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Effects of a COVID-19 lockdown-induced pause and resumption of artificial provisioning on blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*) in French Polynesia (East-Pacific)

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Abstract

The tourism activities linked to artificial provisioning of blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*) on a specific site in French Polynesia were suddenly and completely stopped due to a COVID-19 lockdown that lasted 6 weeks from March 20 until April 30, 2020. Using both drone footage and underwater counting, we were able to track the abundance of those two species before, during, and after reopening and thus investigate the impact of provisioning on wild shark populations. The absence of any stimulus during this long period resulted in almost total desertion of the site by the elasmobranchs. However, 1 day prior to reopening, some individuals of both species positively reacted to the single acoustic stimulus of an engine boat, showing the resilience of conditioning, and some elasmobranchs reacted to acoustic and olfactive stimuli linked to the provisioning practice from the first day after reopening. During the first 2 weeks after reopening, the abundance of both species remained at reduced levels comparable to those observed between 2008 and 2010 for sharks; i.e., around 9 animals in the presence of local tourists. Pre-lockdown abundance levels, reaching approximatively 15 individuals for sharks and 10 for rays, were considered restored 1 and 2 months after reopening for blacktip reef sharks and pink whiprays, respectively. These findings improve our capacity to better understand the potential effects of artificial provisioning tourism on the abundance of elasmobranchs by showing that conditioning is resilient for several weeks, suggesting that intermittent interruption of elasmobranchs feeding would not really help to decrease its impact on animal welfare.

KEYWORDS
anthropause, conditioned behavior, feeding, memory retention, reconditioning delay

1 | INTRODUCTION

Tourism based on elasmobranchs, whereby participants seek contact with sharks and rays in their natural environment, is a fast-growing activity (Clua et al., 2011; Gallagher & Hammerschlag, 2011; Zimmerhackel et al., 2019). To maximize the chances of encounters or to aggregate animals at the same location, many tour operators use provisioning, a practice that includes simple attraction by olfactory stimulus (chumming) and active feeding of elasmobranchs (see review by Gallagher et al., 2015). Shark and ray tourism, attracting more than 500,000 participants expending around USD 314 million per year globally, has clear economic benefits and may lead to greater willingness to conserve these animals by governments and the general public (Cisneros-Montemayor et al., 2013; Clua et al., 2011; Vianna et al., 2012; Zimmerhackel et al., 2018). Accordingly, it may help to meet the urgent need for measures to preserve shark and ray populations, many of which have declined at a worldwide scale and, in some cases, become functionally extinct (Dulvy et al., 2014; Macneil et al., 2020). This conservation application is particularly important because many elasmobranchs are considered keystone species (Stevens et al., 2000).

The provisioning of sharks and rays also raises concerns regarding the potential ecological effects on the animals. Indeed, previous studies highlighted some negative impacts such as modification of the composition of elasmobranch communities (Brunnschweiler et al., 2014; Meyer et al., 2009), reduced mobility or habitat shifts (Bruce & Bradford, 2013; Clua et al., 2010; Corcoran et al., 2013; Huveneers et al., 2013; Mourier et al., 2021), altered activity patterns (Barnett et al., 2016; Bruce & Bradford, 2013; Corcoran et al., 2013), the transmission of ectodermal parasites (Semeniuk et al., 2009; Semeniuk & Rothley, 2008), alteration of physiological characteristics (Semeniuk et al., 2009), and elevated intra- and interspecific competition (Brunnschweiler et al., 2014; Clua et al., 2010; Newsome et al., 2004; Semeniuk & Rothley, 2008). However, other studies did not show any significant negative impacts on ecology and behavior of targeted elasmobranchs species including white sharks (*Carcharodon carcharias*) (Laroche et al., 2007), Caribbean reef sharks (*Carcharhinus perezii*) (Maljković & Côté, 2011), tiger sharks (*Galeocerdo cuvier*) (Hammerschlag et al., 2012), bull sharks (*Carcharhinus leucas*) (Abrantes et al., 2018; Brunnschweiler & Barnett, 2013), and juvenile lemon sharks (*Negaprion brevirostris*) (Heinrich et al., 2021). Thus, shark provisioning appears to have differential effects depending upon practices, with hand or surface feeding facilitating the development of agonistic behavior in sharks for instance (Clua, 2018), and species, with resident species potentially more affected than highly mobile species (Mourier et al., 2021).

Wildlife provisioning also creates unprecedented opportunities for scientific data collection, aggregating animals that are difficult to study without baiting due to their low density, solitary behavior, or pelagic environment (Bègue et al., 2020; Brena et al., 2015,2018; Gallagher & Hammerschlag, 2011; Meyer et al., 2009). Flourishing shark and ray watching also promotes the development of participatory science, involving tourists in the production of scientific research and raising their awareness on elasmobranch conservation (Gallagher et al., 2015; Mieras et al., 2017; Ward-Paige et al., 2020). Finally, the ecological and economic importance of elasmobranchs for local communities has the potential to enhance the creation of protected areas to better conserve these often highly threatened species and potentially benefit the entire ecosystem (Govan et al., 2008; Jupiter et al., 2014; Ward-Paige et al., 2020).

While some effects of chronic feeding on shark and ray populations have been studied, responses to a sudden prolonged break of this stimulus have rarely been observed in the wild (but see Huveneers et al., 2021). In fish, long-term retention of information for activities such as food retrieval is traded-off with the benefits of discarding memory in favor of reduced energy expenditure and flexibility (Fuss & Schluessel, 2015). Thus, elasmobranchs are hypothesized to exhibit memory windows that vary with task and the behavioral ecology of the species considered. Some sharks exhibit considerable information retention capacities ranging from 24 h to more than 40 days in juvenile Port-Jackson sharks (*Heterodontus portusjacksoni*) (Guttridge & Brown, 2014), more than 10 weeks in some adult lemon sharks (*Negaprion brevirostris*) (Clark, 1959), more than 12 weeks in juveniles of the same species (Heinrich et al., 2021), and more than 50 weeks in some juvenile grey bamboo sharks (*Chiloscyllium griseum*) (Fuss & Schluessel, 2015). However, little information, if any, is available on the memory capacities of wild pink whiprays (*Pateobatis fai*) and blacktip reef sharks (*Carcharhinus melanopterus*). These two species are highly targeted by lagoon-based provisioning in French Polynesia, particularly at the touristic site of Tiahura in Moorea. From March 20 to April 30, 2020, a total break of provisioning was observed at the Tiahura site due to a COVID-19 lockdown, as in multiple tourist spots worldwide (Bates et al., 2021). This historic event induced the first globally considerable slowing of human activity, termed “anthropause” (Rutz et al., 2020), where short- and long-term effects on biodiversity are currently being evaluated worldwide (Bates et al., 2020,2021; Corlett et al., 2020). Thus, this 6-week complete break of provisioning activities offered a unique opportunity to contribute to an unprecedent global research effort (Bates et al., 2021).

In elasmobranchs, the deconditioning process (i.e., the decline of response) following cessation of provisioning can manifest as (i) a lower reaction to the noise of boat engines associated with baiting; (ii) augmentation of the distance to human-feeders and tourists; (iii) an increase in the time before contact with a familiar attractant and a reduction in speed of approach when food is released; and (iv) a reduction in the number of individuals seen simultaneously on the site. The reconditioning processes, characterized by a return to usual behavioral responses, have been only described once for wild provisioned white sharks (*Carcharodon carcharias*) in a similar COVID-19 context (Huveneers et al., 2021). Conditioned elasmobranchs targeted in this study were mainly lagoon-resident and may present highly differential behavioral responses relative to those of white sharks. Thus, this situation offered a unique opportunity to investigate the effects of cessation of provisioning and the resumption of touristic activities on the behavior and ecology of elasmobranchs.

2 | MATERIALS AND METHODS

2.1 | Study area and description of provisioning activity

The study was carried out on the Tiahura Marine Reserve, located in the North-West of the island of Moorea (17°30′S; 149°51′W), belonging to the Society Archipelago in French Polynesia (Figure 1a).

This lagoon site is surrounded by a central channel, with depths between 2 and 7 meters, and shallow coral reefs (Kiszka et al., 2016) (Figure 1b). The provisioning site in Tiahura shows a total surface area of approximately 4470 m^2, with a very shallow water area (<1.5 meters) covered by sand where people can easily stand. This convenient access allowed the development of touristic activities on the area, targeting two elasmobranchs species: blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*). These two species share their habitat in the lagoons of French Polynesia, although blacktip reef sharks are also present in the fore-reef area (Gaspar et al., 2008; Mourier et al., 2013). Both species are globally declining in numbers and are listed on the IUCN Red List as “Near threatened” and “Vulnerable”, respectively (Heupel, 2009; Manjaji Matsumoto et al., 2016). Daily and year-round provisioning of both sharks and rays has been carried out on Tiahura since the 1980s (and inconsistently before), usually with fish discards and frozen squids (Clua et al., 2011; Mourier et al., 2021). Both professional operators who can bring up to 50 tourists per boat and individual users can share the area, which receives an average daily human attendance of around 100 people and up to almost 500 for special occasions such as Polynesian holidays when locals mix with tourists (Buray, 2015). Overall, animal-based tourism in French Polynesia attracts around 420,000 participants every year, and shallow water (lagoon) feeding of elasmobranchs accounts for 145,000 tourists per year (35%) through six different islands; Moorea island accounts for an average of 40,000 people per year (9.5%) (Lagouy & Clua, 2016).

Both species are strongly conditioned to people, displaying strong attenuation of their fear of humans when in the presence of an unconditioned stimulus (US) that is related to food and smell and associated as a reward. Consequently, they react positively to a conditioned stimulus (CS, Pavlov, 1927), i.e., the noise of boat motor, increasing their speed, and swimming in a circle. Additionally, sharks and rays are usually fed regularly during the day and consequently anticipate the arrival of boats one or 2 h before feeding hours (Gaspar et al., 2008).

2.2 | Pre-lockdown abundance assessment

Pre-lockdown abundances of elasmobranchs were defined previously in the study site in Tiahura in three studies: Study 1: Mourier et al., 2012; Study 2: Kiszka et al., 2016; Study 3: Buray, 2015 (Table 1). Abundance data from studies 1 and 3 were collected similarly, using in-water sampling, whereas Study 2 used UAV overflights to estimate the number of animals in the area.

Comparisons between data of blacktip reef shark abundances were explored from the original data sets for all three studies. Due to the suddenness and the impossibility to anticipate the lockdown decision, no data were collected right before the closure of the provisioning activity. Nevertheless, according to experts and professional touristic operators, the average abundance of sharks and rays appears to be similar and maximal since Studies 2 and 3. Thus, we defined these values as “Business As Usual” (BAU) and considered them as the pre-lockdown reference for abundance.

2.3 | Lockdown abundance assessment

Following the worldwide spread of the COVID-19 pandemic, an official lockdown was implemented on March 20, 2020, in French Polynesia, which carried out complete removal of human presence and activity in the feeding spot of Tiahura for a 6-week period.

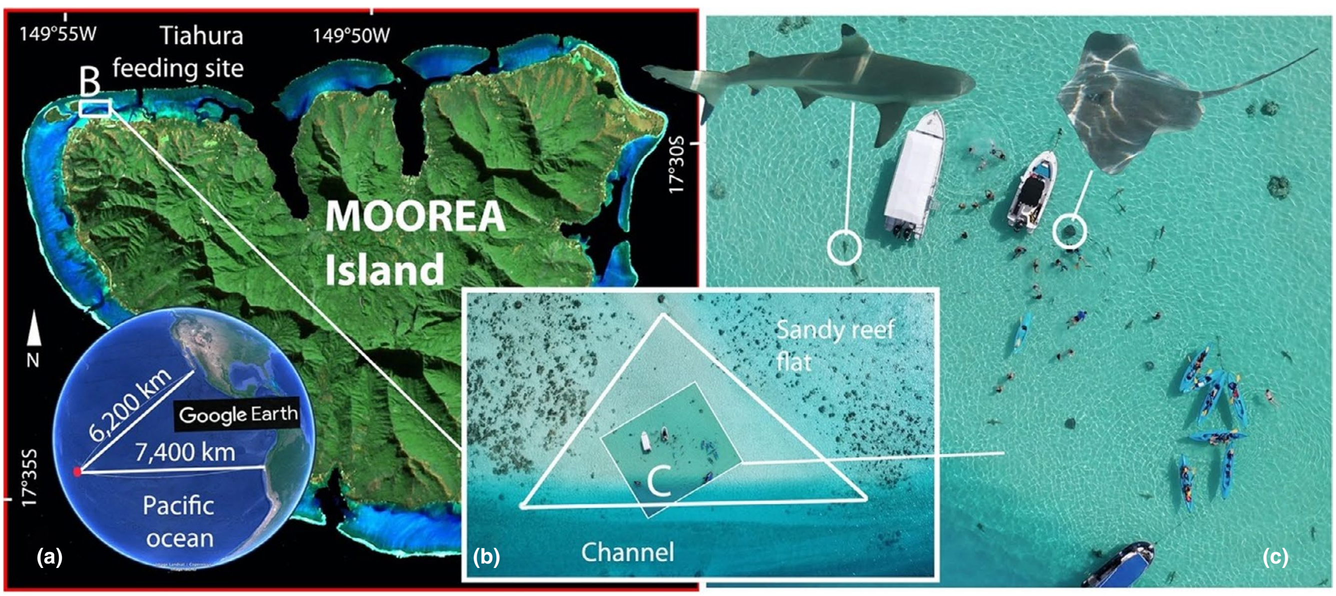

FIGURE 1 Study area. a: Localization of Moorea, French Polynesia. b: Unmanned Aerial Vehicle (UAV) overflight of the Tiahura marine reserve. C: UAV overflight of a provisioning session involving different tour operators and swimmers interacting with blacktip reef sharks (Cacharhinus melanopterus) and pink whiprays (Pateobatis fai)

TABLE 1 Overview of the publications used as references for pre-lockdown assessment in the present study

Study description	Data collection period	Blacktip reef shark abundance	Pink whipray abundance	Reference
Study 1: Evidence of social communities in a spatially structured network of a free-ranging shark species	From March 2008 to June 2010	8.97 ± 0.72 (SD)	NA	Mourier et al., 2012
Study 2: Using unmanned aerial vehicles (UAVs) to investigate shark and ray densities in a shallow coral lagoon	July 2014	15.1 ± 2.77 (SD)	10.00 ± 4.59 (SD)	Kiszka et al., 2016
Study 3: Étude comportementale des requins sur le site touristique du « ray feeding» de Tiahura à Moorea en Polynésie Française.	From July to August 2015	15.4 ± 7.8 (SD)	NA	Buray, 2015

Nevertheless, there remained very marginal sound stimuli emitted by passing boats (around 1 to maximum 3 per day) in the small channel neighboring the feeding site driven by some fishermen on their way to the reef passage. An expert observer was confined in her house right in the front of the Tiahura site at a distance of 200 meters with a direct and exhaustive view facilitated by the water clarity, allowing her to: (i) Confirm the absence of elasmobranchs in the area during the usual peak periods of provisioning and regularly during the daylight hours and (ii) confirm the absence of any significant olfactory or sound stimulus on the Tiahura site itself (C. Gaspar, Pers. Comm.).

In order to confirm the expert observer results and to record the number of sharks and rays simultaneously present, a 10-min UAV survey session was implemented at 10 a.m. on 29 and April 30, 2020. The drone flights were conducted using a DJI Mavic 2 Pro UAV quadcopter equipped with a Hasselblad L1D-20c camera, allowing us to capture 20-megapixel aerial shots and 4K HDR video. The Mavic 2 Pro includes a multi-axis flight controller, GPS, and compass that allow for stable flight, maintenance of a consistently chosen altitude of 60 meters, wind compensation, station holding, and reliable user control.

2.4 | Post-lockdown abundance assessment

The data collection focusing on elasmobranch abundances was carried out 1–3 times a day from May 1, 2020, the day of reopening after lockdown, to May 15, 2020, totaling 31 dives, in the presence of favorable climatic conditions (unaltered visibility, moderate current). Three additional dives were conducted in June 2020 at 10 a.m. in order to record elasmobranch abundance in the area 1 month after reopening. Despite the low amount of data collected in June, samplings sessions were separated into two groups—“early post-lockdown” with May data and “late post-lockdown” with June data—in order to highlight the possible differences in terms of elasmobranchs abundance. Diver results (see below) were compared to UAV data, collected at the beginning (4 days, between 1 and May 5, 2020) and at the end of the post-lockdown period (3 days, during late post-lockdown dives). During lockdown, a 10-min stationary UAV survey was performed with the same equipment, at the same height.

The underwater diver surveys were conducted by a qualified and trained freediver from an independent boat, who counted and identified individual blacktip reef sharks and pink whiprays over 30-min sessions at up to three different times of the day overlapping with provisioning sessions of most professional touristic operators; i.e., at 10 a.m., 12 a.m., and 4 p.m.. During each count, the diver recorded the number of people present in the water, boats with (tour operators, jet skis, private boats) or without motors (standup paddle, kayak, pirogue), and whether provisioning occurred or not. The presence/absence of the sharks and rays targeted was evaluated four times: at the entrance of the diver in the water, after 10 min, after 20 min, and at the end of each session.

The counting of the sharks was carried out with the help of photo-identification techniques such as the identification of individual shape of margins separating black, white, and brown color patterns on both sides of the dorsal fin as well as other distinctive body marks such as scars, notches, and dots (Mourier et al., 2012; Porcher, 2005). Similarly, rays can be differentiated using the dorsal and ventral color shapes and patterns. Sex was determined by the presence or absence of claspers for both species. Such information about shark and ray individual discrimination allowed us to avoid counting them twice and thus to generate more accurate measures of abundance. Identification was facilitated by the excellent visibility of the site (Figure 1), allowing photos and videos to be taken to confirm the identity of the animals observed.

2.5 | Statistical analysis

Statistical analyses were completed using R software (V 2.0.4; R Core Team, 2020). Statistical significance was tested at the *p*-value <.05 level. Anthropogenic variables, including information on boats, and people present on the site, were tested for collinearity using the variance inflation factor (VIF). Low multicollinearity, expressed by a VIF < 5 was revealed, suggesting low collinearity between predictor variables for the abundance of the two species of elasmobranchs. Pearson correlations were performed between the number of sharks and rays and the anthropogenic variables in order to detect possible associations between animal and human presence. Comparisons between drone and observer data were performed using χ^2 tests

FIGURE 2 Photographs from drone surveys showcasing representative abundance of sharks (red circles) and rays (yellow circles) at the Tiahura feeding site on (a) 04/29/2020 (2 days before re-opening) showing the presence of one shark; (b) 04/30/3030 (1 day before re-opening) showing the presence of four sharks and three rays; (c) 05/02/2020 (1 day after re-opening) showing the presence of eleven sharks and five rays; (d) 06/01/2020 (31 day after re-opening), showing the presence of 20 sharks and 9 rays. All images were taken at 10 a.m. and have been adjusted to optimize shark and ray counts

of independence. Comparisons between counts were done using Kruskal-Wallis rank-sum tests and pairwise comparisons post hoc tests. Given the reduced sample size for the late post-lockdown data, a power analysis was used to ensure sufficient power and reliability (power = 0.99; "kwpower" function, R-package "MultNonParam", Kolassa & Jankowski, 2021).

A site fidelity index (SFI), obtained by dividing the number of samplings where the individual was present by the total number of sessions, was calculated for all the elasmobranchs seen at least one time in the Tiahura site. Animals with SFI > 0.5 were considered as residents during the post-lockdown period sampled and thus frequently seen from the reopening of tourism activities. In order to control if the individuals responding to auditory and olfactory cues were consistent post-lockdown and to explore the potential intra-specific difference of presence pattern, the response curve of presence/absence observed during the sampling was fitted with a Loess smoother for all the photo-identified elasmobranchs. Furthermore, an accumulation curve was performed in order to estimate the number of dives needed to observe all the individuals listed.

2.6 | Ethical note and STRANGE statement

This study was conducted under a special permit issued by the Ministry of Culture and Environment of French Polynesia (ref: N°011492/MCE/ENV) from October 16, 2019, and was designed to minimize the disturbance and stress. The following statements on sampling biases are made with reference to the STRANGE framework (Rutz & Webster, 2021; Webster & Rutz, 2020). All individuals photo-identified were in their natural environment where they could interact freely with all the other animals and tourists frequenting the Tiahura site (Social background). In order to take into account the variability of daily energy expenditure of animals in such conditions, three different sessions were sampled, as explained in the "Post-lockdown abundance assessment" section (Natural changes in responsiveness). The elasmobranchs monitored had been targeted by ecotourism practices for years as described above in the "Study area and provisioning activity description" section and thus were highly conditioned to provisioning practices, minimizing the bias that might cause novelty in such a study (Rearing history, Experience). Furthermore, bias linked to potentially higher detectability of bold individuals may exist given that tourists may be perceived as a threat (Biro & Dingemanse, 2008). However, the long-term conditioning phenomenon likely decreased the natural vigilance of the focal animals being fed and viewed by humans and thus likely allowed shyer individuals to be present simultaneously (Bejder et al., 2009). Moreover, the excellent visibility at the site may have allowed the detection of individuals positioned more distantly in the visual field of the diver, and potentially displaying lower levels of boldness (Trappability and self-selection, Genetic make-up). According to the above statements, the STRANGEness of the sampling may be considered as low. All potential biases related to the STRANGE framework that could be due to inter-specific and inter-individual differences are discussed in the "**Discussion**" section.

3 | RESULTS

3.1 | Lockdown abundance assessment

The observer confined at home did not observe any significant presence of sharks during the lockdown duration. A maximum of one animal quickly crossing the area was observed in the absence of any stimulus. Nevertheless, on April 30, 2020, the observer spotted 9 elasmobranchs (6 sharks and 3 rays) aggregating after the arrival of a motorboat at the provisioning site, potentially stimulating the animals acoustically but without any food release. This was the only event where a boat was anchored in the area during the lockdown period.

The UAV videos recorded during the lockdown confirmed these observations with 1 shark and 0 rays counted on April 29, 2020 when no boats were crossing the area (Figure 2a). The shark seen was traveling without any visible change in swimming speed and only stayed for a few seconds in the UAV frame. By contrast, analysis of drone data recorded April 30, 2020 with a motorboat arriving and anchoring in the area highlighted 6 sharks and 3 rays (Figure 2b). Both species remained for several minutes in the area and noticeably increased their speed quickly after the arrival of the boat, with a trajectory directed toward the boat, and circled the boat when it stopped despite the fact that no provisioning occurred.

3.2 | Post-lockdown abundance assessment

UAV data and diver data were considered as independent using χ^2 tests during the mutual surveys (p-value >.05). For subsequent statistical analysis, only freediver counts were used, as they provided more samples. Data collected revealed a significant increase in anthropogenic activity between early and late post-lockdown with an intensification of the number of the motor and non-motorboats, the number of boats feeding and the number of people present on Tiahura (Kruskal–Wallis tests: p-value <.05 for all anthropogenic parameters) (Table 2).

From the first day of reopening, numbers of sharks (10 a.m.: 8, 12 a.m.: 11, 4 p.m.: 10) and rays (10 a.m.: 7, 12 a.m.: 9, 4 p.m.: 4) were sufficient to allow for tourist activity to resume as normal, despite being about half of the pre-COVID levels (Figure 2c). Mean abundance levels of both species for the early post-lockdown part of the survey were 7.82 ± 3.04 sharks and 4.77 ± 2.24 rays, showing some variation between days and time of the day (Table 2). Shark abundance recorded at early post-lockdown was only comparable to the one measured in Study 1, 10 years before (p-value = .667) and was significantly lower than the abundances measured in other two previous studies (p-values <.05) (Figure 3). Early post-lockdown ray abundance was comparable to late post-lockdown ray abundance (p-value = .372), but was significantly lower than the one measured in Study 2, 6 years before (p-value = .041) (Figure 3).

Both species showed an increase in abundance during late post-lockdown compared to early post-lockdown; this increase was significant for sharks (p-value = .040) with a mean of 19.92 ± 2.07 individuals but non-significant for rays (p-value = .372) with a mean of 6.58 ± 1.31 animals (Table 2, Figure 3). One month after reopening, in June 2021, shark abundance appeared fully recovered to pre-COVID levels and comparable to the ones obtained in Study 2 and Study 3, with a minimum of 17 individuals simultaneously present (Figure 3a). Concerning ray abundance, no significant difference was either observed between early and late post-lockdown data or between late post-lockdown and Study 2 counts. This result suggests a return to BAU for rays since June 2020, but with a slower abundance increase than for sharks and a complete recovery fully achieved 1 month later in July 2020 according to tourist operators' estimation (Figure 3b).

Results of the Pearson correlations between elasmobranch abundance and anthropogenic parameters show significant and positive relationships between all the variables and numbers of sharks and rays. Indeed, the increase of the number of provisioning boats, offering both olfactory and acoustic stimuli, was linked to a significant increase in the number of individuals in the area for both species (Pearson correlation: p = .45; p-value <.001). Furthermore, the increase of the total number of boats, with or without an engine, appeared to attract elasmobranchs and showed a significant positive relationship with shark and ray presence (Pearson correlation: p = .64; p-value <.001).

A total of 31 different blacktip reef sharks, including 16 females and 15 males, and of 10 individuals pink whiprays, with 7 females and 3 males, were photo-identified (Appendix S1). Six individuals reached a SFI > 0.5, with 4 female rays and 2 male sharks. No significant correlation between SFI value and species was observed (KW: p-value = .21). Furthermore, no significant link between sex and higher SFI was highlighted for either species (KW: p-value = .053 for sharks and p-value = .73 for rays). The maximal SFI was 0.82 for a

TABLE 2 Description of the data collected on elasmobranch abundance and anthropogenic parameters

Variable		Minimum	Maximum	Mean	SD
Number of blacktip reef sharks	Early post-lockdown	1	16	7.82	3.04
	Late post-lockdown	17	23	19.92	2.07
Number of pink whiprays	Early post-lockdown	0	10	4.77	2.24
	Late post-lockdown	5	9	6.58	1.31
Number of boats provisioning	Early post-lockdown	0	4	1.50	0.81
	Late post-lockdown	1	4	2.83	0.94
Number of motorboats	Early post-lockdown	0	10	2.45	2.09
	Late post-lockdown	3	14	7.33	3.14
Number of non-motorboats	Early post-lockdown	0	6	0.84	1.19
	Late post-lockdown	3	9	6.58	1.83
Number of people	Early post-lockdown	1	45	8.48	8.35
	Late post-lockdown	24	119	60.17	35.70

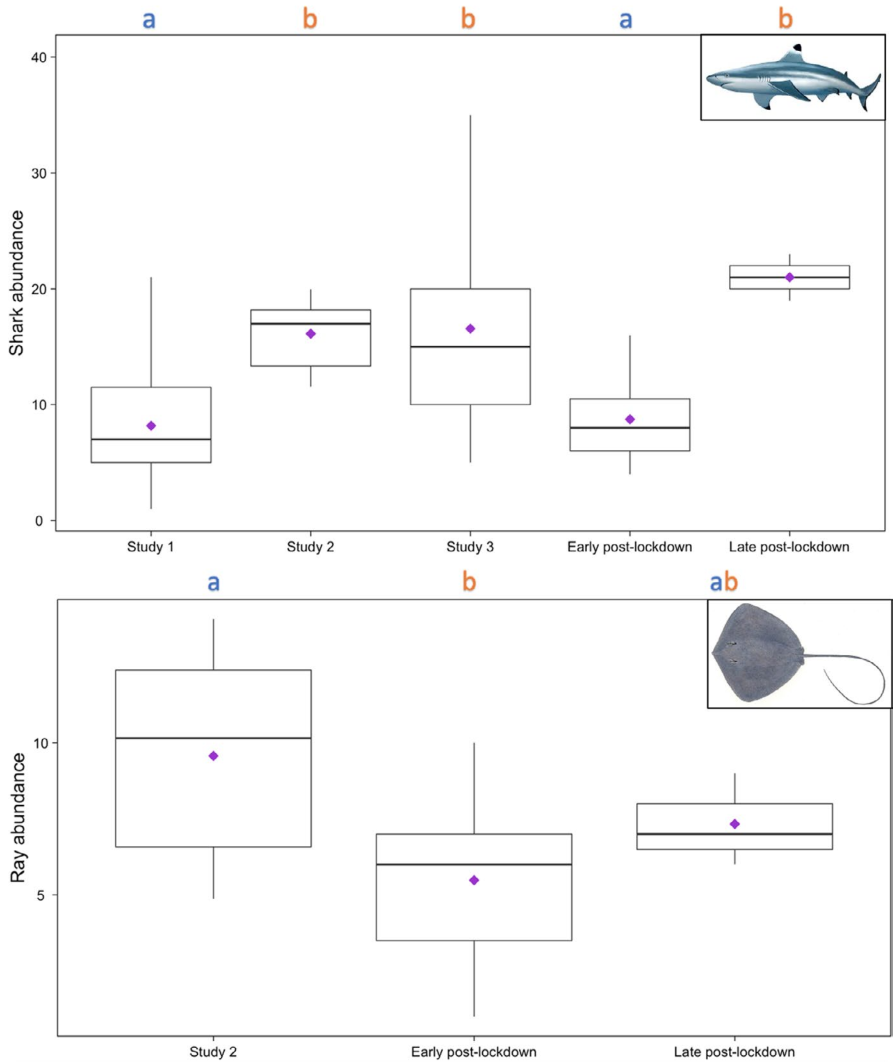

FIGURE 3 Abundance of blacktip reef sharks (Carcharhinus melanopterus) and pink whiprays (Pateobatis fai) furnished by several studies completed in Tiahura. Boxplots not sharing the same letter are significantly different in pairwise comparisons (p-value <.05). Purple dots represent mean values of the abundance for the study considered. Note that the y-axis varies with species

female ray. Nine individuals displayed a SFI < 0.1 (6 sharks and 3 rays) and 2 of them were seen only once (2 female rays).

The probability of individual presence varied among the individuals observed (Appendix S2). Indeed, despite the majority of the animals showing an increase in their presence probability with time, it is interesting to note an inflection of the presence probability during the second week for the majority of individuals present since the beginning, before increasing again at late post-lockdown. Furthermore, 12 individuals from both species (29% of the total number of individuals targeted) showed a maximum in their probability of presence during early post-lockdown, with a reduced probability during late post-lockdown. Among the six individuals spotted from the first day after reopening of tourism activities, only one of them displayed a SFI > 0.5.

Accumulation curves showed a strong increase in the numbers of individual sharks and rays spotted after reopening of the Tiahura site and then asymptotes after half the first week. Indeed, 90% of the animals were seen after 97 samples (beginning of the second week after reopening) for blacktip reef sharks and 63 (end of the first week after reopening) for pink whiprays, both during early post-lockdown. All the rays identified visited Tiahura after 86 samples, and then during early post-lockdown (beginning of the second week after reopening), but three individuals among the sharks we photo-identified were only spotted after 129 samples, from June 1, 2020, during the late post-lockdown (Figure 4).

4 | DISCUSSION

Using drones and underwater observations, we were able to accurately monitor the presence and abundance of two elasmobranch species at a specific feeding site for ecotourism purposes after a 6-week break in provisioning. Based on the reaction of several animals from both species to a single acoustic stimulus (a motorboat) 1 day prior to the re-opening of the site, our findings suggest that sharks and rays can remember stimuli for periods exceeding 6 weeks (i.e., we observed a positive reaction to a CS in both species). This result confirms the resilience of conditioning as described following deliberate cessation of artificial stimuli in previous studies for other elasmobranch species (Clark, 1959; Fuss & Schluessel, 2015; Guttridge & Brown, 2014; Heinrich et al., 2021). The fact that both species were attracted with a single sound stimulus supports previous findings on Pink whipray (Gaspar et al., 2008), white sharks (*Carcharodon carcharias*) (Bruce & Bradford, 2013), and Port-Jackson sharks (*Heterodontus portusjacksoni*) (Pouca & Brown, 2018), showing a possible cognitive connection of two linked stimuli (food being the US). In this study, the noise of the engine appears to be an important stimulus that attracts highly conditioned blacktip reef sharks and pink whiprays. Further studies could explore a potential cognitive association between food reward and splashes (as CS) made by tourists practicing snorkeling or paddling in a highly frequented area. It has been already observed that human-induced noises caused avoidance behavior for whale sharks (*Rhincodon typus*) in the touristic site of Panaon island (Philippines) in 39% of the cases (Araujo et al., 2017). By implication, elasmobranchs may be able to associate other sound stimuli like splashes to negative events (i.e., disturbance to the animals) or positive events (i.e., food reward). Such noises linked to provisioning participants should be, therefore, considered in future codes of conduct to improve the quality and safety of the experience. Indeed, even if all paddling noises cannot be avoided, tour operators could raise awareness about reducing splash entry in the water from boats and loud fin kicking when swimming. Notably, the number of provisioning boats in our study area was significantly higher for late post-lockdown than for early post-lockdown, and the amounts and types of food and the duration of exposure were not standardized and sometimes difficult to assess, possibly biasing our results. Nevertheless, a recent study suggests that the reward magnitude has a limited effect on learning rates (Heinrich et al., 2020) when it is hypothesized that CS could play an important role in associations made by sharks with the presence of baits. Thus, the bias potentially caused by the possible differences in provisioning effort between early and late post-lockdown may be considered as minimal, as CS was present since the first day of reopening.

Previous studies have shown that in some places, focal species, such as bull sharks (*Carcharhinus leucas*) and whitetip reef sharks (*Trianodon obesus*), are not dependent on the provisioning activities as a significant food source (Abrantes et al., 2018). However, heavy dependence has been observed in some other species, such as southern stingrays (*Dasyatis Americana*) (Semeniuk et al., 2007). This could be a sign of potential differential effects of artificial feeding depending on species and practices, which may as well occur at an intraspecific level (Brunnschweiler et al., 2017). Thus, it is expected that elasmobranchs that are fully dependent on daily provisioning activities continue to regularly visit the site, anticipating being fed. Given that the sharks and rays in Tiahura completely deserted the area during the lockdown, they may not depend on this feeding activity to sustain and satisfy their nutritional needs. However, further studies focusing on food intake would be needed to confirm this observation.

The differences observed in presence-absence patterns and return to BAU between sharks and rays could be linked to the different ecologies of these two species. Indeed, blacktip reef sharks are ram ventilators that must remain continuously swimming (Bernal et al., 2012). By contrast, pink whiprays spend most of their time motionless, sitting on (or in) the sand to save energy and avoid predation. Such a difference in their behavioral ecology and respective capacities to explore their environment could explain the slower response of rays compared to sharks to relocate to the provisioning site in spite of the return of daily olfactory and acoustic stimuli. Another explanation could be linked to differences in auditory capacities for sharks relative to rays, with the former being more efficient.

Despite the majority of photo-identified individuals displaying an increased probability of being present at the feeding site with time, strong inter-individual differences were highlighted. This intra-specific variation could be linked to physiological differences. A sudden restart of artificial provisioning could lead to a feeling of satiety owing to important and unexpected food intake. A physiological shift may be needed from natural levels of eating to chronic artificial feeding (Leigh et al., 2017; Papastamatiou et al., 2007). Sharks fed first after the reopening, still in a slow metabolism and slow digestion state, may feel "full" quickly and abandon the feeding site a few days after unnatural levels of eating, leaving space for others.

Another explanation could be linked to competition among individuals due to a rapid increase in the number of elasmobranchs

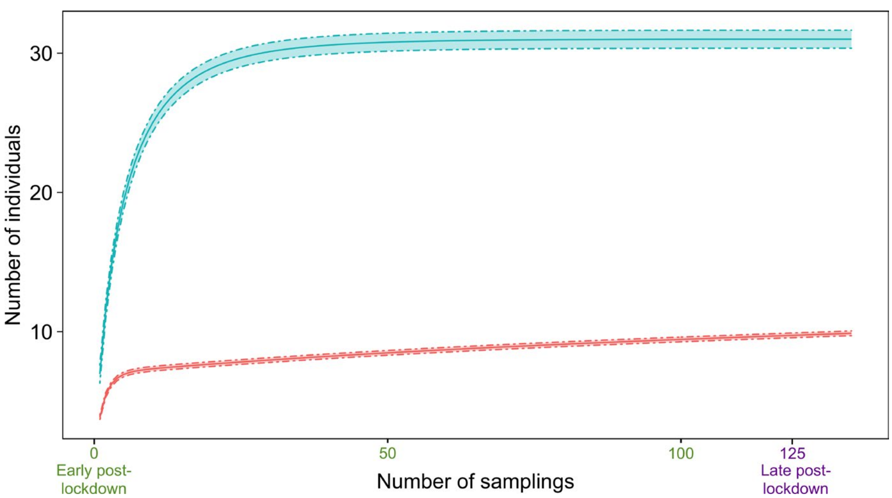

FIGURE 4 Accumulation curve of the individuals photo-identified at the Tiahura site. The blue line represents the accumulation curve for blacktip reef sharks and the red line for pink whiprays. Colored values on the x-axis represent samplings collected during early post-lockdown in green ($n = 124$) and samplings collected during late post-lockdown in purple ($n = 12$). 95% confidence intervals are highlighted for each curve

foraging in the area. Such negative interactions have already been observed for sicklefin lemon sharks (*Negaprion acutidens*) in another feeding site in Moorea, located on the outer reef, where some animals were displaying wounds inflicted during fights for dominance (Clua et al., 2010). Particularly strong dominance interactions could have occurred after reopening, but then progressively attenuated with time, allowing coexistence of different individuals in the same area of interest, as has already been shown for tiger sharks (*Galeocerdo cuvier*) around a blue whale carcass (Clua et al., 2013).

Another explanation could be the existence of clustering in the subpopulation of the elasmobranchs in the Tiahura site, with preferred associations between individuals that did not frequent the site simultaneously, as has been already suggested in the full population of blacktip reef sharks around Moorea island (Mourier et al., 2012). Residency patterns could also be different between identified individuals with resident, semi-resident, or opportunistic individuals as has been observed in sicklefin lemon shark on a provisioning site (Clua et al., 2010). The drop of in the probability of the presence of some sharks after 2 weeks could be linked to individual choices, linked to life-history traits (Mourier et al., 2013) or to individual personality (Finger et al., 2017), with shyer individuals avoiding competition or displaying higher exploratory behavior encouraging foraging on new sites.

Even if it is still too early to evaluate the long-term effects of the COVID-19 pandemic, the present study on the Tiahura provisioning site in Moorea suggests a limited impact on elasmobranch tourism in the area due to the fast recovery to before-lockdown abundances of blacktip reef sharks and pink whiprays. Regarding the sustainability of tourism practices, the near desertion of the site during the Anthropause and the decrease in abundance observed at early post-lockdown provide more evidence that feeding elasmobranchs may not necessarily lead to drastic ecological change that cannot be reversed. Whatever their level of conditioning, our results suggest provisioned sharks and rays can adapt when provisioning stops, and then return when provisioning resumes. Those findings are in line with a growing number of studies showing minimal (if any) negative effects of shark feeding on the biology and ecology of some species (Abrantes et al., 2018; Brunnschweiler & Barnett, 2013; Hammerschlag et al., 2012; Heinrich et al., 2021; Laroche et al., 2007; Maljković & Côté, 2011). Nevertheless, precautionary approaches should be taken to limit the potential negative impact of tourism on species with the high level of residency such as blacktip reef sharks (Mourier et al., 2021), with a necessity to redesign the activity with sustainable management practices if impacts are documented. It is, however, important to place the potential impacts of these tourism activities in the context of the threats faced by sharks and rays (Healy et al., 2020). Indeed, fishing and habitat loss remain the main causes of elasmobranch declines, and addressing these threats should remain the priority of conservation efforts for these species (Dulvy et al., 2014; Healy et al., 2020). Furthermore, the use of codes of conduct standardizing ways to bait animals and to behave in the water during provisioning should help to minimize the potential impacts of this tourism activity on wildlife and on the safety of participants (Abrantes et al., 2018; Clua, 2018; Clua & Torrente, 2015; Gallagher et al., 2015; Healy et al., 2020; Newsome et al., 2004; Zimmerhackel et al., 2019) while increasing the ecological and economic benefits (Semeniuk et al., 2009; Zimmerhackel et al., 2018). Evidence in the wild, including from this study, reveals strong levels of conditioning in sharks and rays strengthens the need for these codes of conduct to be adopted, implemented, and enforced in every provisioning site around the world. Our study reveals that conditioning stability is so strong that a cessation of the activity, even for several weeks (up to six in this case), has no significant impact on the conditioning of the animals. Therefore, efforts to reduce potentially deleterious effects of provisioning on animals should not rely on temporary feeding stoppages and instead focus on standardizing and optimizing both provisioning practices, which currently vary considerably among operators, as well as human behavior in the water.

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DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

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