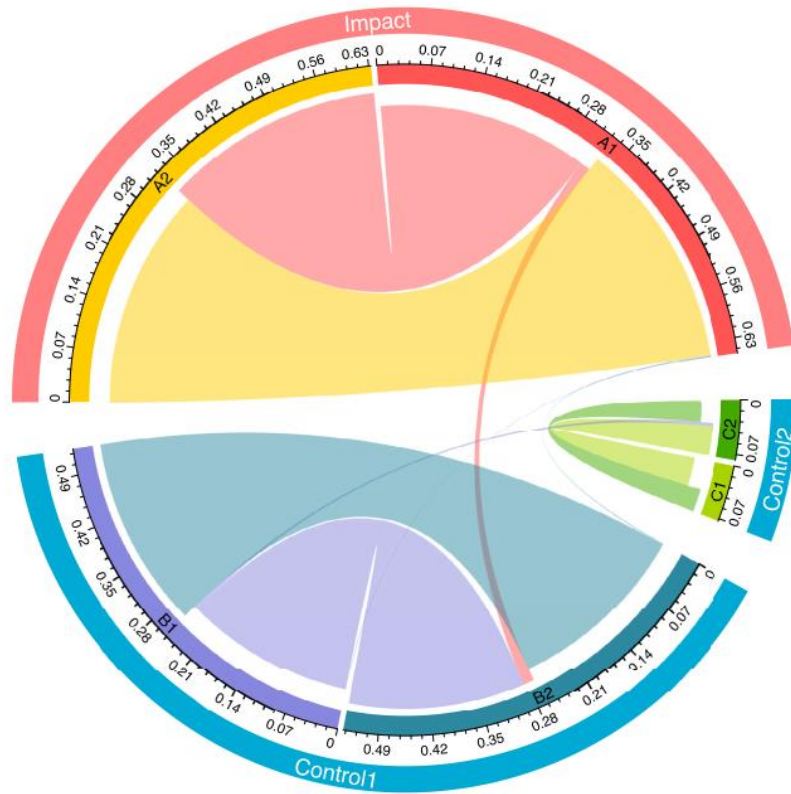


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479 Fig. 1. Map of the study location featuring the Control-Impact design. Receivers are indicated by  
480 circles. Provisioning activities occur on the Northern coast of Moorea at three locations indicated by a  
481 “shark symbol” sign. Red and blue zones indicate the Impact and Control zones used in the analysis,  
482 respectively.

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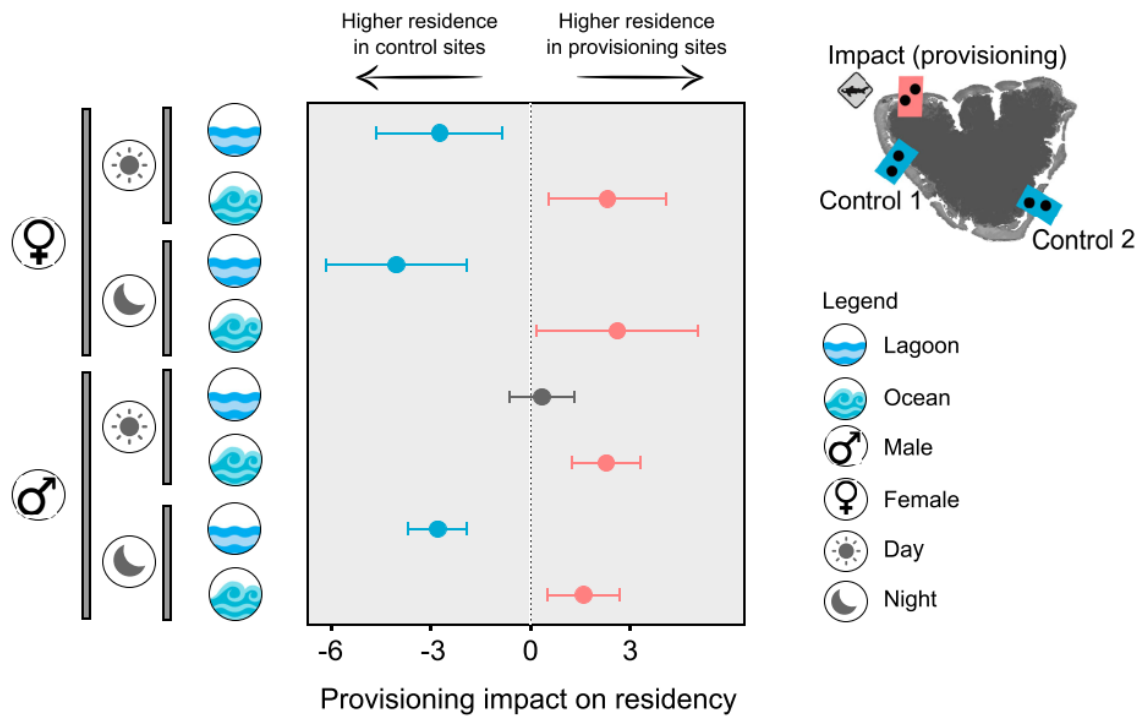


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486 Fig. 2. Connectivity map indicating rate of movement of individual blacktip reef sharks between  
 487 acoustic receiver arrays for each coast. Line thickness is proportional to average daily movements  
 488 between receivers. The Impact and Control sites are indicated by red and blue sections.

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492 Fig. 3. Effects of provisioning on shark residency, split by habitat type, diurnal activity or sex. Effect

493 sizes and their 95% confidence intervals are shown. Statistically significant effects (95 % CI not

494 overlapping 0) are presented in red for positive effects and in blue for negative effects. Non-significant

495 effects (95% CI overlapping 0) are presented in grey.

496