



HAL
open science

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

Johann Mourier, Joachim Claudet, Serge Planes

► **To cite this version:**

Johann Mourier, Joachim Claudet, Serge Planes. Human-induced shifts in habitat use and behaviour of a marine predator: the effects of bait provisioning in the blacktip reef shark. *Animal Conservation*, 2021, 24 (2), pp.230-238. 10.1111/acv.12630 . hal-03208317

HAL Id: hal-03208317

<https://hal.science/hal-03208317>

Submitted on 26 Apr 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Johann Mourier^{1,2,3}, Joachim Claudet^{2,4}, Serge Planes^{1,2}

4

5 ¹ PSL Research University: EPHE-UPVD-CNRS, USR 3278 CRIOBE, 66860 Perpignan, France

6 ² Laboratoire d'Excellence "CORAIL"

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

8 ⁴ National Center for Scientific Research, PSL Research University: EPHE-UPVD-CNRS, USR 3278

9 CRIOBE, Maison des Océans, 195 rue Saint-Jacques 75005 Paris, France

10

11 ORCID:

12 JM, 0000-0001-9019-1717

13 JC, 0000-0001-6295-1061

14 SP, 0000-0002-5689-5371

15

16 Corresponding author:

17 **Johann Mourier**

18 **Email: johann.mourier@gmail.com**

19 Address: MARBEC, Bureau 52 - 1^{er} étage bâtiment principal, Station Ifremer de Sète, Av Jean
20 Monnet, CS 30171 34203 Sète cedex, France

21 Telephone number: +33 672712157

22

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 ± 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 ± 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; Huveneers *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

324 Acknowledgements

325 This study was implemented thanks to the financial support of the Direction à l'Environnement
326 (DIREN) of French Polynesia, the Coordination Unit of the Coral Reef Initiatives for the Pacific
327 (CRISP Program) and Proscience in French Polynesia. We are grateful to the Centre de Recherche
328 Insulaire et Observatoire de l'Environnement (CRIOBE) staff for their technical support, as well as the
329 volunteers and students who assisted in field data collection.

330

331 References

332

- 333 Abrantes, K. G., Brunnschweiler, J. M., & Barnett, A. (2018). You are what you eat: Examining the
334 effects of provisioning tourism on shark diets. *Biol. Conserv.* **224**, 300–308.
- 335 Barnett, A., Abrantes, K. G., Seymour, J., & Fitzpatrick, R. (2012). Residency and Spatial Use by Reef
336 Sharks of an Isolated Seamount and Its Implications for Conservation. *PLOS ONE* **7**, e36574.
- 337 Barnett, A., Payne, N. L., Semmens, J. M., & Fitzpatrick, R. (2016). Ecotourism increases the field
338 metabolic rate of whitetip reef sharks. *Biol. Conserv.* **199**, 132–136.

339 Bond, M. E., Babcock, E. A., Pikitch, E. K., Abercrombie, D. L., Lamb, N. F., & Chapman, D. D. (2012).
340 Reef Sharks Exhibit Site-Fidelity and Higher Relative Abundance in Marine Reserves on the
341 Mesoamerican Barrier Reef. *PLOS ONE* **7**, e32983.

342 Brena, P. F., Mourier, J., Planes, S., & Clua, E. (2015). Shark and ray provisioning: functional insights
343 into behavioral, ecological and physiological responses across multiple scales. *Mar. Ecol.*
344 *Prog. Ser.* **538**, 273–283.

345 Brena, P. F., Mourier, J., Planes, S., & Clua, E. E. (2018). Concede or clash? Solitary sharks competing
346 for food assess rivals to decide. *Proc R Soc B* **285**, 20180006.

347 Brunnschweiler, J. M., Payne, N. L., & Barnett, A. (2018). Hand feeding can periodically fuel a major
348 portion of bull shark energy requirements at a provisioning site in Fiji. *Anim. Conserv.* **21**, 31–
349 35.

350 Brunnschweiler, Juerg M., Abrantes, K. G., & Barnett, A. (2014). Long-Term Changes in Species
351 Composition and Relative Abundances of Sharks at a Provisioning Site. *PLOS ONE* **9**, e86682.

352 Chin, A., Heupel MR, Simpfendorfer CA, & Tobin AJ. (2016). Population organisation in reef sharks:
353 new variations in coastal habitat use by mobile marine predators. *Mar. Ecol. Prog. Ser.* **544**,
354 197–211.

355 Chin, Andrew, Mourier, J., & Rummer, J. L. (2015). Blacktip reef sharks (*Carcharhinus melanopterus*)
356 show high capacity for wound healing and recovery following injury. *Conserv. Physiol.* **3**,
357 cov062.

358 Christiansen, F., McHugh, K. A., Bejder, L., Siegal, E. M., Lusseau, D., McCabe, E. B., Lovewell, G., &
359 Wells, R. S. (2016). Food provisioning increases the risk of injury in a long-lived marine top
360 predator. *R. Soc. Open Sci.* **3**, 160560.

361 Claudet, J., Osenberg, C. W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J. M., Bertocci, I.,
362 Benedetti-Cecchi, L., García-Charton, J.-A., Goñi, R., Borg, J. A., Forcada, A., de Lucia, G. A.,
363 Pérez-Ruzafa, Á., Afonso, P., Brito, A., Guala, I., Diréach, L. L., Sanchez-Jerez, P., Somerfield, P.

364 J., & Planes, S. (2010). Marine reserves: Fish life history and ecological traits matter. *Ecol.*
365 *Appl.* **20**, 830–839.

366 Claudet, Joachim, Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-
367 Ruzafa, Á., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.-M., Dimech, M.,
368 Falcón, J. M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P. J., Stobart, B.,
369 Vandeperre, F., Valle, C., & Planes, S. (2008). Marine reserves: size and age do matter. *Ecol.*
370 *Lett.* **11**, 481–489.

371 Clua, E., Buray, N., Legendre, P., Mourier, J., & Planes, S. (2011). Business partner or simple catch?
372 The economic value of the sicklefin lemon shark in French Polynesia. *Mar. Freshw. Res.* **62**,
373 764.

374 Clua, Eric, Buray, N., Legendre, P., Mourier, J., & Planes, S. (2010). Behavioural response of sicklefin
375 lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Mar.*
376 *Ecol. Prog. Ser.* **414**, 257–266.

377 Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman, D. D., & Harvey, G. M.
378 (2013). Supplemental Feeding for Ecotourism Reverses Diel Activity and Alters Movement
379 Patterns and Spatial Distribution of the Southern Stingray, *Dasyatis americana*. *PLOS ONE* **8**,
380 e59235.

381 Drew, J. A., & McKeon, M. (2019). Shark-based tourism presents opportunities for facultative dietary
382 shift in coral reef fish. *PLOS ONE* **14**, e0221781.

383 Fitzpatrick, R., Abrantes, K. G., Seymour, J., & Barnett, A. (2011). Variation in depth of whitetip reef
384 sharks: does provisioning ecotourism change their behaviour? *Coral Reefs* **30**, 569–577.

385 Gallagher, A. J., Vianna, G. M. S., Papastamatiou, Y. P., Macdonald, C., Guttridge, T. L., &
386 Hammerschlag, N. (2015). Biological effects, conservation potential, and research priorities
387 of shark diving tourism. *Biol. Conserv.* **184**, 365–379.

388 Gaspar, C., Chateau, O., & Galzin, R. (2008). Feeding sites frequentation by the pink whipray
389 Himanturafai in Moorea (French Polynesia) as determined by acoustic telemetry. *Cybium* **32**,
390 153–164.

391 Gu, Z., Gu, L., Eils, R., Schlesner, M., & Brors, B. (2014). circlize implements and enhances circular
392 visualization in R. *Bioinformatics* **30**, 2811–2812.

393 Gurevitch, J., & Hedges, L. V. (1999). Statistical Issues in Ecological Meta-Analyses. *Ecology* **80**, 1142–
394 1149.

395 Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J., & Ault, J. S. (2012). Don't bite the hand that
396 feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator.
397 *Funct. Ecol.* **26**, 567–576.

398 Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The Meta-Analysis of Response Ratios in
399 Experimental Ecology. *Ecology* **80**, 1150–1156.

400 Heupel, M. R., Simpfendorfer, C. A., Espinoza, M., Smoothey, A. F., Tobin, A., & Peddemors, V. (2015).
401 Conservation challenges of sharks with continental scale migrations. *Front. Mar. Sci.* **2**.

402 Huveneers, C., Rogers, P. J., Beckmann, C., Semmens, J. M., Bruce, B. D., & Seuront, L. (2013). The
403 effects of cage-diving activities on the fine-scale swimming behaviour and space use of white
404 sharks. *Mar. Biol.* **160**, 2863–2875.

405 Huveneers, C., Watanabe, Y. Y., Payne, N. L., & Semmens, J. M. (2018). Interacting with wildlife
406 tourism increases activity of white sharks. *Conserv. Physiol.* **6**.

407 Jacoby, D. M. P., Busawon, D. S., & Sims, D. W. (2010). Sex and social networking: the influence of
408 male presence on social structure of female shark groups. *Behav. Ecol.* **21**.

409 Jacoby, D. M. P., Croft, D. P., & Sims, D. W. (2012). Social behaviour in sharks and rays: analysis,
410 patterns and implications for conservation. *Fish Fish.* **13**, 399–417.

411 Kiszka, J. J., Mourier, J., Gastrich, K., & Heithaus, M. R. (2016). Using unmanned aerial vehicles (UAVs)
412 to investigate shark and ray densities in a shallow coral lagoon. *Mar. Ecol. Prog. Ser.* **560**,
413 237–242.

414 Knight, J. (2009). Making Wildlife Viewable: Habituation and Attraction. *Soc. Amp Anim.* **17**, 167–184.

415 Leenhardt, P., Stelzenmüller, V., Pascal, N., Probst, W. N., Aubanel, A., Bambridge, T., Charles, M.,
416 Clua, E., Féral, F., Quinquis, B., Salvat, B., & Claudet, J. (2017). Exploring social-ecological
417 dynamics of a coral reef resource system using participatory modeling and empirical data.
418 *Mar. Policy* **78**, 90–97.

419 Maljković, A., & Côté, I. M. (2011). Effects of tourism-related provisioning on the trophic signatures
420 and movement patterns of an apex predator, the Caribbean reef shark. *Biol. Conserv.* **144**,
421 859–865.

422 Matich, P., Kiszka, J. J., Heithaus, M. R., Le Bourg, B., & Mourier, J. (2019). Inter-individual differences
423 in ontogenetic trophic shifts among three marine predators. *Oecologia* **189**, 621–636.

424 Meyer, L., Pethybridge, H., Beckmann, C., Bruce, B., & Huveneers, C. (2019). The impact of wildlife
425 tourism on the foraging ecology and nutritional condition of an apex predator. *Tour. Manag.*
426 **75**, 206–215.

427 Meyer, L., Whitmarsh, S. K., Nichols, P. D., Reville, A. T., & Huveneers, C. (2020). The effects of wildlife
428 tourism provisioning on non-target species. *Biol. Conserv.* **241**, 108317.

429 Mourier, J., Mills, S. C., & Planes, S. (2013). Population structure, spatial distribution and life-history
430 traits of blacktip reef sharks *Carcharhinus melanopterus*. *J. Fish Biol.* **82**, 979–993.

431 Mourier, Johann, Maynard, J., Parravicini, V., Ballesta, L., Clua, E., Domeier, M. L., & Planes, S. (2016).
432 Extreme Inverted Trophic Pyramid of Reef Sharks Supported by Spawning Groupers. *Curr.*
433 *Biol.* **26**, 2011–2016.

434 Mourier, Johann, & Planes, S. (2013). Direct genetic evidence for reproductive philopatry and
435 associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*)
436 in French Polynesia. *Mol. Ecol.* **22**, 201–214.

437 Mourier, Johann, Vercelloni, J., & Planes, S. (2012). Evidence of social communities in a spatially
438 structured network of a free-ranging shark species. *Anim. Behav.* **83**, 389–401.

439 Orams, M. B. (2002). Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tour.*
440 *Manag.* **23**, 281–293.

441 Osenberg, C. W., Sarnelle, O., Cooper, S. D., & Holt, R. D. (1999). Resolving Ecological Questions
442 Through Meta-Analysis: Goals, Metrics, and Models. *Ecology* **80**, 1105–1117.

443 Papastamatiou, Y. P., Bodey, T. W., Friedlander, A. M., Lowe, C. G., Bradley, D., Weng, K., Priestley, V.,
444 & Caselle, J. E. (2018). Spatial separation without territoriality in shark communities. *Oikos*.

445 Papastamatiou, Y. P., Friedlander, A. M., Caselle, J. E., & Lowe, C. G. (2010). Long-term movement
446 patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra
447 Atoll. *J. Exp. Mar. Biol. Ecol.* **386**, 94–102.

448 Papastamatiou, Y. P., Lowe, C. G., Caselle, J. E., & Friedlander, A. M. (2009). Scale-dependent effects
449 of habitat on movements and path structure of reef sharks at a predator-dominated atoll.
450 *Ecology* **90**, 996–1008.

451 Semeniuk, C. A. D., Bourgeon, S., Smith, S. L., & Rothley, K. D. (2009). Hematological differences
452 between stingrays at tourist and non-visited sites suggest physiological costs of wildlife
453 tourism. *Biol. Conserv.* **142**, 1818–1829.

454 Semeniuk, C. A. D., Speers-Roesch, B., & Rothley, K. D. (2007). Using Fatty-Acid Profile Analysis as an
455 Ecologic Indicator in the Management of Tourist Impacts on Marine Wildlife: A Case of
456 Stingray-Feeding in the Caribbean. *Environ. Manage.* **40**, 665–677.

457 Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., Harcourt, R. G., Stevens, J. D., Babcock, R.
458 C., Pillans, R. D., & Bradshaw, C. J. A. (2016). Reef shark movements relative to a coastal
459 marine protected area. *Reg. Stud. Mar. Sci.* **3**, 58–66.

460 Speed, C. W., Meekan MG, Field IC, McMahon CR, & Bradshaw CJA. (2012). Heat-seeking sharks:
461 support for behavioural thermoregulation in reef sharks. *Mar. Ecol. Prog. Ser.* **463**, 231–244.

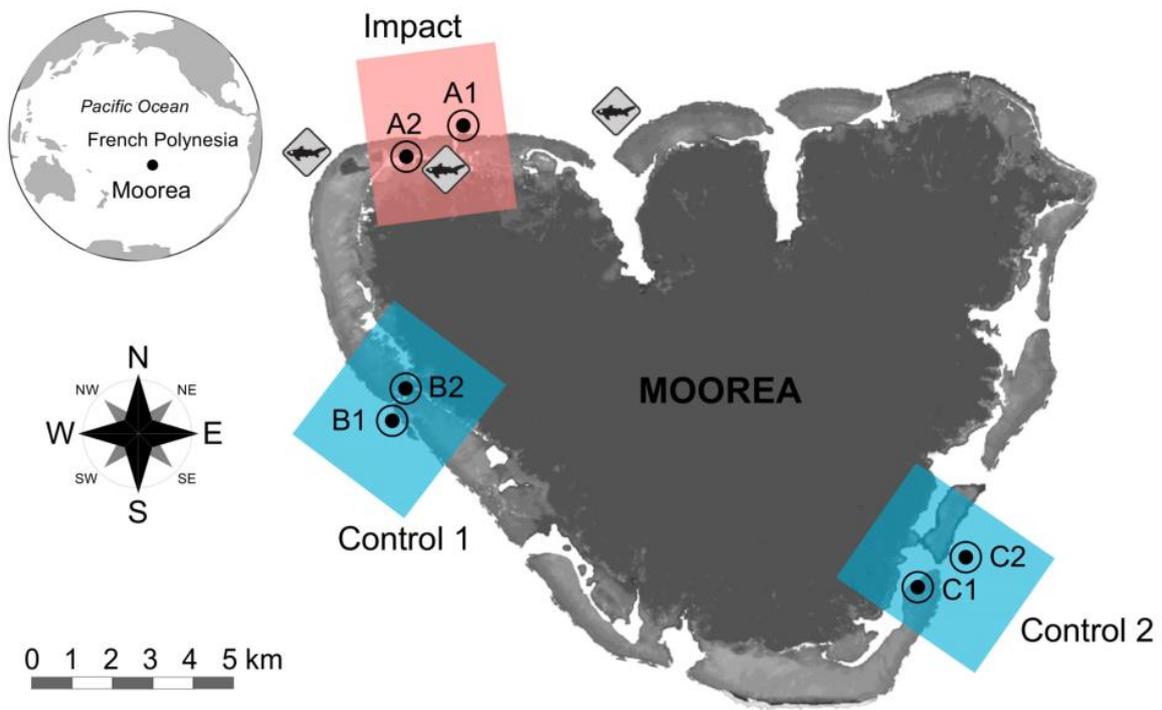
462 Speed, C. W., Meekan MG, Field IC, McMahon CR, Stevens JD, McGregor F, Huveneers C, Berger Y, &
463 Bradshaw CJA. (2011). Spatial and temporal movement patterns of a multi-species coastal
464 reef shark aggregation. *Mar. Ecol. Prog. Ser.* **429**, 261–275.

465 Vignaud, T., Clua, E., Mourier, J., Maynard, J., & Planes, S. (2013). Microsatellite Analyses of Blacktip
466 Reef Sharks (*Carcharhinus melanopterus*) in a Fragmented Environment Show Structured
467 Clusters. *PLOS ONE* **8**, e61067.

468 Vignaud, T. M., Mourier, J., Maynard, J. A., Leblois, R., Spaet, J. L. Y., Clua, E., Neglia, V., & Planes, S.
469 (2014). Blacktip reef sharks, *Carcharhinus melanopterus*, have high genetic structure and
470 varying demographic histories in their Indo-Pacific range. *Mol. Ecol.* **23**, 5193–5207.

471 Vignon, M., Sasal, P., Johnson, R. L., & Galzin, R. (2010). Impact of shark-feeding tourism on
472 surrounding fish populations off Moorea Island (French Polynesia). *Mar. Freshw. Res.* **61**,
473 163–169.

474 Whittaker, D. (1997). Capacity norms on bear viewing platforms. *Hum. Dimens. Wildl.* **2**, 37–49.
475
476

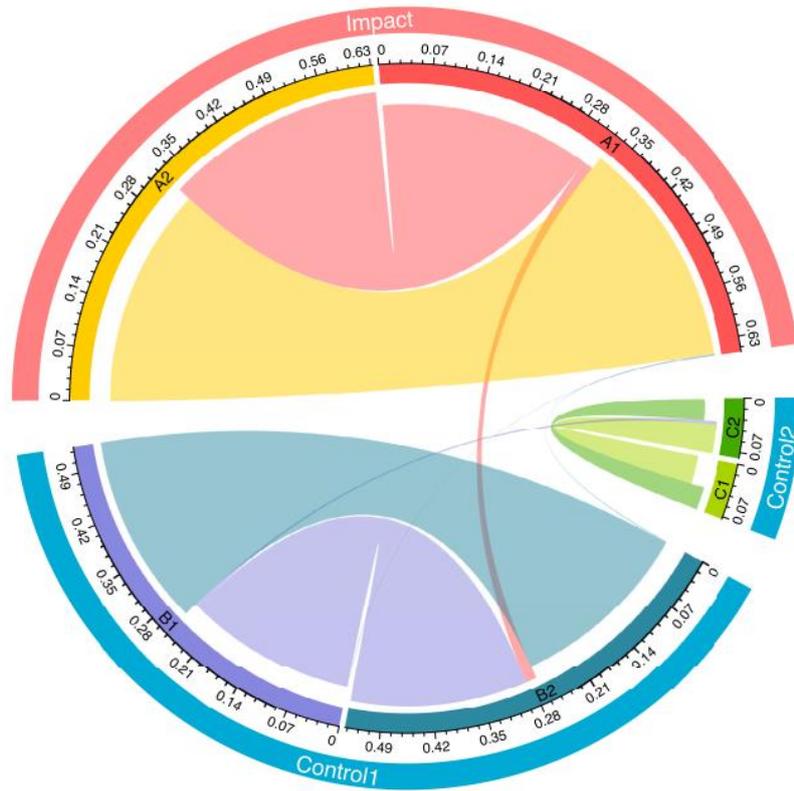


478

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.

483

484

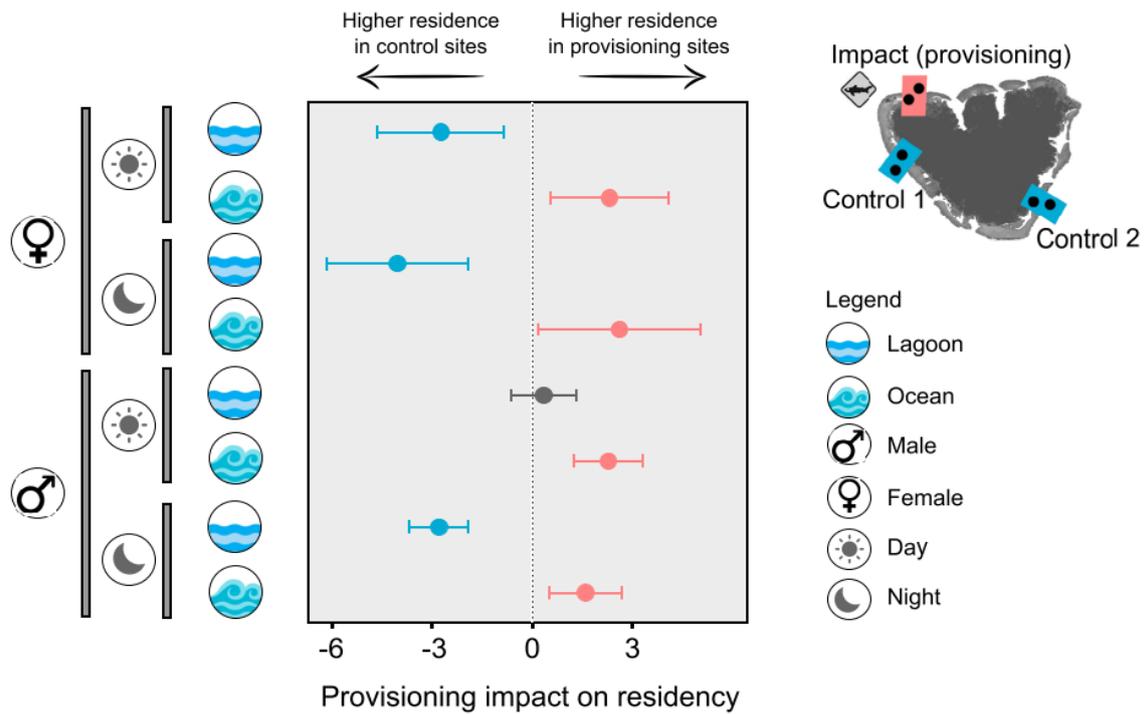


485

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.

489

490



491

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