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

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Abstract

While the negative effects of consumptive pressures on marine predators are well established, the effects of increasing non-consumptive activities such as wildlife tourism are still understudied. As such, the long-term effects of the provision of bait on shark behaviour are still unclear. Here, we assessed the effects of provisioning using a Control-Impact design on the spatial use and level of residency of the blacktip reef shark *Carcharhinus melanopterus* over a 2-year period. We used effect sizes to model the relative changes in residency between provisioning and non-provisioning sites. Sharks showed a high degree of residency and significant changes in their habitat use which persisted overnight while the activity ceased. We suggest that provisioning activities can affect species with high level of residency such as the blacktip reef shark. Further research is needed to better understand how these behavioural modifications can alter the fitness of this species. It is important to adapt shark provisioning activities to limit the induced changes in habitat use.

Introduction

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

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

Alteration of the size of individual home range is one of the changes most commonly observed after provisioning sharks or rays in the same location for long periods of time (several years) (Huveneers *et al*., 2013). Sharks and rays tend to increase their time residency and decrease their activity space following provisioning activities, at least for subsets of the populations (Clua *et al*., 2010; Fitzpatrick *et al*., 2011; Corcoran *et al*., 2013; Kiszka *et al*., 2016). These modifications in space utilization question whether they promote substantive trade-offs in activity budgets and in turn alter energy budget (Barnett *et al*., 2016), individual fitness and overall the structuring role these top predators play in their ecosystem. While most studies have shown that provisioning unlikely affects the long-term and overall population behaviour of large species of sharks (Hammerschlag *et al*., 2012; Meyer *et al*., 2019), less evidence is available on smaller species (<3 m total length) that are potentially more vulnerable to such activities due to restricted movements (Maljković & Côté, 2011; Kiszka *et al*., 2016).

Here, using a Control-Impact design, we investigated potential changes in behaviour induced by provisioning at the individual and population levels of a common reef shark species. In particular, using acoustic telemetry, we assessed how shark provisioning activities restricted to specific locations for the last two decades can affect habitat use of both females and males for a period of more than 2 years.

Materials and methods

Study site and species

The study was conducted at Moorea Island (17°30’S; 149°51’W), French Polynesia. The tourism industry has grown rapidly in Moorea (Clua *et al*., 2011; Leenhardt *et al*., 2017), and has offered activities including interaction with sharks and rays in the lagoon since the 1980’s (Gaspar, Chateau & Galzin, 2008; Kiszka *et al*., 2016) as well as shark-feeding dives on the outer reef of the North coast (Clua *et al*., 2010). There are about 100 000 tourists visiting Moorea every year of whom 80 000 (80%) conduct excursions to the ray provisioning in the lagoon and about 15 000 (15%) dive the fore reef shark provisioning sites. In 2004, Moorea authorities implemented a Management Plan for the Marine Environment (*Plan de Gestion de l’Espace Maritime*) that restricted these shark provisioning activities to two sites on the outer reef in the North (Fig. 1) which primarily sought to attract sicklefin lemon sharks *Negaprion acutidens* and which banned shark provisioning in the lagoon but authorized ray feeding *Himantura fai* that also ended up attracting large numbers of blacktip reef sharks *C. melanopterus* (site A2 in Fig. 1; Kiszka *et al*., 2016). Despite local regulations, another former provisioning site is also used, but on a more sporadic basis (site A1 in Fig. 1). Provisioning location A2 is used during the day by both professional operators who can bring up to 50 tourists per boat and individual users who feed pink whiprays and blacktip reef sharks with fish discards and frozen squid in less than 1.5 m depth on sandy banks. Provisioning has been present along the entire northern coast of Moorea since the 1980’s and here we considered it as representative of an area potentially impacted by provisioning.

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

Control-Impact design

We used an array of 6 VR2W acoustic receivers (VEMCO Ltd., Halifax, Canada) deployed from June 2008 to November 2010 to build a Control-Impact design; for each of the three coasts, a pair of receivers was selected at a pass with one receiver in the lagoon and the other on the fore reef (Fig. 1). Receivers were anchored to the substratum using cement-filled car tires with a single metal bar (150 cm tall) through the centre, to which the receiver was attached. This design included two ‘Impact’ sites on the north coast (i.e. receivers A1 and A2) where provisioning was developed, and two groups of ‘Control’ sites where no provisioning was developed (i.e. Control 1 on the west coast with receivers B1 and B2; and Control 2 on the east coast with receivers C1 and C2) (Fig. 1). This design allowed us to compare the movements of sharks between the lagoon and the outer-reef for sites affected by provisioning activities and control sites where feeding does not occur. Two controls were chosen to account for influence of spatial effects in individual variability of movements. Range testing of the acoustic receiver array was conducted to determine the distance by which most tag emissions were detected by the receivers. Detection probabilities were found to drop at 400 meters from the receiver. For each detection, the receiver recorded the time, date and transmitter number. We retrieved and downloaded receivers every 6 months, from June 2008 to November 2010, in order to back-up the data, clean them from biofouling and change batteries.

Sampling and tagging

Blacktip reef sharks were caught from a boat using a fishing rod with barbless hooks at multiple locations within and outside the lagoon in each area where acoustic receivers were deployed (Fig. 1; Table S1; Mourier *et al*., 2013). They were brought alongside the boat where they were inverted and

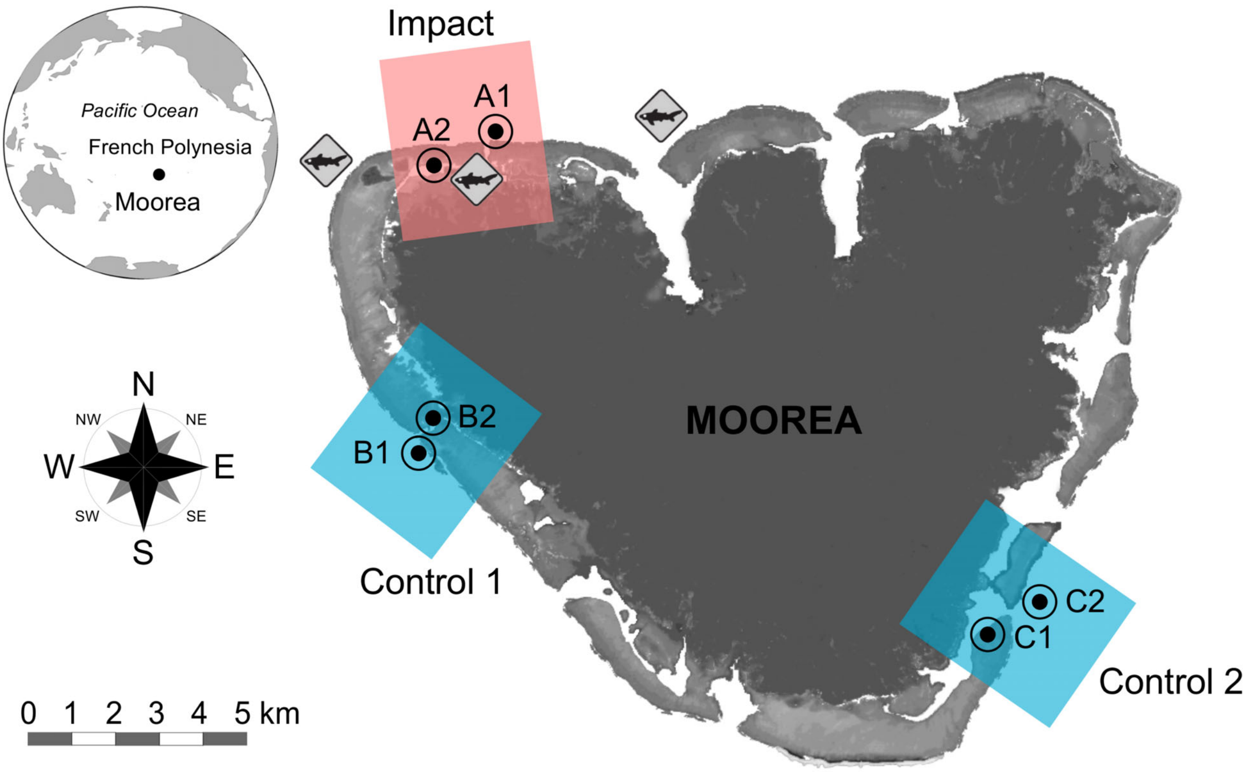

Figure 1 Map of the study location featuring the Control-Impact design. Receivers are indicated by circles. Provisioning activities occur on the Northern coast of Moorea at three locations indicated by a "shark symbol" sign. Red and blue zones indicate the Impact and Control zones used in the analysis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

controlled in tonic immobility. Each individual was sexed and total length (TL) was measured from the snout tip to the end of the upper caudal lobe. Sharks were then equipped with VEMCO V16-4H transmitters (68 mm length × 13 mm width; VEMCO, Halifax, Nova Scotia, Canada). These tags continually transmitted an individual coded pulse, randomly within 40 and 80s intervals, producing a nominal transmission around 60 s apart at a frequency of 69 kHz, with an expected battery life of more than 800 days. The tags were externally attached and secured to the dorsal fins. We analysed data from the 35 blacktip reef sharks equipped with acoustic transmitters, ranging from 102 to 157 cm TL (mean ± SD = 132.7 ± 13.0) including 21 males and 14 females (Table S1).

Data analysis

To determine the amount of connectivity between provisioning sites and control sites and to confirm independency of "impact" and "control" sites, we inferred individual daily rate of movements between receivers defined as the number of total movements between each receiver divided by the total number of days of monitoring. Mean daily movement was used to examine the level of connectivity between sites and coasts. A connectivity plot was therefore constructed based on average daily movements between paired receivers indicating the magnitude of incoming and outgoing movements at receivers from the different coasts (Heupel *et al.*, 2015). The connectivity map was constructed using R package "circlize" package (Gu *et al.*, 2014) in R v.3.3.0 (R Core Team, 2019).

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

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

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

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

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 (i.e. male or female) and diel phase k (i.e. day or night), in impact (I) or control (C) sites respectively.

The variance v_{ijk} associated with each effect size was calculated as follows;

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

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. number of sharks detected by the receivers in habitat i, of sex j, during diel phase k), associated with $\bar{X}_{I,ijk}$ and $\bar{X}_{C,ijk}$, respectively.

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

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

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

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

Results

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

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

On provisioning sites, both male and female sharks were disproportionately more resident on the fore reef than in the lagoon, when compared to control sites. There were significant 5- to 13-fold increases in residency in the fore reef, in comparison to control sites, not only during the day ($R = 2.32 \pm 1.78$, 95% CI for females; $R = 2.29 \pm 1.04$, 95% CI for males; Fig. 3) but also at night ($R = 2.62 \pm 2.42$, 95% CI for females; $R = 1.60 \pm 1.10$, 95% CI for males; Fig. 3).

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

Discussion

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

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

Changes in habitat use induced by provisioning were different for males and females. Females lost some residency time in the lagoon at provisioning sites when compared to control sites, not only during the day (when provisioning occurs) but also at night. These patterns likely reflect a shift in habitat use via a translocation of their activity space from lagoon to fore reef habitats when under provisioning influence. While previous studies on the effects of provisioning on sharks have shown an increased residency at provisioning sites (Clua *et al.*, 2010), reduced activity space (Huveneers *et al.*, 2013) or change in depth niche during provisioning (Fitzpatrick *et al.*, 2011), no studies have shown evidence of a clear long-term shift in habitat use in any shark species.

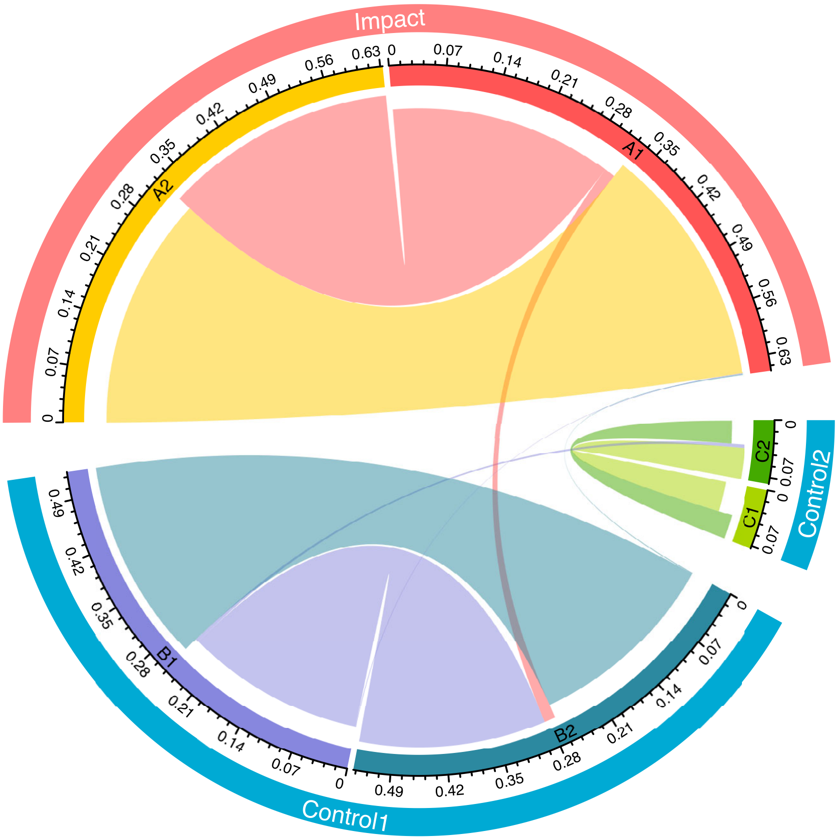

Figure 2 Connectivity map indicating rate of movement of individual blacktip reef sharks between acoustic receiver arrays for each coast. Line thickness is proportional to average daily movements between receivers. The Impact and Control sites are indicated by red and blue sections.

The presence of three official provisioning sites within a ~10 km portion of reef both in the lagoon and fore reef in Moorea may partially explain the increase in time spent by sharks on the fore reef and a decrease in the level of residency in the lagoon. In fact, sharks likely increased movements and exchanges between these sites, simultaneously dividing their spatial use between different habitats.

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

A high level of male harassment can drive spatial segregation of the sexes. In many species of elasmobranch, sexual dimorphism in body size or differential activity budget between the sexes may be sufficient to cause very different behavioural strategies and movement patterns (Jacoby, Croft & Sims, 2012). These differences may select for male sharks to invest more time in pursuit of mates than female sharks that may themselves allocate a higher percentage of time in search of suitable environmental conditions to aid gestation (Speed *et al*., 2012). As a consequence of mating, females often sustain bite marks and serious abrasions to the body and pectoral fins (Chin, Mourier & Rummer, 2015) which may in turn favour sexual segregation. Females need to avoid energetically expensive and potentially damaging multiple mating events, a mechanism which leads to sexual segregation. More research is needed to understand whether this change in sexual segregation patterns due to provisioning negatively affects reproduction in blacktip reef shark, and in turn fitness and population dynamics.

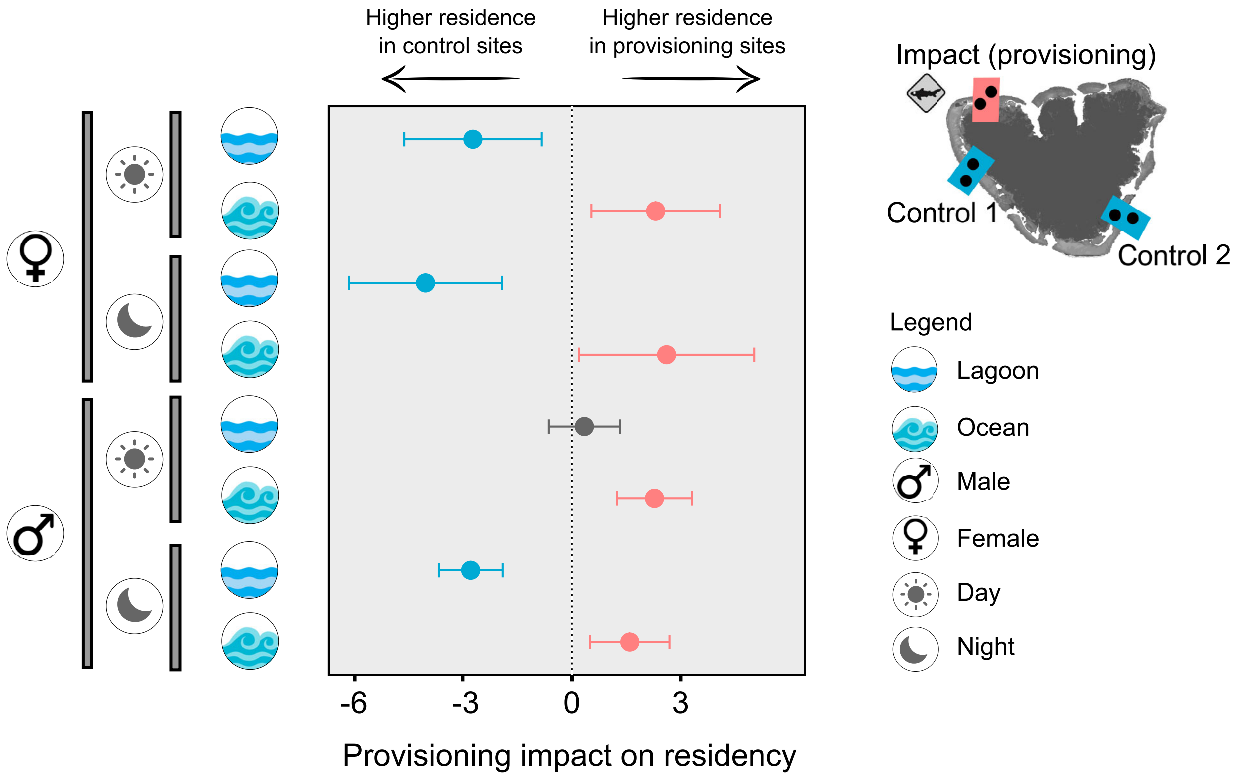

Figure 3 Effects of provisioning on shark residency, split by habitat type, diurnal activity or sex. Effect sizes and their 95% confidence intervals are shown. Statistically significant effects (95 % CI not overlapping 0) are presented in red for positive effects and in blue for negative effects. Non-significant effects (95% CI overlapping 0) are presented in grey.

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

Sharks from provisioning sites may allocate less time and energy in search of food and food should therefore be easier to acquire than under natural conditions. While food quantity delivered at the provisioning site in the lagoon is non-negligible (Gaspar *et al.*, 2008), the quantity of food that blacktip reef sharks may acquire at the fore reef provisioning locations may be much lower as blacktip reef sharks also have to compete for food with larger sharks such as the sicklefin lemon shark (Clua *et al.*, 2010) and with higher numbers of conspecifics due to increased female's residency. Nothing is currently known about the quantity of food that sharks may acquire from provisioning activities and what proportion of their diet it represents. Previous work on bull sharks in Fiji found that the amount of provisioned food was unlikely a significant contributor to the daily food budget (Abrantes, Brunnschweiler & Barnett, 2018), although it can depend on the individual degree of residency (Brunnschweiler *et al.*, 2018). Still, the observed changes in activity space may explain observed intraspecific variation in trophic interactions documented in blacktip reef sharks in Moorea (Matich *et al.*, 2019). Therefore, future research is required to better understand the influence of provisioning activities on diet, trophic ecology, metabolism and the health of sharks in Moorea. In particular, it may help us to understand whether food acquired easily from provisioning can offset the loss of energy allocation for reproduction, specifically in females.

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

Wildlife tourism, including shark provisioning, has the potential to contribute significantly to the conservation of animals. However, both tourists and management agencies have the obligation to carefully consider the potential negative effects on health, fitness and long-term behaviour of targeted species and to ensure a sustainable activity by guaranteeing best practice/least impact tourism. If mobility and habitat use is modified for one sex (in our case for female sharks), this activity could have cryptic long-term detrimental impact on the local population, potentially affecting reproduction and population dynamics of resident, long-living fish like reef sharks. Further research is required to determine whether the results of the present study represent an isolated case and to what extend they apply to other localities for blacktip reef sharks and other taxa, as shark and ray provisioning is a popular activity throughout French Polynesia involving many species. In particular, it will be important to address provisioning management from an ecosystem perspective (Vignon *et al*., 2010; Drew & McKeon, 2019; Meyer *et al*., 2020) as non-targeted species can also be affected, potentially leading to cascading effects within the ecosystem.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Information for individual tagged sharks including ID, tagging location, sex and total length (TL). For each individual and each receiver, respective residency indices (= proportion of hours spent at a receiver) are provided with a color proportional to the degree of residency for improved clarity.