



# **Ecological evaluation of a marine protected area network: A Progressive-Change BACIPS approach**

## **Prepared as a research article for Ecosphere**

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1   **Ecological evaluation of a marine protected area**  
2   **network: A Progressive-Change BACIPS approach**

3

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5

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20    **Abstract**

21    Marine Protected Area (MPA) networks, with varying degrees of protection and use,  
22    can be useful tools to achieve both conservation and fisheries management benefits.  
23    Assessing whether MPA networks meet their objectives requires data from before the  
24    establishment of the network to better discern natural spatio-temporal variation and pre-  
25    existing differences from the response to protection. Here, we use a Progressive-Change  
26    BACIPS approach to assess the ecological effects of a network of five fully and three  
27    moderately protected MPAs on fish communities in two coral reef habitats (lagoon and  
28    fore reef) based on a time-series of data collected 5 times (over 3 years) before and 12  
29    times (over 9 years) after the network's establishment on the island of Moorea, French  
30    Polynesia. At the network scale, on the fore reef, density and biomass of harvested  
31    fishes increased by 19.3 and 24.8 %, respectively, in protected areas relative to control  
32    fished areas. Fully protected areas provided greater ecological benefits than moderately  
33    protected areas. In the lagoon, density and biomass of harvested fishes increased, but  
34    only the 31% increase in biomass in fully protected MPAs was significant. Non-  
35    harvested fishes did not respond to protection in any of the habitats. We propose that  
36    these responses to protection were small, relative to other MPA assessments, due to  
37    limited compliance and weak surveillance, although other factors such as the occurrence  
38    of a crown-of-thorns starfish outbreak and a cyclone after the network was established  
39    may also have impeded the ability of the network to provide benefits. Our results  
40    highlight the importance of fully protected MPAs over moderately protected MPAs in  
41    achieving conservation objectives, even in complex social-ecological settings, but also  
42    stress the need to monitor effects and adapt management based on ongoing assessments.

43  
44    **Key words:** conservation; coral reef; impact assessment design; Progressive-Change

45 BACIPS; protection regime, marine spatial planning; partially protected areas;

46        **Introduction**

47        Marine Protected Areas (MPAs) are an important management tool to conserve or  
48        restore fish populations inside their borders (Kerwath *et al.* 2013; Lubchenco & Grorud-  
49        Colvert 2015) and export biomass to surrounding fishing grounds (McClanahan &  
50        Mangi 2000; Harmelin-Vivien *et al.* 2008; Goñi *et al.* 2008; Di Lorenzo *et al.* 2016).  
51        Studies have shown that ecological effects of MPAs depend on MPA age (Claudet *et al.*  
52        2008; Molloy *et al.* 2009; Friedlander *et al.* 2017), network design (Jupiter & Egli 2011;  
53        Green *et al.* 2014a,b), species traits (McClanahan *et al.* 2007; Claudet *et al.* 2010;  
54        Abesamis *et al.* 2014) and degree of compliance (Guidetti *et al.* 2008; Campbell *et al.*  
55        2012; Gill *et al.* 2017). The most compelling evidence for beneficial effects of MPAs  
56        arises from meta-analyses that synthesize data from many empirical studies (Côté *et al.*  
57        2001; Micheli *et al.* 2004; Claudet *et al.* 2008; Lester *et al.* 2009; Gill *et al.* 2017).

58        Despite accumulated evidence suggesting far-reaching benefits of MPAs, assessment  
59        designs of individual MPAs or MPA networks often have substantive limitations,  
60        including the lack of data from Before the establishment of the MPA (Willis *et al.*  
61        2003). As a result, most assessments cannot discern effects of the MPA from pre-  
62        existing differences or spatio-temporal variability (Guidetti 2002; Halpern *et al.* 2004;  
63        Osenberg *et al.* 2006, 2011). Even studies with Before samples tend to have a limited  
64        time-series, often only one survey, making it difficult to attribute any observed temporal  
65        trends to effects of the MPA or MPA network (Osenberg *et al.* 2006, 2011).

66        When Before data are available, the BACIPS (Before-After Control-Impact Paired-  
67        Series) assessment design (Stewart-Oaten *et al.* 1986; Osenberg *et al.* 1994; Stewart-  
68        Oaten & Bence 2001) provides a powerful tool to overcome many of the limitations of  
69        typical studies (e.g. Guidetti, 2002; Osenberg et al., 2006, 2011). Repeated assessments  
70        *before* enforcement provide an estimate of the spatial variability between the Control

71 and Impact sites in the absence of an effect of the MPA. In its simplest application, a  
72 change from *before* to *after* the establishment of the MPA in the differences ( $\Delta$ ) in  
73 density (or other response parameter) between the Control and Impact sites (i.e.,  $\Delta_{\text{After}} -$   
74  $\Delta_{\text{Before}}$ ) provides an estimate of the local effect of the MPA (see Stewart-Oaten and  
75 Bence, 2001 for a more detailed discussion of the BACIPS analysis and Osenberg et al.,  
76 2006, 2011 for discussion of the BACIPS method applied to marine reserves). However,  
77 this step-change from  $\Delta_{\text{Before}}$  to  $\Delta_{\text{After}}$  is unlikely in most MPA systems. For example,  
78 enforcement *after* MPA establishment may be gradual or the response of long-lived  
79 species may be slow to accumulate (e.g., Russ and Alcala, 2010). In such cases, the  
80 effect of the MPA may follow more complex dynamics (Babcock *et al.* 2010). Recently  
81 a more flexible approach, the Progressive Change BACIPS, was proposed (Thiault *et al.*  
82 2017b) that allows quantification of various patterns of temporal change (e.g., linear,  
83 asymptotic, sigmoid) in addition to the traditional step-change. Although the need for  
84 Before data is widely acknowledged when implementing and assessing an MPA  
85 (Claudet & Guidetti 2010) and although BACIPS studies are increasingly used (Castilla  
86 & Bustamante 1989; Lincoln-Smith *et al.* 2006; Claudet *et al.* 2006; Shears *et al.* 2006;  
87 Moland *et al.* 2013; Grorud-Colvert *et al.* 2014; Fletcher *et al.* 2015), they remain rare  
88 (Osenberg et al. 2011).

89 Existing MPA assessments have focused almost exclusively on no-take, or fully  
90 protected, marine reserves. Partially protected areas, where some extractive activities are  
91 allowed but still regulated, are often used to balance trade-offs between conservation  
92 and exploitation. Partially protected MPAs are often favored to reach international  
93 targets of MPA coverage over the more arduous task of seeking approval for fully  
94 protected areas (Lubchenco & Grorud-Colvert 2015; Claudet 2018). Existing  
95 assessments of partially protected areas show that their ecological benefits are smaller

96 than those achieved with full protection (Shears *et al.* 2006; Lester & Halpern 2008; Di  
97 Franco *et al.* 2009; Giakoumi *et al.* 2017; Zupan *et al.* 2018).

98 Here, we assess the ecological effectiveness of a network of 8 MPAs, consisting of  
99 five fully and three moderately protected MPAs (*sensu* Horta e Costa *et al.* 2016) in  
100 Moorea, French Polynesia. We use a 12-year time series with three years of Before data  
101 and nine years of After data. We apply the Progressive-Change BACIPS design to detect  
102 and quantify the pattern of response of fish communities to the establishment of the  
103 MPA network. We assessed the effects of the MPA network as a whole, and at the sub-  
104 network scales of fully and moderately protected MPAs.

## 105 **Material and methods**

### 106 **Data collection**

107 The MPA network in Moorea, French Polynesia, was officially designated in October  
108 2004, although establishment and enforcement required several additional years (Lison  
109 de Loma *et al.* 2008). MPAs were delimited inside the lagoon using buoys in September  
110 2005. The first information campaign and police patrols were conducted in 2006. A  
111 second information campaign was initiated in 2007, and police monitoring was  
112 subsequently increased (and accomplished by hiring a local mediator/enforcement agent  
113 and purchasing a boat). We therefore consider January 1, 2007 to constitute the start of  
114 enforcement (Lison de Loma *et al.* 2008).

115 MPAs within the network were classified using the Regulation-Based Classification  
116 System for MPAs (Horta e Costa *et al.* 2016). The network consists of five fully  
117 protected MPAs where all fishing activities are prohibited (i.e. equivalent to no-take  
118 zones), and three moderately protected MPAs where restrictions only apply to particular  
119 fishing practices and species (Fig. 1 and Supporting Information Table S1). Other areas  
120 are open to fishing but subject to general restrictions, such as species size regulations.

121 Within these other areas, we selected five control sites that were paired with one, two or  
122 three of the MPA sites (Fig. 1) based upon their geographic proximity and physical  
123 characteristics.

124 [Figure 1]

125 Fish communities and benthic assemblages were sampled from 2004-2015, with  
126 sampling surveys (which we refer to as “dates”) conducted once in 2004 (during the dry  
127 season), twice each year from 2005-2009 (during both the dry and wet seasons), and  
128 once each year thereafter (during the wet season). Thus, our dataset consists of five sets  
129 of surveys from the Before period (i.e., prior to January 2007) and 12 sets of surveys  
130 from the After period (i.e., after January 2007). We refer to each set of surveys as a date,  
131 even though data across the whole island were obtained over an approximately week-  
132 long period.

133 At each MPA and Control site we sampled one location on the fore reef and two  
134 locations in the lagoon (Fig. 1). Fishes were identified to species and enumerated along  
135 3, 25 m x 2 m underwater belt transects at each location. Total length of each fish was  
136 estimated to the nearest centimeter for isolated fish, and mean length was estimated for  
137 schools of fish.

138 We also quantified the density of crown-of-thorns starfish (COTS, *Acanthaster*  
139 *planci*), a coral predator, as well as the cover of live coral and algae. Coral and algal  
140 cover were estimated using a point-intercept transect method, using the line that was  
141 deployed for fish transects. A total of 50 points were used, spaced equally along each  
142 transect. All point contacts were done after the fish surveys to minimize disruption to the  
143 fish assemblage.

144 **The Progressive-Change BACIPS design and analysis**

145 We categorized fish species as harvested or non-harvested based on local expert

146 knowledge, and converted all lengths to wet mass (g) using species-specific length-mass  
147 relationships (Kulbicki *et al.* 2005). Sharks, rays and pelagic species were excluded  
148 from the analyses because the transects were not designed to count those highly vagile  
149 species. Within each date and habitat, data were averaged across transects (n=3 transects  
150 for each fore reef site and n=6 transects for each lagoon site). For each habitat (lagoon or  
151 fore reef) and fish group (harvested or non-harvested), we then determined the  
152 difference,  $\Delta$ , between the MPA and its paired Control site (see Fig. 1) after log-  
153 transformation (Lison de Loma *et al.* 2008):

154 
$$\Delta_{P,i} = \ln(N_{MPA,P,i} + a) - \ln(N_{Control,P,i} + a) \quad (\text{Eq. 1})$$

155 where N is the average target fish density or biomass (across the three or six transects) at  
156 either the MPA or Control site, during the i<sup>th</sup> date in the P<sup>th</sup> period (P=Before or  
157 P=After), and a is a constant that was added to avoid taking logarithms of zero. To use  
158 the smallest plausible value of 'a' we chose a value for each fish group that represented  
159 the addition of one fish to one of the n (n=3 or 6) transects (i.e., a = 1/n for analyses of  
160 density, and a = [average mass of a fish in all surveys]/n for analyses of biomass).

161 We evaluated whether protection had an ecological effect by assessing if the  
162 difference in density or biomass,  $\Delta$ , changed from Before to After the establishment of  
163 the MPAs. The classic BACIPS approach assumes a step-change in  $\Delta$ . Instead of a  
164 step-change in  $\Delta$ , we hypothesized that the temporal change in  $\Delta$  might exhibit a more  
165 complex pattern because: (1) fish assemblages can take several decades after protection  
166 to fully recover from fishing (Russ & Alcala 2004; Babcock *et al.* 2010; MacNeil *et al.*  
167 2015), and, perhaps more importantly, (2) enforcement of the MPAs in the network was  
168 gradually phased in after January 2007. Therefore, we applied a Progressive-Change  
169 BACIPS by comparing four competing models: step-change (Eq. 2), linear (Eq. 3),  
170 asymptotic (Eq. 4) and sigmoid models (Eq. 5). As for any BACIPS analysis, we

171 assumed that in the Before period,  $\Delta$  was stationary through time (i.e., there was no  
172 consistent temporal trend in  $\Delta_{\text{Before}}$ ), but After enforcement,  $\Delta$  changed with time, with  
173 an increase indicating a positive effect of the MPA and a decrease indicating a negative  
174 effect. Thus, the differences between an MPA and its Control After enforcement ( $\Delta_{\text{After}}$ )  
175 could be described as:

176 Step change response:  $\Delta_{\text{After},i} = M + \Delta_{\text{Before}} + \varepsilon_i$  (Eq. 2)

177 Linear response:  $\Delta_{\text{After},i} = rt_i + \Delta_{\text{Before}} + \varepsilon_i$  (Eq. 3)

178 Asymptotic response:  $\Delta_{\text{After},i} = \frac{Mt}{L+t} + \Delta_{\text{Before}} + \varepsilon_i$  (Eq. 4)

179 Sigmoid response:  $\Delta_{\text{After},i} = \frac{M(t/L)^K}{1+(t/L)^K} + \Delta_{\text{Before}} + \varepsilon_i$  (Eq. 5)

180 where  $t$  is time (in years) since 1 January 2007 associated with the  $i^{\text{th}}$  sampling survey;  
181  $\Delta_{\text{Before}}$  is the underlying spatial variation between the two sites in the absence of an MPA  
182 effect (and was estimated during the Before period);  $r$  and  $M$  are the rate of divergence  
183 and magnitude of change between the MPA site and Control (due to the establishment of  
184 the MPA), respectively;  $L$  is the time required to achieve half of the long-term effect;  $K$   
185 is a scaling parameter in the sigmoid model that affects the steepness of the curve; and  $\varepsilon$   
186 is the error associated with the  $i^{\text{th}}$  survey. Each model was fitted setting all Before data  
187 to have  $t=0$ , and the magnitude of the response of fish to protection (hereafter referred to  
188 as effect size) was then measured based on the predictions of the best-fit model (highest  
189 AICc score) at  $t=9$  (i.e., 2015), the last year of the survey (Thiault *et al.* 2017b).

190 Having first checked assumptions of normality, homogeneity of variance and absence  
191 of autocorrelation (Supporting Information Table S2), we assessed the effect of (i) the  
192 whole network (i.e., the island-wide effect of the MPA network), (ii) the two sub-  
193 networks (i.e., the networks of fully protected and moderately protected MPAs), and (iii)  
194 individual MPAs. To avoid pseudo-replication, and because we expected that each  
195 MPA would have its own response, we included MPA as a random effect for all the

196 parameters describing the effect size (i.e., M, r, K and L). Season was not included in  
197 the model to maximize statistical power and because the BACIPS design reduces the  
198 effect of seasonality. All analyses were performed using the R statistical software (R  
199 Core Team 2017).

200 **Results**

201 Fishes were generally more abundant on the fore reef compared to the lagoon (Fig.  
202 2). Coral and algal cover changed dramatically over the period of study on the fore reef  
203 following a crown-of-thorns starfish (COTS; *Acanthaster planci*) outbreak between  
204 2007 and 2012 and cyclone Oli in 2010: as COTS increased, coral cover decreased by  
205 more than 90% between October 2006 and March 2010, and algae increased by 34%  
206 (Fig. 2).

207 [Figure 2]

208 **Effect of protection on harvested and non-harvested fishes**

209 Estimated statistical power to detect MPA effects was high at the MPA network and  
210 sub-networks scales, suggesting that we would be able to detect changes if they did  
211 occur. For example, the probability of detecting a 100% increase (typically seen in other  
212 MPA assessments) was 0.97 on average across the 24 comparisons (Supporting  
213 Information Fig. S2). Power to detect responses at individual MPAs was considerably  
214 lower. Therefore, we focus on the network and sub-network responses; results for  
215 individual MPAs are presented in the Supporting Information (Supporting Information  
216 Table S3).

217 The pattern of change in response to protection provided more support for the step-  
218 change model (asserting an immediate shift in density in the MPA relative to the Control  
219 site) than for the linear model (in which the difference increases linearly with time since  
220 protection). In no case was the asymptotic or sigmoid model better supported by the

221 data. In 25% of cases, the likelihood ( $\omega$ ) of the second best-fit model was comparable to  
222 that of the best-fit model (i.e.,  $\omega_{\text{best-fit}} - \omega_{\text{second best fit}} \leq 10\%$ ). For consistency, we only  
223 present results derived from the best-fit model (Fig. 3).

224 [figure 3]

225 On the fore reef, at the network scale, harvested fish biomass increased significantly  
226 by 24.8 % in MPAs relative to the paired Controls (Fig. 3); the relative increase in  
227 density was similar in magnitude (19.3 %), although not significant. This increase was  
228 mostly due to the response in fully protected MPAs (where all fishing is prohibited),  
229 where density and biomass of harvested fish increased significantly by 43.2 % and 31  
230 %, respectively. No significant increase in either density or biomass was observed for  
231 the sub-network of moderately protected MPAs, where fishing restrictions apply to only  
232 a subset of fishing methods and species (Fig. 3). Protection benefited herbivores,  
233 invertivores and piscivores (Supporting Information Fig. S2), the large majority of  
234 which are targeted by fishing.

235 For harvested fish inside the lagoon, the only significant effect that we detected was  
236 on biomass in the fully protected MPA sub-network, which showed an increase of 31.1  
237 %. Although positive, the effect on densities was non-significant.

238 Effects on non-harvested fishes were generally smaller in magnitude and more often  
239 negative (Fig 3 and Supporting Information Fig. S2). However, none of these responses  
240 differed from zero, whether for the whole network or for the two sub-networks.

## 241 Discussion

242 Disentangling the effects of management interventions from other sources of  
243 spatiotemporal variation is a challenging but necessary task to derive robust inferences  
244 that can inform evidence-based decisions. BACIPS designs are particularly powerful

245 tools to address this challenge, yet, although there have been hundreds of assessments of  
246 Marine Protected Areas (MPAs), very few include data from Before the establishment of  
247 the MPA and even fewer have multiple surveys from Before (Castilla & Bustamante  
248 1989; Lincoln-Smith *et al.* 2006; Shears *et al.* 2006). As a result, most assessments are  
249 unable to unequivocally isolate the effects of the MPA from pre-existing differences  
250 (Osenberg *et al.* 2006). To our knowledge, this is the first time a Progressive-Change  
251 BACIPS approach –which expands the scope of BACIPS analyses beyond the step-  
252 change response assumed in previous assessments– has been used to assess the impact  
253 of a network of MPAs on fish communities.

254 We expected continuous changes in the response of fish to protection due to  
255 ecological processes combined with gradual enforcement in the After period. Yet,  
256 asymptotic and sigmoid models were never selected among the competing models, and  
257 the linear model was only selected twice. The lack of support for complex, non-linear  
258 responses likely resulted from the low effect sizes combined with relatively high  
259 spatiotemporal variability. This likely led to the selection of simple (step-change and  
260 linear) models over more complex ones (Thiault *et al.* 2017b).

261 The establishment of the MPA network in Moorea provided positive, but limited,  
262 ecological benefits. Network-wide, harvested fish biomass had increased by 24.8% on  
263 the fore reef eight years after the start of enforcement, in protected areas relative to  
264 controls. Importantly, this positive, network-scale effect was mostly driven by responses  
265 where fishing was entirely prohibited (i.e., in the fully protected MPAs, biomass and  
266 density increased +30% and +43.2%, respectively). Indeed, no positive effect was  
267 detected in either habitat within moderately protected MPAs (*sensu* Horta e Costa *et al.*  
268 2016). This results is consistent with a recent meta-analysis that found that fully and  
269 highly protected areas consistently conferred ecological benefits, but moderately

270 protected MPAs provided ecological benefits only when immediately adjacent to fully  
271 protected areas (Zupan *et al.* 2018).

272 The response in fully protected MPAs, although the largest effect we detected, was  
273 relatively small compared to effects documented in other published MPA meta-analyses,  
274 in which harvested organisms were generally 2-3 times more abundant inside MPAs  
275 compared to fishing grounds (Halpern 2003; Claudet *et al.* 2008, 2011). The lower  
276 effect measured in this study could be due to a combination of factors, which we  
277 elaborate upon below, including (i) overestimation of the effect size in previous studies  
278 due to the lack of Before data (Osenberg *et al.* 2006, 2011), (ii) limited compliance and  
279 enforcement (Guidetti *et al.* 2008; Campbell *et al.* 2012), and (iii) dramatic ecosystem  
280 disturbance following enforcement due to the crown-of-thorns starfish (COTS) outbreak  
281 and cyclone (Adam *et al.* 2011; Lamy *et al.* 2015, 2016).

282 MPAs are often strategically implemented in sites with higher densities than  
283 surrounding areas. The absence of Before data precludes the incorporation of these  
284 initial, and potentially large, differences, which may then become confounded with  
285 effects of MPAs. As a result, studies that lack Before data may overestimate the benefits  
286 of MPAs. Indeed, it has been suggested that up to half of the commonly observed  
287 "increase" in density inside MPAs may be due to these pre-existing differences  
288 (Osenberg *et al.* 2006, 2011). Our smaller than expected effect sizes support this  
289 interpretation. They also support Osenberg et al.'s (2011) conjecture that by identifying  
290 Control sites before MPA enforcement, siting and MPA effects are less likely to be  
291 confounded: e.g., effect sizes from a Control-Impact analysis of our data yielded effects  
292 that were comparable in magnitude to (i.e., not larger than) effects from the BACIPS  
293 analyses (Supporting Information Fig. S3). The Control-Impact comparison, however,  
294 revealed two important differences. First, variation in the effects was greater for the

295 Control-Impact analyses, presumably because initial differences between sites added to  
296 the variation in the Control-Impact effects (relative to the effects quantified with  
297 BACIPS). Secondly, the confidence intervals on the effects were smaller for the  
298 Control-Impact estimates, likely because Control-Impact studies only capture spatial  
299 variation while BACIPS analyses capture spatio-temporal variation. These results not  
300 only suggest that Control-Impact studies might overestimate effects, but that they might  
301 also give a false sense of confidence in the estimates because they fail to incorporate  
302 spatio-temporal variance. The BACIPS approach circumvents these problems, and likely  
303 leads to smaller, more accurate, but less precise, estimates of effect sizes.

304 Limited public appreciation about the benefits of MPAs and an understaffed  
305 management team may have limited compliance, and therefore ecological outcomes  
306 associated with the Moorea MPA network (Gaspar & Bambridge 2008; Guidetti *et al.*  
307 2008; Edgar *et al.* 2014; Gill *et al.* 2017). Surveillance reports made by the local  
308 mediator (Gaspar & Bambridge 2008) and surveys completed by local experts  
309 (Supporting Information Table S5) suggest that enforcement was heterogeneous, being  
310 mostly limited to the north shore, where the largest beneficial effects were observed  
311 (Supporting Information Figs S4-5). Furthermore, the lagoon habitat is highly fished at  
312 night with light attractors, and surveillance is non-existent at night. The fore reef is less  
313 accessible and more hazardous, and, as a result, less likely to experience night poaching  
314 (Thiault *et al.* 2017a), potentially explaining why the responses on the fore reef were  
315 greater than in the lagoon (Fig. 3).

316 The whole island underwent severe natural disturbances since the network's  
317 establishment. A COTS outbreak occurred starting in 2007 and was followed by a  
318 cyclone in 2010. This resulted in a dramatic (90%) decline in live coral cover, especially  
319 on the fore reef, and an increase in turf and macro-algae (Fig. 2). These shifts in

320 microhabitats led to changes in the composition of reef-associated fishes, but after a  
321 time lag of several years (Adam *et al.* 2011; Lamy *et al.* 2015; Han *et al.* 2016). These  
322 types of dramatic temporal changes can cause problems with some types of assessments  
323 (e.g., Before–After comparisons). BACIPS, in theory, can handle such regional  
324 phenomena because the Control site should reflect the effects of the regional processes  
325 (i.e., the natural disturbance) but not the local factors (i.e., MPA). Surveys confirmed  
326 that similar impacts of COTS and the hurricane were simultaneously observed at the  
327 MPA and Control sites (Kayal *et al.* 2012; Lamy *et al.* 2015). This, combined with the  
328 fact that functional groups that are highly sensitive to habitat changes did not respond to  
329 protection (Supporting Information Fig. S2) suggest that observed MPA effects are not  
330 confounded with COTS and cyclone effects. These issues underscore the importance of  
331 implementing BACIPS designs for future MPA assessments.

332 Our results have been communicated to some local community members and to local  
333 administrations to facilitate the ongoing revision of the marine spatial management plan  
334 in Moorea. The marine spatial management plan of Moorea is currently being revised to  
335 better engage local communities and foster better compliance. Monitoring of the current  
336 and future MPA network in Moorea will continue, but will be revised to increase  
337 sampling effort: e.g. more numerous and larger transects should facilitate future MPA-  
338 specific assessments as well as network-wide results. We believe the Progressive-  
339 Change BACIPS approach used here represents a meaningful advance that could  
340 facilitate and inform management interventions in other social-ecological settings.

341

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554

555 **Figure legends**

556 **Figure 1:** Network of marine protected areas (MPAs) around the island of Moorea, French  
557 Polynesia. The network consists of five fully protected MPAs (on the north and west shores) and  
558 three moderately protected MPAs (on the east shore) using the regulation-based classification system  
559 for MPAs (Horta e Costa et al. 2016). Numbers in parentheses after MPA names refer to the Control  
560 site to which it was paired. Sampling at each MPA and Control was conducted in two distinct  
561 habitats (in the lagoon at two locations and on the fore reef at one location), 5 times (over 3 years)  
562 before and 12 times (over 9 years) after implementation.

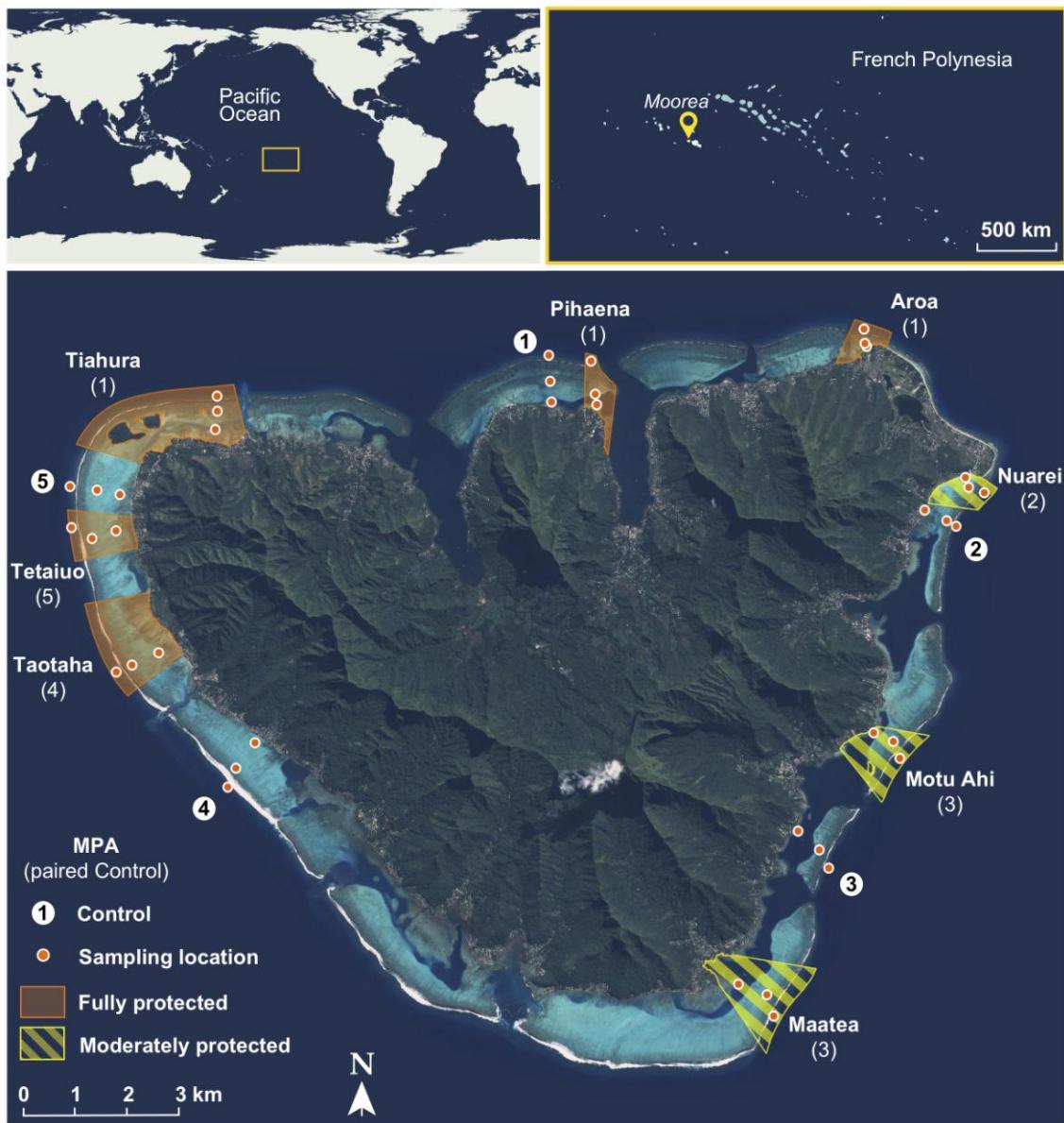
563 **Figure 2:** Temporal variation in key ecological components of the studied coral reef ecosystem.  
564 From top to bottom: density of Acanthaster planci (red), living coral cover (yellow), algal cover  
565 (green), biomass of harvested (blue) and non-harvested fish (purple) in the lagoon (left column) and  
566 fore reef (right column). Lines are the mean of the eight MPAs (solid line) and five Control sites  
567 (dashed line) and ribbons represent standard deviations (the darker ribbon corresponds to the  
568 Controls). MPA enforcement started in January 2007, which separates the Before (2004-2006) from  
569 the After (2007-2015) periods.

570 **Figure 3:** Effect sizes measured at the whole network scale, and for fully protected MPAs and  
571 moderately protected MPAs separately, in the lagoon and fore reef, for density and biomass of  
572 harvested and non-harvested fishes. Effect sizes are expressed as the change in the log-ratio of the  
573 density or biomass in the MPA relative to its Control ( $\Delta$ ) from  $t=0$  (i.e., <2007) to  $t=9$  (i.e., 2015) as  
574 predicted by the best-fit model. Changes by a factor of 2 correspond to effects sizes of -0.7 (halving)  
575 or 0.7 (doubling) over the 9-year period of protection. Positive effects are depicted in red and  
576 negative effects in blue. Filled symbols indicate that the 95% confidence interval of the effect does  
577 not overlap zero. Shapes indicate the best-fit model: step-change (circle) and linear (triangle). There  
578 were no cases in which the asymptotic or sigmoid model was best supported by the data. See  
579 Supporting Information Table S3 for results at the individual MPA-scale and Supporting Information  
580 Figure S1 for results broken down by trophic group.

581

582 **Figures**

583 Figure 1



584

585

Figure 2

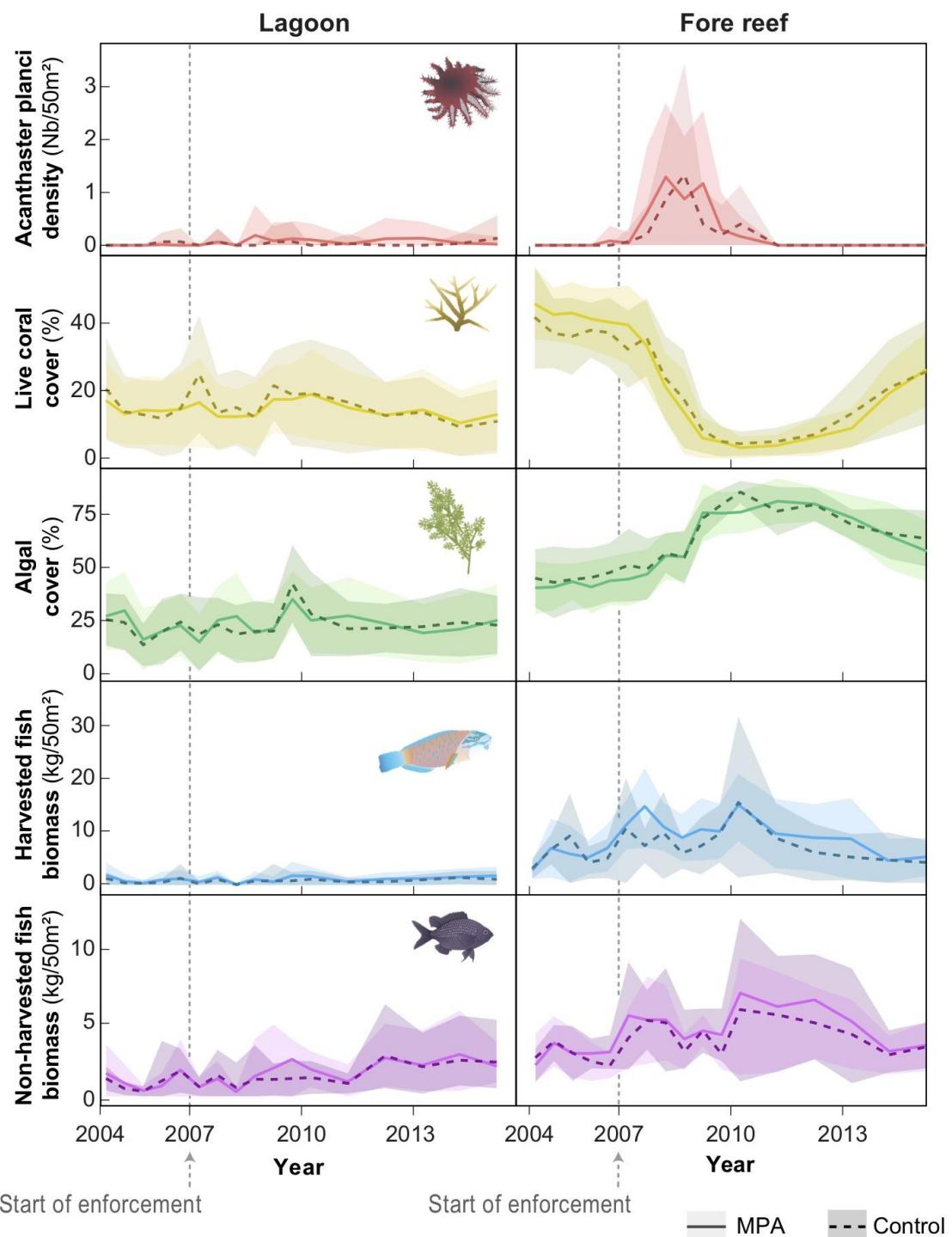


Figure 3

