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Ecological evaluation of a marine protected area network: a progressive-change BACIPS approach

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Abstract. Marine protected area (MPA) networks, with varying degrees of protection and use, can be useful tools to achieve both conservation and fisheries management benefits. Assessing whether MPA networks meet their objectives requires data from Before the establishment of the network to better discern natural spatiotemporal variation and preexisting differences from the response to protection. Here, we use a Progressive-Change BACIPS approach to assess the ecological effects of a network of five fully and three moderately protected MPAs on fish communities in two coral reef habitats (lagoon and fore reef) based on a time series of data collected five times (over three years) Before and 12 times (over nine years) After the network's establishment on the island of Moorea, French Polynesia. At the network scale, on the fore reef, density and biomass of harvested fishes increased by 19.3% and 24.8%, respectively, in protected areas relative to control fished areas. Fully protected areas provided greater ecological benefits than moderately protected areas. In the lagoon, density and biomass of harvested fishes increased, but only the 31% increase in biomass in fully protected MPAs was significant. Non-harvested fishes did not respond to protection in any of the habitats. We propose that these responses to protection were small, relative to other MPA assessments, due to limited compliance and weak surveillance, although other factors such as the occurrence of a crown-of-thorns starfish outbreak and a cyclone after the network was established may also have impeded the ability of the network to provide benefits. Our results highlight the importance of using fully protected MPAs over moderately protected MPAs to achieve conservation objectives, even in complex social–ecological settings, but also stress the need to monitor effects and adapt management based on ongoing assessments.

Key words: conservation; coral reef; impact assessment design; marine spatial planning; partially protected areas; progressive-change BACIPS; protection regime.

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Introduction

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

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

When Before data are available, the BACIPS (Before–After Control–Impact Paired-Series) assessment design (Stewart-Oaten et al. 1986, Osenberg et al. 1994, Stewart-Oaten and Bence 2001) provides a powerful tool to overcome many of the limitations of typical studies (e.g., Guidetti 2002, Osenberg et al. 2006, 2011). Repeated assessments Before enforcement provide an estimate of the spatial variability between the Control and Impact sites in the absence of an effect of the MPA. In its simplest application, a change from Before to After the establishment of the MPA in the differences (Δ) in density (or other response parameter) between the Control and Impact sites (i.e., $\Delta_{\text{After}} - \Delta_{\text{Before}}$) provides an estimate of the local effect of the MPA (see Stewart-Oaten and Bence 2001 for a more detailed discussion of the BACIPS analysis and Osenberg et al. 2006, 2011 for discussion of the BACIPS method applied to marine reserves). However, this step-change from Δ_{Before} to Δ_{After} is unlikely in most MPA systems. For example, enforcement after MPA establishment may be gradual or the response of long-lived species may be slow to accumulate (e.g., Russ and Alcala 2010). In such cases, the effect of the MPA may follow more complex dynamics (Babcock et al. 2010). Recently, a more flexible approach, the Progressive-Change BACIPS, was proposed (Thiault et al. 2017*b*) that allows quantification of various patterns of temporal change (e.g., linear, asymptotic, sigmoid) in addition to the traditional step-change. Although the need for Before data is widely acknowledged when implementing and assessing an MPA (Claudet and Guidetti 2010) and although BACIPS studies are increasingly used (Castilla and Bustamante 1989, Claudet et al. 2006, Lincoln-Smith et al. 2006, Shears et al. 2006, Moland et al. 2013, Grorud-Colvert et al. 2014, Fletcher et al. 2015), they remain rare (Osenberg et al. 2011).

Existing MPA assessments have focused almost exclusively on no-take, or fully protected, marine reserves. Partially protected areas, where some extractive activities are allowed but still regulated, are often used to balance tradeoffs between conservation and exploitation. Partially protected MPAs are often favored to reach international targets of MPA coverage over the more arduous task of seeking approval for fully protected areas (Lubchenco and Grorud-Colvert 2015, Claudet 2018). Existing assessments of partially protected areas show that their ecological benefits are smaller than those achieved with full protection (Shears et al. 2006, Lester and Halpern 2008, Di Franco et al. 2009, Giakoumi et al. 2017, Zupan et al. 2018).

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

Methods

Data collection

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

Marine protected areas within the network were classified using the Regulation-Based Classification System for MPAs (Horta e Costa et al. 2016). The network consists of five fully protected MPAs where all fishing activities are prohibited (i.e., equivalent to no-take zones) and three moderately protected MPAs where restrictions only apply to particular fishing practices and species (Fig. 1; Appendix S1: Table S1). Other areas are open to fishing but subject to general restrictions, such as species size regulations. Within these other areas, we selected five Control sites that were paired with one, two, or three of the MPA sites (Fig. 1) based upon their geographic proximity and physical characteristics.

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

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

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

The progressive-change BACIPS design and analysis

We categorized fish species as harvested or non-harvested based on local expert knowledge and converted all lengths to wet mass (g) using species-specific length–mass relationships (Kulbicki et al. 2005). Sharks, rays, and pelagic species were excluded from the analyses because the transects were not designed to count those highly vagile species. Within each date and habitat, data were averaged across transects (n = 3 transects for each fore reef site and n = 6 transects for each lagoon site). For each habitat (lagoon or fore reef) and fish group (harvested or non-harvested), we then determined the difference, Δ, between the MPA and its paired Control site (see Fig. 1) after log-transformation (Lison de Loma et al. 2008):

$$\Delta_{P,i} = \ln(\mathrm{N}_{\mathrm{MPA},P,i} + a) - \ln(\mathrm{N}_{\mathrm{Control},P,i} + a) \quad (1)$$

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

We evaluated whether protection had an ecological effect by assessing if the difference in density or biomass, Δ, changed from Before to After the establishment of the MPAs. The classic BACIPS approach assumes a step-change in Δ. Instead of a step-change, we hypothesized that the temporal change in Δ might exhibit a more complex pattern because (1) fish assemblages can take several decades after protection to fully recover from fishing (Russ and Alcala 2004, Babcock et al. 2010, MacNeil et al. 2015), and, perhaps more importantly, (2) enforcement of the

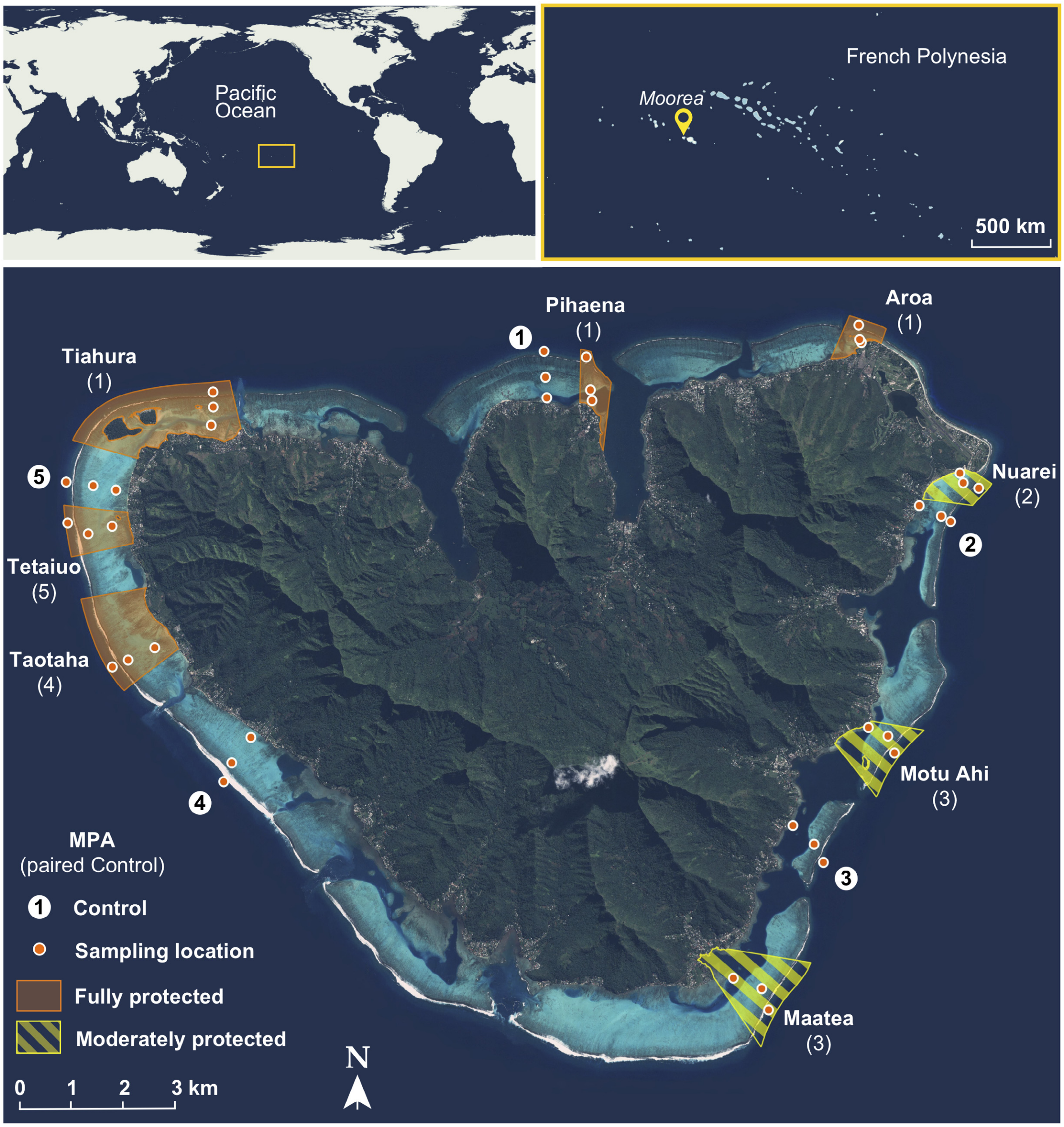

Fig. 1. Network of marine protected areas (MPAs) around the island of Moorea, French Polynesia. The network consists of five fully protected MPAs (on the north and west shores) and three moderately protected MPAs (on the east shore) using the regulation-based classification system for MPAs (Horta e Costa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

MPAs in the network was gradually phased in after January 2007. Therefore, we applied a Progressive-Change BACIPS by comparing four competing models: step-change (Eq. 2), linear (Eq. 3), asymptotic (Eq. 4), and sigmoid models (Eq. 5). As for any BACIPS analysis, we assumed that in the Before period, Δ was stationary through time (i.e., there was no consistent temporal trend in Δ_{Before}), but After enforcement, Δ changed with time, with an increase indicating a positive effect of the MPA and a decrease indicating a negative effect. Thus, the differences between an MPA and its Control After enforcement (Δ_{After}) could be described as

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

$$\text{Linear response: } \Delta_{\text{After},i} = \text{r}t_i + \Delta_{\text{Before}} + \varepsilon_i \quad (3)$$

$$\text{Asymptotic response: } \Delta_{\text{After},i} = \frac{\text{M}t}{L+t} + \Delta_{\text{Before}} + \varepsilon_i \quad (4)$$

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

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

Having first checked assumptions of normality, homogeneity of variance, and absence of autocorrelation (Appendix S1: Table S2), we assessed the effect of (1) the whole network (i.e., the island-wide effect of the MPA network), (2) the two sub-networks (i.e., the networks of fully protected and moderately protected MPAs), and (3) individual MPAs. To avoid pseudo-replication, and because we expected that each MPA would have its own response, we included MPA as a random effect for all the parameters describing the effect size (i.e., M, r, K, and L). Season was not included in the model to maximize statistical power and because the BACIPS design reduces the effect of seasonality. All analyses were performed using the R statistical software (R Core Team 2017).

Results

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

Effect of protection on harvested and non-harvested fishes

Estimated statistical power to detect MPA effects was high at the MPA network and sub-networks scales, suggesting that we would be able to detect changes if they did occur. For example, the probability of detecting a 100% increase (typically seen in other MPA assessments) was 0.97 on average across the 24 comparisons (Appendix S1: Fig. S2). Power to detect responses at individual MPAs was considerably lower. Therefore, we focus on the network and sub-network responses; results for individual MPAs are presented in Appendix S1 (Table S3).

The pattern of change in response to protection provided more support for the step-change model (asserting an immediate shift in density in the MPA relative to the Control site) than for the linear model (in which the difference increases linearly with time since protection). In no case was the asymptotic or sigmoid model better supported by the data. In 25% of cases, the likelihood (ω) of the second best-fit model was comparable to that of the best-fit model (i.e., $\omega_{\text{best-fit}} - \omega_{\text{second best-fit}} \leqq 10\%$). For consistency, we only present results derived from the best-fit model (Fig. 3).

On the fore reef, at the network scale, harvested fish biomass increased significantly by 24.8% in MPAs relative to the paired Controls (Fig. 3); the relative increase in density was similar in magnitude (19.3%), although not significant. This increase was mostly due to the response in fully protected MPAs (where all

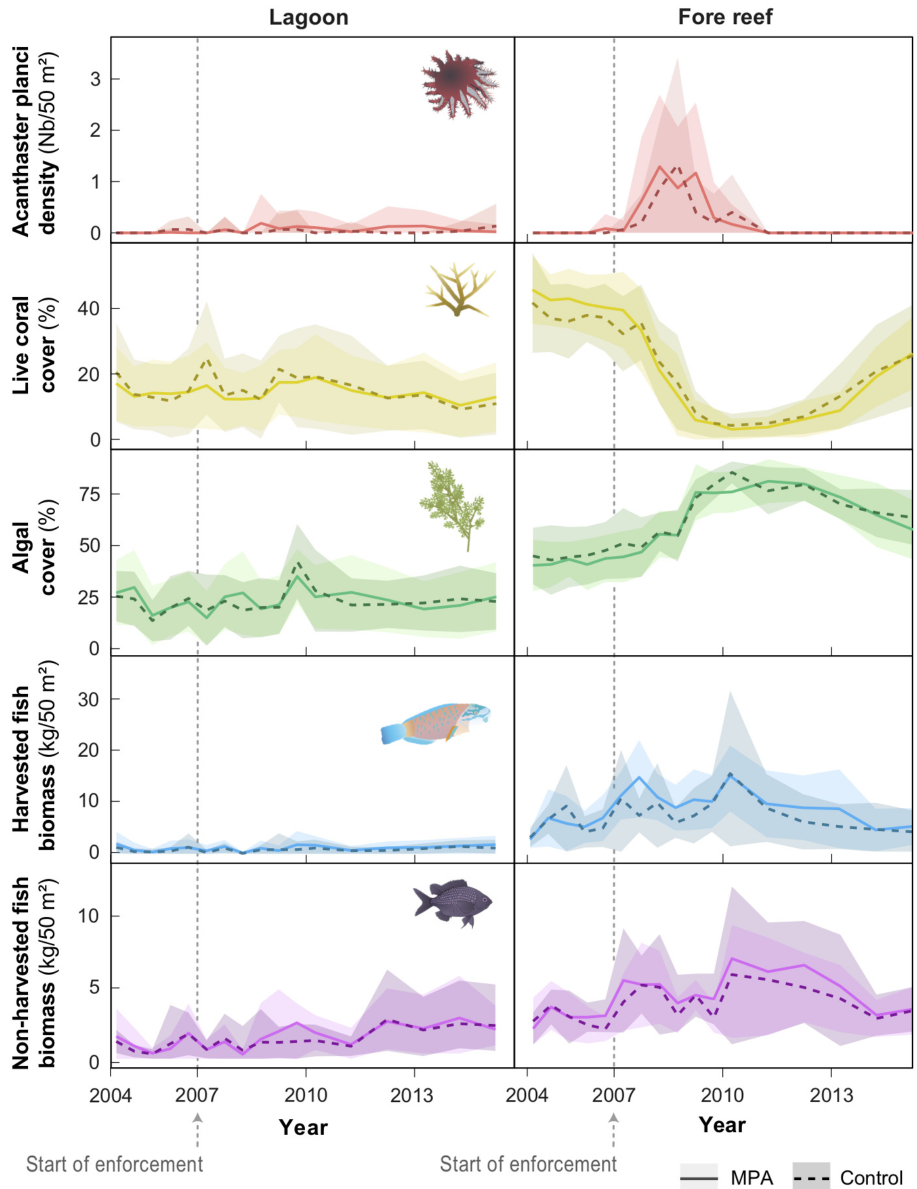

Fig. 2. Temporal variation in key ecological components of the studied coral reef ecosystem. From top to bottom: density of *Acanthaster planci* (red), living coral cover (yellow), algal cover (green), biomass of harvested (blue), and non-harvested fish (purple) in the lagoon (left column) and fore reef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

fishing is prohibited), where density and biomass of harvested fish increased significantly by 43.2% and 31%, respectively. No significant increase in either density or biomass was observed for the sub-network of moderately protected MPAs, where fishing restrictions apply to only a subset of fishing methods and species (Fig. 3). Protection benefited herbivores, invertivores, and piscivores (Appendix S1: Fig. S2), the large majority of which are targeted by fishing.

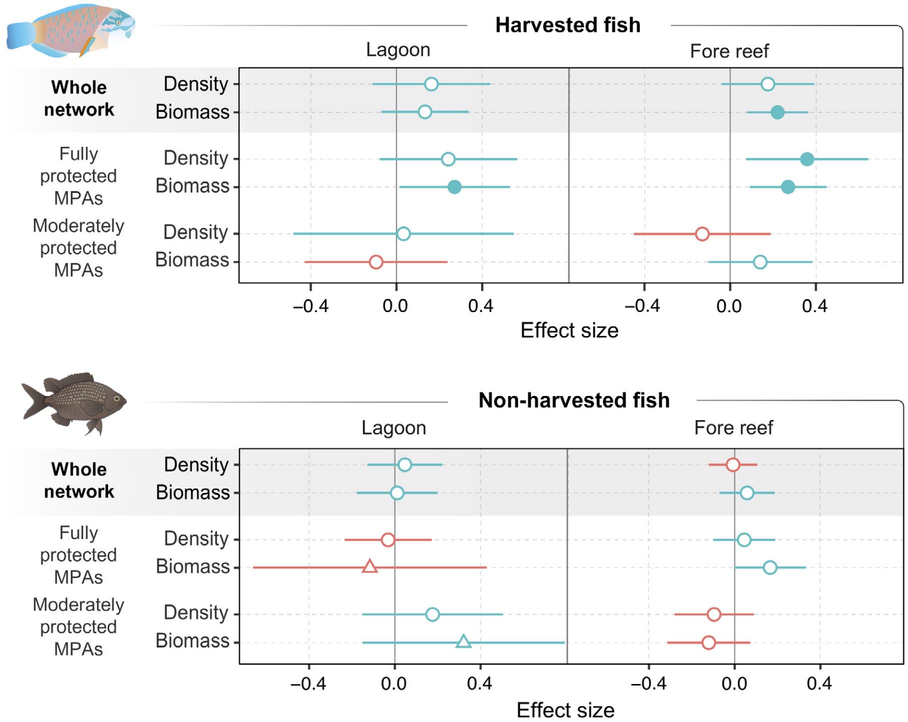

Fig. 3. Effect sizes measured at the whole network scale, and for fully protected marine protected areas (MPAs) and moderately protected MPAs separately, in the lagoon and fore reef, for density and biomass of harvested and non-harvested fishes. Effect sizes are expressed as the change in the log-ratio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

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

Effects on non-harvested fishes were generally smaller in magnitude and more often negative (Fig. 3; Appendix S1: Fig. S2). However, none of these responses differed from zero, whether for the whole network or for the two sub-networks.

Discussion

Disentangling the effects of management interventions from other sources of spatiotemporal variation is a challenging but necessary task to derive robust inferences that can inform evidence-based decisions. Before-After Control-Impact Paired-Series designs are particularly powerful tools to address this challenge, yet, although there have been hundreds of assessments of MPAs, very few include data from Before the establishment of the MPA and even fewer have multiple surveys from Before (Castilla and Bustamante 1989, Lincoln-Smith et al. 2006, Shears et al. 2006). As a result, most assessments are unable to unequivocally isolate the effects of the MPA from preexisting differences (Osenberg et al. 2006). To our knowledge, this is the first time a Progressive-Change BACIPS approach—which expands the scope of BACIPS analyses beyond the step-change response assumed in previous assessments—has been used to assess the impact of a network of MPAs on fish communities.

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

The establishment of the MPA network in Moorea provided positive, but limited, ecological benefits. Network-wide, harvested fish biomass had increased by 24.8% on the fore reef eight years after the start of enforcement, in protected areas relative to Controls. Importantly, this positive, network-scale effect was mostly driven by responses where fishing was entirely prohibited (i.e., in the fully protected MPAs, biomass and density increased +30% and +43.2%, respectively). Indeed, no positive effect was detected in either habitat within moderately protected MPAs (sensu Horta e Costa et al. 2016). This result is consistent with a recent meta-analysis that found that fully and highly protected areas consistently conferred ecological benefits, but moderately protected MPAs provided ecological benefits only when immediately adjacent to fully protected areas (Zupan et al. 2018).

The response in fully protected MPAs, although the largest effect we detected, was relatively small compared to effects documented in other published MPA meta-analyses, in which harvested organisms were generally 2–3 times more abundant inside MPAs compared to fishing grounds (Halpern 2003, Claudet et al. 2008, 2011). The lower effect measured in this study could be due to a combination of factors, which we elaborate upon below, including (1) overestimation of the effect size in previous studies due to the lack of Before data (Osenberg et al. 2006, 2011), (2) limited compliance and enforcement (Guidetti et al. 2008, Campbell et al. 2012), and (3) dramatic ecosystem disturbance following enforcement due to the crown-of-thorns starfish (COTS) outbreak and cyclone (Adam et al. 2011, Lamy et al. 2015, 2016).

Marine protected areas are often strategically implemented in sites with higher densities than surrounding areas. The absence of Before data precludes the incorporation of these initial, and potentially large, differences, which may then become confounded with effects of MPAs. As a result, studies that lack Before data may overestimate the benefits of MPAs. Indeed, it has been suggested that up to half of the commonly observed increase in density inside MPAs may be due to these preexisting differences (Osenberg et al. 2006, 2011). Our smaller-than-expected effect sizes support this interpretation. They also support Osenberg et al.'s (2011) conjecture that by identifying Control sites Before MPA enforcement, siting and MPA effects are less likely to be confounded: For example, effect sizes from a Control-Impact analysis of our data yielded effects that were comparable in magnitude to (i.e., not larger than) effects from the BACIPS analyses (Appendix S1: Fig. S3). The Control-Impact comparison, however, revealed two important differences. First, variation in the effects was greater for the Control-Impact analyses, presumably because initial differences between sites added to the variation in the Control-Impact effects (relative to the effects quantified with BACIPS). Secondly, the confidence intervals on the effects were smaller for the Control-Impact estimates, likely because Control-Impact studies only capture spatial variation while BACIPS analyses capture spatiotemporal variation. These results not only suggest that Control-Impact studies might overestimate effects, but that they might also give a false sense of confidence in the estimates because they fail to incorporate spatiotemporal variance. The BACIPS approach circumvents these problems and likely leads to smaller, more accurate, but less precise, estimates of effect sizes.

Limited public appreciation about the benefits of MPAs and an understaffed management team may have limited compliance and therefore ecological outcomes associated with the Moorea MPA network (Gaspar and Bambridge 2008, Guidetti et al. 2008, Edgar et al. 2014, Gill et al. 2017). Surveillance reports made by the local mediator (Gaspar and Bambridge 2008) and surveys completed by local experts (Appendix S1: Table S5) suggest that enforcement was heterogeneous, being mostly limited to the north shore, where the largest beneficial effects were observed

(Appendix S1: Figs. S4 and S5). Furthermore, the lagoon habitat is highly fished at night with light attractors, and surveillance is non-existent at night. The fore reef is less accessible and more hazardous, and, as a result, less likely to experience night poaching (Thiault et al. 2017*a*), potentially explaining why the responses on the fore reef were greater than in the lagoon (Fig. 3).

The whole island underwent severe natural disturbances since the network's establishment. A COTS outbreak occurred starting in 2007 and was followed by a cyclone in 2010. This resulted in a dramatic (90%) decline in live coral cover, especially on the fore reef, and an increase in turf and macro-algae (Fig. 2). These shifts in microhabitats led to changes in the composition of reef-associated fishes, but after a time lag of several years (Adam et al. 2011, Lamy et al. 2015, Han et al. 2016). These types of dramatic temporal changes can cause problems with some types of assessments (e.g., Before–After comparisons). Before-After Control-Impact Paired-Series, in theory, can handle such regional phenomena because the Control site should reflect the effects of the regional processes (i.e., the natural disturbance) but not the local factors (i.e., MPA). Surveys confirmed that similar impacts of COTS and the hurricane were simultaneously observed at the MPA and Control sites (Kayal et al. 2012, Lamy et al. 2015). This, combined with the fact that functional groups that are highly sensitive to habitat changes did not respond to protection (Appendix S1: Fig. S2), suggests that observed MPA effects are not confounded with COTS and cyclone effects. These issues underscore the importance of implementing BACIPS designs for future MPA assessments.

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

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2576/full

Ecosphere

Ecological evaluation of a marine protected area network: a progressive-change BACIPS approach

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Appendix S1

Appendix S1: Supplementary Analyses

1. Classifying MPAs

We classified each of the eight MPAs based on the system described by Horta e Costa et al. (2016), in which each area type allows different activities. Among the five possible classes, we identified five fully protected areas and three moderately regulated areas (Fig. 1). Individual regulations are provided in Table S1.

Table S1: *Regulation-based classification of the eight MPAs implemented on Moorea's reefs. FPA: Fully protected area; ModPA: Moderately protected area.*

Name	Regulations	Classification
Tiahura	• No fishing allowed; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	FPA
Taotaha	• No fishing allowed; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	FPA
Tetaiuo	• No fishing allowed; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	FPA
Aora	• No fishing allowed; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	FPA
Pihaena	• No fishing allowed; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	FPA
Maatea	• No fishing allowed except line fishing and beach net on the shore, and spearfishing by day and net fishing <50m beyond reef passages; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	ModPA
Motu Ahi	• No fishing allowed except line fishing and trolling net; • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	ModPA
Nuarei	• No fishing allowed except line fishing and pelagic species (ouma, inaa, and skipjack). • No other extractive activities allowed; • Boating and anchoring allowed but anchoring is restricted to particular areas or mooring buoys.	ModPA

2. Autocorrelation Analyses

Our model assumed an absence of autocorrelation. To test this assumption, we fitted one-lag autoregressive models to each time series of residuals ($\Delta_{observed} - \Delta_{fitted}$) for each model and determined the correlation (r) between the residual at the x^{th} sampling date and the residual at the $(x+1)^{th}$ sampling date. This approach assumes that the residuals are autoregressive in the sense that only ε_{t-1} is important when predicting ε_t. Results show that temporal autocorrelation was small, indicating the overall robustness of our models (Table S2).

Table S2: *Summary of the residual autocorrelation analysis. Numbers indicate Pearson 's product moment correlation coefficient.*

	Harvested fish		*Non-harvested fish*	
	Lagoon	**Fore reef**	**Lagoon**	**Fore reef**
Whole network				
Density	0.16	0.17	0.22	0.24
Biomass	0.14	0.16	0.35	-0.02
Fully protected areas				
Density	0.19	0.13	0.41	0.25
Biomass	0.16	0.15	0.43	0.02
Moderately protected areas				
Density	-0.01	0.16	-0.12	0.12
Biomass	-0.17	0.07	0.08	-0.25

3. RESULTS OF THE MPA-SCALE ANALYSIS

We applied a Progressive-Change BACIPS by competing four models: step-change, linear, asymptotic and sigmoid models (Thiault et al. 2017). The magnitude of the response of fish to protection (hereafter referred to as effect size) was then measured based on the predictions of the best-fit model (highest AICc score) at t=2015, which corresponds to the last year in our dataset. We assessed the effect of (i) the whole network (i.e., the island-wide effect of the MPA network), (ii) the two sub-networks (i.e., the network of fully protected and moderately protected MPAs, respectively) and (iii) each individual MPA using all $\Delta_{P,i}$ calculated for each pair of sites (i.e., eight pairs for each date). Note that due to limited power (Table S3), MPA-level analyses should be interpreted with caution.

Table S3: *Effect sizes [and 95% confidence intervals] measured at the whole network scale, at the fully protected MPAs and moderately protected MPAs sub-networks scale, and at the MPA-scale, in the lagoon reef and fore reef, for density and biomass of targeted and non-targeted fishes. Tiahura, Tetaiuo, Taotaha, Pihaena and Aroa are fully protected MPAs; Nuarei, Motu Ahi, and Maatea are moderately protected MPAs. Effect sizes are expressed as the log-ratio of the density or biomass in the MPA relative to its Control (Δ) as predicted by the best-fit model at t=2015. Changes by a factor of 2 thus correspond to values of -0.7 (halving) or 0.7 (doubling) over the 9-yer period of protection. Estimates with 95% CIs that do not include 0 are indicated in bold.*

		Harvested fish		Non-harvested fish	
		Lagoon	Fore reef	Lagoon	FORE REEF
WHOLE NETWORK					
	Density	0.16 [-0.11-0.44]	0.18 [-0.04-0.39]	0.05 [-0.13-0.22]	-0.01 [-0.12-0.11]
	Biomass	0.13 [-0.07-0.34]	**0.22 [0.08-0.36]**	0.01 [-0.18-0.2]	0.06 [-0.07-0.19]
FULLY PROTECTED					
	Density	0.24 [-0.08-0.56]	**0.36 [0.07-0.64]**	-0.03 [-0.23-0.17]	0.04 [-0.1-0.19]
	Biomass	**0.27 [0.01-0.53]**	**0.27 [0.09-0.45]**	-0.12 [-0.66-0.43]	0.17 [0-0.33]
Aroa	Density	0.16 [-0.85-1.16]	0.84 [-0.3-1.97]	-0.6 [-1.89-0.69]	0.05 [-0.58-0.68]
	Biomass	0.29 [-0.59-1.16]	0.44 [-0.26-1.15]	-0.58 [-1.27-0.12]	0.67 [-0.29-1.63]
Pihaena	Density	-0.7 [-1.97-0.57]	**1.46 [0.54-2.37]**	-0.4 [-0.97-0.18]	-0.36 [-0.81-0.1]
	Biomass	0.31 [-0.4-1.02]	0.59 [-0.08-1.27]	-0.81 [-1.54--0.08]	-0.36 [-1.09-0.38]
Taotaha	Density	0.57 [-0.64-1.78]	0.29 [-0.72-1.3]	0.21 [-0.47-0.9]	0.16 [-0.38-0.69]
	Biomass	0.34 [-0.62-1.31]	0.25 [-0.43-0.92]	0.32 [-0.45-1.08]	0.19 [-0.37-0.76]
Tetaiuo	Density	0.5 [-0.55-1.54]	0.33 [-0.55-1.2]	0.32 [-0.62-1.26]	0.3 [-0.12-0.72]
	Biomass	0.33 [-0.45-1.12]	0.27 [-0.26-0.81]	0.39 [-0.26-1.04]	0.2 [-0.11-0.5]
Tiahura	Density	-0.28 [-1.52-0.96]	0.75 [-0.32-1.81]	-0.47 [-1.37-0.42]	0.33 [-0.36-1.02]
	Biomass	-0.32 [-1.54-0.91]	0.15 [-0.43-0.72]	-0.65 [-1.46-0.16]	-0.03 [-0.52-0.45]
MODERATELY PROTECTED					
	Density	0.03 [-0.48-0.55]	-0.13 [-0.45-0.19]	0.18 [-0.15-0.5]	-0.09 [-0.28-0.09]
	Biomass	-0.09 [-0.43-0.24]	0.14 [-0.1-0.38]	0.32 [-0.15-0.79]	-0.12 [-0.31-0.07]
Maatea	Density	-0.23 [-1.27-0.82]	-1.06 [-2.01--0.1]	0.36 [-0.57-1.29]	0.07 [-0.52-0.66]
	Biomass	-0.19 [-1.05-0.68]	0.11 [-0.42-0.63]	0.71 [-0.14-1.56]	-0.5 [-1.12-0.11]
Motu Ahi	Density	0.36 [-0.43-1.16]	0.11 [-0.87-1.09]	0.18 [-0.72-1.08]	-0.59 [-1.08--0.1]
	Biomass	0.49 [-0.53-1.5]	0.2 [-0.47-0.87]	0.48 [-0.61-1.57]	-0.16 [-0.63-0.31]
Nuarei	Density	-0.12 [-2.09-1.85]	0.1 [-0.6-0.81]	0.14 [-0.74-1.02]	0.09 [-0.36-0.55]
	Biomass	-0.31 [-1.13-0.52]	0.12 [-0.56-0.79]	0.35 [-0.54-1.25]	0.07 [-0.43-0.57]

4. RESULTS FOR TROPHIC GROUPS

We also assessed the effect of (i) the whole network (i.e., the island-wide effect of the MPA network) and (ii) the two sub-networks (i.e., the network of fully protected and moderately protected MPAs, respectively) on the density and biomass of six trophic groups: coralivores, herbivores, invertivores, omnivores, piscivores and planktivores. Results show that herbivores, piscivores and invertivores (most of which are targeted locally) had larger (and significant) effect sizes, but no particular difference in the response was observed (Fig. S1), probably as a result of high within-transect variability (see Discussion in the main text). In contrast, coralivores, planktivores and omnivores (which are virtually not targeted in Moorea) did not respond significantly to protection (Fig. S1).

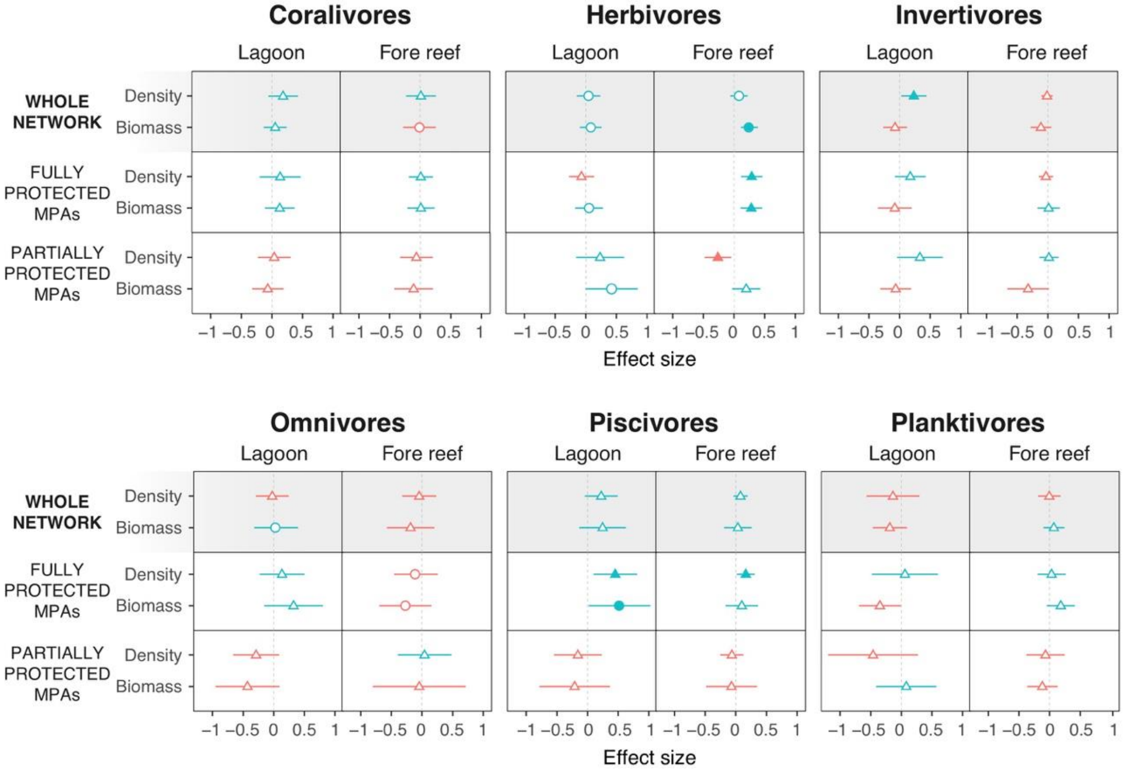

Figure S1: Results of the Progressive-Change BACIPS analysis on the density and biomass of six functional groups. Effect sizes are expressed as the log-ratio of the density or biomass in the MPA relative to its Control (Δ) as predicted by the best-fit model at t=2015. Changes by a factor of 2 correspond to effects sizes of -0.7 (halving) or 0.7 (doubling) over the 9-year period of protection. Positive effects are depicted in red and negative effects in blue. Filled symbols indicate that the 95% confidence interval of the effect does not overlap zero. Shapes indicate the best-fit model: step-change (circle) and linear (triangle). There were no cases in which the asymptotic or sigmoid model was best supported by the data.

5. Power Analyses

Limited statistical power might have prevented us from detecting effects, especially at the individual MPA-scale. The power of a BACIPS design is determined by the number of transects, sampling dates, and MPAs (the latter is relevant for network analyses) and the degree of spatio-temporal variation in density and biomass, which is driven by sampling (i.e., among-transect) error as well as true spatio-temporal variability (Osenberg et al., 1994). Using estimates of variation, and an effect size observed in prior studies (i.e., a doubling in density inside the MPA relative to the control) we conducted power analyses and found that we had very high power to detect a 100% increase in density or biomass in the MPAs at the whole network scale (Fig. S2): for variables presented in the main text (harvested and non-harvested fish density and biomass), power always exceeded 97% and was usually 100%. At the sub-network scale, power was also very high, exceeding 92% in all but 1 of the 16 comparisons. In contrast, power to detect effects at the scale of an individual MPA was much lower: i.e., over half of the comparisons had power <80% and 9/64 comparisons had power that did not exceed 50%. Interestingly, error varied systematically among the two habitats we sampled: it was smallest on the fore reef and greatest in the lagoon, and as a result, power was almost always greater for comparisons based on the fore reef (Fig. S2). This high variability in the lagoon may have resulted from the greater habitat heterogeneity (Galzin, 1987). We observed similar patterns observed when analyzing functional groups (Fig. S2).

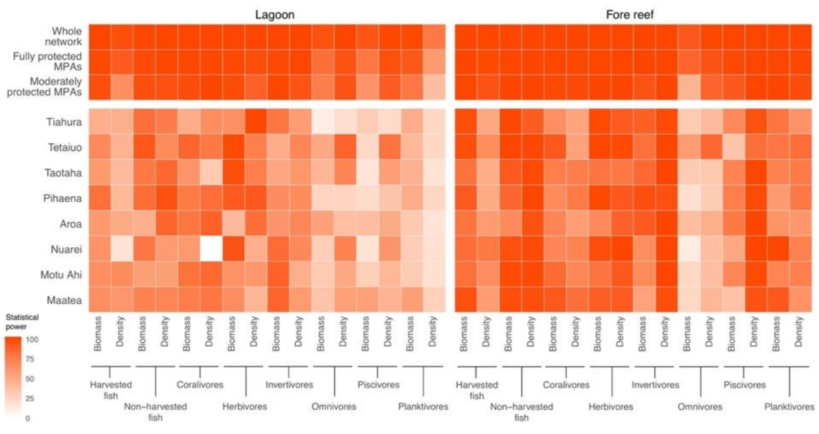

Figure S2: *Power analyses for BACIPS designs. Given are the percentage of times that the null hypothesis would be rejected assuming a 100% increase in density (a change in Δ equal to 0.7) in the MPA(s), and using the sampling design and observed variation from our study. Results are given separately for harvested, non-harvested fishes and the functional groups in two habitats (lagoon and fore reef) when evaluated at the scale of individual MPAs, sub-networks of fully and moderately MPAs, and the whole network.*

6. Comparing Progressive-Change BACIPS with Control-Impact

We explored the consequence of implementing a Progressive-Change BACIPS design versus the more commonly used Control-Impact design by comparing effect sizes and their confident intervals for the two methods. For each possible comparison (each unique combination of MPA site, harvest category, and habitat), effect sizes from the Control-Impact approach were calculated using data from the last sampling date (t=2015) with confidence intervals based on spatial variation among transects. These means and associated 95% CIs were then plotted against effects sizes and 95% CIs from the Progressive-Change BACIPS (Fig. S1).

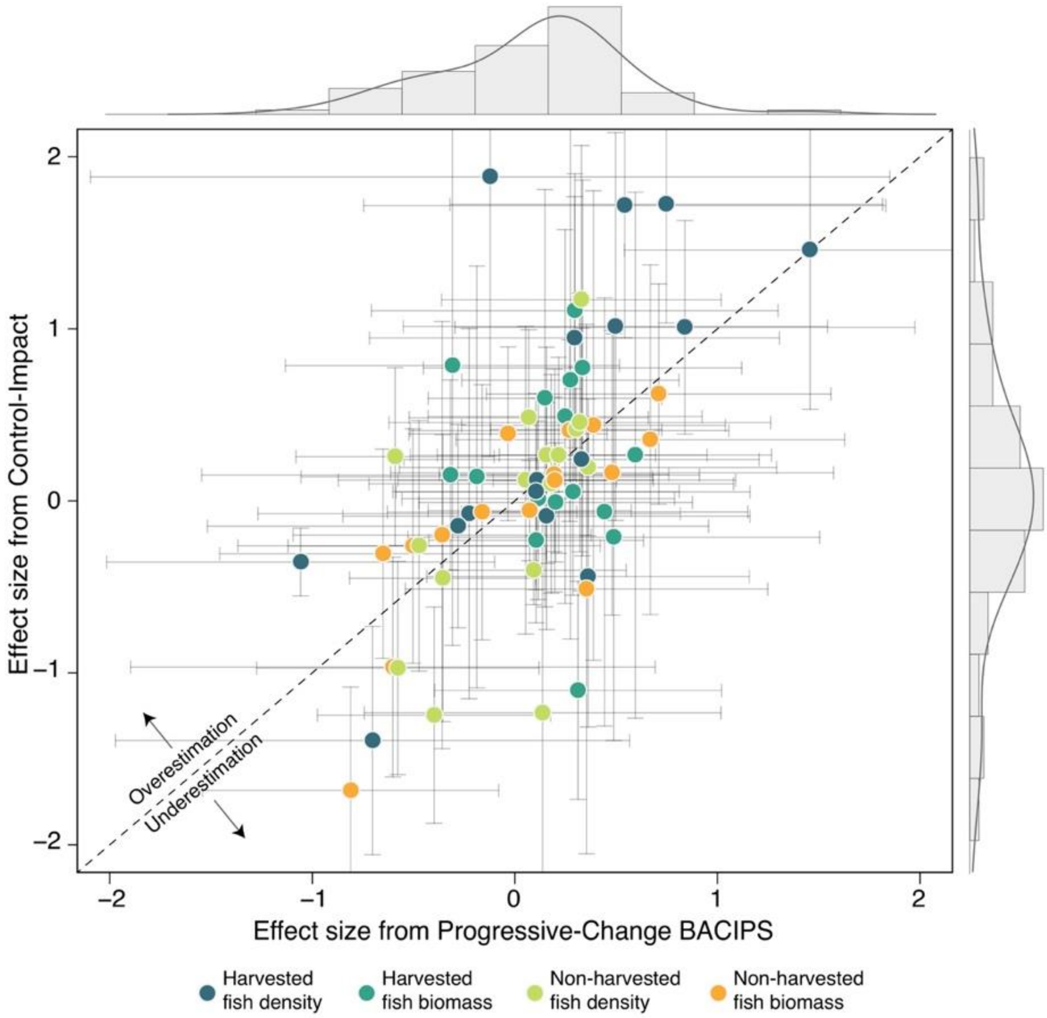

Figure S3: *Comparison of effect sizes as estimated by the Progressive-Change BACIPS approach and the more traditional Control-Impact method. Each point represents an effect-size (+/- 95% confidence intervals) measured at the individual MPA-scale and colors indicate the variable considered. The 1:1 line shows where the two methods provide equal effect sizes; deviation from this line indicates situations where the Control-Impact method underestimates and overestimates the effect size relative to the more robust Progressive-Change BACIPS approach used in this study. Histograms indicate the distribution of effect sizes along the x and y axes.*

Although patterns were similar for the two types of analyses, use of the Control-Impact approach led to an increase in the number of significant effects from 4 to 18, probably because estimated effects tended to be more extreme (i.e., more dispersed with larger positive and negative effects) and confidence intervals tended to be smaller (Fig. S1).

By applying a BACIPS design, our goal was to more effectively quantify the benefits of MPAs. Osenberg et al. (2011) suggested that Control-Impact studies may yield biased effects because MPAs may be placed in non-representative (better) areas. They further surmised that when sites are sampled Before, the pre-existing differences may be reduced because the Before period allows investigators to select sites that are, a priori, more similar to one another. Our results support this conjecture: effect sizes from a Control-Impact comparison in our BACIPS study were comparable in magnitude as the effects from the BACIPS analyses (Fig. S1). However, there were two important differences. First, the variation in the effects was greater for the Control-Impact analyses, presumably because initial differences between sites added to the variation in the Control-Impact effects (relative to the effects quantified with BACIPS). Secondly, the confidence intervals on the effects were smaller for the Control-Impact estimates, likely because Control-Impact studies only capture spatial variation while BACIPS captures spatio-temporal variation. These results not only suggest that Control-Impact studies might overestimate effects (Osenberg et al. 2011), but that they might also give a false sense of confidence in the estimates because they fail to incorporate temporal variance.

Due to the low statistical power of our local, MPA-scale, analyses (Table S4), these results should be interpreted with caution.

7. Temporal Trends in Fish Communities Across Moorea.

Data presented in the main text, provide overall summaries of the analyses, including effect sizes. Here, we also present the time series of the data (log-transformed densities or biomasses) and the differences from which those summaries were derived.

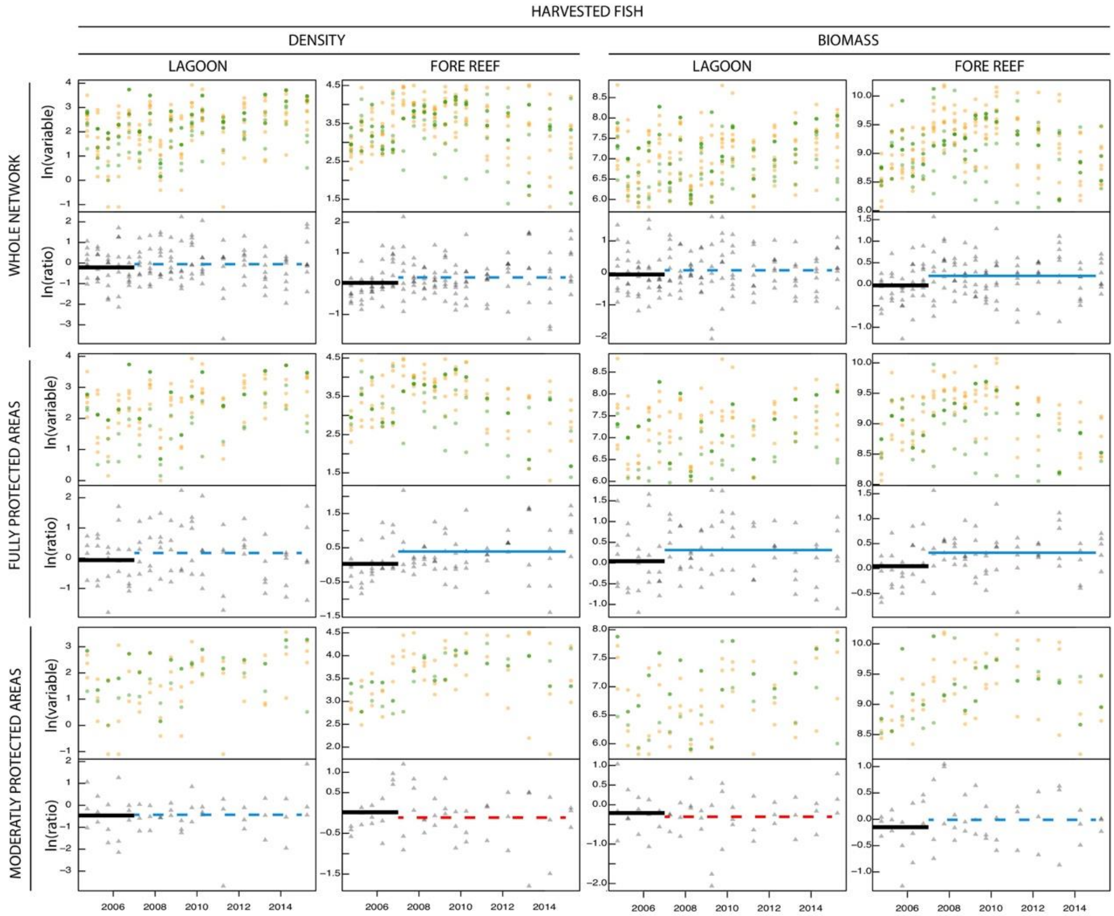

Figure S4: *Time series of raw counts for density and biomass (log$_e$-transformed) inside (yellow dots) and outside (green dots) the MPAs, and differences (i.e., log-ratios; grey triangles) in the whole network, fully protected areas and partially protected areas, on each habitat (lagoon and fore reef), for harvested fishes. Each black solid line gives the estimated difference Before MPA enforcement. Dashed and solid lines, respectively, indicate non-significant and significant changes in Δ from Before to After MPA enforcement (2007) as measured by the Progressive-Change BACIPS approach, with blue lines indicating increases and red lines indicating decreases in density or biomass. A change of +/- 0.7 from Before to After represents a doubling or halving in density or biomass. All panels for log(ratio) give effects estimated from the step-change model.*

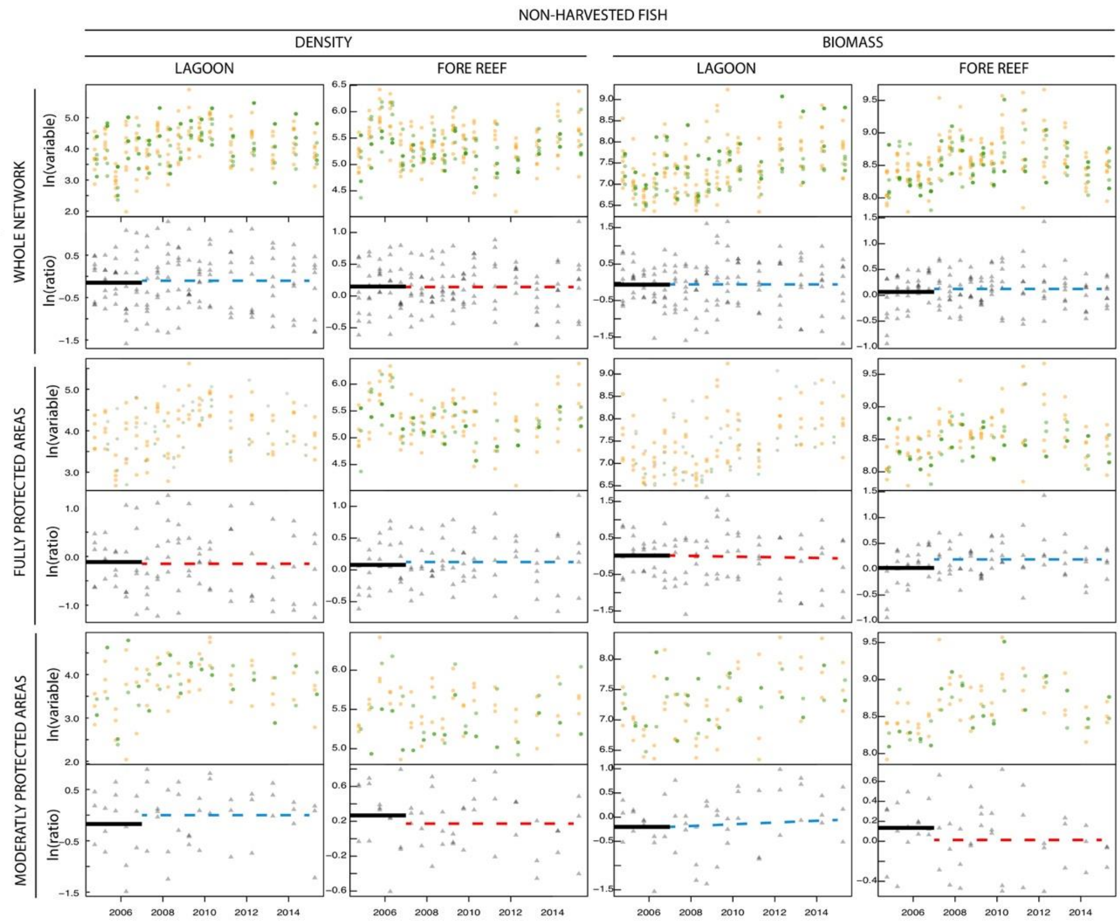

Figure S5: *Time series of raw counts for density of biomass (log-transformed) inside (yellow dots) and outside (green dots) and log-ratio (grey triangles) in the whole network, fully protected areas and partially protected areas, on each habitat (lagoon and fore reef), for non-harvested fishes. Dashed and solid lines respectively indicate insignificant and significant change in Δ between Before and After MPA enforcement (2007) as measured by the Progressive-Change BACIPS approach. Panels for log(ratio) give effects estimated from either the step-change model (all but two cases) or the linear model (for lagoon biomass in both the fully and moderately protected areas).*

8. SURVEILLANCE EFFORT

Face-to-face surveys were administered to 10 local experts including three managers, three scientists, two staff from environmental agencies, an independent environmental consultant, and a member of an environmental association. Respondents were asked to rate their perceived level of surveillance effectiveness for each individual MPA since 2007 on a 5-point scale (1=ineffective surveillance; 5-=highly effective surveillance). Surveillance effectiveness included surveillance formally carried out by local authorities (fisheries department, etc.), but also informally via residents or local stakeholders' groups. Anonymized answers are provided in Table S5. We followed the Code of Ethics adopted by CRIOBE and validated by the Ethics Committee of the CNRS. Accordingly, experts involved in the study were informed about the purpose of the questionnaire and use of the resulting data.

Table S5: *Results of the surveys performed with 10 local experts on their perception of the surveillance effort of each MPA. 1- ineffective surveillance, 5-high surveillance effectiveness. Fully protected areas in orange; Moderately protected areas in yellow.*

	Fully protected MPAs					**Moderately protected MPAs**		
	Tiahura	Pihaena	Aroa	Tetaiuo	Taotaha	Nuarei	Motu Ahi	Maatea
Expert 1	3	4	2	2	2	3	3	2
Expert 2	3	4	2	1	1	3	2	2
Expert 3	3	4	2	2	2	2	2	2
Expert 4	4	4	3	3	3	4	4	3
Expert 5	3	3	3	2	2	2	2	2
Expert 6	3	4	2	2	2	3	2	2
Expert 7	4	3	3	2	2	3	2	2
Expert 8	4	5	4	4	4	4	4	4
Expert 9	5	3	3	4	4	4	3	3
Expert 10	2	4	2	2	2	2	2	2
Mean	**3.4**	**3.8**	**2.6**	**2.4**	**2.4**	**3**	**2.6**	**2.4**
+/-SD	+/-0.8	+/-0.6	+/-0.7	+/-0.9	+/-0.9	+/-0.8	+/-0.8	+/-0.7

Results from our survey show that, overall, surveillance effectiveness was perceived as low (2.8+/-0.9), highlighting the general lack of enforcement island-wide. Local experts ranked surveillance in Maatea (moderately protected area), Tetaiuo (full protected area) and Taotaha (fully protected area) as being the least effective. Interestingly, surveillance effectiveness was ranked highest in the MPA locally enforced by an environmental association (Pihaena, fully protected area).

9. References

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