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**Ecological evaluation of a marine protected area network: A Progressive-Change BACIPS approach
Prepared as a research article for Ecosphere**

L. Thiault, L. Kernaléguen, C. W Osenberg, T. Lison de Loma, Y. Chancerelle, G. Siu, Joachim Claudet

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

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4 Prepared as a research article for Ecosphere

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6 **L. Thiault^{a,b,c,d}, L. Kernaléguen^e, C.W. Osenberg^f, T. Lison de Loma^{a,b}, Y.**
7 **Chancerelle^{a,b}, G. Siu^{a,b}, J. Claudet^{a,b}**

8
9 ^a National Center for Scientific Research, PSL Université Paris, CRIOBE, USR 3278
10 CNRS-EPHE-UPVD, Maison des Océans, 195 rue Saint-Jacques, 75005 Paris, France

11 ^b Laboratoire d'Excellence CORAIL, France

12 ^c Museum National d'Histoire Naturelle, PALOC, UMR 208 MNHN-IRD, 75231 Paris,
13 France

14 ^d Center of Applied Ecology and Sustainability (CAPES) and Centro de Conservación
15 Marina, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile,
16 Alameda 340, Santiago, Chile

17 ^e Deakin University, Geelong, School of Life and Environmental Sciences (Burwood
18 Campus), Victoria, Australia

19 ^f Odum School of Ecology, University of Georgia, Athens, GA, 30602, USA

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 (Δ) in
73 density (or other response parameter) between the Control and Impact sites (i.e., $\Delta_{\text{After}} -$
74 Δ_{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 Δ_{Before} to Δ_{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, Δ , between the MPA and its paired Control site (see Fig. 1) after log-
153 transformation (Lison de Loma *et al.* 2008):

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

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^{th} date in the P^{th} 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 $a = [\text{average mass of a fish in all surveys}]/n$ for analyses of biomass).

161 We evaluated whether protection had an ecological effect by assessing if the
162 difference in density or biomass, Δ , changed from Before to After the establishment of
163 the MPAs. The classic BACIPS approach assumes a step-change in Δ . Instead of a
164 step-change in Δ , we hypothesized that the temporal change in Δ 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, Δ was stationary through time (i.e., there was no
 172 consistent temporal trend in Δ_{Before}), but After enforcement, Δ 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 (Δ_{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^{th} sampling survey;
 181 Δ_{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 ε
 186 is the error associated with the i^{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 (ω) 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.

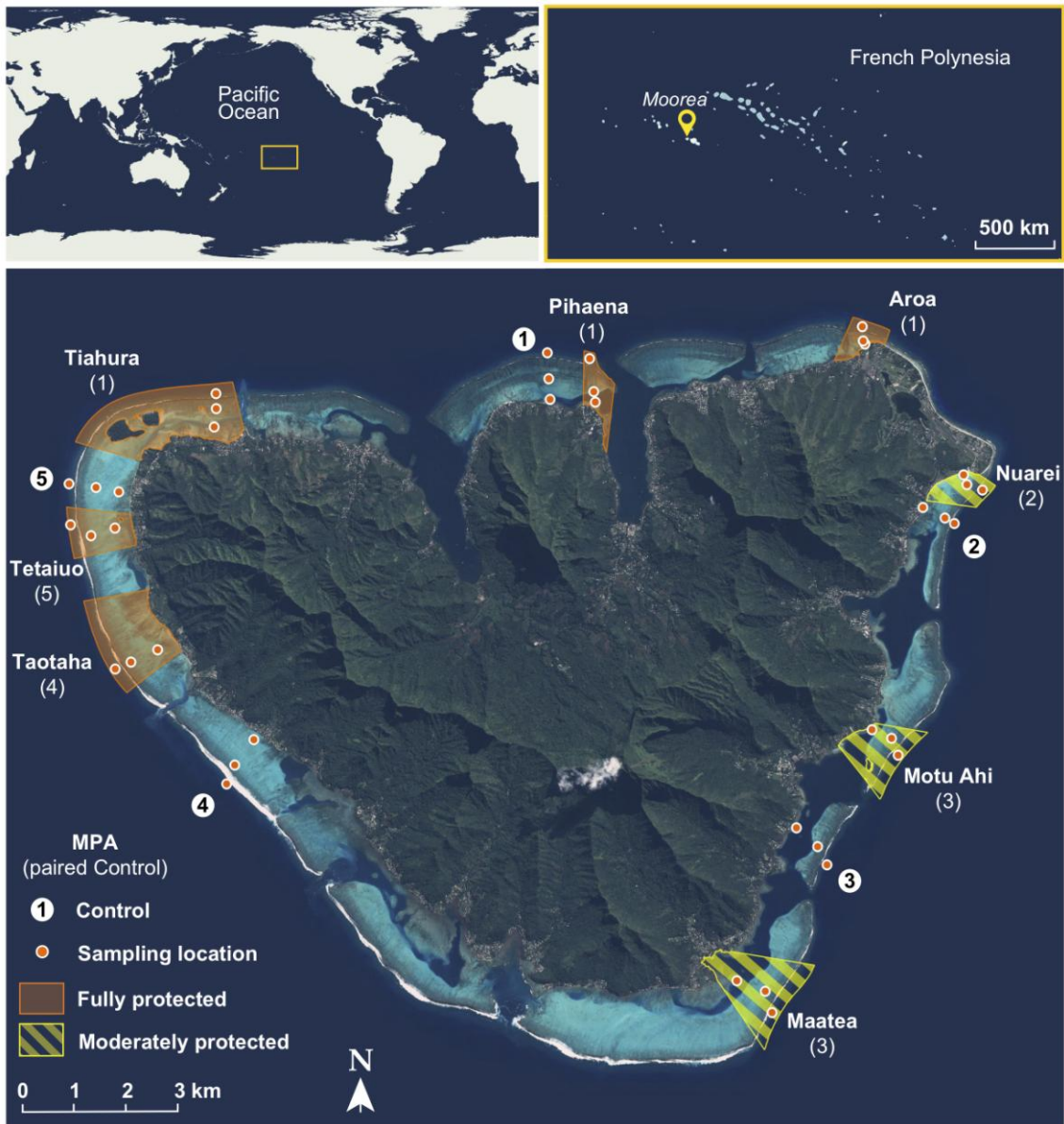
563 **Figure 2:** Temporal variation in key ecological components of the studied coral reef ecosystem.
564 From top to bottom: density of *Acanthaster planci* (red), living coral cover (yellow), algal cover
565 (green), biomass of harvested (blue) and non-harvested fish (purple) in the lagoon (left column) 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 (Δ) 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

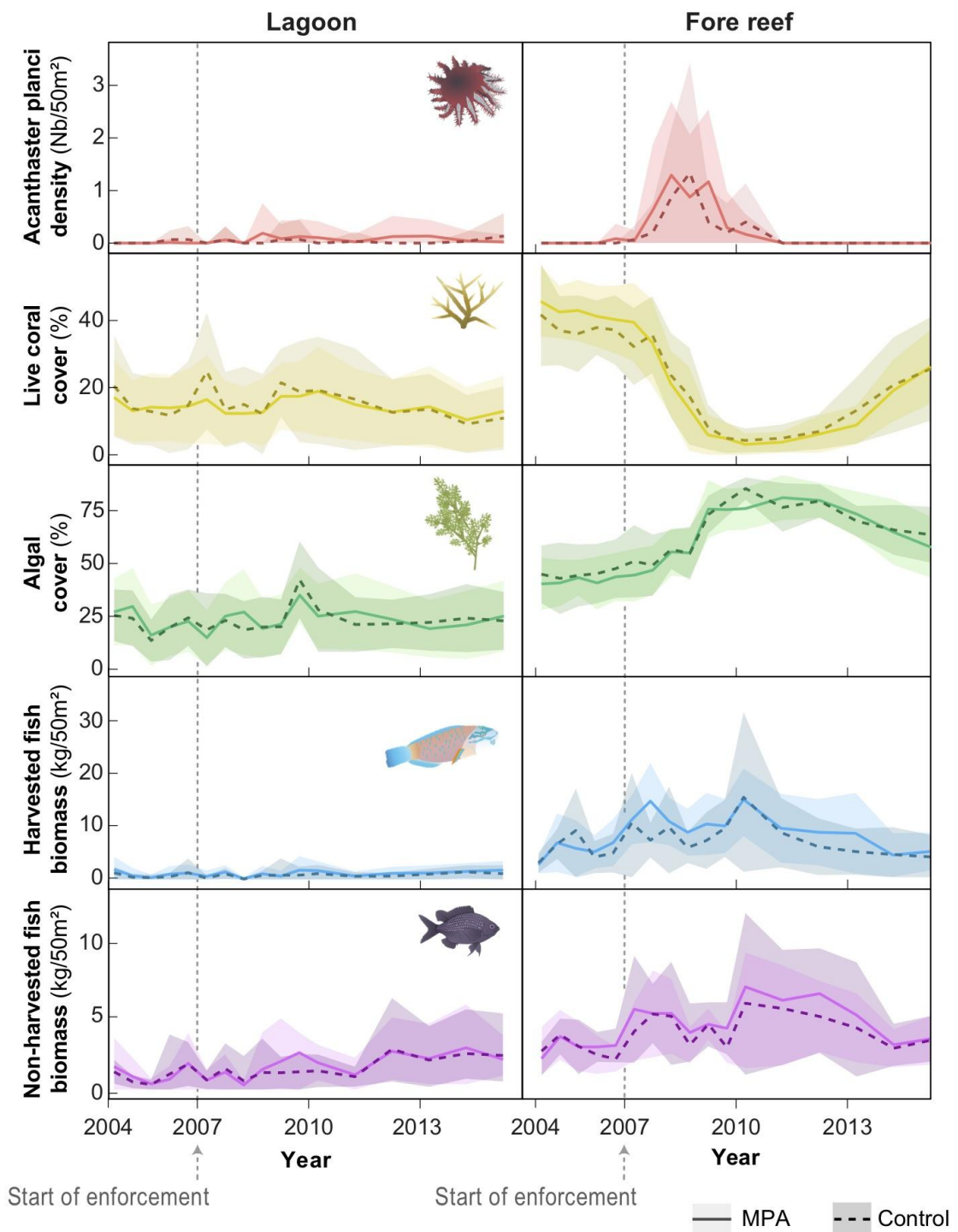


Figure 3

