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Effects of COVID-19 lockdown on the observed density of coral reef fish along coastal habitats of Moorea, French Polynesia

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Abstract

During the first COVID-19 lockdown in 2020, levels of coastal activities such as subsistence fishing and marine tourism declined rapidly throughout French Polynesia. Here, we examined whether the reduction in coastal use led to changes in fish density around the island of Moorea. Two natural coastal marine habitats (bare sand and mangrove) and one type of man-made coastal structure (embankment) were monitored on the west coast of the island before and after the first COVID-19 lockdown. At the end of the lockdown (May 2020), significantly higher apparent densities of juvenile and adult fish, including many harvested species, were recorded compared to levels documented in 2019 at the same period (April 2019). Fish densities subsequently declined as coastal activities recovered; however, 2 months after the end of the lockdown (July 2020), densities were still higher than they were in July 2019 with significant family-specific variation across habitats. This study highlights that short-term reductions in human activity can have a positive impact on coastal fish communities and may encourage future management policy that minimizes human impacts on coastline habitats.

Keywords Anthropause · Coral reef fish · COVID-19 · Coastline habitat · Human activities · Recreational activities

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Background

Coastal habitats and environments associated with coral reefs support a wide range of essential socio-economic (e.g. food production, tourism, biotechnology) and biophysical (e.g. fish nursery area, coastal protection) processes (Lecchini et al. 2013; Aouiche et al. 2016; Madi Moussa et al. 2019) that provide direct benefits to at least 500 million people living in tropical coastal regions worldwide (Wilkinson and Salvat 2012; Costanza et al. 2014; Hoegh-Guldberg 2015). While it is clear that the constant presence of humans affects coastal environments (Hughes et al. 2017; Moritz et al. 2018; Morrison et al. 2019), the COVID-19 pandemic and associated government-mandated lockdowns that occurred in 2020 created a window during which the degree of human impact could be isolated and quantified (Corlett et al. 2020; Rice et al. 2020; Sandford 2020). Many studies have noted that the reduction of human activities quickly leads to positive effects on the environment and on wild organisms (e.g. Arora et al. 2020; Rosenbloom and Markard 2020; Zambrano-Monserrate et al. 2020; Bertucci et al. 2021; Kumar et al. 2021). Thus, lockdowns initially appeared to relieve marine ecosystems of anthropogenic pressure (Bates et al. 2021); however, the cessation of tourism led to a greater dependence

of some populations on natural resources (Buckley 2020), and COVID-19-related restrictions have negatively impacted small-scale fisheries (Bennet et al. 2020; Campbell et al. 2021).

The first COVID-19 infection was identified in French Polynesia on March 10, 2020, and the World Health Organization declared COVID-19 a pandemic on March 11, 2020. The country immediately started to prohibit international boats from stopping or anchoring in French Polynesian waters. On March 18, inter-island flights were strictly limited to travels that could not be postponed (with presentation of an exemption form) and international flights were cancelled on March 19. Between March 11 and March 19, approximately 3000 tourists left French Polynesia. The country instituted a total lockdown from March 20, during which public movements were restricted to short trips of up to 1 h per day and within a maximum radius of 2 km of households. Only a few grocery stores remained open for basic purchases (www.polynesie-francaise.pref.gouv.fr/Dossiers/Information-COVID-19/Textes-officiels/2020/Textes-officiels). As a result, the majority of maritime and tourism activities ceased for 6 weeks (until May 4, 2020). Many residents lost their jobs (permanently or temporarily) and turned to subsistence fishing along the coastline to feed themselves and their families, with spear or line fishing rather than the usual boat fishing, due to movement limitations (TB and DL personal observations). This differential pressure on local resources to meet food and subsistence needs along the coast, as well as the decrease in human presence at sea, is therefore likely to have affected fish communities (Hoffman 2020). In a recent study, Lecchini et al. (2021) showed that fish density at ecotourism sites in Bora-Bora (French Polynesia) increased significantly from March to May 2020 in the absence of humans and returned to pre-lockdown levels in August 2020 (12 weeks after the lockdown), after most human activities and tourism resumed. Another study performed on the inner and outer barrier reefs inside and outside marine protected areas of Moorea (Feeney et al., 2022) compared fish densities between 2011 and 2020, with densities observed in May and July 2020. The study recorded an increase in post-lockdown densities compared to this long-term average on sites where human activity decreased (inner barrier reefs) but not in areas where human activity was already lower (outer barrier reefs). These results likely suggest that fish have moved into less frequented areas.

The present study aims to provide new information on the effects of the COVID-19 lockdown on observed coral reef fish density along coastal habitats in Moorea, French Polynesia. Specifically, we intend to identify whether the reduction in local fishing and boating activities in the Moorea lagoon caused changes in fish densities after the 2020 lockdown. We hypothesize that fish densities along the coastline

should have increased during the lockdown period, but that this benefit should have been short-lived and thus densities would return to pre-lockdown levels when human activities resumed.

Methods

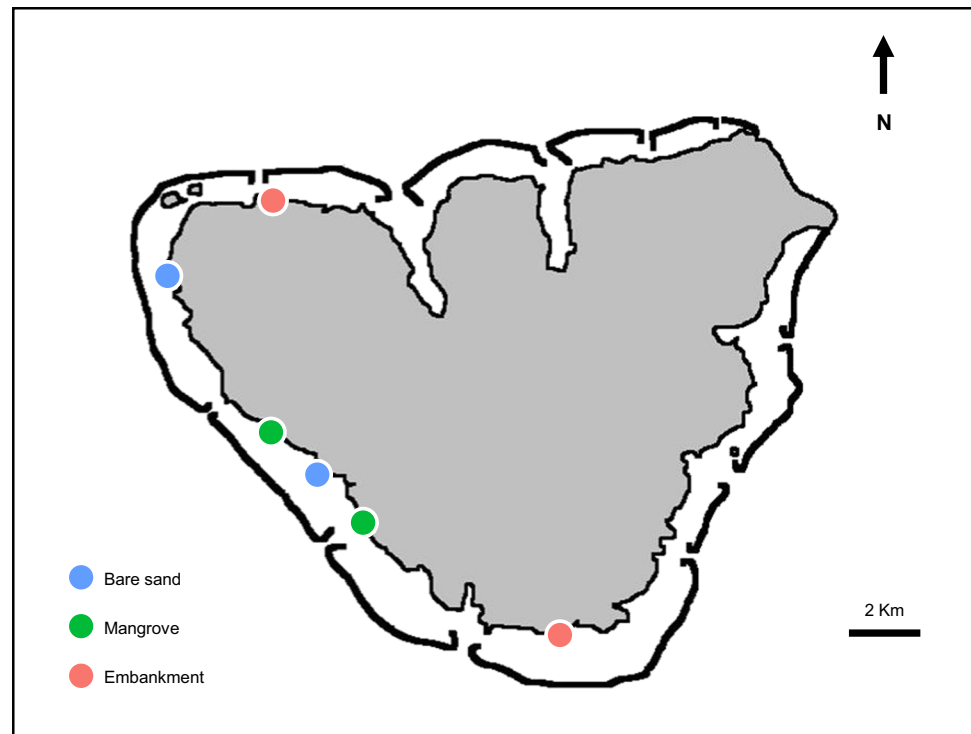
Fish surveys

Fish density was assessed in two natural coastal marine habitats (bare sand and mangrove) and near a human-engineered shore structure (embankment) made of rocks and concrete on the island of Moorea (Madi Moussa et al. 2019) (Fig. 1). In each coastal habitat, two sites were selected, and visual surveys were conducted using SCUBA along three transects per site (30 m long and 2 m wide = 60 m²) extending 30 m perpendicular to the shoreline (Lecchini et al. 2009). Along each transect, all observable fishes were counted and identified to the species level along with their ontogenetic stage (adult vs. juveniles). The distinction between juvenile and adult stages was based on size, colour, pattern and behaviour (Lecchini and Galzin 2005). Count data were standardized to densities by dividing the total number of fish observed by the area covered by the 6 transects (360 m²). Surveys took place between 10:00 and 16:00 both in 2019 and 2020. In 2019, visual surveys were conducted in February, March, April, July, September and November, and densities were averaged across months in order to obtain baseline fish density data for 2019 for each coastal habitat type (see Online Resource 1 for inter-annual variability). In 2020, no surveys could be conducted prior to lockdown and the first fish density surveys were conducted immediately after lockdown (first week of May 2020, in order to best capture the environment following six weeks of lockdown) and then 1 and 2 months after lockdown (June and July 2020, respectively). By the July sampling period, international flights and associated tourism activities had resumed. The same survey protocol was used for the 2019 and 2020 surveys. Although tidal fluctuations in Moorea are minimal (less than 0.4 m), all surveys were conducted at high tide for consistency. Water depth along all transects varied between 0.5 and 1 m in all coastal habitats.

Statistical analysis

All statistical analyses were conducted using R-Studio version 1.3.1093 (R version 4.0.3) (R Core Team 2020; R Studio Team 2020). To assess whether juvenile, adult and harvested fish densities changed after the period of reduced human presence due to the lockdown, generalized linear mixed effects models were run using the *lme4* package (Bates et al. 2015). Full models included fish density as the

Fig. 1 Map of Moorea Island showing the location of the different study sites. Map was drawn by the authors using PhotoFiltre 7 software (version 7.1.2—www.photofiltre.com) from an aerial photograph taken by the CRIOBE in 2008 from a private plane



dependent variable; sampling periods, i.e. 2019 average, end of lockdown, 1 month and 2 months after the end of lockdown, as the categorical fixed effect; and coastline habitats, i.e. bare sand, mangrove and embankment as a random effect with transect nested within habitat. Density did not follow a Normal distribution (Shapiro–Wilk tests, $W=0.50–0.60$, all $P < 0.001$). The probability distribution that best fit the data was determined graphically using the packages *car* and *MASS* and the function “*qqp*” (see Online Resource 2). Three separate models were then fit using a log-normal distribution, each with the same covariates described above, for juveniles (including all species), adults (including all species) and harvested fish at the adult stage (i.e. species targeted by recreational, subsistence and commercial fishers). A significant effect of the fixed effect, i.e. sampling period, was assessed at the significance level $\alpha=0.05$.

In order to take into account inter-annual variations, the fish densities recorded in April 2019 were compared to the densities of early May 2020, i.e. at the end of the lockdown (Table 1), and densities recorded in July 2019 were compared to the densities of July 2020, i.e. 2 months after the end of the lockdown (Table 2). Comparisons were made for each type of habitat (embankment, mangrove and bare sand) by measuring the effect sizes calculated as the change in the log ratio of the 2020 densities of fishes recorded at the end of the lockdown and 2 months after it in the different habitats relative to the densities recorded in April and July 2019 respectively. The same approach was taken at the family level by considering the eight families showing the

highest densities of individuals (juvenile and adult stages), i.e. Acanthuridae, Chaetodontidae, Labridae, Lutjanidae, Mugilidae, Mullidae, Pomacentridae and Scaridae. Differences were considered significant when the 95% confidence interval (95% CI) of the effect size was different from zero.

Results

A significant effect of the sampling period was found on juvenile density (Table 3) with significantly higher densities at the end of the lockdown, 1 month and 2 months after the end of lockdown compared to the average density of 2019 (Table 3). A similar significant effect of the sampling period was also found on adult density (Table 4) with significantly higher densities at the end of the lockdown, 1 month and 2 months after the end of lockdown than in 2019 (Table 4). Again, a significant effect of the sampling period was found on harvested fish density (Table 5) with significantly higher densities observed at the end of the lockdown, 1 month and 2 months after the end of lockdown compared to the 2019 average density (Table 5).

The overall density of juveniles at the end of the lockdown (May 2020) did not change compared to the same period in 2019 (0.09 fish per m^2 in April 2019 vs. 0.09 fish per m^2 in May 2020). Despite that, densities were 25% higher near embankments (0.08 fish per m^2 in April 2019 vs. 0.10 fish per m^2 in May 2020), or decreased by 50% in mangroves (0.06 fish per m^2 in April 2019 vs. 0.03 fish per

Table 1. List of adult (AD) and juvenile (JUV) fish species observed in the different habitats in April 2019 and May 2020, i.e. at the end of the lockdown. Species in grey are harvested species (fisheries targets). Numbers are the total number of observations made along the 6 transects (3 transects 2 sites) of each habitat

Family	Species	Bare sand				Mangrove				Embankment				
		April 2019		May 2020		April 2019		May 2020		April 2019		May 2020		
		AD	JUV	AD	JUV	AD	JUV	AD	JUV	AD	JUV	AD	JUV	
Acanthuridae	<i>Acanthurus nigricauda</i>				3						30		2	
	<i>Acanthurus olivaceus</i>										1			
	<i>Acanthurus triostegus</i>	3	4	21	31	1	6		1	18	32	82	26	
	<i>Ctenochaetus striatus</i>				1					5	28	35	22	
	<i>Naso lituratus</i>										1			
	<i>Naso unicornis</i>										5			
Apogonidae	<i>Apogon exostigma</i>												2	
	<i>Cheilodipterus quiquelineatus</i>												1	
	<i>Ostorhinchus angustatus</i>	8		4	3					1				
	<i>Pristiapogon kallopterus</i>												1	
Balistidae	<i>Ballistapus undulatus</i>								1					
	<i>Rhinecanthus aculeatus</i>	6		1	10			1	1	8	18	9	7	
Bothidae	<i>Bothus mancus</i>												1	
Carangidae	<i>Caranx melampygus</i>			83	12		4			1		1	1	
	<i>Caranx sexfasciatus</i>										9			
Chaetodontidae	<i>Chaetodon auriga</i>	9	6	4	8	7	4			2	10	3	17	
	<i>Chaetodon citrinellus</i>	4								8	6	12	2	
	<i>Chaetodon ephippium</i>				6	1						4		
	<i>Chaetodon lunula</i>	12	8	6	5	4			2	1	14			
	<i>Chaetodon lunulatus</i>									2			2	
	<i>Chaetodon trifascialis</i>	1												
	<i>Chaetodon unimaculatus</i>										3			
	<i>Chaetodon vagabundus</i>			9	20				1				24	9
	<i>Heniochus chrysostomus</i>													1
Dasyatiidae	<i>Himantura fai</i>			2										
Fistulariidae	<i>Fistularia commersoni</i>									2	3			
Gobiidae	<i>Asterropteryx semipunctata</i>			5	2			11	9				17	
	<i>Fusigobius neophytus</i>			4				6						
	<i>Gnatholepis anjerensis</i>	2				1	1							
	<i>Valenciennesa strigata</i>									1				
Holocentridae	<i>Neoniphon microstoma</i>												2	
	<i>Neoniphon sammara</i>			6	2									
Labridae	<i>Cheilinus chlorourus</i>		37		1		2				2		9	
	<i>Cheilinus trilobatus</i>		2										1	
	<i>Coris aygula</i>										7			
	<i>Coris gaimard</i>											9	1	
	<i>Gomphosus varius</i>											1		
	<i>Halichoeres hortulanus</i>				1								5	
	<i>Halichoeres margaritaceus</i>				26				1			9	39	
	<i>Halichoeres trimaculatus</i>	7	13	99	115	12	27	19	2	8	28	52	6	
	<i>Stethojulis bandanensis</i>		1	13	45	1				6	5	26	35	
	<i>Thalassoma hardwicke</i>	12	9	13	28	1	1			8	15	64	31	
	<i>Thalassoma purpurum</i>											1	1	
Lethrinidae	<i>Gnathodentex aureolineatus</i>												3	
	<i>Lethrinus nebulosus</i>												1	
	<i>Monotaxis grandoculis</i>											15	1	
Lutjanidae	<i>Lutjanus fulvus</i>	2	2	31		2	2	21	1	1	1	11		
	<i>Lutjanus kasmira</i>			1										
	<i>Lutjanus monostigma</i>				5									
Mugilidae	<i>Crenimugil crenilabis</i>	117		31	195	87	124	15		3	178		60	
	<i>Ellochelon vaigiensis</i>	156				114	4						160	
	<i>Liza vaigiensis</i>				100			141	39					
Mullidae	<i>Mulloidichthys flavolineatus</i>	827	35	139		360		138		1827	100		540	
	<i>Mulloidichthys vanicolensis</i>	12		19						1			1082	
	<i>Parupeneus barberinus</i>									3				
	<i>Parupeneus ciliatus</i>												1	
	<i>Parupeneus multifasciatus</i>	1		2		1				11	10		14	
Muraenidae	<i>Echidna nebulosa</i>			1									1	
	<i>Gymnothorax javanicus</i>		1	1									1	
Ostraciidae	<i>Ostracion cubicus</i>					1						1		
Pomacentridae	<i>Centropyge flavissima</i>									1			1	
Pomacentridae	<i>Abudefduf septemfasciatus</i>					3	7		10	9	1		1	
	<i>Abudefduf sexfasciatus</i>	2	6	11	10		1			10	15	43	10	
	<i>Abudefduf sordidus</i>	1			1		1		10	16	7	2	26	
	<i>Chromis viridis</i>	97	185	100	338									
	<i>Chrysiptera brownriggii</i>										2		3	
	<i>Chrysiptera glauca</i>	11		8	5								2	
	<i>Dascyllus aruanus</i>	77	99	146	455		5				1			
	<i>Dascyllus trimaculatus</i>				1									
	<i>Pomacentrus pavo</i>	2									2			
	<i>Stegastes albifasciatus</i>				25									3
	<i>Stegastes fasciolatus</i>												12	
	<i>Stegastes nigricans</i>	82	32	132	116	16	2	1		185	5	65	83	
	Scaridae	<i>Calotomus carolinus</i>												7
		<i>Chlorurus spilurus</i>	1	159		67				1		315		233
<i>Hipposcarus longiceps</i>		1		3	34				2				39	
<i>Scarus psittacus</i>			208		120			41			274	15	110	
<i>Scarus rubroviolaceus</i>								13						
<i>Scarus schlegelii</i>				40	55								5	
	<i>Chlorurus sordidus</i>				170							5	85	
Serranidae	<i>Epinephelus merra</i>					2			1				3	
Siganiidae	<i>Siganus argenteus</i>		6			2	23				22	5		
	<i>Siganus spinus</i>		6								14	2		
Syngnathidae	<i>Corythoichthys flavofasciatus</i>												2	
Synodontidae	<i>Synodus binotatus</i>									1				
	<i>Saurida gracilis</i>												3	
Zanclidae	<i>Zanclus cornutus</i>	1								2	4	2	1	

m² in May 2020) and 25% on bare sand (0.12 fish per m² in April 2019 vs. 0.09 fish per m² in May 2020), 95% CI of the effect sizes did not differ from 0 for the three habitats (Fig. 2). In adults, the overall density increased by 50% (0.02 fish per m² in April 2019 vs. 0.03 fish per m² in May 2020) and was significantly higher near embankments and on bare sand (Fig. 2). Despite a 33% increase (0.03 fish per m² in April 2019 vs. 0.04 fish per m² in May 2020), the 95% CI of the effect size did not differ from 0 in mangroves. Overall harvested species density increased by 25% compared to 2019 (0.036 fish per m² in April 2019 vs. 0.045 fish per m² in May 2020). In mangroves, it increased by 197% (0.06 fish per m² in April 2019 vs. 0.19 fish per m² in May 2020), but the 95% CI of the effect size did not differ from 0. Densities significantly increased by 520% near embankments (0.005 fish per m² in April 2019 vs. 0.03 fish per m² in May 2020) and 1325% on bare sand (0.004 fish per m² in April 2019 vs. 0.057 fish per m² in May 2020) (Fig. 2).

The densities recorded 2 months after the end of the lockdown (July 2020) were significantly higher in juveniles for all types of habitats compared to densities recorded in July 2019. Overall density increased by 257% for juveniles (0.016 fish per m² in July 2019 vs. 0.059 fish per m² in July 2020), ranging from a 119% increase on bare sand (0.036 fish per m² in July 2019 vs. 0.079 fish per m² in July 2020) to a 345% increase in mangroves (0.011 fish per m² in July 2019 vs. 0.049 fish per m² in July 2020) and a 557% increase on embankments (0.007 fish per m² in July 2019 vs. 0.046 fish per m² in July 2020). In adults, the overall density increased by 24% in comparison with the densities recorded in July 2019 (0.015 fish per m² in July 2019 vs. 0.019 fish per m² in July 2020), with relative variation ranging from 18% on bare sand to 28% in mangroves and 168% near embankments. Differences were significant only for bare sand and embankments (Fig. 2). Similar results were found in harvested species (Fig. 2), with a 61% increase in the overall density (0.016 fish per m² in July 2019 vs. 0.026 fish per m² in July 2020). Despite a 62% increase in mangroves (0.03 fish per m² in July 2019 vs. 0.049 fish per m² in July 2020), however, the 95% CI of the effect size did not differ from 0. Differences were significant near embankments with a 437% increase (0.004 fish per m² in July 2019 vs. 0.022 fish per m² in July 2020) and also on bare sand with a 537% increase (0.004 fish per m² in July 2019 vs. 0.026 fish per m² in July 2020) (Fig. 2).

The observed increases did not apply equally across the sampled Families. At the end of the lockdown (May 2020), the densities of Acanthuridae (harvested species), Lutjanidae (harvested species), Mugilidae (harvested species), Mullidae (harvested species), Pomacentridae (non-harvested species) and Scaridae (harvested species) were not significantly different from those observed in the same period in 2019 (all 95% CI of the effect size did not differ

from zero). However, in Chaetodontidae (non-harvested species), densities were significantly higher near embankments (95% CI: -0.80 to -0.15) and significantly lower in mangroves (95% CI: 0.14–3.20) in May 2020 compared to April 2019. Labridae (non-harvested species) were also significantly more abundant in May 2020 near embankments (95% CI: -1.83 to -0.74) and on bare sand (95% CI: -2.57 to -0.45) compared to April 2019 (Fig. 3). Two months after the end of the lockdown (July 2020), all families but Lutjanidae and Mugilidae (all 95% CI of the effect size did not differ from zero) showed significantly higher densities in at least one habitat compared to July 2019. Near embankments, Acanthuridae (95% CI: -2.57 to -1.99), Labridae (95% CI: -3.50 to -2.52), Pomacentridae (95% CI: -2.26 to -1.82) and Scaridae (95% CI: -3.04 to -1.31) were more abundant in 2020 than in 2019. In mangroves, only Mullidae (95% CI: -7.04 to -1.04) and Pomacentridae (95% CI: -3.17 to -0.63) showed higher densities in July 2020 compared to July 2019. On bare sand, Chaetodontidae (95% CI: -2.99 to -0.67), Labridae (95% CI: -2.95 to -1.09) and Scaridae (95% CI: -6.64 to -0.23) appeared significantly more abundant in July 2020 compared to July 2019 (Fig. 3).

Discussion

Coastal surveys conducted on the island of Moorea in May 2020 revealed significantly higher densities of adults and harvested species of fish near embankments and bare sand sites immediately after a 6-week lockdown, compared to densities observed at a similar time in 2019. Due to the sudden nature of the lockdown and the unpredictable course of the coronavirus pandemic, it was not possible to plan any survey in early 2020. Thus, the higher density of fish observed in May might be the result of comparatively higher recruitment in early 2020 (Lecchini and Galzin 2005). However, the lack of significant differences in juveniles at the end of the lockdown compared to 2019 suggests that this explanation is unlikely. In addition, the period from May to August usually corresponds to the period of lowest sea surface temperatures in French Polynesia, when fishes are generally less abundant and larval recruitment is lower (Galzin 1987; Lo-Yat et al. 2011). Therefore, the higher apparent density of fish observed in May, June and July 2020 compared to the overall 2019 average could be related to behavioural changes due to the lockdown period (similar to Feeney et al. 2022).

Moorea's coastal sites are generally subject to high human pressure as they are frequented by local residents and international tourists. Therefore, the decrease in activity resulting from the lockdown was likely to affect the density of fish observed by affecting the behaviour of individuals and causing more fish to venture to the study sites or by

Table 2. List of adult (AD) and juvenile (JUV) fish species observed in the different habitats in July 2019 and July 2020, i.e. 2 months after the end of the lockdown. Species in grey are harvested species (fisheries targets). Numbers are the total number of observations made along the 6 transects (3 transects 2 sites) of each habitat

Family	Species	Bare sand				Mangrove				Embankment			
		July 2019	July 2020	AD	JUV	July 2019	July 2020	AD	JUV	July 2019	July 2020	AD	JUV
Acanthuridae	<i>Acanthurus nigricauda</i>												
	<i>Acanthurus triostegus</i>	2	3	6		10	9	11		5	4	42	63
	<i>Ctenochaetus striatus</i>			14						5	11	28	127
	<i>Naso unicornis</i>												1
Apogonidae	<i>Apogon novemfasciatus</i>												3
Ballistidae	<i>Ballistapus undulatus</i>												
	<i>Rhinecanthus oculateatus</i>		1	5		2				6	8	1	10
Carangidae	<i>Caranx melampygus</i>							4					
	<i>Caranx sexfasciatus</i>								4				
Chaetodontidae	<i>Chaetodon auriga</i>	1	1	11	6	7	4			5	11	2	1
	<i>Chaetodon citrinellus</i>									5		8	
	<i>Chaetodon ephippium</i>			1						2			
	<i>Chaetodon lunula</i>	2	3	4	2		2		4				4
	<i>Chaetodon lunulatus</i>									2			
	<i>Chaetodon trifascialis</i>			2									2
	<i>Chaetodon ulietensis</i>		1										
	<i>Chaetodon unimaculatus</i>										3		
	<i>Chaetodon vagabundus</i>			14	10			5				9	10
	<i>Heniochus chrysostomus</i>									3			
Gobiidae	<i>Asterropteryx semipunctata</i>	2					1					1	
	<i>Fusigobius neophytus</i>							1					
Kuhliidae	<i>Kuhlia mugil</i>			2									
	<i>Kuhlia sandvicensis</i>												12
Labridae	<i>Cheilinus trilobatus</i>												1
	<i>Epibulus insidiator</i>									1			1
	<i>Halichoeres hortulanus</i>												6
	<i>Halichoeres margaritaceus</i>			1	8		1				1	4	57
	<i>Halichoeres trimaculatus</i>	6	4	27	36	4	1	9	3	2	2	28	29
	<i>Stethojulis bandanensis</i>	1		5								6	10
	<i>Thalassoma hardwicke</i>	2		21				2		4	1	37	44
Lethrinidae	<i>Monotaxis grandoculis</i>												1
Lutjanidae	<i>Lutjanus fulvus</i>			17			5	1	35				5
	<i>Lutjanus monostigma</i>						2						
Mugilidae	<i>Crenimugil crenilabris</i>	1	24	45	165		1	70	148				
	<i>Ellochelon vaigiensis</i>			35	160			36	85				
	<i>Liza vaigiensis</i>		38			64	13						
Mullidae	<i>Mulloidichthys flavolineatus</i>			30	13			1	27		1		
	<i>Mulloidichthys vanicolensis</i>								30				
	<i>Parupeneus barberinus</i>												1
	<i>Parupeneus multifasciatus</i>												3
													13
Muraenidae	<i>Echidna nebulosa</i>												1
Ostraciidae	<i>Ostracion cubicus</i>												1
Pomacanthidae	<i>Centropyge flavissima</i>												1
Pomacentridae	<i>Abudefduf septemfasciatus</i>		1	11		2		5	20	5	2	18	18
	<i>Abudefduf sexfasciatus</i>			8				2	14	2	2	8	15
	<i>Abudefduf sordidus</i>	2				3	1			2	1		
	<i>Chromis viridis</i>	7	64	70	230								
	<i>Chrysiptera brownriggii</i>										1	1	
	<i>Chrysiptera glauca</i>		1	3	6			3				4	19
	<i>Chrysiptera leucopoma</i>							3				2	16
	<i>Dasycyllus aruanus</i>	104	98	83	247								
	<i>Pomacentrus pavo</i>			8	26								
	<i>Stegastes albifasciatus</i>			7	20								13
	<i>Stegastes fasciolatus</i>									1			
	<i>Stegastes nigricans</i>	112	64	59	125		1			14	4	40	117
Scaridae	<i>Chlorurus spilurus</i>		5					15				35	
	<i>Hipposcarus longiceps</i>						18	12		2	2		
	<i>Scarus psittacus</i>	1	7	105									73
	<i>Scarus schlegeli</i>												2
	<i>Chlorurus sordidus</i>			85									37
													90
Serranidae	<i>Epinephelus merra</i>										1		1
Siganidae	<i>Siganus argenteus</i>	2								2	2		
	<i>Siganus spinus</i>						7				4	1	
Syngnathidae	<i>Corythoichthys flavofasciatus</i>										2		
Synodontidae	<i>Saurida gracilis</i>												1
Tetraodontidae	<i>Arothron hispidus</i>			1									
	<i>Arothron meleagris</i>												1
	<i>Canthigaster jentinopectera</i>												1
Zanclidae	<i>Zanclus cornutus</i>						1				1		

making the local cryptic species bolder and more visible (Januchowski-Hartley et al. 2011, 2015; Wong and Candolin 2015; Goetze et al. 2017; Emslie et al. 2018; Ruppert et al. 2018). Indeed, some species like *Chaetodon vagabundus* (Chaetodontidae), *Halichoeres margaritaceus* (Labridae) or *Chlorurus sordidus* (Scaridae), which is fisheries target species, were only observed in May and July of 2020. These species may be more negatively affected than others by normal human activities and may therefore have become more visible when this pressure was relieved. This hypothesis of

a change in behaviour further highlights a known potential bias in the effectiveness of traditional visual monitoring of fish populations by SCUBA divers in areas frequented by humans, where fish have already been shown to remain at a greater distance and hide from divers (Kulbicki 1998; Lindfield et al. 2014; Gray et al. 2016). This suggests that complementary and less invasive methods, such as environmental DNA or video monitoring, might also be useful in future surveys in order to provide more precise evaluation of biodiversity. Additionally, current surveys often consider

Table 3 Summary of the generalized linear mixed effects model analysis performed on the density of juveniles with sampling periods as the fixed effect (N=148). 2019 average density is the reference period

	Density	SE	t-value	P
May 2020	0.245	0.029	8.36	<10 ⁻³
June 2020	0.078	0.030	2.63	0.01
July 2020	0.247	0.026	9.53	<10 ⁻³
Correlations	Intercept	May 2020	June 2020	
May 2020	-0.134	0.166	0.190	
June 2020	-0.130	0.191		
July 2020	-0.150			

only diurnal communities while populations are known to display marked biological rhythms (Galzin 1987; Galzin and Legendre, 1987). To investigate whether a diminution in human activities, which occur mainly during daytime, would also benefit nocturnal organisms, the use of passive acoustic monitoring would appear as a particularly suited alternative to investigate potential impacts on communities without further disturbing marine organisms (Bertucci et al. 2020, 2021).

Before the lockdown, nautical activities were mainly present near the bare sand sites, with three family guesthouses (ca. 15 rooms in total and provision of kayaks for tourists), a campsite (ca. 50 people) and a diving club (two sea trips per day and open all year round). Likewise, the mangroves were mainly used as fishing areas from kayaks and pirogues by local fishermen, and embankments were used as launching sites (boats to bring surfers close to the ocean waves) and for fishing on foot or with rods by local fishermen (TB and DL personal observations). In contrast to Hoffman (2020), the present ecological surveys showed that the density of adults and harvested species was significantly greater at the end of the lockdown and 2 months after for juveniles, adults and harvested species. Unfortunately, there are no data or indicators to quantify the change in human use of the areas in question nor is there a control site such as a no-entry marine reserve that would have been less or not at all impacted by the lockdown. However, despite the inability to statistically compare the relationship between fish density and nautical/fishing activities on the three coastline habitats, we can postulate that any change in the fish community would mainly depend on the degree of human activity existing at the location ordinarily and the intensity of the change after the lockdown, as this has been suggested by other recent studies (e.g. Edward et al. 2021; Lecchini et al. 2021; Feeney et al. 2022). Furthermore, at Moorea, we are not aware of any particular variations or events (potentially related to weather, cyclone, coral bleaching or environmental conditions) that may have occurred during

Table 4 Summary of the generalized linear mixed effects model analysis performed on the density of adults with sampling periods as the fixed effect (N=146). 2019 average density is the reference period

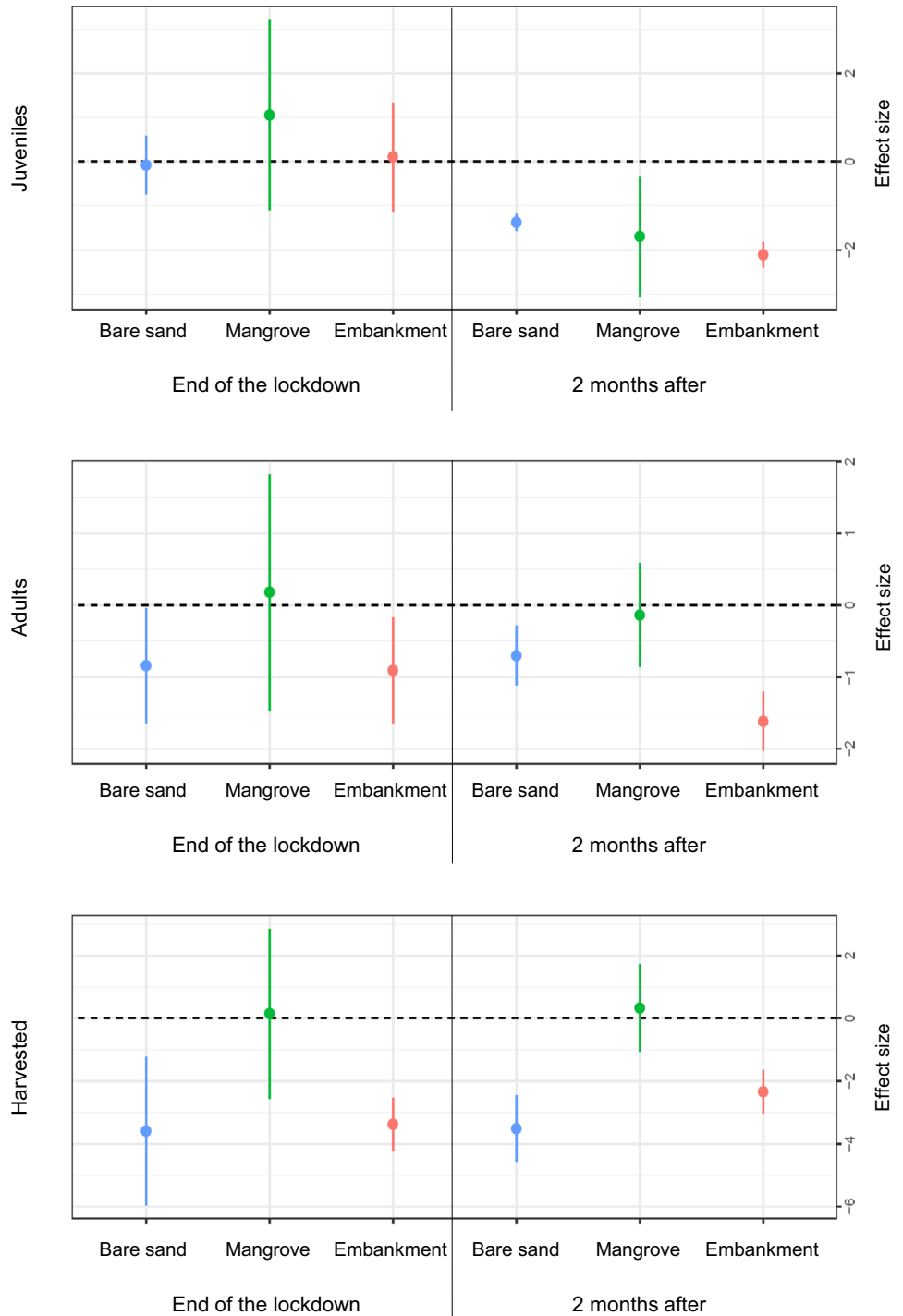
	Density	SE	t-value	P
May 2020	0.228	0.019	11.77	<10 ⁻³
June 2020	0.129	0.021	6.18	<10 ⁻³
July 2020	0.127	0.020	6.18	<10 ⁻³
Correlations	Intercept	May 2020	June 2020	
May 2020	-0.216	0.204	0.195	
June 2020	-0.200	0.211		
July 2020	-0.207			

the same period that could explain the observed changes. Zambrano-Monserrate et al. (2020) showed that some internationally known beaches, which welcome millions of tourists every year (e.g. Acapulco in Mexico, Barcelona in Spain and Salinas in Ecuador) looked cleaner and had crystal clear waters during the early 2020 lockdown. This resembles our results, where the impact of reduced human activity appears strong in areas where human presence is usually high. At Moorea, the main change was due to the absence of human activities along the coastline during the lockdown. For instance, the lockdown seems to have had a strong impact on adult and harvested fish densities on bare sand sites which are frequently used for nautical activities and by many locals and tourists. In contrast, even though mangrove habitats are good fishing grounds, few local people actually use the sites studied and no significant effect of the reduced human activity could be detected (April 2019 vs. May 2020) for juveniles, adults or harvested species at the end of the lockdown. Additionally, the existence of a greater number of refuges potentially used by fish when humans are present would support the hypothesis of a change in the behaviour of individuals venturing outside their shelters (Gotanda et al. 2009; Madin et al. 2010;

Table 5 Summary of the generalized linear mixed effects model analysis performed on the density of harvested species (fisheries targets) with sampling periods as the fixed effect (N=152). 2019 average density is the reference period

	Density	SE	t-value	P
May 2020	0.277	0.023	11.83	<10 ⁻³
June 2020	0.067	0.026	2.54	0.01
July 2020	0.096	0.025	3,81	<10 ⁻³
Correlations	Intercept	May 2020	June 2020	
May 2020	-0.250	0.185	0.168	
June 2020	-0.223	0.189		
July 2020	-0.234			

Fig. 2 Effect sizes \pm 95% confidence interval measured on bare sand, mangroves and embankments, in juveniles, adults and harvested fish, for densities at the end of the lockdown (May 2020) and two months after the lockdown (July 2020). Effect sizes are expressed as the change in the log ratio of the 2020 densities in the different habitats relative to their levels in April and July 2019 respectively. Higher negative values of effect size indicate higher densities in 2020 and are considered significant when the 95% confidence interval of the effect does not overlap zero



Januchowski-Hartley et al. 2011). As an example, species of wrasse (Labridae), which often hide in sand or lie against hard substrate were more abundant near embankments and on bare sand sites in May 2020 (at the end of the lockdown) than in April 2019. Embankments likely showed large effect sizes because they typically host fishing and recreational activities even though these are practiced by a limited number of people. These sites may also have experienced a reduction

in boat engine noise associated with human activities and, as a consequence, fish may have been less stressed (Buckley 2020; Ferrier-Pagès et al. 2021). However, the potential effects of the lockdown (April 2019 vs. May 2020) remained non-significant for the most abundant fish families.

After the lockdown, schools remained closed, there were many public holidays, and economic activities (especially in hotels) remained low. However, by mid-June, schools

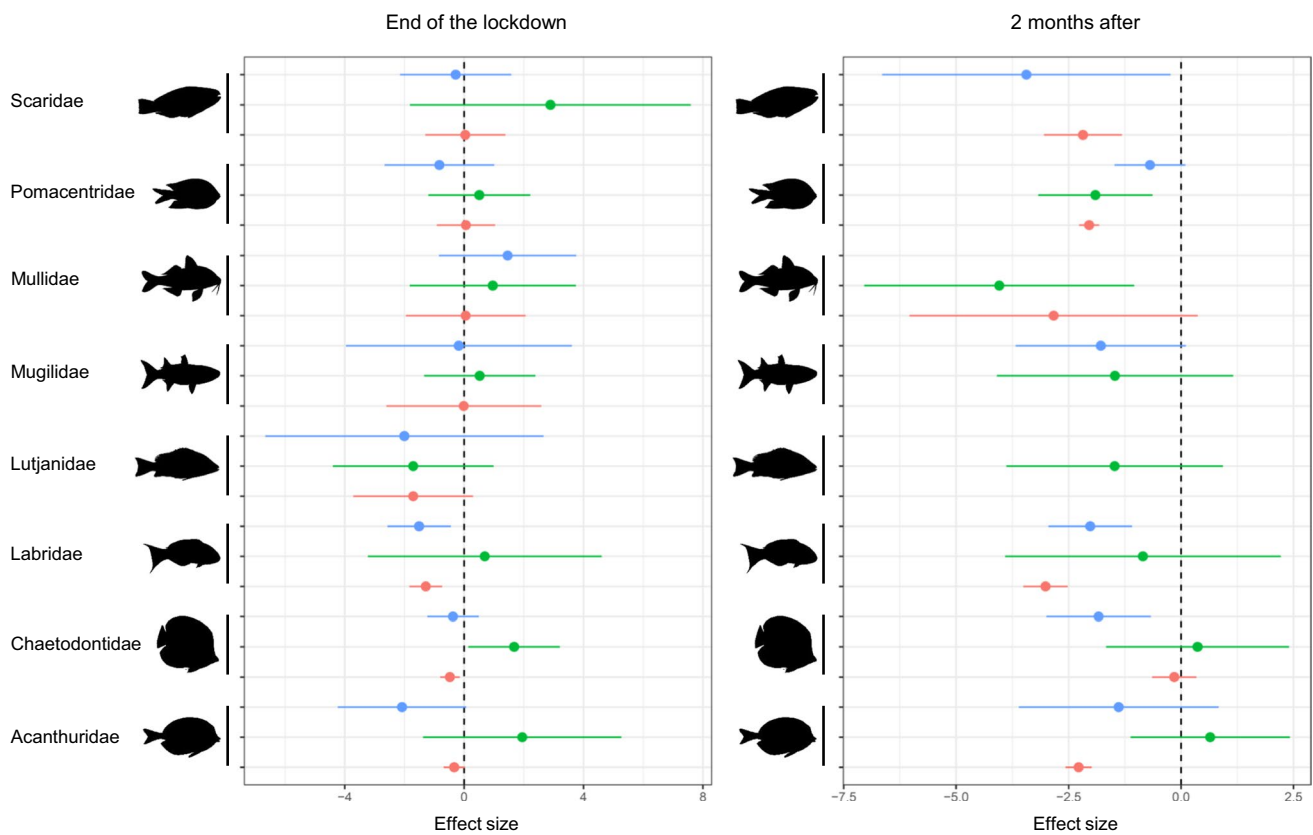


Fig. 3 Effect sizes \pm 95% confidence interval measured on bare sand (blue), mangroves (green) and embankments (red), in all species of families Scaridae, Pomacentridae, Mullidae, Mugilidae, Lutjanidae, Labridae, Chaetodontidae and Acanthuridae at all stages (juveniles and adults), for densities at the end of the lockdown (May 2020) and two months after the lockdown (July 2020). Effect sizes are expressed as the change in the log ratio of the 2020 densities in the different

habitats relative to their levels in April and July 2019 respectively. Higher negative values of effect size indicate higher densities in 2020 and are considered significant when the 95% confidence interval of the effect does not overlap zero. Missing points in the right panel could not be calculated due to the low number of individuals observed in those habitats

reopened, there were no more holidays, and more economic sectors resumed their activities (www.polynesie-francaise.pref.gouv.fr/content/download/45236/273700/file/). Correspondingly, fish density along the Moorea coastline appeared to be lower at the end of June. These results may indicate that although there were apparently more fish in the coastal habitats at the end of the lockdown, the resumption of local activity with the return of international tourists may have led to a decrease in the observed fish density. However, when comparing densities observed 2 months after the end of the lockdown, fish were still more abundant than in 2019 at the same time. This was also the case for juveniles in all habitats including mangroves, where an increase in density was observed in all families in at least one habitat type, including the parrotfishes (Scaridae) which comprise many species usually targeted by fishermen. Increased damselfish (Pomacentridae) density was also observed in mangroves and near embankments, which generally support substantial levels of boating and fishing activities and hence high noise levels. Species in this family have been shown to be particularly sensitive to noise pollution with negative effects on

larval survival, altered response to predators, reduced fast-start kinetics, altered swimming behaviour and increased aggressive behaviour (Jain-Schlaepfer et al. 2018; McCormick et al. 2019; Mills et al. 2020). This again illustrates the possible benefit of reduced human activity along the coastline and may inspire long-term management plans in which access to certain areas by tourists or fishermen is reduced and/or allowed only at certain times of the year in order to allow species, particularly those of commercial value, to reproduce and also in order to promote biodiversity. Such achievement could be realized within the framework of the United Nations Sustainable Development Goals (SDGs). Tourism is an important source of income and employment in many developing and island countries and can hardly be banned. Developing sustainable tourism, i.e. that considers economic, social and environmental impacts, that meets the needs of visitors and professionals, would align with SDG 8 “Decent work and economic growth” which intends to “promote sustained, inclusive and sustainable economic growth, employment and decent work for all”. Monitoring potential impacts of such activities on sustainable development is

also central in the SDG 12 “Responsible consumption and production”. The present results finally support that these efforts will benefit biodiversity and promote the conservation and sustainable use of the oceans, seas and marine resources as encouraged by the SDG14 “Life below water”.

The COVID-19 pandemic has raised awareness of our dependence on a functional food system (Gordon 2020). To understand the effects of future similar pandemics, it is essential to acquire data on the impact of alternating breaks and recoveries of human activities on the resilience of fish, humans and their interactions. Several studies have suggested that a rapid reduction in anthropogenic stressors can lead to behavioural changes in animals. For instance, many wild species moved closer to rural and urban areas, including parks and beaches, where they have not been seen for many years, when traffic and other human activities were reduced (e.g. Bates et al. 2021, Kumar et al. 2021). Our study suggests that limiting human presence in coastal areas that are highly affected by tourism and nautical activities may be an effective management policy to minimize total human impacts on coastline habitats in the future. The COVID-19 crisis has thus called for a new balance between sustainable management of common resources, such as coral reef fish for Pacific Island fisheries and tourism (Bambridge et al. 2020), and human well-being.

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

Declarations

Conflict of interest The authors declare no competing interests.

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