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Effects of COVID-19 pandemic restrictions on coral reef fishes at eco-tourism sites in Bora-Bora, French Polynesia

David Lecchini a, b, *, Rohan M. Brooker c, Viliame Waqalevu b, d, Emma Gairin b, e, Lana Minier a, b, Cécile Berthe a, b, Rainui Besineau b, Guilhem Blay b, Tehani Maueau b, Vincent Sturry f, Tamatoa Bambridge a, b, Gaston Tong Sang f, Frédéric Bertucci b, k

a PSL Université Paris, EPHÉ-UPVD-CNRS, USR3278 CRIOBE, 98729, Moorea, French Polynesia
b School of Life and Environmental Sciences, Deakin University, Queenstown, 3225, Australia
c School of Marine Studies, University of the South Pacific, 679, Suva, Fiji
d Laboratoire D’Excellence “CORAIL”, 66100, Perpignan, France
e School of Marine Studies, University of the South Pacific, 679, Suva, Fiji
f Comité Du Tourisme de Bora Bora & de Bora Bora Activités, 98730, Bora-Bora, French Polynesia
g Lagoon Service & Reef Discovery, 98730, Bora-Bora, French Polynesia
h Association Ia Vai Ma Noa Bora-Bora, 98730, Bora-Bora, French Polynesia
i Polynésie des Eaux, Vaitape, 98730, Bora-Bora, French Polynesia
j Association Ia Vai Ma Noa Bora-Bora, 98730, Bora-Bora, French Polynesia
k Town Hall, Vaitape, 98730, Bora-Bora, French Polynesia

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A B S T R A C T

The COVID-19 pandemic led to a global lockdown in mid-2020, leading to a rapid decline in international travel and tourism. In French Polynesia, marine-based tourism activities ceased in March 2020 with the suspension of international flights (i.e., 45 days - between 20th March and 04th May, 2020), slowly restarting between May-July as domestic and international visitors returned. The impacts of this rapid change in human activity at reef tourism sites on associated reef fishes was examined at Bora-Bora Island through underwater surveys of five control and nine eco-tourism sites. Our results showed that fish density significantly increased from March to May (i.e., the overall density of fishes increased by 143% and harvested species by 215%), but returned to pre-lockdown levels by August 2020. At the usually busy eco-tourism sites, fish diversity, notably of piscivores, omnivores, and benthic feeders, was higher in the absence of tourists. The impact observed is almost certainly related to short term changes in fish behavior, as any density fluctuations at the population level are unlikely to have happened over such a short time frame. Overall, these findings highlight the influence of human activities on fish communities and underline the need for further research to evaluate the environmental impacts of eco-tourism.

1. Introduction

Although coral reefs comprise only 0.1% of the ocean’s surface, they contain at least 25% of the world’s marine biodiversity (Reaka-Kudla and Wilson, 1997; Spalding et al., 2001). Moreover, humans have a close cultural and socioeconomic relationship with coral reefs. Around 850 million people live within 100 km of a reef, many of whom rely on them for their food and livelihood (Burke et al., 2011). In addition, around 30% of coral reefs also support varying forms of tourism activities, with reef-based tourism involving over 100 countries and territories (Spalding et al., 2017). However, tourism also has the potential to be a major cause of coral reef degradation (Spalding et al., 2017). For instance, tourism may impact reefs through activities where humans come into direct contact with the reef and its inhabitants, such as boating, fish feeding, diving and snorkeling (Rouphael and Inglis, 2001), as well as indirectly as a result of coastal development or resource extraction (e.g., Hawkins and Roberts, 1992; Hawkins et al., 1999; Tratalos and Austin, 2001; Uyarra and Côté, 2007; Siriwong et al., 2018). Despite these potential impacts tourism can also be an asset to reef protection, for instance helping to reduce overfishing by offering...
financial or social incentives for sustainable management (Spalding et al., 2017). Thus, seeking a balance between providing ecosystem services and ensuring ecological resilience should be an essential component of effective conservation management (Albuquerque et al., 2015; Prinz, 2017; Wen et al., 2018).

In 2020, the COVID-19 pandemic lead to dramatic restrictions on human activities worldwide. The resulting ‘anthropause’ (Rutz et al., 2020) provided an opportunity to quantify the degree to which human perturbations such as tourism, fishing, and boat traffic impact coral reefs and associated economically important resources such as fishes. For example, Bennett et al. (2020) suggests that the COVID-19 pandemic has had negative consequences on most small-scale fisheries across the Pacific due to the complete shutdown of some fisheries, knock-on economic effects from market disruptions, and increased health risks for fishers. Similarly, tourism has been one of the industries most affected by COVID-19 (Sigala, 2020). In May 2020, the United Nations World Tourism Organization estimated that international tourist travel dropped by 78%, causing a loss of 1.2 trillion USD in export revenues and directly leading to the loss of 120 million tourism-related jobs (UNWTO 2020). In French Polynesia, the health crisis linked to the first ‘wave’ (from March to June 2020) of the pandemic was relatively limited, with only 60 people infected and no linked deaths (World Health Organisation 2020). However, many French Polynesians subsequently lost their jobs in the tourism sector or in the black pearl industries, both of which rely on a steady stream of tourists (Blondy 2010, 2016). During the lockdown, all tourism activities ceased, with these gradually restarting in stages with the subsequent return of first domestic and then international tourists.

We aimed to opportunistically use the rapid cessation of tourism and its gradual resumption to examine the effects of related activities on coral reef fishes at eco-tourism sites at Bora-Bora, French Polynesia. Impacts of COVID-19 on the tourism sector have been profound, particularly in countries like French Polynesia, where tourism is one of the main economic activities (UNWTO, 2020). Tourism, if done sustainably, can provide multiple benefits to local communities and can even strengthen global conservation efforts (Spalding et al., 2017). Thus, understanding how different tourism activities influence coastal ecosystems, including coral reefs, is important to inform stakeholders and ensure sustainable management of ecotourism. We aimed to address this by evaluating reef fish density and diversity between multiple eco-tourism sites in different time periods corresponding to pre-lockdown, during lockdown, and post-lockdown measures in Bora-Bora.

2. Methods

2.1. The COVID-19 lockdown at Bora-Bora Island

In an attempt to slow the transmission of COVID-19 in French Polynesia, a six-week total lockdown was implemented between 20th March and 04th May 2020, suspending all international and domestic flights. During this period, all marine tourism ceased with only professional fishermen allowed to operate within coastal waters (French Polynesia tourism Department, 2020).

At Bora-Bora, the post-lockdown period consisted of three stages. Between 05–24 May, flights between Tahiti and Bora-Bora remained cancelled. Between 25th May and 30th June, domestic flights between Tahiti and Bora-Bora resumed; however, international flights to French Polynesia did not and, as a consequence, all hotels and other guest accommodation on Bora Bora remained closed. Flights from Europe and North America to Tahiti resumed on 01st July and 13th July respectively, with all hotels also reopening on 13th July. All marine and other recreational activities also resumed at that time to coincide with the return of local and international tourists. Under normal circumstances, around 100,000 tourists visit Bora Bora each year, with over 90% coming from the USA. July and August 2020 each saw around 1,200 tourists visiting Bora-Bora with marine tourism activities conducted at around half the rate of that seen in 2019 (French Polynesia tourism Department, 2020).

In addition to the decline in tourist numbers, around 10–20% of the local Bora-Bora population inhabitants relocated to smaller islets around the Bora-Bora lagoon at the outset of the lockdown, often on their family’s ancestral land. As there were minimal police controls on the islets during the lockdown and no food market, many inhabitants undertook subsistence fishing on the hoa (the small open channel between the reef and the ocean) and on the reef flat. In contrast, on the main island of Bora-Bora, lockdown rules were strictly enforced and so recreational and subsistence fishing were minimal (French Polynesia tourism Department, 2020).

2.2. Sampling sites

At Bora-Bora, 14 eco-tourism sites in the lagoon and 1 eco-tourism site on the outer slope were identified by the Mayor and the tourism committee (eco-tourism site: coral reef site related tourism - Spalding et al., 2017; Jossinet, 2020). Six of these sites are used for shark and ray feeding, five within the lagoon and the one site on the outer slope (Jossinet, 2020). Some tourism companies continued to provide food at these sites during the initial post-lockdown period to encourage the continued presence of animals. However, as we did not have information about the frequency of this activity, data pertaining to these sites was not used in the present study. Therefore, the remaining nine eco-tourism sites within the lagoon (without fish feeding) were selected for this study: four on the fringing reef, four on the barrier reef, and one in the hoa (Fig. 1). Prior to the pandemic, these sites were visited at least five times a week by tourism operators, with an average of 20 snorkelers per visit/boat (Jossinet, 2020). In addition, five control sites (without tourism activities) were selected: two on the fringing reef, two on the barrier reef, and one in the hoa (Fig. 1).

![Fig. 1. Map of Bora-Bora with the location of the 14 surveyed sites. Black rectangles represent control sites and white circles represent eco-tourism sites. BR: barrier reef, FR: fringing reef. Hoa is a small open channel between the reef and the ocean. Dark grey represents land areas, light grey represents reef areas.](image-url)
2.3. Fish surveys

Fish density (number of fishes per m$^2$) and species richness (number of species per m$^2$) were recorded at the nine eco-tourism sites and the five control sites from 02–06 March 2020 (before the lockdown), between 25–29 May (after the lockdown and when flights to and from Tahiti resumed), between 8–12 July (before the return of international tourists to French Polynesia) and between 21–25 August (during the peak of the tourism season in 2020). At each site, three replicate 25 × 4 m transects were conducted in order to record the fish community. Two passes were performed per transect; mobile, more visible fishes were recorded during the first pass and more cryptic fishes were recorded on the second pass (Lecchini and Galzin, 2005). At each site, a 25 m gap was left between each transect in order to ensure independence of the replicates. All adult fishes were identified to the species level, and fish species targeted by recreational, subsistence, and commercial fishers were then categorized as harvested species (Siu et al., 2017).

2.4. Statistical analysis

All statistical analyses were conducted using R-Studio (R version 3.6.3) at the significance level $\alpha = 0.05$. Non-normality of density and species richness data for both total fish and harvested species was identified using Shapiro-Wilk’s tests ($W = 0.87–0.98$, all $P < 10^{-3}$). Kruskal-Wallis tests were subsequently used to compare these factors between the four sampling periods (March, May, July and August), eco-tourism and control sites, and the barrier reef, fringing reef and hōa. Where significant differences were found, Dunn’s post-hoc tests for multiple pairwise comparisons were performed in order to identify the comparisons driving this difference.

Species data was then used to examine differences in fish assemblages between the four sampling periods using a Non-metric Multidimensional Scaling analysis (NMDS). This analysis was performed on the Bray–Curtis similarity matrix using the vegan package in R (version 2.5–7, Oksanen et al., 2020). One-way ANOSIM (analysis of similarity) with 9999 permutations was then used to investigate differences identified by NMDS according to the sampling period.

![Fig. 2. Box plots of the total density (number of fish per m$^2$) of all fish species (top) and of harvested species (bottom) calculated at barrier reefs (A, D), at fringing reefs (B, E) and at the hōa (C, F). Control sites are in blue, eco-tourism sites are in red. Boxes represent the first and third quartiles, thick horizontal bars are the median (second quartile), whiskers correspond to the distribution range (min-max) and circles are all the observations. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)](image-url)
Fish species observed at the adult stage were divided into six trophic guilds: herbivores, omnivores, mobile benthic invertebrate feeders (MBIF), corallivores, planktivores and piscivores, based on their general feeding preferences (Legendre et al., 1997; Viviani et al., 2019). Normality of densities for all trophic guilds were verified using Shapiro-Wilk’s tests ($W = 0.74–0.93$, all $P < 0.01$). Kruskal-Wallis tests were then used to compare densities between the four sampling periods (March, May, July, and August) in eco-tourism sites for all species and for harvested species.

3. Results

In March 2020, fish density was $1.31 \pm 0.16$ fish per m$^2$ (mean ± SD) at the five control sites and $0.94 \pm 0.06$ fish per m$^2$ at the nine eco-tourism sites (Fig. 2). In August 2020, there was $1.26 \pm 0.21$ fish per m$^2$ in the control sites and $1.28 \pm 0.09$ fish per m$^2$ in the eco-tourism sites. Total fish density was not significantly different between March and August at control and eco-tourism sites (Kruskal-Wallis, $\chi^2 = 1.81–6.55$, $P = 0.08–0.61$) (Fig. 2).

However, between these two dates, the fish density increased to $1.70 \pm 0.26$ and $1.41 \pm 0.15$ at the control sites and to $3.12 \pm 0.32$ and $2.31 \pm 0.20$ at the eco-tourism sites in May and July respectively (Fig. 2). The only site where a decrease in density was observed was the hōa control site (from $1.52 \pm 0.28$ fish per m$^2$ in March to $0.65 \pm 0.01$ in May). Kruskal-Wallis tests showed that total fish density was significantly different between March and May at the barrier reef ($\chi^2 = 27.65$, $P < 10^{-3}$; Dunn, $Z = 4.88$, $P < 10^{-3}$) and fringing reefs ($\chi^2 = 12.45$, $P = 0.006$; Dunn, $Z = 3.30$, $P = 0.005$) ecotourism sites. At barrier reef sites, fish density remained significantly higher in July (Dunn, $Z = 3.22$, $P = 0.005$), before numbers decreased to initial levels (i.e. those seen in March) in August both at barrier and fringing reefs (Fig. 2A and B). Overall, total fish density increased on average by 29% in the control sites and by 230% in the eco-tourism sites between March and May, and by 7% in the control sites and by 145% in the eco-tourism sites between March and July.

The same significant variations were observed for the harvested species subset (Kruskal-Wallis, $\chi^2 = 10.49–28.42$, $P < 10^{-3}$) (Fig. 2D and E). Even though a similar pattern occurred (i.e. density increasing...
from March to July, then decreasing in August), differences in total density and harvested fish density were not significant at the hōa ecotourism sites (Kruskal-Wallis, $\chi^2 = 3.17$–4.17, $P = 0.24$–0.37) (Fig. 2C and F).

Species richness for both total and harvested species significantly varied temporally for both control (Kruskal-Wallis, $\chi^2 = 8.55$, $P = 0.036$) and in eco-tourism barrier reef sites (Kruskal-Wallis, $\chi^2 = 19.95$, $P < 10^{-2}$) with a significant increase from March to May (Kruskal-Wallis, $\chi^2 = 8.55$–21.18, $P = 0.03$–$10^{-5}$; Dunn, $Z = 2.91$–4.45, $P < 0.05$). At the eco-tourism sites, species such as the striped large-eye bream (*Gnathodentex aureolineatus*, Lethrinidae), the shadowfin soldierfish (*Myripristis adusta*, Holocentridae) and yellowstripe goatfish (*Mulloidichthys flavolineatus*, Mullidae) were recorded in May while they had not been observed in March. Species richness significantly decreased at eco-tourism sites between May and August (Kruskal-Wallis, $\chi^2 = 3.37$, $P = 0.08$) highlighting the sensitivity of these fish assemblages to the presence of human activity. These changes are likely to be primarily behaviorally driven, with more fishes moving into tourism areas in the absence of humans.

During the lockdown at Bora-Bora, the overall densities of fish, and that of harvested species increased on average by 143% (from 1.07 ± 0.07 fish per m$^2$ in March to 2.61 ± 0.26 fish per m$^2$ in May) and 215% (from 0.39 ± 0.08 fish per m$^2$ in March to 1.23 ± 0.20 fish per m$^2$ in May) respectively in the 14 surveyed sites. Similar to reports about the sudden effects of lockdown on pollution levels (He et al., 2020; Venter et al., 2020; Yunus et al., 2020), our results suggest that the sudden removal of human activities related to marine tourism, fishing and recreation had a positive effect on the density and behaviour of associated fish populations (Figs. 2 and 3). For some countries that are highly dependent on tourism, the decline in global travel had devastating impacts on local livelihoods and led to increased pressure on local resources to meet food and livelihood needs (Hoffman, 2020). However, impacts on local resources are highly variable. For example, Feeney et al. (2021) showed a dramatic increase in harvested fishes at Moorea Island (French Polynesia) during the six-week lockdown across the inner barrier reef sites of three Marine Protected Areas (MPA), while no significant difference was observed across the non-MPA sites. According to the town hall and police at Bora-Bora, the lockdown was respected by the majority of local inhabitants, with the resulting reduction in water activity around the island itself potentially explaining the increase in fish density between March and May (Fig. 2). The only site where the fish density decreased during the lockdown was the control site at the hōa (47% drop in harvested fish density: from 0.65 ± 0.31 fish per m$^2$ in March to 0.35 ± 0.10 in May). As noted, many local inhabitants relocated to outlying islets at the outset of lockdown, and as there was no police control on the islets, there was a continued fishing pressure on the hōa (Fig. 2). Due to the time frames involved, the changes observed in fish populations during the lockdown are likely driven by the behavior of fishes. For instance, fishes may be bolder and more visible in the absence of fishing, swimming activities and boat traffic (e.g., Goetze et al., 2017; Numes et al., 2018; Samia et al., 2019). This hypothesis of a behaviorally driven response in fishes also underlines a potential issue

![Fig. 4](non-metric multidimensional scaling (NMDS) plot of the similarity of fish assemblages calculated from the Bray–Curtis distances on the total number of fish of each species recorded in the eco-tourism sites.)
could be partly explained by natural seasonal changes, our results suggest a pattern similar to the one observed in the first two months of the lockdown (Fig. 2), although this temporal pattern was not observed in the following months (Fig. 3). Although this temporal pattern was not observed in the following months (Fig. 3), it is clear that tourism has an effect on the ecology of coastal environments (e.g., Hawkins and Roberts, 1992; Hawkins et al., 1999; Tratalos and Austin, 2001; Siriwong et al., 2018), and this effect is often difficult to isolate due to the constant presence of human activity (Bessa et al., 2017). Based on our findings, it appears that fish assemblages are altered as a result of tourism activities, and the COVID-19 pandemic provided an opportunity to collect data to this effect. Thus, our study showed a significant decrease in fish density on the control sites during March and May corresponding with the return of domestic visitors. Density decreased by a further 44% between March and May during the lockdown then decreased by 26% between May and July corresponding with the return of international tourists. Densities decreased by a further 44% between July and August corresponding with the return of international tourists, reopening of all hotels and resumption of recreational activities. Over the same periods, the fish density on the control sites increased by 23% and then decreased by 17% and 11%. As the vast majority of Bora-Bora’s local population work in the tourism industry, the eco-tourism sites are often protected from fishing as unofficial Marine Protected Areas (Jossinet, 2020). Many studies have shown a negative effect of fish feeding such as habituation to human presence, increased aggressiveness, and short-term changes in species distribution (e.g., Burgin and Hardiman, 2015; Albuquerque et al., 2015; Cruz de Paula et al., 2018; Wen et al., 2018). However, fewer studies have highlighted the effects of snorkeling on fishes (e.g., Rouphael and Inglis, 2001; Binney, 2009; Dearden et al., 2010). For instance, Di Franco et al. (2013) and Riera et al. (2016) showed that in some areas, fish follow scuba-divers or snorkelers to wait for them to touch and disturb the substratum, which may provide opportunistic foraging opportunities. Bessa et al. (2017) outlined several negative effects of human presence on fishes even when no interaction takes place, such as an increase of cortisol production and the modification of activity patterns and habitat use. Intensive tourism activities could also reduce fish density and lead to changes in fish community composition by creating conditions favorable to generalist species but that exclude specialists (Bessa et al., 2017). In our study, the NMDS analysis did not show any consistent changes in species composition (Fig. 4). However, when examining the different trophic guilds, only the densities of MBIF, omnivores and piscivores increased in May at the eco-tourisms sites (Fig. 5). Thus, in general the same species were seen but with variable densities correlating with patterns of human activity (Bessa et al., 2017; Spalding et al., 2017). The stable densities of corallivores, herbivores and planktivores during and after the lockdown suggest that these guilds are less sensitive to the presence of tourists and could maintain important ecosystem processes (Fig. 5). For instance, herbivorous comprise keystone species across the world’s coral reefs, and the diversity of species within this guild provides various ecosystem services, including those that may aid in the recovery of live hard coral (e.g., Bouchon et al., 2006; Jackson et al., 2014; Cornohorsky et al., 2015; Altman-Kurosaki et al., 2018). By contrast, other species such as farming Stegastes damselfish can control other organisms through predation, influence sediment dynamics, mediate nutrient fluxes, and act as ecosystem engineers by favouring the local development of algal turfs (e.g., Ceccarelli et al., 2001; Precht et al., 2010; Emslie et al., 2012; Casey et al., 2014; Randazzo-Eisemann et al., 2019). Conversely, the sensitivity of mobile benthic invertebrate feeders (MBIF), omnivores and piscivores and their decreased density in the presence of human may reveal subtle impacts of tourism activity on the ecosystem as species within these guilds play important roles in regulating fish and invertebrate biodiversity (Ceccarelli et al., 2001; Glaser et al., 2018). However, we should acknowledge that our experimental design may not be suitable for the detection of rare and/or mobile species, due to a low number of replications and
the relatively small area covered at each site.

5. Conclusion

Early reports of improved air and water quality following the onset of the global lockdown (He et al., 2020; Venter et al., 2020; Yunus et al., 2020) suggested that the dramatic reductions in human activity can correspond with positive effects on the environment. However, somewhat unsurprisingly, subsequent reports suggest that any environmental benefit was largely short lived (Le Quéré et al., 2020). Our results are consistent with this, demonstrating a significant increase in fish density in the absence of human activity and a subsequent return to pre-lockdown levels correlating with the gradual return of local and then international tourists (Fig. 2). Nonetheless, this finding highlights the impact that the presence of humans can have on coastal communities of fishes. To date, half of the world’s coral reefs have been lost since the early 1980s, mainly due to ocean acidification and warming, as well as to increasing levels of pollution, unsustainable coastal development, over-fishing, and outbreaks of coral predators (Hoegh-Guldberg et al., 2019; Hughes et al., 2017; Woodhead et al., 2018). Disturbance to coral reefs due to recreational activities have been largely overlooked in comparison to these other perturbations (Spalding et al., 2017). According to the results of the present study, it is clear that tourism activities have the potential to alter coral reef biodiversity, and may impact aspects of associated organisms ecology such as physiology and behavior (e.g., Hawkins et al., 1999; Tratalos and Austin, 2001; Cruz de Paula et al., 2018; Wen et al., 2018). The influence of tourism activities on animal health has been well examined in terrestrial systems and marine megafauna (Orams, 2002; Valentine et al., 2004; Murray and Becker, 2016). Similar efforts should evaluate the impacts of tourism activities on coral reef fishes more broadly as this is critical for effective management of eco-tourism areas and the sustainable use of coral reefs in the future. Reducing the human carrying capacities of those places or activities on coral reef fishes more broadly as this is critical for effective behavior (e.g., Hawkins et al., 1999; Tratalos and Austin, 2001; Cruz de Paula et al., 2018; Wen et al., 2018). The influence of tourism activities on animal health has been well examined in terrestrial systems and marine megafauna (Orams, 2002; Valentine et al., 2004; Murray and Becker, 2016). Similar efforts should evaluate the impacts of tourism activities on coral reef fishes more broadly as this is critical for effective management of eco-tourism areas and the sustainable use of coral reefs in the future.}

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