Oecologia
https://doi.org/10.1007/s00442-024-05589-w

ORIGINAL RESEARCH

Coral reef fish density at a tourist destination responded rapidly to COVID-19 restrictions

Emma Gairin[1] · Frédéric Bertucci[2] · Natacha Roux[3] · Lana Minier[4,5] · Cécile Berthe[4] · Viliame Waqalevu[6] · Tehani Maueau[7] · Vincent Sturny[5] · Gaston Tong Sang[8] · Suzanne C. Mills[3,4] · David Lecchini[3,4]

Received: 10 March 2023 / Accepted: 1 July 2024

Abstract

Throughout the world, anthropogenic pressure on natural ecosystems is intensifying, notably through urbanisation, economic development, and tourism. Coral reefs have become exposed to stressors related to tourism. To reveal the impact of human activities on fish communities, we used COVID-19-related social restrictions in 2021. In French Polynesia, from February to December 2021, there was a series of restrictions on local activities and international tourism. We assessed the response of fish populations in terms of changes in the species richness and density of fish in the lagoon of Bora-Bora (French Polynesia). We selected sites with varying human pressures—some dedicated to tourism activities, others affected by boat traffic, and control sites with little human presence. Underwater visual surveys demonstrated that fish density and richness differed spatially and temporally. They were lowest on sites affected by boat traffic regardless of pandemic-related restrictions, and when activities were authorised; they were highest during lockdowns. Adult fish density increased threefold on sites usually affected by boat traffic during lockdowns and increased 2.7-fold on eco-tourism sites during international travel bans. Human activities are major drivers of fish density and species richness spatially across the lagoon of Bora-Bora but also temporally across pandemic-related restrictions, with dynamic responses to different restrictions. These results highlight the opportunity provided by pauses in human activities to assess their impact on the environment and confirm the need for sustainable lagoon management in Bora-Bora and similar coral reef settings affected by tourism and boat traffic.

Keywords Human impacts · Fish · Coral reef · Boat traffic · COVID-19 · Fishing

Introduction

Human activities in natural ecosystems worldwide are intensifying due to demographic increase, economic development, industrialisation, urbanisation, and the rise in mass tourism. Whilst not minimising its considerable human cost, the COVID-19 pandemic provided a unique opportunity to study the impact of human activities on ecosystems. Pandemic-related travel and activity restrictions led to a global 'anthropause' (Rutz et al. 2020) which, in many areas, translated into a decrease in human pressures on ecosystems and in the exploitation of natural resources. From 2020, studies began to highlight reductions in human activities

Communicated by Brian Shuter.

✉ Emma Gairin
emma.gairin@hotmail.fr

1 Marine Eco-Evo-Devo Unit, Okinawa Institute of Science and Technology, 1919-1 Tancha, Onna-son, Kunigami District, Okinawa 904-0495, Japan

2 UMR MARBEC, University of Montpellier-CNRS-IFREMER-IRD, 87 Av. Jean Monnet, CS 30171, 34203 Sète Cedex, France

3 Laboratoire d'Excellence "CORAIL", Perpignan, France

4 PSL Research University: EPHE-UPVD-CNRS, UAR 3278 CRIOBE BP 1013, 98729 Papetoai, Moorea, French Polynesia

5 Polynésienne Des Eaux, Vaitape, Bora-Bora, French Polynesia

6 Yas SeaWorld Research and Rescue Center, Abu Dhabi, United Arab Emirates

7 Association Ia Vai Ma Noa Bora-Bora, 98730 Bora-Bora, French Polynesia

8 Town Hall, Commune de Bora-Bora, Vaitape, 98730 Bora-Bora, French Polynesia

in the marine realm, notably a global reduction in marine traffic (March et al. 2021) coupled with improvements in water quality in coastal zones throughout the world (review from Mallik et al. 2021). Tourism was highly affected by the COVID-19 pandemic due to a large decrease in international travel. For instance, the fall in tourism and business led to an improvement in water quality and reduced turbidity in Vembanad Lake, India (Yunus et al. 2020) and in the canals of Venice (Braga et al. 2020; Spalding et al. 2021). Reduced tourism during lockdowns also indirectly increased the numbers of burrowing crabs on beaches and dunes in Latin America, due to the reduction in noise, frequentation, littering, and activities (Soto et al. 2021). On coral reefs in Guadeloupe, lower recreational boat noise pollution during lockdowns led to a reduction in vocalisation sounds produced by fish, which may indicate that their communication was more efficient, with less sound needing to be produced, in the absence of boat traffic (Bertucci et al. 2021). Furthermore, the cessation of white shark cage-diving tourism over 51 days in South Australia led to a reduction in activity space of yellowtail kingfish (*Seriola lalandi*) as it did not have to stray far to avoid boats (Huveneers et al. 2021). However, the impacts of tourism at the level of the ecosystem or community, as revealed through COVID-19 pandemic-related decreases in tourism, have been less studied.

Coral reefs are key resources for marine-based tourism in over a hundred countries and territories worldwide (Spalding et al. 2017) and whilst ocean warming and acidification are global drivers of coral reef degradation (Pörtner et al. 2019), at a local scale, tourism can be a major cause of damage and stress on reefs and the organisms that they shelter (Spalding et al. 2017). These issues notably arise through boat traffic, diving, and snorkelling (Rouphael and Inglis 2001), but also because of indirect activities such as coastal urbanisation and the extraction of resources to accommodate tourists (Tratalos and Austin 2001; Uyarra and Côté 2007; Siriwong et al. 2018; Gairin et al. 2021; Giraud-Renard et al. 2022). Coral reefs are an important ecosystem affected by tourism that should be studied in the context of the pandemic-related 'anthropause' (term coined in Rutz et al. 2020). Among studies performed during restriction periods, it was shown that recreational boating greatly decreased in Australia, particularly in the Great Barrier Reef, with an 88% reduction in visitor numbers between March and June 2020 compared to the previous year (Huveneers et al. 2021). In Hawai'i, fish biomass increased in shallow habitats usually visited by tourists during COVID-19 restrictions, and returned to pre-restriction levels when tourism resumed (Weng et al. 2023). In the Gulf of Aqaba in Israel, zones where shore divers enter the sea showed elevated species diversity and evenness, although there was no change in their abundance, during COVID-19 lockdowns (China et al. 2021).

In this study of the lagoon of Bora-Bora, in the Society Archipelago of French Polynesia, in the South Pacific, we extend upon a previous study on the same island that compared coral reef fish communities before, during, and after 2020 pandemic-related restrictions over six months (Lecchini et al. 2021). In this updated study conducted during the following year, in 2021, we compared the impact of pandemic restrictions on fish communities across ten months on sites with little human activities, with tourism, and with boat traffic. Bora-Bora is a French Polynesia island, famous worldwide for its blue lagoon and coral reefs. More than 95% of tourists visiting the island come from outside of the region, among whom many take part in lagoon-based activities and consume local fish. From the start of the pandemic in March 2020 to early 2022, there have been numerous openings and closures of French Polynesia borders to international tourists, as well as partial and total lockdowns and restrictions on local economic activities. These restrictions led to a 70% and 65% reduction in tourists visiting French Polynesia in 2020 and 2021, respectively, compared to 2019 (230,000 tourists versus 70,000–80,000). In 2021, 60% of the 80,000 tourists travelled between October and December (data from French Polynesia Tourism Department, https://tahititourisme.fr/). On average, 75% of tourists travelling to French Polynesia stay on the island of Bora-Bora for 2–4 days. During the pandemic-related restrictions, very few tourists were present in French Polynesia, and almost all tourism vendors in Bora-Bora were closed. As such, Bora-Bora represents an ideal setting to characterise how fish communities responded to the changes in lagoon usage. Prior to the COVID-19 pandemic, Bora-Bora had been continuously visited by tourists over the past few decades.

In 2021, there were three levels of pandemic-related restrictions in French Polynesia: a ban of international tourism travel, a partial lockdown during the weekends accompanied by a curfew on weekdays, a complete lockdown. These periods occurred in rapid succession from February to December 2021 (Fig. 1). This alternation in different pandemic-related restrictions allowed us to study their impacts on fish population dynamics through a timeseries.

We hypothesize that (i) fish populations will be more numerous and diverse on sites with less human pressure regardless of restriction period, and that (ii) a succession of pandemic-related restriction periods with varying levels of socioeconomical activities will translate into shifts in the distribution of the reef fish community on the study sites in the lagoon of Bora-Bora. We expect that the changes in density and diversity of the fish populations (juveniles, adults, harvested or non-harvested) observed on the different sites will be related to the level of pandemic-related

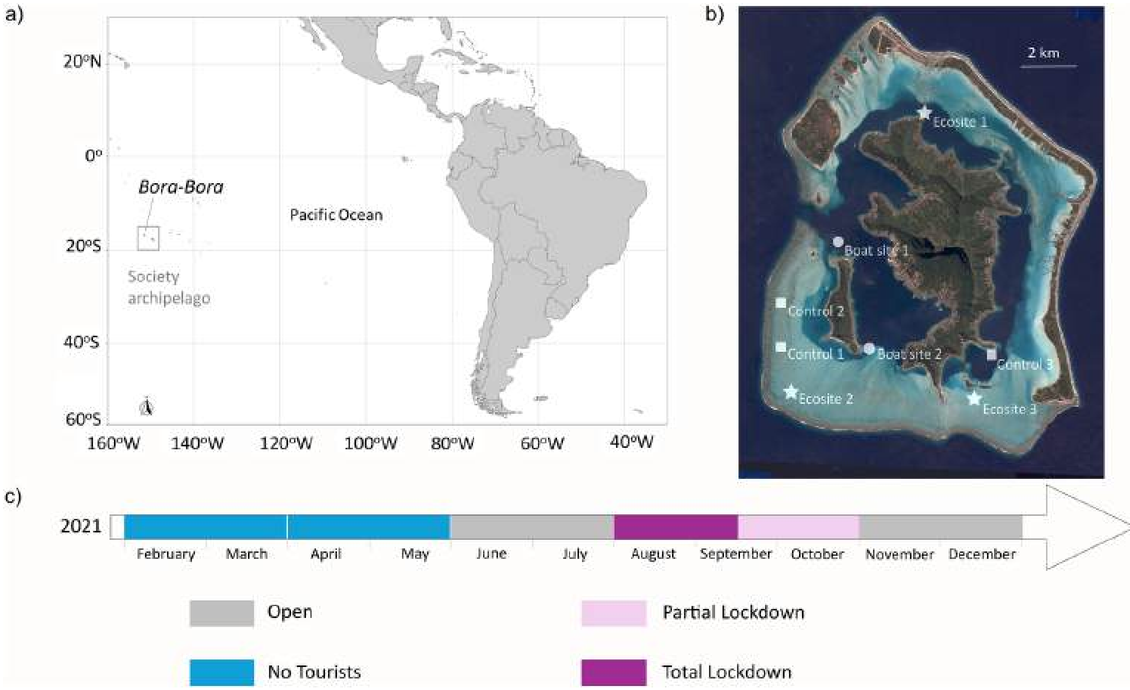

Fig. 1 Maps of (**a**) the location of the Society archipelago in the Southern Pacific Ocean, and of (**b**) the 8 surveyed sites on Bora-Bora. Squares represent control sites, stars represent eco-tourism sites and circles represent boat traffic sites. Background satellite image from CNES/Airbus, April 2014. **c** Timeline of the study with different socio-economical restriction periods

restrictions—with the greatest changes compared during the most stringent restriction, *i.e.,* total lockdown.

Materials and methods

Pandemic-related restriction periods

In 2021, coral reef fish populations were exposed to different periods of pandemic-related restrictions which we subdivided into six periods for this analysis: from February to March (no tourists 1) and from April to May (no tourists 2), when there were few tourism activities due to the absence of international tourists; from June to July (open 1) and from November to December (open 2), when no restrictions were in place and all tourism activities were occurring; from August to mid-September (total lockdown) when there were no human activities in the lagoon; and from mid-September to the end of October (partial lockdown) when tourism activities were only allowed during the week, with a complete lockdown during the weekend (Fig. 1).

Sites under varying human pressures

We selected a total of eight sites exposed to three different levels of human pressures: control (no human pressure); eco-tourism sites (low–medium human pressure); and boat traffic sites (high human pressures). Three control sites were surveyed: two on the barrier reef (control 1 & control 2) and one on the fringing reef (control 3; Fig. 1). In 2019, Bora-Bora's mayor and tourism committee designated 14 eco-tourism sites (location of coral reef-related tourism; Spalding et al. 2017) in the lagoon (on the fringing and inner side of the barrier reef) and 1 eco-tourism site on the outer barrier reef (outer slope) (Lecchini et al. 2021). Prior to the pandemic, these eco-tourism sites were visited at least five times a week by tourism operators, with an average of 20 snorkelers per visit/boat (Jossinet 2020). Eco-tourism sites are also de facto Marine Protected Areas with no fishing activities (Jossinet 2020). We selected three eco-tourism sites to survey: one on the fringing reef (eco-tourism site 1) and two on the barrier reef (eco-tourism site 2 & eco-tourism site 3; Fig. 1). We also selected two sites located in the vicinity of high boat traffic (from fishermen and tourism operators on their way to eco-tourism sites), where fishing is not restricted (boat

Table 1 Generalized Linear Model selection using Akaike's information criterion for small sample sizes (AICc) and where AICc weight is equivalent to the probability of each model

		Description	df	logLik	AICc	Weight
All species						
Density	Model 1	Dens~ Site*Restriction + (1|Month)	19	− 156.25	361.7	0
	Model 2	**Dens~ Site + Restriction + (1|Month)**	**9**	**− 162.39**	**345.1**	**0.99**
	Model 3	Dens~ Restriction + (1|Month)	7	− 176.04	367.5	0
	Model 4	Dens~ Site + (1|Month)	4	− 172.82	354.1	0.01
	Model 5	Dens~ (1|Month)	2	− 186.51	377.2	0
Richness	Model 1	Rich~ Site*Restriction + (1|Month)	19	− 264.75	578.7	0
	Model 2	**Rich~ Site + Restriction + (1|Month)**	**9**	**− 270.79**	**561.9**	**0.72**
	Model 3	Rich~ Restriction + (1|Month)	7	− 392.28	800	0
	Model 4	Rich~ Site + (1|Month)	4	− 277.63	563.7	0.28
	Model 5	Rich~ (1|Month)	2	− 399.31	802.8	0
Harvested species						
Density	Model 1	Dens~ Site*Restriction + (1|Month)	19	− 124.75	298.7	0
	Model 2	**Dens~ Site + Restriction + (1|Month)**	**9**	**− 128.67**	**277.6**	**0.44**
	Model 3	Dens~ Restriction + (1|Month)	7	− 131.52	278.4	0.29
	Model 4	Dens~ Site + (1|Month)	4	− 135.48	279.5	0.18
	Model 5	Dens~ (1|Month)	2	− 138.33	280.8	0.09
Richness	Model 1	Rich~ Site*Restriction + (1|Month)	19	− 208.27	465.7	0
	Model 2	Rich~ Site + Restriction + (1|Month)	9	− 214.09	448.5	0.25
	Model 3	Rich~ Restriction + (1|Month)	7	− 262.15	539.7	0
	Model 4	**Rich~ Site + (1|Month)**	**4**	**− 218.93**	**446.3**	**0.75**
	Model 5	Rich~ (1|Month)	2	-267.01	538.2	0

Dens = total density of fish (number of individuals per m^2) and Rich = species richness (number of species per 100 m^2), for all species at adult and juvenile stages and harvested species at adult and juvenile stages; Site = the different sites corresponding to the level of human pressures (control, eco-tourism site, boat traffic); Restriction = the six periods with different types of socio-economic restrictions (n tourists 1, no tourists 2, open 1, open 2, partial lockdown, total lockdown); Month = time of the year from February to December 2021. Selected models are indicated in bold

df degrees of freedom, *logLik* log likelihood

traffic site 1 & boat traffic site 2; Fig. 1). These boat traffic sites are located near coral pinnacles surrounded by a deeper sandy bottom.

Fish community measures

On each site, three replicate 25 m long and 4 m wide transects (100 m^2) were conducted by one expert taxonomist (DL) by snorkelling to record the fish community based on visual identification and using waterproof paper. Surveying was conducted within the seven days centred around the new moon. The surveys were conducted once per month (no survey in August): two surveys were conducted for the no tourists periods (no tourists 1 and no tourists 2), two for the open periods (open 1 and open 2), one for the total lockdown, and one for the partial lockdown. Two passes were performed per transect, at a 5-min interval; more mobile and visible fishes were recorded during the first pass and more cryptic fishes were recorded on the second pass (Lecchini and Galzin 2005). On each site, a 25 m gap was left between each transect to ensure independence. All fishes were identified to the species level and according to their ontogenetic stage based on their size and colour pattern (juveniles *vs*. adults). Fish species targeted by recreational, subsistence, and commercial fishers were categorized as harvested species (Siu et al. 2017). The average fish density (number of fishes per m^2) and species richness (number of species on each transect) for each month were calculated for all adults and juveniles and for adults and juveniles of harvested species.

Statistical analysis

Fish count data were first used to describe differences in species assemblages between the control, eco-tourism, and boat traffic sites under varying temporal human pressure using a Non-metric Multi-Dimensional Scaling analysis (NMDS). This analysis was performed on the Bray–Curtis dissimilarity matrix using the "metaMDS" function of the *vegan* package in R (version 2.6–2, Oksanen et al. 2020). Permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis distance with 9999 permutations was then used to investigate

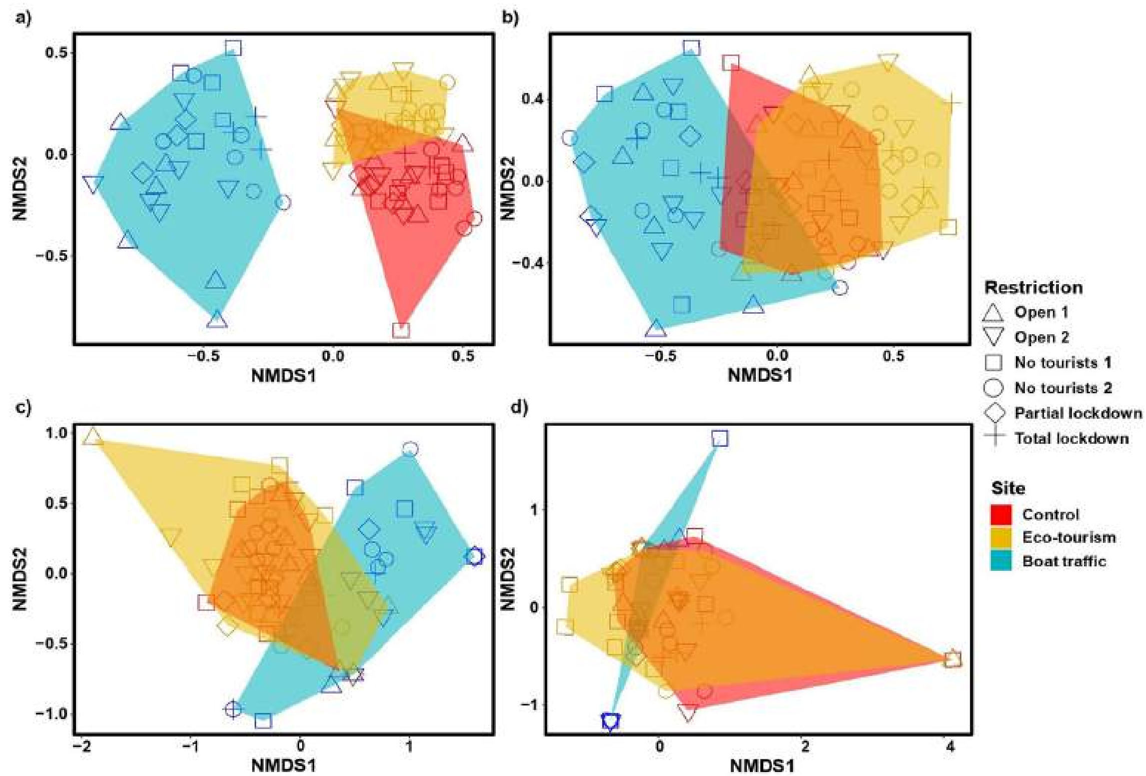

Fig. 2 Non-metric multidimensional scaling (NMDS) plots of the similarity of fish assemblages calculated from the Bray–Curtis distances on the number of **a**) all adult fish, **b** all juvenile fish, **c** harvested adult fish, and **d** harvested juvenile fish in the different sites during the six restriction periods on control (red), eco-tourism (yellow), and boat traffic (blue) sites. Note that on panel c, the control sites overlap the eco-tourism sites

differences in species assemblages using the "adonis2" function. Four models were run for adults and juveniles of all species and harvested species with restriction period, month, and site as factors. Species which were most responsible for the differences in fish assemblages between groups were identified through an indicator species analysis using the "multipatt" function of the *indicspecies* package (version 1.7.12, De Cáceres et al. 2010) by running 9999 permutations.

Secondly, the effect of the restriction periods and of the type of sites on the total density and total species richness (adults and juveniles together) for all species and harvested species was investigated by running generalised linear models (GLMs) using the *lme4* package (Bates et al. 2015). Density or richness were set as the dependent variables for all species and harvested species. The restriction periods (no tourists 1, no tourists 2, open 1, open 2, partial lockdown, and total lockdown) and the type of sites (control, eco-tourism site, and boat traffic) were set as categorical effects. For all models, no tourists 1 and control sites were set as the reference groups for restriction periods and sites, respectively. Potential temporal correlation and the lack of independence in density and richness within each restriction period and site were accounted for by setting the month as a random effect. The models were fitted with Poisson distributions. The full model was dredged, creating a set of new models containing all possible combinations of the factors, with the "dredge" function of the *MuMIn* package (Bartoń 2003). These models were ranked based on the decreasing model fit, using Akaike's information criterion corrected for small sample size (AICc) weight; the smaller the weight, the lower its contribution to parameter estimates (Burnham & Anderson 2002) (Table 1). The goodness of fit of the selected model (with the highest weight) was measured with the deviance goodness of fit test (all P values > 0.05, suggesting no overdispersion).

All statistical analyses were conducted using R-Studio (R version 4.2.0) at the significance level $\alpha = 0.05$.

Results

Fish assemblages in relation to human pressure, month, and restriction period

The NMDS analysis (Fig. 2) graphically revealed that adult fish assemblages (of all species and of harvested species) varied with human pressure both spatially and temporally. There were significant differences for all

Table 2 List of species that were identified as significantly responsible for the differences in fish assemblages across one or two human pressures (control, eco-tourism site, boat traffic, and combinations) at the adult and juvenile stages

Adults

Control			Ecosite			Boat traffic			Control + Ecosite			Boat traffic + Ecosite		
Species	stat	P	Species	stat	P	Species	stat	P	Species	stat	P	Species	stat	P
Chromis viridis	0.72	< 10-3	*Lutjanus fulvus*	0.64	< 10-3	*Dascyllus flavicaudus*	0.83	< 10-3	*Myripristis pralina*	0.63	< 10-3	*Zebrasoma scopas*	0.48	< 10-3
Chaetodon trifasciatus	0.61	< 10-3	*Gnathodentex aurolineatus*	0.56	< 10-3	*Centropyge bispinosa*	0.41	< 10-3	*Stegastes nigricans*	0.56	< 10-3	*Pomacentrus pavo*	0.38	< 10-3
Chrysiptera leucopoma	0.49	< 10-3	*Abudefduf sexfasciatus*	0.54	< 10-3	*Pygoplites diacanthus*	0.35	0.003	*Halichoeres hortulanus*	0.51	< 10-3			
Chaetodon ephippium	0.49	< 10-3	*Balistapus undulatus*	0.53	< 10-3	*Chromis iomelas*	0.33	0.003	*Labroides dimidiatus*	0.40	< 10-3			
Acanthurus triostegus	0.48	< 10-3	*Naso lituratus*	0.46	< 10-3	*Forcipiger longirostris*	0.32	0.001	*Heniochus chrysostomus*	0.38	< 10-3			
Neocirrhites armatus	0.42	< 10-3	*Zebrasoma veliferum*	0.39	< 10-3	*Fistularia commersonii*	0.29	0.011	*Neoniphon sammara*	0.34	0.004			
Caracanthus maculatus	0.41	< 10-3	*Abudefduf septemfasciatus*	0.39	< 10-3	*Diodon histrix*	0.26	0.04	*Halichoeres trimaculatus*	0.32	0.007			
Dascyllus aruanus	0.40	< 10-3	*Siganus spinus*	0.38	< 10-3				*Thalassoma hardwicke*	0.31	0.011			
Coris aygula	0.39	< 10-3	*Thalassoma purpureum*	0.36	< 10-3				*Halichoeres margaritaceus*	0.25	0.036			
Coris gaimard	0.38	0.004	*Chaetodon ulietensis*	0.34	0.001				*Cheilinus trilobatus*	0.25	0.045			
Chrysiptera glauca	0.32	0.004	*Chaetodon auriga*	0.34	0.003									
Sargocentron spiniferum	0.32	0.002	*Acanthurus nigricans*	0.27	< 10-3									
Stethojulis bandanensis	0.28	0.019	*Aulostomus chinensis*	0.25	0.040									
Ctenochaetus flavicauda	0.27	0.024												
Paracirrhites arcatus	0.26	0.032												
Parupeneus multifasciatus	0.25	0.046												
Scarus psittacus	0.25	0.045												
Scarus oviceps	0.24	0.020												

Juveniles

Control			Ecosite			Boat traffic			Control + Ecosite		
Species	stat	P	Species	stat	P	Species	stat	P	Species	stat	P
Chaetodon trifasciatus	0.62	< 10-3	*Monotaxis grandoculis*	0.32	0.006	*Pomacentrus pavo*	0.42	< 10-3	*Thalassoma hardwicke*	0.53	< 10-3
Halichoeres hortulanus	0.47	< 10-3				*Ctenochaetus striatus*	0.26	0.04	*Scarus sordidus*	0.52	< 10-3
Gomphosus varius	0.47	< 10-3							*Stegastes nigricans*	0.51	< 10-3
Scarus psittacus	0.32	0.022							*Halichoeres margaritaceus*	0.27	0.041
Chromis viridis	0.30	0.013									
Chrysiptera leucopoma	0.29	0.019									
Chaetodon citrinellus	0.27	0.034									

Species highlighted in grey are harvested species. Species are ranked in decreasing order according to the value of their association statistic. P values are the result of an indicator species analysis run with 9999 permutations

species between the study sites exposed to different human pressures (PERMANOVA, $F_{2,76} = 20.39$, $P < 0.001$), as well as between months ($F_{4,76} = 1.53$, $P = 0.027$) and restriction periods ($F_{5,76} = 4.45$, $P < 0.001$). For harvested species, there were significant differences in adult fish assemblages between the study sites exposed to different human pressures (PERMANOVA, $F_{2,76} = 11.18$, $P < 0.001$) and between restriction periods ($F_{5,76} = 4.85$, $P < 0.001$). The differences between months were close to significance ($F_{4,76} = 1.45$, $P = 0.052$). For juveniles, there were significant differences for all species between the study sites exposed to different human pressures (PERMANOVA, $F_{2,69} = 9.50$, $P < 0.001$), between months ($F_{4,69} = 1.51$, $P = 0.031$). No significant differences were found between restriction periods ($F_{5,69} = 1.31$, $P = 0.089$). In harvested species, there were significant differences in juvenile fish assemblages between the study sites exposed to different human pressures (PERMANOVA, $F_{2,60} = 6.71$, $P < 0.001$), between restriction periods ($F_{5,60} = 1.66$, $P = 0.035$), and between months ($F_{4,60} = 1.73$, $P = 0.032$).

Of the total of 133 adult species observed, 50 were significantly responsible for the differences in fish assemblages between the sites with different human pressure (Table 2). Similarly, for juveniles, 16 species were responsible for the differences in fish assemblages between sites (Table 2). Differences in fish assemblages between the control sites and the other sites were linked to 18 species for adults and 7 for juveniles, with 4 species in common. 41 species were responsible for the differences between the fish communities of control and eco-tourism sites compared with the boat traffic sites (Table 2). The boat traffic sites were associated with only 7 adult species and 4 juvenile species. For harvested adults, out of the total of 49 harvested species observed, 12 were responsible for the differences in fish assemblages across restriction periods at the adult stage and 4 at the juvenile stage (Table 2). None of the harvested species were associated with the boat traffic sites at the adult stage, and only 1, *Ctenochaetus striatus*, was associated at the juvenile stage.

The density of fish at adult and juvenile stages showed significant differences between sites with different human pressures, with significantly lower densities on the boat traffic sites compared to the control sites for both all species and harvested species. An effect of restriction period was found with lower densities of all fish species during the open periods compared with the no tourists 1 condition, and significantly higher densities during the total lockdown period compared with no tourists 1 (Table 3; Fig. 3). Of note, on boat traffic sites, the average density of adults of all species and of harvested species increased threefold during the total lockdowns, and twofold during the partial lockdown and no tourist periods, compared to the open periods. The largest increase on eco-tourism sites was during the no tourist period compared to the open period, with a 2.7-fold increase in the adult density for all fish. No change beyond 1.5-fold for any of the adult or juvenile densities was observed between periods on control sites (Fig. 3). The total species richness for adult and juvenile stages showed significant spatial differences between human pressures, with lower densities on the boat traffic sites compared to the

Table 3 Summary of the generalized linear model analysis performed on the total density of fish (all species at adult and juvenile stages and harvested species at adult and juvenile stages)

		Estimate	SE	*z* value	*P*
All species					
	Intercept	**1.89**	**0.12**	**15.8**	**< 0.001**
Human pressures	**Boat traffic**	**− 0.62**	**0.13**	**− 4.84**	**< 0.001**
	Eco-tourism	− 0.09	0.11	− 0.86	0.39
Restriction periods	No tourists 2	0.06	0.14	0.44	0.66
	Open 1	**− 0.52**	**0.17**	**− 3.08**	**0.002**
	Total lockdown	**0.36**	**0.16**	**2.35**	**0.02**
	Partial lockdown	− 0.04	0.18	-0.21	0.83
	Open 2	**− 0.50**	**0.17**	**− 2.99**	**0.003**
Harvested species					
	Intercept	**1.01**	**0.18**	**5.59**	**< 0.001**
Human pressures	**Boat traffic**	**− 0.41**	**0.18**	**− 2.32**	**0.021**
	Eco-tourism	− 0.11	0.16	− 0.68	0.49
Restriction periods	No tourist 2	0.13	0.22	0.58	0.56
	Open 1	− 0.45	0.25	− 1.78	0.07
	Total lockdown	0.45	0.24	1.87	0.06
	Partial lockdown	0.13	0.26	0.48	0.63
	Open 2	− 0.34	0.24	− 1.40	0.16

No tourists 1 and control sites were set as the reference groups for restriction periods and human pressures, respectively. Significant differences are highlighted in bold

control sites for both all species and harvested species. The species richness of harvested species was also significantly higher on eco-tourism sites compared to the control sites (Table 4, Fig. 3). Restriction period affected the richness of all species, with significantly less species during the two open periods compared with no tourists 1 condition (Table 4) (Fig. 3).

Discussion

This study took advantage of the global COVID-19 pandemic-related activity and travel restrictions in 2021 to determine the impact that human activities exert on coral reef fish communities (Rutz et al. 2020). We explored the effect of restriction periods on fish assemblages on sites along a gradient of human pressures—control, eco-tourism sites and boat traffic sites—in the lagoon of Bora-Bora, a tourism destination in French Polynesia. Our study finds that throughout 2021, fish communities rapidly responded to restriction periods, at the scale of weeks to months. To the best of our knowledge, this is a one-of-kind study demonstrating rapid fish community response to tourism-related human activities. Our results showed that from February to December 2021, a period marked by multiple COVID-19-related travel restrictions and fluctuations in the number of international tourists visiting the island, the density and species richness of lagoonal juvenile and adult fish populations for all species, as well as for harvested fish species, showed rapid and dynamic responses corresponding to the level of restrictions on travel and tourism activities.

Irrespective of pandemic-related restrictions, fish populations were relatively similar (Fig. 2), with high density and diversity, on the eco-tourism sites, where tourists snorkel and scuba-dive, and on the control sites with limited human presence (Fig. 3). On the other hand, boat traffic sites, where fishing and intense boat passage occur, had a different fish species assemblage (Fig. 2) with less abundant and diverse populations (Fig. 3). Only one harvested species was associated with boat traffic sites at the juvenile stage, the striated surgeonfish (*Ctenochaetus striatus*), and none at the adult stage. The presence of boats and fishing activities may be driving commercially important species to avoid this area of the lagoon of Bora-Bora (Table 2). Boat-related noise pollution can affect coral reef marine organisms (Barber et al. 2011; Duarte et al. 2021). Anthropogenic noise is one of the characteristic symptoms of human activity in marine ecosystems; it can be used as a proxy of human activity (Ferrier-Pagès et al. 2021). Boat noise represents a major stress for adult and juvenile fish, increasing the levels of stress hormones and interfering with communication and social interactions, disrupting reproduction as well as feeding and/or anti-predatory behaviour (Hanache et al. 2020; Mills et al. 2020; Gairin et al. 2021; Nedelec et al. 2022). This can decrease survival (Simpson et al. 2016; Ferrari et al. 2018; McCormick et al. 2018). Alterations in behaviour and physiology impact inter-species interactions (Nedelec et al. 2017) and are likely to compromise population dynamics, community structure (as potentially highlighted here), and underlying ecological functions (Shafiei Sabet et al. 2016). In addition to noise pollution, fishing pressure may lead to further straining of the fish communities living in the boat traffic sites. Boat noise and fishing may have direct impacts on fish survival and indirect impacts through changes in habitat preferences as juveniles (*e.g.,* avoidance of noisy areas by coral reef fish larvae, Holles et al. 2013; and pelagic fish, Kok et al. 2021). Few studies focus on the impact of human activities of juvenile fish in the field; here, they are shown to be less abundant and diverse on sites exposed to boat traffic. Despite the major potential consequences of fishing and noise pollution on coral reef fish, which are key resources for both tourism and fisheries, our knowledge of the impacts of anthropogenic stress on juvenile reef fish survival and habitat preference remains limited.

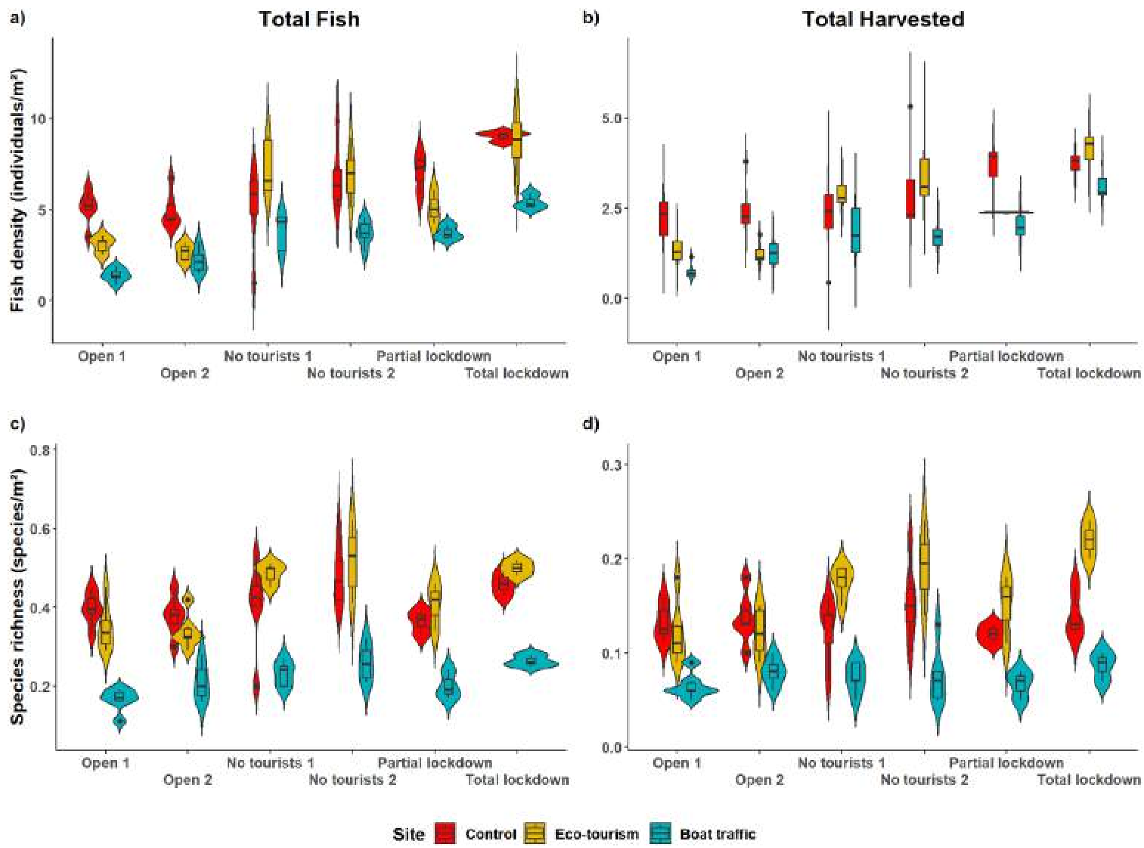

Fig. 3 Box plots and violin plots of the total density (number of individuals per m^2) of (**a**) all fish species and (**b**) harvested species as well as total species richness (number of species per m^2 transect, with three transects per site) of (**c**) all fish and (**d**) harvested species at all stages observed during the six types of restriction periods in Bora-Bora in boat traffic sites (blue), control sites (red), and eco-tourism sites (yellow). Boxes represent the first and third quartiles, thick horizontal bars are the median (second quartile), whiskers correspond to the extreme quantile values and dots are potential outliers. Violin plots describe the distribution of the data for each group

In addition to spatial differences, we observed temporal variations in fish communities in response to human pressures. In agreement with our predictions, temporal changes in the density of fish populations were related to the level of pandemic-related restriction, with the greatest fish densities observed during the most stringent restrictions, *i.e.*, the total lockdown period (Fig. 3). Inversely, periods of unrestricted activities (open periods) were associated with the lowest density of all fish and of harvested species on all sites. Strikingly, there was a threefold increase in adult density during the total lockdown compared to the open periods on boat traffic sites, and a 2.7-fold increase in adult density on eco-tourism sites during no tourist periods (Fig. 3). These results echo results from other locations—for instance, a 2.5-fold increase in fish density was observed during lockdowns in a marine reserve of Mexico, which was suggested to be linked to a return of fish to sites usually affected by noise and human presence due to boat diving activities (Olán-González et al. 2023). These results are also in accordance with surveys performed before, during, and after the lockdown period of 2020 on Bora-Bora, which found that fish density more than doubled on eco-tourism sites during lockdown periods (Lecchini et al. 2021).

As the different restriction periods were implemented over the course of a single year, we cannot exclude a seasonality effect in the results. However, we did not observe significant differences between the two open periods (June–July, during French Polynesia's cool and dry winter and November–December, during the hotter and more humid summer) nor between the two no tourists periods (February–March, end of summer and April–May, start of winter). In addition, there were no major weather or bleaching events on Bora-Bora during the study period. Over the 2021 timeseries, the most striking result is the variation in fish density on the sites, correlated to changes in restriction levels. This tight relationship highlights the fast temporal association and consistent response of fish to human presence. Restrictions started in March 2020 and their subsequent implementations and removals, which can be referred to as 'anthropulses' (Rutz 2022), continued to cause significant changes in fish presence on habitats in 2021. These fluctuations are scenarios that, before

Table 4 Summary of the generalized linear model analysis performed on the total species richness (all species at adult and juvenile stages and harvested species at adult and juvenile stages). No tourists 1 and control sites were set as the reference groups for restriction periods and human pressures, respectively. Significant differences are highlighted in bold

		Estimate	SE	*z* value	*P*
All species					
	Intercept	**3.77**	**0.06**	**63.24**	**< 0.001**
Human pressures	**Boat traffic**	**− 0.64**	**0.49**	**− 13.08**	**< 0.001**
	Eco-tourism	0.03	0.40	0.71	0.48
Restriction periods	No tourists 2	0.12	0.07	1.55	0.12
	Open 1	**− 0.21**	**0.08**	**− 2.57**	**0.01**
	Total lockdown	0.09	0.09	0.98	0.32
	Partial lockdown	− 0.14	0.09	− 1.43	0.15
	Open 2	**− 0.19**	**0.08**	**− 2.34**	**0.02**
Harvested species					
	Intercept	**2.59**	**0.06**	**42.15**	**< 0.001**
Human pressures	**Boat traffic**	**− 0.60**	**0.08**	**− 7.14**	**< 0.001**
	Eco-tourism	**0.15**	**0.07**	**2.30**	**0.02**

the COVID-19 pandemic, had rarely occurred and been sparsely documented by environmental impact studies. The COVID-19 pandemic has had a drastic impact on underwater ecosystems across the world. On reefs, a study conducted during a lockdown in Guadeloupe confirmed a significant decrease (− 6 to − 10 dB) in the mean underwater sound level and suggested that the decrease in anthropogenic noise was accompanied by a decrease in animal sound production, with less sound needed for effective communication (Bertucci et al. 2021). On coral reefs, fish may acclimate to boat noise when chronically exposed (Nedelec et al. 2016), and may similarly acclimate to regular human presence, as noted in laboratory experiments (Baker et al. 2013) and predicted for wild coral reef fish (Geffroy et al. 2015). This acclimation may also be individual- or species-specific, and context-dependent; a behavioural study examining acclimation to cameras and observers found no acclimation of the fish to the presence of observers (Nanninga et al. 2017). The random and month-scale alternation between periods of anthropogenic presence and absence caused by pandemic-related restrictions in French Polynesia was a novel situation with unknown effects on wild organisms. Here, we show that fish communities, which can be presumed to have acclimated to the constant presence of human presence and noise pollution in the lagoon of Bora-Bora over the past few decades, respond dynamically to the presence of humans in the lagoon.

Interestingly, fish population assemblages were more different spatially than temporally (Fig. 2); while density varied, the community composition, in terms of the proportion of different species, remained relatively constant throughout the different socioeconomical restrictions. The functioning of the trophic webs might have remained stable throughout 2021 on each study site. We hypothesise that overall ecosystem functioning may not have drastically changed during the short-term variations in pandemic-related restrictions. Such results were also found on the sites studied during the previous year (Lecchini et al. 2021), with community compositions that did not differ temporally across restriction periods. However, longer term decreases in human pressures, for instance through the implementation of management plans, with limited tourism, fishing, and boat traffic over multiple fish generations, could lead to positive shifts in community composition and differences in ecosystem functioning. It is difficult to predict such consequences through the lens of the short-term 2021 COVID-19-related restrictions in French Polynesia. Throughout the world, the noticeable and rapid beneficial effects of lockdowns on natural ecosystems highlighted the harmful impacts of humans on the environment and have led scientists to call for a reduction in activities, most notably regarding fisheries (Kemp et al. 2020; Coll et al. 2021) but also tourism (Rume and Islam 2020).

Our study confirms that COVID-19-related restrictions can be used to explore the human-related drivers of fish assemblages in natural settings, such as in a busy coral reef lagoon. In terms of conservation objectives, this study highlights the direct links between tourism-related human activities and fish communities. The creation of no-take zones and restriction of boat access in key parts of the lagoon of Bora-Bora and other marine settings worldwide could rapidly result in fish communities returning to locations they may have previously avoided, which can be beneficial in terms of survival, reproduction, population maintenance, and resilience (Arthington et al. 2016). Regulating fishing catches and boat passage in intensely frequented areas may be a rapid remedial measure to increase fish density. In Bora-Bora, human presence is particularly intense near the only pass of the barrier reef circling the island. However, the pass is a key zone for fish reproduction, notably with reproductive aggregations (Domeier and Colin 1997; Sadovy De Mitcheson et al. 2008). Regulating fishing practices and boat passage during reproduction events may be of high importance to increase fish stocks. In Bora-Bora, a locally managed Marine Protected Area called 'rahui' will be put in place to restrict access to the southern edge of the lagoon. Through this study, we predict that the rahui will allow fish to rapidly return to the ex-fishing grounds in high numbers and contribute to a long-term increase of the marine biomass and biodiversity of the island.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-024-05589-w.

Acknowledgements We would like to thank the staff of 'Polynésienne des Eaux', 'Ia Vai Ma Noa Bora-Bora and the 'Commune de Bora-Bora' for their help.

Author contribution statement DL originally formulated the idea, DL and FB developed methodology, DL, LM, CB, FB, VW conducted the formal analysis and investigation, FB and EG wrote the original draft, FB, EG, SCM, NR reviewed and edited the manuscript, DL acquired the funding, TM, VS, GTS provided resources.

Funding This work has received several grants: Fondation de France (2019–08602), Polynésienne des Eaux, ANR-19-CE34-0006-Manini and ANR-19-CE14-0010-SENSO, ANR-23-SSRP-0020–01, ANRT grant (CIFRE 2021/1268).

Data availability The script and datasets used and/or analysed during the current study are publicly available on FigShare (https://doi.org/10.6084/m9.figshare.24227932).

Declarations

Conflict of interest All authors declare that they have no conflicts of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

References

Arthington AH, Dulvy NK, Gladstone W, Winfield IJ (2016) Fish conservation in freshwater and marine realms: status, threats and management. Aquat Conserv Mar Freshw Ecosyst 26:838–857. https://doi.org/10.1002/aqc.2712

Baker MR, Gobush KS, Vynne CH (2013) Review of factors influencing stress hormones in fish and wildlife. J Nat Conserv 21:309–318

Barber JR, Burdett CL, Reed SE et al (2011) Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. Landsc Ecol 26:1281–1295. https://doi.org/10.1007/s10980-011-9646-7

Bertucci F, Lecchini D, Greeven C et al (2021) Changes to an urban marina soundscape associated with COVID-19 lockdown in guadeloupe. Environ Pollut Barking Essex 289:117898. https://doi.org/10.1016/j.envpol.2021.117898

Braga F, Scarpa GM, Brando VE et al (2020) COVID-19 lockdown measures reveal human impact on water transparency in the Venice Lagoon. Sci Total Environ 736:139612. https://doi.org/10.1016/j.scitotenv.2020.139612

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer New-York, New York

China V, Zvuloni A, Roll U, Belmaker J (2021) Reduced human activity in shallow reefs during the COVID-19 pandemic increases fish evenness. Biol Conserv 257:109103. https://doi.org/10.1016/j.biocon.2021.109103

Coll M, Ortega-Cerdà M, Mascarell-Rocher Y (2021) Ecological and economic effects of COVID-19 in marine fisheries from the Northwestern Mediterranean Sea. Biol Conserv 255:108997. https://doi.org/10.1016/j.biocon.2021.108997

De Cáceres M, Legendre P, Moretti M (2010) Improving indicator species analysis by combining groups of sites. Oikos 119:1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci 60:698–726

Duarte CM, Chapuis L, Collin SP et al (2021) The soundscape of the Anthropocene ocean. Science 371:eaba4658. https://doi.org/10.1126/science.aba4658

Ferrari MCO, McCormick MI, Meekan MG et al (2018) School is out on noisy reefs: the effect of boat noise on predator learning and survival of juvenile coral reef fishes. Proc R Soc B Biol Sci 285:20180033. https://doi.org/10.1098/rspb.2018.0033

Ferrier-Pagès C, Leal MC, Calado R et al (2021) Noise pollution on coral reefs?—a yet underestimated threat to coral reef communities. Mar Pollut Bull 165:112129. https://doi.org/10.1016/j.marpolbul.2021.112129

Gairin E, Collin A, James D et al (2021) Spatiotemporal trends of bora bora's shoreline classification and movement using high-resolution imagery from 1955 to 2019. Remote Sens 13:4692. https://doi.org/10.3390/rs13224692

Geffroy B, Samia DSM, Bessa E, Blumstein DT (2015) How nature-based tourism might increase prey vulnerability to predators. Trends Ecol Evol 30:755–765. https://doi.org/10.1016/j.tree.2015.09.010

Giraud-Renard E, Dolique F, Collin A et al (2022) long-term evolution of the Guadeloupean Shoreline (1950–2017). J Coast Res 38:976–987. https://doi.org/10.2112/JCOASTRES-D-21-00161.1

Hanache P, Spataro T, Firmat C et al (2020) Noise-induced reduction in the attack rate of a planktivorous freshwater fish revealed by functional response analysis. Freshw Biol 65:75–85. https://doi.org/10.1111/fwb.13271

Holles S, Simpson SD, Radford AN et al (2013) Boat noise disrupts orientation behaviour in a coral reef fish. Mar Ecol Prog Ser 485:295–300. https://doi.org/10.3354/meps10346

Huveneers C, Jaine FRA, Barnett A et al (2021) The power of national acoustic tracking networks to assess the impacts of human activity on marine organisms during the COVID-19 pandemic. Biol Conserv 256:108995. https://doi.org/10.1016/j.biocon.2021.108995

Jossinet F (2020) Les bouts du monde touristiques: Gérer un milieu exceptionnel entre ressource et patrimoine (Bora-Bora, Polynésie française) Master report. University of Paris

Kemp PS, Froese R, Pauly D (2020) COVID-19 provides an opportunity to advance a sustainable UK fisheries policy in a post-Brexit brave new world. Mar Policy 120:104114. https://doi.org/10.1016/j.marpol.2020.104114

Kok ACM, Bruil L, Berges B et al (2021) An echosounder view on the potential effects of impulsive noise pollution on pelagic fish around windfarms in the North Sea. Environ Pollut 290:118063. https://doi.org/10.1016/j.envpol.2021.118063

Lecchini D, Galzin R (2005) Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). Mar Biol 147:47–58. https://doi.org/10.1007/s00227-004-1543-z

Lecchini D, Brooker RM, Waqalevu V et al (2021) Effects of COVID-19 pandemic restrictions on coral reef fishes at eco-tourism sites in Bora-Bora, French Polynesia. Mar Env Res 170:105451–105451

Mallik C, Gadhavi H, Lal S et al (2021) Effect of lockdown on pollutant levels in the delhi megacity: role of local emission sources and chemical lifetimes. Front Environ Sci. https://doi.org/10.3389/fenvs.2021.743894

March D, Metcalfe K, Tintoré J, Godley BJ (2021) Tracking the global reduction of marine traffic during the COVID-19 pandemic. Nat Commun 12:2415. https://doi.org/10.1038/s41467-021-22423-6

McCormick MI, Allan BJM, Harding H, Simpson SD (2018) Boat noise impacts risk assessment in a coral reef fish but effects depend on engine type. Sci Rep 8:3847. https://doi.org/10.1038/s41598-018-22104-3

Mills SC, Beldade R, Henry L et al (2020) Hormonal and behavioural effects of motorboat noise on wild coral reef fish. Environ Pollut Barking Essex 262:114250. https://doi.org/10.1016/j.envpol.2020.114250

Nanninga GB, Côté IM, Beldade R, Mills SC (2017) Behavioural acclimation to cameras and observers in coral reef fishes. Ethology 123:705–711. https://doi.org/10.1111/eth.12642

Nedelec SL, Mills SC, Lecchini D et al (2016) (2016) Repeated exposure to noise increases tolerance in a coral reef fish. Environ Pollut Barking Essex 216:428–436. https://doi.org/10.1016/j.envpol.2016.05.058

Nedelec SL, Mills SC, Radford AN et al (2017) Motorboat noise disrupts co-operative interspecific interactions. Sci Rep 7:6987. https://doi.org/10.1038/s41598-017-06515-2

Nedelec SL, Radford AN, Gatenby P et al (2022) Limiting motorboat noise on coral reefs boosts fish reproductive success. Nat Commun 13:2822. https://doi.org/10.1038/s41467-022-30332-5

Oksanen J, Blanchet FG, Friendly M, et al (2020) vegan community ecology package version 2.5–7 November 2020

Olán-González M, Reyes-Bonilla H, Arreola-Alarcón IM et al (2023) Ecotourism impacts on reef fishes in a marine reserve during the COVID-19 era. Front Ecol Environ 21:317–323. https://doi.org/10.1002/fee.2657

Pörtner HO, Roberts DC, Masson-Delmotte V (2019) The ocean and cryosphere in a changing climate: special report of the intergovernmental panel on climate change, 1st edn. Cambridge University Press

Rouphael AB, Inglis GJ (2001) "Take only photographs and leave only footprints"?: AN experimental study of the impacts of underwater photographers on coral reef dive sites. Biol Conserv 100:281–287. https://doi.org/10.1016/S0006-3207(01)00032-5

Rume T, Islam SMD-U (2020) Environmental effects of COVID-19 pandemic and potential strategies of sustainability. Heliyon 6:e04965. https://doi.org/10.1016/j.heliyon.2020.e04965

Rutz C (2022) Studying pauses and pulses in human mobility and their environmental impacts. Nat Rev Earth Environ 3:157–159. https://doi.org/10.1038/s43017-022-00276-x

Rutz C, Loretto M-C, Bates AE et al (2020) COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat Ecol Evol 4:1156–1159. https://doi.org/10.1038/s41559-020-1237-z

Sadovy De Mitcheson Y, Cornish A, Domeier M et al (2008) A global baseline for spawning aggregations of reef fishes. Conserv Biol J Soc Conserv Biol 22:1233–1244. https://doi.org/10.1111/j.1523-1739.2008.01020.x

Shafiei Sabet S, Wesdorp K, Campbell J et al (2016) Behavioural responses to sound exposure in captivity by two fish species with different hearing ability. Anim Behav 116:1–11. https://doi.org/10.1016/j.anbehav.2016.03.027

Simpson SD, Radford AN, Nedelec SL et al (2016) Anthropogenic noise increases fish mortality by predation. Nat Commun 7:10544. https://doi.org/10.1038/ncomms10544

Siriwong S, True JD, Piromvarakorn S (2018) Number of tourists has less impact on coral reef health than the presence of tourism infrastructure. Songklanakarin J Sci Technol 40:1437–1445. https://doi.org/10.14456/sjst-psu.2018.175

Siu G, Bacchet P, Bernardi G et al (2017) Shore fishes of French Polynesia. Cybium. https://doi.org/10.26028/CYBIUM/2017-413-003

Soto EH, Botero CM, Milanés CB et al (2021) How does the beach ecosystem change without tourists during COVID-19 lockdown? Biol Conserv 255:108972. https://doi.org/10.1016/j.biocon.2021.108972

Spalding M, Burke L, Wood SA et al (2017) Mapping the global value and distribution of coral reef tourism. Mar Policy 82:104–113. https://doi.org/10.1016/j.marpol.2017.05.014

Spalding M, Burke L, Fyall A (2021) Covid-19: implications for nature and tourism. Anatolia 32:126–127. https://doi.org/10.1080/13032917.2020.1791524

Tratalos JA, Austin TJ (2001) Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. Biol Conserv 102:67–75. https://doi.org/10.1016/S0006-3207(01)00085-4

Uyarra MC, Côté IM (2007) The quest for cryptic creatures: impacts of species-focused recreational diving on corals. Biol Conserv 136:77–84. https://doi.org/10.1016/j.biocon.2006.11.006

Weng KC, Friedlander AM, Gajdzik L et al (2023) Decreased tourism during the COVID-19 pandemic positively affects reef fish in a high use marine protected area. PLoS ONE 18:e0283683. https://doi.org/10.1371/journal.pone.0283683

Yunus AP, Masago Y, Hijioka Y (2020) COVID-19 and surface water quality: improved lake water quality during the lockdown. Sci Total Environ 731:139012. https://doi.org/10.1016/j.scitotenv.2020.139012