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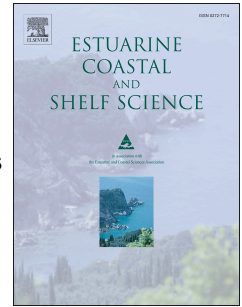
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# 1 Restoring the reef: coral restoration yields rapid impacts on certain fish assemblages

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23

24

## 25 Authorship contribution statement

26 SK, CC, JS, TM, and JC conducted the investigation. SK, DL, and XR worked on the methodology. SK and XR  
27 wrote the initial draft. SK, EM, LS, LM, NR, FB, DL, and XR reviewed and edited the final manuscript. SK,  
28 XR, and DL oversaw project administration. DL and XR conceptualized the study. XR implemented the code in  
29 R, validated the analyses, and conducted formal analysis, managed data curation and visualization. XR and DL  
30 supervised the project. JC and DL provided resources, and DL managed funding acquisition.

31

32

33 **Abstract**

34 Coral reefs harbor one of the highest biodiversity on Earth but increasing disturbances have  
35 often led to rapid shifts from coral to algal states, prompting the development of conservation  
36 methods, including coral restoration. While most studies have focused on the medium and  
37 long-term effects of restoration on fish assemblages, less is known about its short-term effects  
38 (i.e., within one month) on associated communities. This study explored the short-term  
39 impacts (< 1 month) of coral restoration, including four restoration conditions, on fish  
40 abundance, diversity, and assemblages in a marine educational area (a small coastal area  
41 managed by a school in the frame of an eco-citizen pedagogical program) in Bora Bora,  
42 French Polynesia. Sixteen dead reef patches previously covered by macroalgae were grouped  
43 into four conditions as follows: four were non-restored (control condition), four were restored  
44 to 25% living coral cover (condition 25%), four to 50% living coral cover (condition 50%),  
45 and four were restored to 75% living coral cover (condition 75%). The abundance of fish at  
46 adult and juvenile stages was assessed, before and after coral restoration, using the fixed-  
47 point method for a period of 5 minutes on each of the 16 reef patches. Two successive  
48 observation periods were conducted for each patch: one focusing on more visible and mobile  
49 fish, and another on more cryptic species. Surveys were conducted one day and three days  
50 prior to restoration, and then 24 days and 28 days post-restoration. For adults, the difference  
51 in abundance, number of species, and diversity before and after restoration were not  
52 significant between the conditions. Similarly, for juveniles, no significant differences were  
53 observed when considering the conditions and restoration. Before restoration, the fish  
54 assemblages were randomly distributed between the four conditions for both adults and  
55 juveniles. After the restoration, the inter-conditions similarity decreased significantly for  
56 adults, but not for juveniles. Some species were associated with the more restored patches  
57 (*Chaetodon citrinellus*, *Halichoeres trimaculatus*, and *Zanclus cornutus*). Finally, the

58 restoration seemed to have variable effects depending on the trophic groups. Coral restoration  
59 has short-term effects on fish assemblages, indicating the effectiveness of restoration efforts  
60 even within a brief period. These rapid changes underscore the remarkable ability of adult  
61 fish to adapt to rapidly changing environments.

62

63 **Keywords:** fish communities, French Polynesia, restoration efforts, diversity, abundance, Marine educational  
64 area, Bora Bora, Society Islands, algal states, short-term

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## 66 INTRODUCTION

67           Although coral reefs cover slightly less than 0.1% of the ocean's surface, they host  
68 one of the most extensive taxonomic biodiversity on Earth (Porter and Tougas, 2001).  
69 However, the increasing frequency and intensity of disturbances linked to climate change and  
70 local human activities are causing rapid degradation of coral reefs (Hughes et al., 2017;  
71 Noisette et al., 2022). In response, various monitoring and conservation methods, such as  
72 coral restoration, have been developed (Boström-Einarsson et al., 2020; Clark and Edwards,  
73 1995).

74           The International Science and Policy Working Group of the Society for Ecological  
75 Restoration defines coral restoration as “the process of helping to recover an ecosystem that  
76 has been degraded, damaged, or destroyed” (SER, n.d.). Traditional methods of active reef  
77 restoration include physical restoration (*e.g.*, reprofiling the sea floor, consolidating the reef  
78 structure, and installing artificial structures) and/or biological restoration (*e.g.*, direct coral  
79 transplantation, coral gardening, micro-fragmentation, and repopulation with larvae)  
80 (Boström-Einarsson et al., 2020; Romon, 2018). In the last decade, new types of restoration  
81 have emerged, including the modification of coral phenotypic plasticity (Thériault-Gauthier,  
82 2017), acoustic enrichment (Gordon et al., 2019), the introduction of herbivorous species  
83 (Krimou et al., 2023), and microbiome manipulation to mitigate heat stress (Voolstra et al.,  
84 2023), which are interconnected (Thériault-Gauthier, 2017). For instance, acoustic  
85 enrichment coupled with active coral restoration can enhance fish assemblages (Gordon et al.,  
86 2019). However, caution must be exercised to prevent pushing a restoration technique to its  
87 extreme, as exemplified by the re-introduction of species, which, if done excessively, may  
88 result in invasive species concerns and disrupt the ecological balance. In light of these  
89 elements, it appears that coral restoration is widely employed to address declines in coral  
90 cover. While it is necessary to monitor the dynamics of fish in restored areas to assess

91 restoration progress (Zakaria et al. 2020, Alvarez-Filip et al. 2015), very few studies have  
92 focused on the temporal response of fish communities to coral restoration (Hein et al. 2020).

93 The term ‘succession’ refers to the changes observed in an ecological community  
94 because of a disturbance that opens up a relatively large area. These changes often include a  
95 sequence of species and increases in biomass and diversity (Connell and Slatyer, 1977).  
96 Ecological succession has mainly been studied in terrestrial ecosystems in studies focusing on  
97 a broad range of topics such as primary and secondary plant succession, arthropod succession  
98 in mangroves and carcasses, or in link with carbon sequestration (Anderson, 2007; Liu et al.,  
99 2023), but studies are generally more recent in the marine realm (Harrison and Whitfield,  
100 2004; Jouval et al., 2020, Toledo et al., 2020, Mathews et al., 2021, Li et al., 2022, Vicente et  
101 al., 2022, McDevitt et al., 2023).

102 Understanding the impact of habitat fragmentation and consumer loss on coral reefs is  
103 crucial for comprehending how habitat characteristics moderate the effects of consumer-  
104 resource interactions on successional dynamics (Gonzalez et al., 2020). The architectural  
105 complexity of the coral reef environment, mainly driven by the abundance of hermatypic  
106 corals, plays an influential role in shaping the community structure of reef-associated  
107 organisms (Komyakova et al., 2013).

108 In response to acute disturbances such as coral bleaching, cyclones, or other events,  
109 fish assemblages exhibit a wide range of responses (Pratchett et al., 2011; Wilson et al.,  
110 2006). This variability includes scenarios where there is no perceived change, declines, or  
111 even increases in the abundance of certain fish species (Bellwood et al., 2006; Garpe et al.,  
112 2006; Munday et al., 2008). Notably, fish species highly specialized and dependent on corals,  
113 such as coral-feeding butterflyfish, are particularly sensitive to coral loss (Pratchett et al.,  
114 2008). While numerous studies have explored the crucial role of some fish species in coral  
115 reef resilience (Adam et al., 2011; Hughes et al., 2007), there is also a focus on artificial or

116 restored natural reefs in understanding the mechanisms of ecological succession in aquatic  
117 ecosystems (Santos et al., 2011; Wang et al., 2021).

118         The structure and diversity of fish assemblages can serve as valuable indicators to  
119 assess the success of restoration projects (Harrison and Whitfield, 2004; Zakaria and  
120 Syaifullah, 2020, Sangil et al., 2024). While some restoration projects have directly assessed  
121 fish populations, fish are often studied as secondary qualitative observations, and research on  
122 the effects of adding live coral cover and complexity on fish is still in its early stages  
123 (Seraphim et al., 2020). Few studies exist on how the addition of structural complexity during  
124 coral restoration can restore reef ecosystems (Opel et al. 2017). Specifically, the effect of  
125 adding coral cover and complexity on fish lacks scientifically validated research (Seraphim et  
126 al. 2020).

127         Moreover, the effect of coral restoration on fish assemblages varies strongly over  
128 time, whether for the short term (*i.e.*, within the first month), medium term, or long term (*i.e.*,  
129 at least one year). After a week of outplanting, it has been demonstrated that there was an  
130 increase in fish abundance, species richness, and a significant shift in fish community  
131 composition (Opel et al., 2017). More research is needed to confirm the trends observed in  
132 this Caribbean reef. While there is generally a positive effect of coral reef restoration in the  
133 medium/long-term, often resulting in increased fish diversity and abundance after months or  
134 years (Fadli et al., 2012), responses of fish assemblages to coral restoration have been shown  
135 to be very complex, with region-, site-, and size-specific patterns (Hein et al., 2020). For  
136 example, while a higher abundance of damselfish at restored sites seems consistent, the  
137 increased abundance of herbivorous fish appears to be limited to individual reefs (Ladd et al.,  
138 2019).

139         Patterns of fish abundance and richness during the first months following coral  
140 restoration can be complex and variable, with fluctuations occurring during this period. In a



141 study from a non-reef environment, Santos et al. (2011) demonstrated that fish abundance  
142 and richness may initially increase following the installation of an artificial reef, but then  
143 decline within the first six months. These observations were associated with an increase in  
144 biomass, with variations noted depending on the type of material used for the artificial reef.  
145 Other studies indicated drops in fish abundances six months after structural addition (Smith  
146 1978, Golani and Dimant 1999). An explanation could be that the initial high abundance  
147 reaches a plateau (Bohnsack and Sutherland 1985).’

148 Our study aims to compare fish abundance, diversity, and assemblages before and  
149 after coral restoration in the Marine Educational Area (MEA) of Bora Bora (French  
150 Polynesia) to evaluate short-term fish changes occurring within one month. A marine  
151 educational area is an eco-citizen pedagogical concept that involves a small coastal area  
152 managed by students from a school under the supervision of a scientific mentor and their  
153 teacher(s). Therefore, analysis over a short-term period will enable us to understand the early  
154 mechanisms of ecological succession in fish and their evolution over time within a month.  
155 Our hypothesis is that within a month, changes in abundance and diversity would not be yet  
156 significant while we expect to observe initial signs of modifications in fish assemblages.

## 157 **MATERIALS AND METHODS**

### 158 **Study sites**

159 The study was conducted at a Marine Educational Area (MEA), located on the  
160 fringing reef of Bora Bora (French Polynesia, Fig. 1). The MEA is a 40,000 m<sup>2</sup> area located  
161 on the west coast of the south part of the main island (16°31’29” S, 151°44’20” W). Sixteen  
162 dead reef patches with a size range from 5 to 12 m<sup>2</sup> were identified and grouped into four  
163 conditions as follows: four were non-restored (control condition), four were restored to 25%  
164 living coral cover (condition 25%), four to 50% living coral cover (condition 50%), and four  
165 were restored to 75% living coral cover (condition 75%).

166 Prior to the restoration efforts, the reef patches had less than 1% living coral cover  
167 and were dominated by macroalgae, especially by *Dictyota* spp., *Halimeda* spp., *Padina*  
168 *boryana*, and *Turbinaria ornata*, which covered over 85% of the reef surface. To restore the  
169 reef patches, healthy coral colonies (size between 10 x 5 x 5 cm and 15 x 30 x 10 cm),  
170 naturally present near the MEA zone, were manually glued (using a mix of SikaLatex,  
171 cement, and sand) individually in less than two days. The coral colonies used in this study  
172 were relocated prior to the construction of a new infrastructure, which is located 500 meters  
173 away from the AME. The proportion of different coral species used on each reef patch was as  
174 follows: 70% *Acropora* spp., 18% *Porites rus*, and 12% *Porites lobata* (Fig. 1). This  
175 distribution was based on the coral cover found on the fringing reef close to the MEA  
176 (Lecchini et al., 2021). Coral colonies were transplanted from a similar and nearby fringing  
177 reef to the studied patches. Macroalgae were manually removed before attaching new corals.  
178 In addition, throughout the experiment, macroalgae that settled on the coral patches were  
179 removed daily (McClanahan et al., 2001, 2000).

## 180 **Fish survey**

181 The abundance of fish at adult and juvenile stages was assessed, before and after coral  
182 restoration, using the fixed-point method for a period of 5 minutes on each of the 16 reef  
183 patches (method adapted from Dethier *et al.* 1993). The mean depth was approximately 1 m  
184 and the maximal depth was approximately 1.4 m. Each site was surveyed across the entire  
185 patch. The potential effect of the size of the patches was not directly accounted for during the  
186 survey, but it was considered in the statistics (see Statistical analysis section). Visual  
187 estimates were employed because they are deemed to be more accurate, especially for rare  
188 species, compared to other methods involving random points (Dethier et al. 1993). Surveys  
189 were conducted one day (D-1) and three days (D-3) prior to restoration, and then 24 days  
190 (D24) and 28 days (D28) post-restoration. Abundances at D-1 and D-3 characterized the

191 pre-restoration period, and values at D24 and D28 characterized the post-restoration period.  
192 Abundance and life stage (adult vs. juvenile) were determined for each species, excluding  
193 small cryptic species from the families *Blenniidae*, *Carapidae*, *Gobiidae*, and *Tripterygiidae*  
194 (Siu et al., 2017). The size of the individuals allowed to distinguish between juveniles and  
195 adults. In addition, the pigmentation patterns and the behavior were also used to differentiate  
196 adults from juveniles (Lecchini and Galzin 2005).

197 S.K. conducted all the surveys during one hour and a half between 10 AM and 4 PM.  
198 Due to the limited tidal range at Bora-Bora, which reaches a maximum of 40 cm during  
199 spring tides (Pirazzoli et al. 1985), there is no temporal effect (e.g., day of sampling).

## 200 **Statistical analysis**

201 All statistical analyses were performed using R software 4.1.1 (R Core Team). The  
202 abundance (Ab, *i.e.*, the total number of fish), the number of species (NoSp), and the  
203 Shannon diversity index ( $H'$ ) were calculated for each of the four conditions (control, 25%,  
204 50%, and 75% conditions), each patch (A, B, C, and D), each period (before vs. after coral  
205 restoration), and replicates (1 vs. 2). Linear mixed-effects models were used, with one for  
206 juveniles and another for adults (function *lme*, library *nlme*. To account for site-level  
207 differences, the site was treated as a random variable. For each feature (Ab, NoSp, and  $H'$ ),  
208 the interaction of the condition and the period was examined. Homoscedasticity of variances  
209 and normality assumptions were checked and met. The similarities in fish assemblages'  
210 composition among the four conditions (control, 25%, 50%, and 75%) were tested using  
211 analyses of similarities (ANOSIM) based on Bray-Curtis dissimilarity matrices using the  
212 package *vegan* (Bray & Curtis 1957). The output is a metric called R with  $R \in [-1, 1]$ . Null R  
213 values indicate random grouping, positive R values indicate greater similarity within groups,  
214 and negative R values indicate greater similarity between than within groups (Warton *et al.*  
215 2012).

216 A permutation-based test was used to test the multivariate homogeneity of group  
217 variance (functions *permutest* and *betadisper*, *vegan* package) on distance matrices that were  
218 previously standardized (function *decostand*, method = normalize). The homogeneity of  
219 variance was confirmed after this standardization (Fisher tests: Df = 3, F = 1.70 and 0.40, P =  
220 0.18 and 0.77). Therefore, permutational multivariate analyses of variance (PerMANOVA)  
221 based on distance matrices (function *adonis2*) were used to determine whether the fish  
222 assemblage's composition varied with restoration (group 1 = control, group 2 = 25%, group 3  
223 = 50%, and group 4 = 75%) (Anderson 2017). The method of Bray was used to calculate  
224 pairwise distances. Canonical Correspondence Analysis (CCA) was used to visualize the fish  
225 assemblages and the effect of the restoration. A first CCA was conducted on the data before  
226 the restoration, and a second CCA on the data after the restoration. The "restoration" variable  
227 was added only on the ordination plot of the second CCA. The same analyses were conducted  
228 separately for adult and juvenile fish.

229 Fish species were then classified into seven trophic groups (Viviani et al., 2019): (1)  
230 grazers, (2) herbivorous scrapers or excavators, (3) herbivorous detritivores, (4) omnivores,  
231 (5) planktivores, (6) piscivores, and (7) benthic invertebrates' feeders. As only one species  
232 was herbivorous detritivore, it was excluded from the trophic level analysis. Nevertheless, it  
233 was included when considering all species collectively. It was neither abundant nor  
234 significant, constituting only 3% of observations. The differences in the three ecological  
235 features (Ab, NoSp, and H') before and after the restoration for each condition were  
236 calculated (e.g.,  $\Delta H' = H'_{\text{after}} - H'_{\text{before}}$ ). The difference between the mean number of  
237 individuals before and after restoration ( $\Delta$ ) was calculated in each trophic group. Kruskal-  
238 Wallis tests were used to compare the four conditions (0%, 25%, 50%, and 75%).

## 239 **RESULTS**

240 During the study, 53 fish species from 19 families were observed. The most abundant  
241 families were Labridae (10 species), Pomacentridae (8 species), Scaridae (7 species),  
242 Chaetodontidae (6 species), and Acanthuridae (4 species). The total fish abundance before  
243 restoration was  $16.47 \pm 10.30$  individuals per patch reef (mean  $\pm$  SD), which increased to  
244  $20.97 \pm 10.98$  individuals per patch reef (overall mean for the four conditions together) after  
245 the restoration (Fig. 2). For adults, the difference in abundance (Ab), number of species  
246 (NoSp), and diversity ( $H'$ ) before and after restoration were not significant between the  
247 conditions (Ab:  $F = 1.81$ ,  $P = 0.16$ ; NoSp:  $F = 1.97$ ,  $P = 0.13$ ; and  $H'$ :  $F = 1.40$ ,  $P = 0.26$ ;  
248 Table SP5). Similarly, for juveniles, no significant differences were observed when  
249 considering the conditions and restoration (Ab:  $F = 1.37$ ,  $P = 0.27$ ; NoSp:  $F = 2.36$ ,  $P =$   
250  $0.085$ ; and  $H' = 1.14$ ,  $P = 0.35$ ; Table SP6). For both adults and juveniles, irrespective of the  
251 period, no significant differences were observed between the conditions (for Ab, NoSp, and  
252  $H'$ : all  $P > 0.05$ , Table SP5 and SP6), indicating homogeneity in the patches within the study  
253 area. In contrast, without considering the conditions, significant differences were observed  
254 between the two periods for adults (all  $P \leq 0.0003$ , Table SP5), indicating high variability in  
255 the fish species present. For juveniles, fish abundance was equivalent ( $P = 0.78$ ) but not the  
256 number of species or diversity (both  $P < 0.0001$ , Table SP6).

257 Before restoration (D-1 and D-3), the fish assemblages were randomly distributed  
258 between the four conditions (control, 25%, 50%, and 75%) for both adults and juveniles  
259 (ANOSIM,  $R = 0.057$  and  $0.024$ ,  $P = 0.15$  and  $0.25$ , respectively). After the restoration, the  
260 inter-conditions similarity decreased significantly for adults (ANOSIM,  $R = 0.27$ ,  $P = 0.001$ ),  
261 but not for juveniles (ANOSIM,  $R = 0.068$ ,  $P = 0.11$ ). The fish assemblages were equivalent  
262 between the four groups (0%, 25%, 50%, and 75%) before the restoration for both adults and  
263 juveniles (PerManova,  $df = 3$ ,  $F = 0.16$ ,  $P = 0.15$ ;  $df = 3$ ,  $F = 1.33$  and  $P = 0.20$ , respectively),  
264 while after the restoration a significant difference was observed for adults (PerManova,  $df =$

265 3,  $F = 2.72$ ,  $P = 0.001$ ), but not for juveniles (PerManova,  $df = 3$ ,  $F = 1.16$ ,  $P = 0.29$ ). Thus,  
266 after the restoration, the CCA concentration ellipses of fish assemblages were distributed  
267 along the CCA1 axis illustrating the effect of the restoration on the fish assemblages (Fig 3).  
268 After the restoration, adults and juveniles were distributed in the CCA plot according to two  
269 axes: CCA1 reflected coral restoration while CCA2 reflected variability in some patch reefs  
270 restored at 25%. Some species were associated with the more restored patches (*C. citrinellus*,  
271 *H. trimaculatus*, and *Z. cornutus*; scores:  $-0.94$ ,  $-0.96$ , and  $-1.3$ ). When considering 95%  
272 confidence interval ellipses, there was no overlap between the 75% and the 0% assemblages.

273       When considering each trophic group at adult stage separately, the maximal  $\Delta$  in the  
274 mean number of individuals was observed at 50% restoration for all trophic groups (i.e.,  
275 herbivorous grazers, herbivorous scrapers/excavators, omnivores, and benthic invertebrates'  
276 feeders), except piscivores and planktivores (Fig. 4). Maximal values for piscivores were  
277 observed at 75% restoration, while for planktivores, they were observed when there was no  
278 restoration. However, differences among the four conditions were not statistically significant  
279 (Kruskal-Wallis:  $\chi^2 = 0.24 - 4.51$ ;  $df = 3$ ;  $P = 0.21 - 0.97$ ). The restoration has variable  
280 effects on each of the various trophic groups when compared to one another. For grazers,  
281 positive  $\Delta$  values were obtained, while negative values were observed for planktivores in all  
282 restored patches.

## 283 **DISCUSSION**

284       While restored reefs remain vulnerable to global factors such as climate change,  
285 pollution, and diseases, coral restoration can enhance essential ecological functions and  
286 services for reefs that have undergone significant degradation and lack resilience for natural  
287 recovery (Rinkevich, 2008) or in cases where expedited recovery is desired. For instance,  
288 when sites have been degraded to the point of rubble, fast natural recovery without human  
289 intervention is generally unlikely (Fox et al., 2003). In the context of restoration projects, the

290 structure and diversity of fish assemblages can serve as valuable indicators for evaluating  
291 success (Harrison and Whitfield, 2004). An increase in fish abundance and diversity is  
292 commonly observed after a significant period, typically months or years, following the start  
293 of the restoration process (Fadli et al., 2012). If artificial reefs are known to be rapidly (i.e., >  
294 1 day) colonized by fish (Bohnsack and Sutherland 1985, Golani and Dimant 1999), the  
295 colonization in coral restoration processes is not widely studied (Opel et al. 2017). Our study  
296 specifically investigated the short-term effects of coral restoration on fish assemblages in the  
297 Bora Bora reef over a period of 24 to 28 days. The results suggest a rapid shift in some adult  
298 fish assemblages with coral restoration, without significant changes in richness, diversity, and  
299 abundance. In other words, our findings conclude that early restoration effects did not  
300 manifest as differences in abundance or diversity but rather in the type of assemblage present.  
301 In the Caribbean, it has been shown that restoration leads to a change in community  
302 composition, resulting in no overlap between controls and outplants seven months later, very  
303 similar to what we observed between our control and 75% restoration condition.

304 More specifically, the results underscored that the short-term effects of coral  
305 restoration were primarily attributed to adult fish at Bora-Bora. This distinction could be due  
306 to the fact that newly recruited juvenile fish might not have had sufficient time to establish  
307 themselves on the newly restored patches. In longer-term studies, changes in abundance and  
308 diversity can be influenced by both the specimens that were already present and those that  
309 recruited to the area (Fadli et al., 2012). On the contrary, in short-term studies, the timeframe  
310 is too brief to consider new juveniles resulting from recruitment. Newly recruited individuals  
311 often exhibit cryptic behavior, making them challenging to identify, and they are typically not  
312 counted in visual estimations. Additionally, the requirements of juvenile fish may differ from  
313 those of adults, encompassing variations in feeding habitats and nursery preferences (Mumby  
314 et al., 2004; Nagelkerken et al., 2002, 2000; Ogden and Quinn, 1984). The findings

315 underscore the importance of considering the life history of fish when planning and  
316 evaluating coral reef restoration efforts. Juvenile fish recruits play a critical role in the long-  
317 term success of restoration efforts, contributing to the replenishment of populations and the  
318 maintenance of functional roles within the ecosystem (Seraphim et al., 2020). Consequently,  
319 it is essential to incorporate considerations for the recruitment and survival of juveniles into  
320 restoration planning (Seraphim et al., 2020).

321 One of the unique aspects of our study lies in not altering the species proportion of  
322 restored coral, but rather quantifying coral cover using the same species, while considering  
323 the area of coral cover. In our case, the species of coral restored were consistent across the  
324 experiment (*Acropora* spp., *Porites rus*, and *Porites lobata*) and only their abundance varied  
325 (control, 25, 50 vs. 75% coral cover). Restoration efforts can involve creating habitat  
326 mosaics, establishing multiple habitat types within a single restoration project (Henningson et  
327 al., 2015). On the other hand, artificial reefs may yield different assemblages from those  
328 required due to the preference of certain organisms for specific substrates (Burt et al., 2009).  
329 Maintaining connected coral colonies is crucial for sustaining prey fish assemblages, as a low  
330 coral cover can create wide-open spaces that increase predator densities (Stewart and Jones,  
331 2001). Moreover, high levels of coral cover and species richness generally favor high levels  
332 of fish abundance and species richness (Komyakova et al., 2013). Furthermore,  
333 architecturally complex coral morphologies, such as branching forms, support a higher  
334 number of individuals and fish species than less architecturally complex morphologies, such  
335 as mounding forms (Holbrook et al., 2002). This general relationship is likely due to the  
336 increase in architectural complexity and, thus, in 3D space, which translates into increased  
337 quantities of resources for fish (i.e., food/prey and shelter) (Graham and Nash, 2013). The  
338 associations between fish assemblages and habitat parameters were predominantly positive in  
339 Hawaii (Fukunaga et al., 2020), confirming earlier research findings: greater architectural



340 complexity of habitats is associated with higher levels of fish abundance and diversity  
341 (Graham and Nash, 2013; Holbrook et al., 2002; Komyakova et al., 2013). In contrast, a high  
342 percentage of scleractinian coral cover may suggest a less heterogeneous fish fauna.  
343 Therefore, a study focused on coral restoration by coral species could enhance our  
344 understanding of fish preferences, assemblage dynamics, and ecological succession.

345

346 The latest finding in our study concerned differences between trophic groups. In the  
347 literature, Fukunaga (et al. 2020) noted that certain herbivorous fish assemblages prefer  
348 habitats with high levels of small- and large-scale architectural complexity associated with all  
349 types of coral morphologies (similarly to our 50% condition) but not necessarily habitats with  
350 high architectural complexity (similarly to our 75% condition). Different successions seem to  
351 occur for small herbivorous grazers/corallivores (e.g., butterflyfish and some damselfish) that  
352 appear to prefer habitats containing a high level of small-scale architectural complexity  
353 associated with branching and/or encrusting corals (Fukunaga et al., 2020). Regarding  
354 planktivores, it is known that their abundance could be more strongly correlated with current  
355 strength and predator abundance than with topographic complexity or branching coral cover  
356 (Thresher, 1983). In our study, the percentage of coral cover did not appear to be correlated  
357 with the abundance of planktivores. This highlights the limitations of generalizing habitat-  
358 fish interactions without considering trophic variability and underscores the importance of  
359 conducting formal assessments with individual species when there are a priori specific  
360 species of interest or when data analyses reveal potential species of importance (Fukunaga et  
361 al., 2020).

## 362 **Conclusion**

363 This study unveils the effect of coral restoration on fish assemblages in a short time  
364 frame. These rapid changes prove the effectiveness of coral restoration and showcase the  
365 incredible adaptability of adult fish to a rapidly changing environment.

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376 The authors declare no competing interest.

**377 Ethics approval**

378 Not applicable

**379 Consent to participate**

380 Not applicable

**381 Consent for publication**

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**383 Availability of data and material**

384 The data that support the findings of this study are openly available in Zenodo at  
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**386 Code availability**

387 Not applicable

**388 Authors' contributions**

389 Stéphanie Krimou: Investigation, Methodology, Writing – original draft, Writing – review  
390 and editing, Project administration. Xavier Raick: Conceptualization, Methodology,

391 Software, Validation, Formal analysis, Data curation, Writing – original draft, Writing –  
 392 review and editing, Visualization, Supervision, Project administration. Ethel Mery: Writing –  
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696 **FIGURES CAPTIONS**

697 **Fig. 1.** Location of the study site. (A) Bora Bora with the zone of interest highlighted in red, (B) Detail of the  
698 Marine Educational Area (MEA) outlined with a dashed white line. The imagery used is from Airbus and has  
699 been modified from Google Earth. Each study patch is denoted by a yellow circle. (C and D) Examples of non-  
700 restored vs. a restored patch in the MEA, respectively.

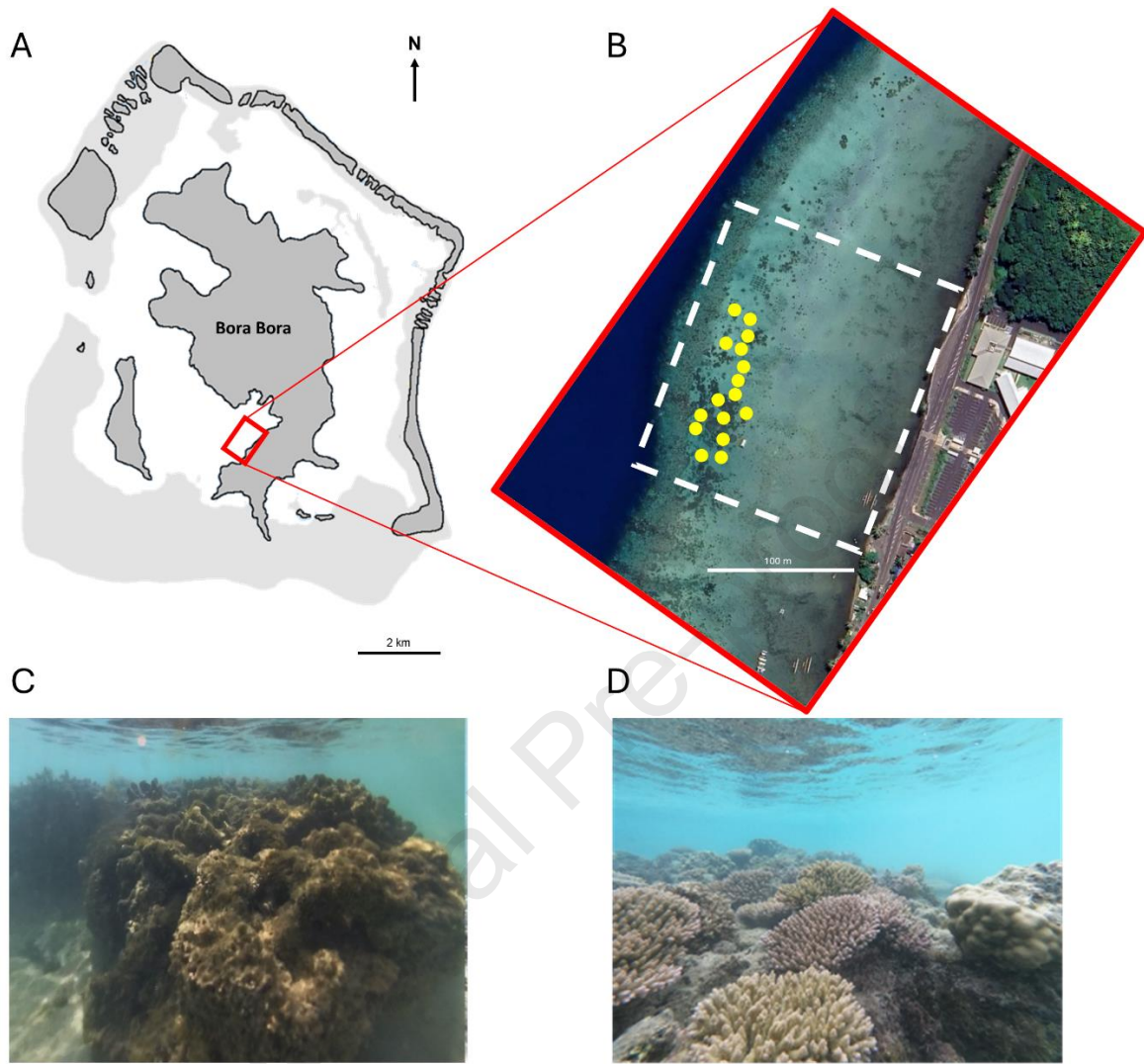
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702 **Fig. 2** Violin plots illustrating probability distribution with boxplots illustrating the median and the interquartile  
703 range to illustrate the differences in (A) the number of species ( $\Delta\text{NoSp}$ ), (B) the diversity ( $\Delta H'$ ), and (C) the  
704 abundance ( $\Delta\text{Ab}$ ) before and after the restoration for the four restoration conditions (0%, 25%, 50%, and 75%).

705  
706 **Fig. 3** Canonical correspondence analysis ordination plot displaying the composition of the adult fish  
707 assemblages after the restoration based on Bray-Curtis dissimilarities, with 95% confidence intervals  
708 represented by ellipses. The colors red, orange, yellow, and green correspond to the four restoration conditions  
709 (0%, 25%, 50%, and 75%, respectively). The pink dots correspond to each site replicate and the fish icons to the  
710 fish species. A different icon was used for each fish family.

711  
712 **Fig. 4**  $\Delta$  mean number of individuals (mean  $\pm$  SE) for the different trophic groups. (A) herbivorous grazers, (B)  
713 herbivorous scrapers or excavators, (C) omnivores, (D) planktivores, (E) piscivores, and (F) benthic  
714 invertebrates' feeders.

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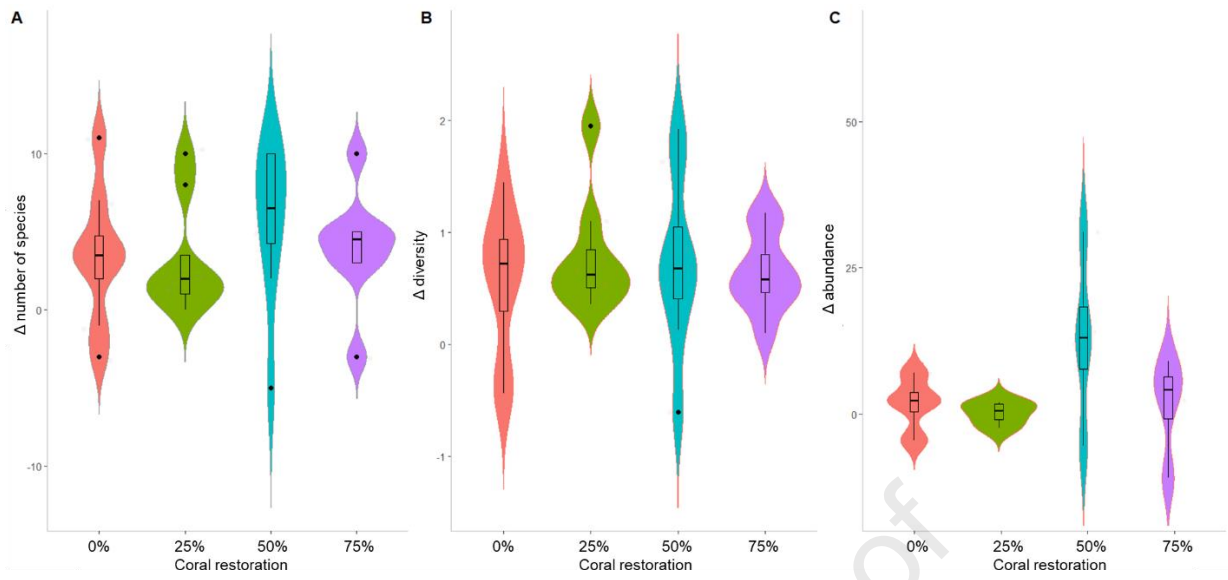
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717 **FIGURES**

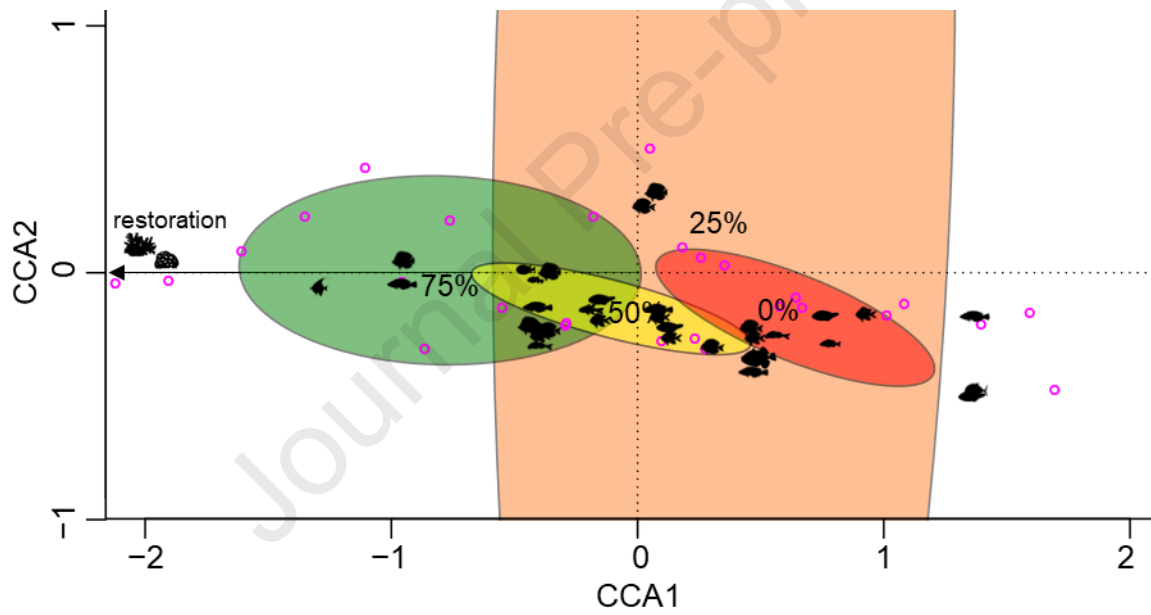
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719 **Fig. 1**

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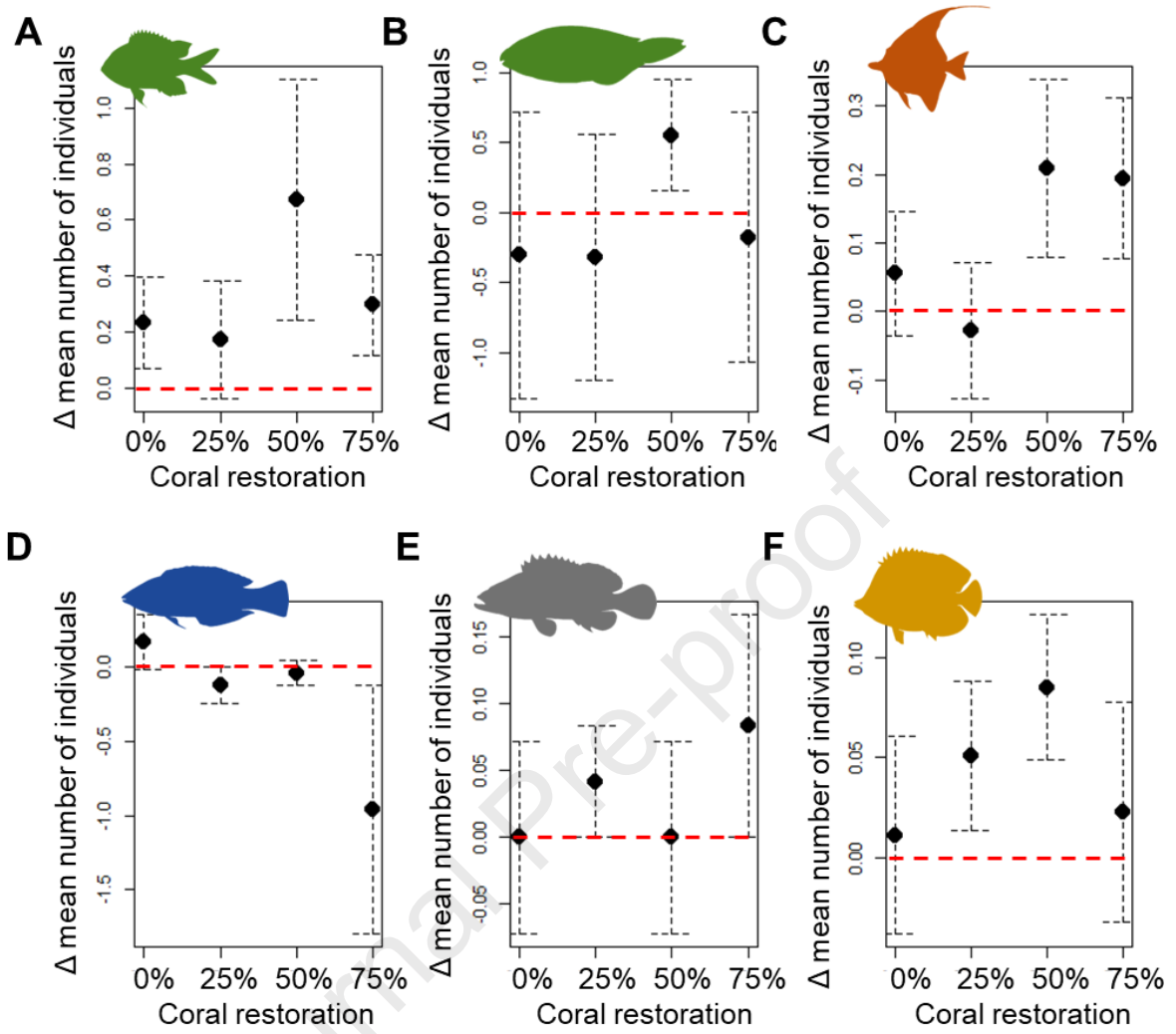


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722 **Fig. 2**

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724 **Fig. 3**



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726 **Fig. 4**

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**Highlights**

- Short-term impacts (< 1 month) of coral restoration on fish abundance, diversity, and assemblages in a marine educational area in Bora Bora were studied.
- Some species were associated with the more restored patches (*Chaetodon citrinellus*, *Halichoeres trimaculatus*, and *Zanclus cornutus*).
- There was no short-term effect on abundance and diversity but there was a significant modification of adult assemblages.
- It indicates the effectiveness of restoration efforts even within a brief period.
- These rapid changes underscore the remarkable ability of adult fish to adapt to rapidly changing environments.

**Conflicts of interest/Competing interests**

The authors declare no competing interest.

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