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1 **COVID-19 lockdown highlights impact of recreational activities on the behaviour of**
2 **coral reef fishes**

3

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22 **Abstract**

23 The SARS-CoV-2 (COVID-19) pandemic led to a drastic reduction of human activities and
24 restriction of all but essential movement for much of the world's population. This abrupt
25 'anthropause' has been attributed to drastic increases in air and water quality; however, its
26 effects on animal populations remains less clear. Extending on long-term monitoring efforts,
27 we examined how coral reef fish populations were affected by the government-mandated
28 lockdown across a series of Marine Protected Area (MPA) and non-Marine Protected Area
29 (nMPA) sites around Moorea Island, French Polynesia. We found that during the six-week
30 lockdown, a dramatic increase in both harvested and non-harvested fishes were observed
31 across the MPA inner barrier reef sites, while no difference was observed across the nMPA
32 sites and the outer barrier MPA sites. Interviews with local amateur and professional fishers
33 indicated that while rules regarding MPA boundaries were generally followed, some
34 subsistence fishing continued in spite of lockdown, including within MPAs. However, as the
35 primary activities occurring within MPA sites are recreational and non-extactive, these data
36 suggest that **these activities affect how fish use space** and that their behaviour can rapidly
37 change in our absence.

38

39 **Introduction**

40 The ongoing SARS-CoV-2 (COVID-19) pandemic has resulted in the unprecedented closing
41 of international borders, halting of commercial activities and lockdown of resident
42 populations¹. These sudden changes have dramatically recalibrated the impacts humans are
43 having on the world's ecosystems, with early reports suggesting increases in air and water
44 quality², as well as the drastic reduction of various pollutants^{3,4}. While the impacts of
45 lockdown may offer initial relief to ecosystems, the resulting breakdown of supply chains and
46 reduction in employment may also present challenges, especially to remote populations,

47 leading to a greater reliance on harvesting resources directly from the surrounding
48 environment⁵. Under these circumstances, this ‘anthropause’ presents a unique opportunity to
49 investigate the impacts that human activities have on animal populations⁶.

50

51 Over the past half century, the remote island nations of the Pacific have transitioned from
52 relying on subsistence agriculture and fishing to emerging economies that rely primarily on
53 tourism⁷. For instance, the tourism-dominated services sector of French Polynesia accounted
54 for 85% of total value added to its economy in 2012, with 17% of the workforce being
55 employed within the tourism industry^{8,9}. Despite this ongoing transformation, the populations
56 of these countries still rely heavily on local fisheries, with fish comprising the primary source
57 of protein throughout the region and most families having at least one member who fishes in
58 either an amateur or professional capacity to help feed their family¹⁰. Following the first
59 COVID-19 infection in French Polynesia being identified on 10 March 2020 and the World
60 Health Organization declaring COVID-19 a pandemic on 11 March 2020, the country
61 enforced a total lockdown from 20 March 2020 – 4 May 2020 (i.e. 6 weeks)^{11,12}. In the week
62 preceding the lockdown, approximately 3000 tourists were repatriated from French Polynesia
63 and during lockdown all international travel was suspended, with inter-island travel within
64 French Polynesia only possible on presentation of an exemption¹¹. Thus, during the lockdown
65 period, French Polynesia became totally isolated from the rest of the world, with all tourism-
66 based marine activities stopped and only professional fishers being allowed to go to sea.
67 Lockdown then eased across two steps: 1) from 5 May to 30 June, 2020, there were no
68 international flight and all hotels remained closed, but residents were allowed to travel
69 between islands; 2) from 1 July, 2020, international flights began resuming and hotels started
70 opening to local and international tourism¹¹.

71

72 In 2004, the Fisheries Service of French Polynesia and the Centre de Recherches Insulaires et
73 Observatoire de l'Environnement (CRIOBE) set up a monitoring plan allowing a statistically
74 rigorous assessment of the biological effects of implementing the Marine Protected Areas at
75 Moorea Island¹³. Thus, each February, eight Marine Protected Area (MPA) and five non-
76 Marine Protected Area (nMPA) sites are surveyed along fixed transects around the island
77 (Fig. 1). In response to the pandemic and associated lockdown/reduction in normal human
78 activities across the reefs, CRIOBE's resident scientists conducted surveys in May,
79 immediately (<48h) following lockdown period, across a limited number of sites to
80 investigate the effect of lockdown on the fish populations ("lockdown" surveys), and again
81 approximately two months later in July after the tourism industry began opening back up
82 ("post-lockdown" surveys). Given the widespread reliance on tourism for much of the
83 nation's employment, social surveys were also deployed to local fishers to examine how
84 lockdown affected subsistence fishing practices during this period. Here, we examine how the
85 abrupt reduction of marine-based activities during lockdown affected fish populations within
86 and outside of MPAs at Moorea Island, as well as the impacts this had on fishing practices.

87

88 **Materials and Methods**

89 *Fish surveys across an MPA network around Moorea*

90 Each February (2004 – 2020), CRIOBE conducts transects at three permanent monitoring
91 sites within three MPAs and three non-MPAs (nMPAs)¹³. Surveyed areas extend from the
92 shore to the outer reef slope, with each permanent monitoring site within an MPA/nMPA
93 falling within one of three distinct habitat types: the shallow reef flat (or fringing reef), the
94 barrier reef, and the outer slope (at 12m depth) (Fig. 1). Three 25m transects are conducted at
95 each permanent monitoring site between 8:00am and 11:00am, during which all fish within
96 2m of the transect tape are recorded. Therefore, nine transects (three within each habitat type)

97 are conducted at each MPA/nMPA with a total of 54 transects conducted at Moorea Island
98 during each monitoring period¹⁴. As a result of the COVID-19 pandemic, CRIOBE
99 experienced reduced research capacity as many researchers returned to their home countries
100 prior to lockdown starting. However, three MPA and three non-MPA (nMPA) sites from the
101 barrier and outer slope sites were chosen to investigate the effect of lockdown on fish
102 abundance: one MPA/nMPA site on the West coast, one MPA/nMPA site on the North coast,
103 and one MPA/nMPA site on the East coast of Moorea (Fig. 1). The barrier and outer slope
104 sites were prioritized as they host the majority of adult fish^{15,16}. Consequently, no fringing
105 reef sites were included in this study.

106

107 Transects were conducted in May, within 48h of lockdown being lifted (“lockdown” surveys),
108 and in July, approximately two months following lockdown being lifted and when
109 international tourists were present again at Moorea (“post-lockdown” surveys) and followed
110 standard protocols. At each site, three replicate 25m transects were conducted at each of the
111 two reef types (barrier reef: 1-2 m depth; and outer slope: 10-12m depth) with two passes
112 conducted per transect¹⁷. Mobile fish were recorded during the first pass as they can quickly
113 leave the survey area, and more cryptic fishes were the focus of the second pass. Transects at
114 a given location were conducted with a 25m gap between each replicate. During each transect,
115 all adult fishes were identified to species, which were then classified as either harvested by
116 fishers or not harvested by fishers¹⁷. We included data from 2011–2020 in our analysis. Data
117 from previous years were not included as Moorea experienced a crown-of-thorn starfish
118 (*Acanthaster planci*) outbreak between 2006 – 2009, and a cyclone in 2010, which comprise
119 disturbances not relevant to this study^{14,18}.

120

121 ***Fisher sentiment and COVID-19***

122 Following lockdown, 69 fishers (six professional and 63 amateur) were interviewed using a
123 standardized set of binary-choice questions about the health and economic crisis facing
124 Moorea Island's resident population; as well as whether eating habits, use of local fisheries,
125 and respect for no-take rules within MPAs had been affected by the lockdown. Only residents
126 of Moorea (maximum one member per household) that self-identified as professional or
127 amateur fishers were interviewed. Interviews were conducted in French, with exception of
128 fish names, which were discussed in Tahitian. The study sample included inhabitants from
129 around the island, including people that lived in front of MPAs and nMPAs.

130

131 *Statistical analysis*

132 To test if the abundances of harvested and non-harvested fish species were affected by the
133 COVID-19 lockdown, we investigated whether fish numbers differed within MPA and nMPA
134 barrier reef and outer slope sites during the lockdown and post-lockdown transects compared
135 to the 10 year average (Feb 2011–Feb 2020) using either a one-way analysis of variance
136 (ANOVA) or a Kruskal-Wallis test, if ANOVA assumptions (homogeneity of variance and
137 normality) were not met. Where the ANOVA or Kruskal-Wallis test indicated a significant
138 difference in group means, post-hoc tests (Tukey's HSD or Dunn test, respectively) were
139 conducted to determine which specific groups differed.

140

141 **Results**

142 *Fish surveys across an MPA network around Moorea*

143 There was a significant different in abundance of both harvested ($\chi^2=11.2$, $P=0.004$, Fig. 2A)
144 and non-harvested ($F_{2,2}=17.5$, $P<0.001$, Fig. 2E) fishes between the three time periods
145 (lockdown, post-lockdown and 10-year 'long-term' average) at the barrier reef MPA sites.
146 Post-hoc tests indicated that fish abundance recorded during the lockdown period was

147 significantly greater than the long-term average for both harvested ($P=0.009$; Dunn's test) and
148 non-harvested ($P<0.001$; Tukey's test) species. For non-harvested species, the fish abundance
149 recorded during the lockdown period was also significantly greater than that recorded post-
150 lockdown ($P<0.001$; Tukey's test). However, there was no significant difference observed
151 between these two time periods for harvested species, and no difference in fish abundance
152 measured post-lockdown compared to the long-term average for either harvested ($P=0.150$;
153 Dunn's test) or non-harvested species ($P=0.960$; Tukey's test). No significant difference in
154 fish abundance across the three time periods was observed at the nMPA barrier reef sites for
155 either harvested species ($\chi^2_2=5.4$, $P=0.067$; Fig. 2B) or non-harvested ($\chi^2_2=1.9$, $P=0.388$; Fig.
156 2F) species. Similarly, for the outer slope sites, there was no significant difference in fish
157 abundance across the three time periods at the MPA sites for either harvested ($\chi^2_2=2.4$, $P=0.3$;
158 Fig. 2C) or non-harvested ($F_{2,2}=1.4$, $P=0.259$; Fig. 2G) species, nor at the nMPA sites for
159 either harvested ($\chi^2_2=0.8$, $P=0.672$, Fig. 2D) or non-harvested ($F_{2,2}=0.071$, $P=0.932$, Fig. 2H)
160 species.

161
162 Within the MPA barrier reef site, a taxonomically and functionally diverse range of species
163 recorded an increase in abundance compared to the long-term average. For instance, the five
164 harvested species that experienced the most dramatic increase, included: *Acanthurus*
165 *triestegus* (3.7 long-term average compared to 230 during lockdown), *Epinephelus merra* (1.0
166 long-term average compared to 34 during lockdown), *Gnathodentex aureolineatus* (1.4 long-
167 term average compared to 46 during lockdown), *Lutjanus fulvus* (1.3 long-term average
168 compared to 46 during lockdown) and *Sargocentron spiniferum* (0.3 long-term average
169 compared to 6 during lockdown) (Fig. S1 and summary data available in Table S1). Five
170 species (*Acanthurus guttatus* [1 recorded during lockdown], *Myripristis pralinia* [75 recorded
171 during lockdown], *Naso lituratus* [12 recorded during lockdown], *Sargocentron tere* [3

172 recorded during lockdown] and *Scarus sordidus* [293 recorded during lockdown]) were also
173 recorded for the first time during the lockdown (Fig. S1 and summary data available in Table
174 S1). Similar patterns were also found for the non-harvested species at the MPA barrier reef
175 site, with notable increases recorded in: *Abudefduf sexfasciatus* (0.4 long-term average
176 compared to 30 during lockdown), *Abudefduf sordidus* (0.9 long-term average compared to 62
177 during lockdown), *Thalassoma amblycephalum* (0.5 long-term average compared to 23 during
178 lockdown), *Paracirrhites arcatus* (0.6 long-term average compared to 62 during lockdown)
179 and *Pseudocheilinus hexataenia* (1.2 long-term average compared to 30 during lockdown)
180 (Fig. S1 and summary data available in Table S1). Again, five species (*Arothron hispidus* [1
181 recorded during lockdown], *Chaetodon trifasciatus* [24 recorded during lockdown],
182 *Forcipiger brevirostris* [2 recorded during lockdown], *Ostracion melagris* [3 recorded during
183 lockdown] and *Thalassoma purpureum* [1 recorded during lockdown]) were also recorded for
184 the first time during the lockdown (Fig. S1 and summary data available in Table S1).

185

186 ***Fisher sentiment and COVID-19***

187 The majority of fishers (91%, 63 of 69) indicated that they were afraid of catching COVID-
188 19, with most (74%, 51 of 69) stating that they or at least one member of their family was
189 financially impacted by the crisis. Most (80%, 55 of 69) indicated that the lockdown led to
190 them and their families changing their diet, turning to a heavier reliance on locally harvested
191 fruits and vegetables, as well as fish from nearby reefs, rather than relying on food purchased
192 from stores. Of the six professional fishers that we interviewed, four said that they continued
193 to fish as usual during the lockdown period, while the other two said that their business
194 primarily relied on selling to local restaurants and hotels and as these businesses were closed
195 they did not fish. Of the amateur fishers, most (71%, 45 of 63) respected the lockdown, with
196 most stating that the risk of punishment (\$150 USD fine for first breach of lockdown, rising to

197 \$2,800 USD for each re-offense) was not worth the potential reward. Most of those that did
198 breach the lockdown (83%, 15 of 18) said that they fished from the coast, rather than from a
199 boat, and fished near dawn or dusk (89%, 16 of 18) to minimize their likelihood of being
200 caught by the authorities. While most amateur fishers respected MPA no-catch restrictions,
201 four (6% of 63) stated that they fished within MPA boundaries. Interestingly, all of these
202 people lived directly in front of an MPA and **stated that they did this as they required fish for**
203 **subsistence** and were worried about the risk of being caught if they travelled to nMPA zones
204 and thus had “no choice”.

205

206 **Discussion**

207 The COVID-19 lockdown highlights the chronic effects that recreational activity has on coral
208 reef fish communities, and that the behaviour of animals in human-impacted environments
209 can rapidly change in our absence. During the six week lockdown period, no tourists were
210 allowed to the island and residents were under a strict lockdown regime. This led to a sudden
211 halt to the recreational use of the inner barrier reef MPA locations, which are adjacent to
212 many of the island’s hotels **and used for tourism-related recreational activities**, and this
213 reduction in recreational use was associated with a dramatic increase in fish abundance during
214 the lockdown period. By contrast, non-MPA and outer barrier reefs experienced non-
215 significant changes in fish abundance during lockdown. Interviews with locals indicated that
216 the fear of catching COVID-19 and being issued heavy fines led to most amateur fishers
217 respecting the lockdown. Professional fishers kept fishing unless they were dependent on
218 selling their catches to the businesses that rely on tourists (e.g. hotels and restaurants), in
219 which case they too ceased activity. Overall, similar to reports of sudden effects of lockdown
220 on pollution levels¹⁹⁻²¹ **and terrestrial species, such as birds^{22,23}**, our results indicate that the

221 sudden removal of human activity has similar positive effects on the behaviour of fish
222 populations.

223

224 These results resemble lockdown-related changes in the physical environment and are
225 consistent with anecdotal reports of increased space use by animals during lockdown⁶. Early
226 reports of increased air and water quality following the onset of lockdown¹⁹⁻²¹ highlighted
227 that drastic reductions in human activity can have rapid positive effects for the environment.
228 Unfortunately, subsequent reports are suggesting that these effects can be short lived². Our
229 results are consistent with the latter, demonstrating a significant increase in the number of fish
230 detected within the barrier reef MPA sites during lockdown (areas commonly used for human
231 recreation), and a subsequent return to pre-lockdown levels following easing of lockdown
232 regulations. As our surveys were conducted on adult fish, these patterns may be explained by
233 either fish rapidly recolonizing these areas, or by resident cryptic species becoming more
234 conspicuous (i.e. venturing further from crevices) in the absence of human activity.
235 Considering that we recorded increases in broad spread of species, spanning those that are
236 typically site attached (e.g. damselfishes and hawkfishes) to those that actively roam (e.g.
237 surgeonfishes and parrotfishes), our data is consistent with both possibilities, suggesting that
238 the abrupt removal of human activity has general benefits for coral reef fish communities,
239 which is consistent with comparable terrestrial research²⁴.

240

241 While a significant increase in fish abundance was seen within the barrier reef sections of the
242 MPAs this pattern did not extend to their outer slope sections. An increase was observed at
243 the barrier reef non-MPA sites; however, this was not significant, and no difference was
244 observed on the outer slope sections of the non-MPA areas surveyed (Fig. 2). This suggests
245 that the effects of the lockdown did not have a uniform effect on coral reef fish communities,

246 which may reflect the baseline level of human activity occurring at each site. For instance,
247 given their distance from shore, outer reef slope sites are likely subject to less human activity
248 than inshore locations, which provide a recreation space for a wider array of local residents
249 and tourists. Subsequently, the difference in activity, and associated disturbance to fish
250 communities during the lockdown was likely less, resulting in the minimal change in
251 abundance observed²⁵⁻²⁷. The lack of a significant difference in abundance in either location
252 may also reflect the baseline level of activity prior to the lockdown. As noted, tourist and non-
253 extractive recreational activity by locals is high within the protected areas, with these
254 locations generally set aside for swimming and water sports (i.e. the municipally managed
255 public beach at Nuarei, and the numerous resort hotels at Tiahura and Temae). Thus, the net
256 change in human activity within these areas may have been higher, leading to more distinctive
257 behavioural changes²⁸. In addition, fishes within fished areas may be more wary of humans in
258 general due to the status of the environment²⁹⁻³¹ and so any change in abundance may have
259 been harder to identify using diver-based survey methods. Finally, the greater abundance of
260 fishes inside the barrier reef MPA areas may reflect the underlying benthic characteristics of
261 these areas. While our surveys only considered fish abundance, the MPA conditions also
262 prohibit the collection of invertebrates such as urchins, shellfish, and lobster - species that can
263 support the health of benthic communities and for which traditional collection methods can
264 cause damage to the underlying structural complexity³². If fishes did recolonize near-shore
265 areas in the absence of humans, they may have been drawn towards the MPA areas, as
266 opposed to the adjacent non-MPA areas, if habitat quality, and subsequently food availability,
267 was higher.

268

269 The COVID pandemic has resulted in hundreds of thousands of deaths worldwide and has led
270 to a global economic downturn that will have long-term and unpredictable consequences³³⁻³⁵.

271 The government-mandated lockdowns, which occurred worldwide in early 2020 following the
272 initial spike in cases, were similarly unprecedented and resulted in a sudden drop in human
273 activity in many of the world's wild spaces. As a side effect, this provided an opportunity to
274 rapidly quantify the influence of human presence on animal behaviour, and acquire a snapshot
275 of these spaces in our absence⁶. Our results provide evidence that the sudden decline in
276 human activity was correlated with an increase in the abundance of fishes within locally-
277 managed MPAs near to shore, although no significant change was seen outside of MPAs or
278 on the outer slope of MPA barrier reefs. This suggests that human activities have a variable,
279 but generally negative, influence on the behaviour of both harvested and non-harvested fish
280 species and that these communities are highly responsive to reductions in human activity, at
281 least where fishing is prohibited. Surveys of the local fishing community showed that, while
282 most fishers limited their activity during the lockdown, fishing in and outside of the MPA
283 network continued, which reflected the greater reliance on harvesting seafood as stores and
284 other commercial supply lines ground to a halt. This in turn highlights the ongoing challenges
285 faced in maintaining effective MPA networks in an ever changing world, particularly in
286 locations where subsistence harvesting is an important part of life for local communities. In
287 all, this study highlights the dramatic and by in large unseen effect that our presence has on
288 the ecological communities with which we interact, and shows the speed with which these
289 communities can rapidly change when we are removed from the equation.

290

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374

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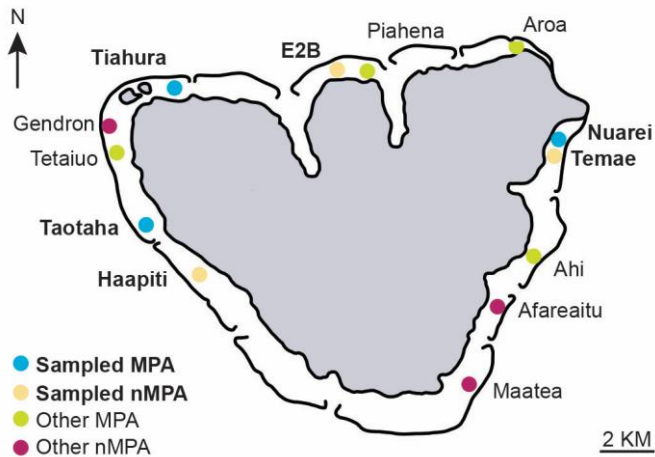
388 **Data and material availability:** An R Markdown file containing all analyses contained
389 within this manuscript is published in the Supplementary Materials. The authors confirm that
390 all data used in this manuscript will be archived prior to the work being published.

391

392 **Supplementary Materials**

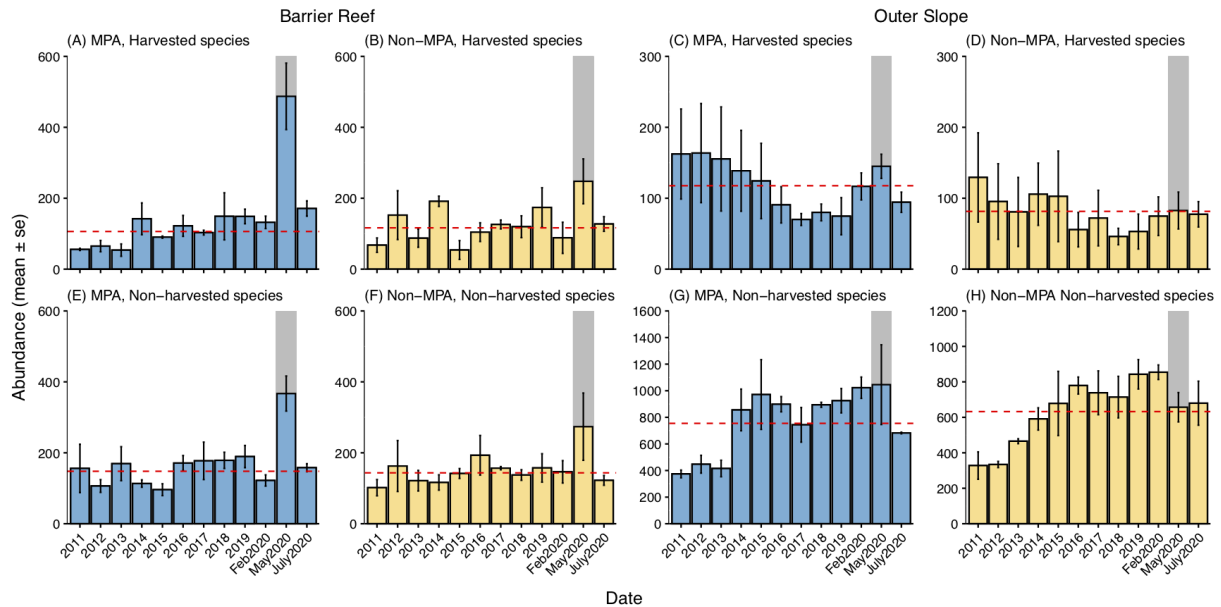
393 R Markdown file of all analyses presented in this manuscript.

394 **Figures and Tables**



395

396 **Figure 1.** Map of sampling sites around Moorea Island, French Polynesia.



397

398 **Figure 2.** Abundance (mean \pm SE) of harvested (A-D) and non-harvested (E-H) fish between
 399 2011-2020 at six locations (3 MPA [A,C,E,G] and 3 non-MPA [B,D,F,H]), measured on both
 400 the barrier reef (A,B,E,F) and outer slope (C,D,G,H). Surveys were conducted during
 401 February between 2011-2020, with additional surveys conducted in May 2020 (immediately
 402 following the six-week COVID-19 lockdown, i.e. “lockdown” survey) and July 2020 (two
 403 months following the removal of COVID-19 lockdown, i.e. “post-lockdown” survey). Dashed
 404 red line indicates the 10-year “long-term” average (calculated from abundance measurements
 405 from 2011-Feb 2020).