




A global assessment of the direct and indirect benefits of marine protected areas for coral reef conservation

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Abstract

Aim: Marine protected areas (MPAs) are increasingly implemented to conserve or restore coral reef biodiversity, yet evidence of their benefits for enhancing coral cover is limited and variable.

Location: 30 MPAs worldwide and nearby sites (within 10 km).

Taxa: Cover of key functional groups for coral (total, branching, massive and tabular), and algae (total, filamentous, foliose) and total biomass of reef fish trophic groups (excavator, scraper, browser, higher carnivore).

Methods: We used a global dataset obtained using standardized survey methods at 465 sites associated with 30 MPAs in 28 ecoregions to test the effects of five key MPA attributes (>10 years old, well-enforced, no-take, large and isolated) on coral cover, algal cover and reef fish biomass. We also tested the direct (reducing disturbance by human activities) versus indirect pathways (increasing grazing potential through recovering populations of herbivorous fishes) by which MPAs can influence coral and algal cover.

Results: Only well-enforced, no-take and old (>10 years) MPAs had higher total coral cover (response ratio 1.08–1.19 \times) than fished sites, mostly due to the increased cover of massive coral growth forms (1.34–2.06 \times). This effect arose through both the direct influence of protection and indirect benefits of depressed algal cover by recovering herbivorous fish biomass. Neither the direct (standardized coefficient = 0.06) nor indirect effects (standardized coefficient = 0.04) of no-take protection on coral cover were particularly strong, likely reflecting regional differences in fishing gear, targeted species and trophic webs.

Conclusions: MPAs promote the persistence of some functional groups of corals, and thus represent an important management tool, globally.

KEYWORDS

algal cover, fish biomass, herbivorous fishes, impacts of fishing, marine reserves, predatory fishes, Reef Life Survey, trophic interactions

1 | INTRODUCTION

Coral reefs cover $\leq 1\%$ of the world's oceans, but host $>25\%$ of their biodiversity (Plaisance, Caley, Brainard, Knowlton, & Roopnarine, 2011; Small, Adey, & Spoon, 1998). They sustain millions of human livelihoods along tropical coastlines (Teh, Teh, & Sumaila, 2013). Their high diversity maintains important ecosystem functions, including habitat provision for associated species (Nyström, Folke, & Moberg, 2000), biotic, physical, biogeochemical, social and cultural services (Liquete et al., 2013), and increased resilience to disturbance (Mora et al., 2011). This diversity is now globally threatened by climate change, coastal pollution and runoff, direct destruction and overexploitation of key species (Bellwood, Hughes, Folke, & Nyström, 2004). Worldwide, $\sim 30\%$ of live coral cover has been lost from coral reefs in the last 50 years (Bruno & Selig, 2007; Jackson, Donovan, Cramer, & Lam, 2014), with recent severe bleaching causing mass mortality of corals in all tropical ocean basins (Baker, Glynn, & Riegl, 2008; Hughes et al., 2017; Stuart-Smith et al., 2018). The protection of coral reefs and their biodiversity is therefore recognized as a global priority for effective marine conservation (UNEP, 2003).

Marine protected areas (MPAs) have increasingly been implemented to conserve or restore key species, fisheries or coral reef habitats (Cinner et al., 2016; Selig & Bruno, 2010; Soler et al., 2015). These MPAs usually aim to prevent or limit human fishing pressure in specific locations (Emslie et al., 2015). Management techniques include no-take regulations, bans on the use of particular gear types, spatial and temporal closures, and/or use of size limits, quotas or permits (Campbell, Edgar, Stuart-Smith, Soler, & Bates, 2017; Cinner et al., 2009; Côté, Mosqueira, & Reynolds, 2001). These options can lead to an increase in coral cover directly by limiting destructive fishing methods (Bellwood et al., 2004) and/or indirectly, through the flow on effects of increases in the biomass of exploited fishes, especially herbivores (Mumby et al., 2006). Nevertheless, many studies have found that MPAs make no detectable contribution towards the protection of coral reef habitats, beyond the species targeted by local or regional fisheries (Coelho & Manfrino, 2007; Cox, Valdivia, McField, Castillo, & Bruno, 2017; Huntington, Karnauskas, & Lirman, 2011; Toth et al., 2014).

Specific attributes can hinder or enhance the performance of MPAs and determine which components of the ecosystem show the greatest response (Claudet et al., 2008; Micheli, Halpern, Botsford, & Warner, 2004). A recent study highlighted the importance of five key planning and management attributes for enhancing the biomass of large fishes in MPAs: no-take regulations, well-enforced compliance, >10 years old, large and isolated by habitat boundaries (Edgar et al., 2014). No-take fishing regulations, coupled with efficient enforcement of those regulations, provide the best direct and indirect protection, leading to increased abundance, biomass, and size of species and changes in assemblage structure (Micheli et al., 2004; Palumbi, 2001). Increasing the size of the MPA can broaden the range of species that gain adequate protection, such as wide-ranging or migratory species, and can ensure that habitats are protected in

their entirety (Claudet et al., 2008). Older MPAs are more likely to protect long-lived species (Claudet et al., 2008). In the case of habitats that occur in discrete patches, such as coral reefs, protection of the entire "patch," and isolation of that patch by deep water or sand, can also enhance the effectiveness of protection (Edgar et al., 2014). The taxa and trophic groups that benefit most from protection in MPAs depend largely on exploitation history and the species targeted by local fishers. While these general principles are widely acknowledged, a detailed understanding of the effect and interactions between these five key attributes is lacking for coral reefs.

The direct and indirect benefits of MPA protection for coral reefs will vary between locations and depend on the fisheries targets (Babcock et al., 2010; Campbell et al., 2017; Edwards et al., 2014; Soler et al., 2015). For example, on the Great Barrier Reef, the protection of higher carnivores has resulted in lower biomass of herbivorous fishes (Graham, Evans, & Russ, 2003), which could potentially indirectly affect algal and coral cover. In contrast, in other regions where herbivores are fished, elevated biomass of this trophic group can reduce the algal cover within MPA boundaries (Mumby & Steneck, 2008; Mumby et al., 2006), which can indirectly benefit coral recruitment and growth (Hughes, Rodrigues, et al., 2007). Additionally, in places such as the Caribbean, the Coral Triangle and the west Indian Ocean, where destructive fishing practises are common, MPAs can also directly protect the benthic community (Mumby & Harborne, 2010). Although several studies have assessed the effects of MPAs on coral reefs across large spatial scales (Cinner et al., 2016; Selig & Bruno, 2010; Soler et al., 2015), none have empirically evaluated the relative importance of these direct versus indirect pathways for coral cover in MPAs.

The effects of MPA protection could also vary between different functional groups on coral reefs (Babcock et al., 2010; Bellwood, Hughes, & Hoey, 2006; Soler et al., 2015). Directly, MPA protection could promote higher cover of total corals, or those of branching or tabular forms, that are valued for tourism but are also easily damaged by fishing gear and other recreational activities (McManus, Rodolfo, Reyes, Cleto, & Nanola, 1997; Roberts et al., 2003). Indirectly, MPA protection could lead to higher biomass of excavating and scraping herbivorous fishes, which clean the reef surface through their feeding activities and are believed to promote coral recruitment and growth (Bellwood et al., 2004; Hughes, Bellwood, Folke, McCook, & Pandolfi, 2007), or browsers, which consume foliose algae (Bellwood et al., 2006), potential competitors with corals for space and light.

In this study, we used the Reef Life Survey (www.reeflifesurvey.com) dataset to assess direct and indirect effects of MPA protection on key functional groups of corals across a wide range of locations and environmental conditions. The different components of coral reef ecosystems investigated comprise fishes (higher carnivores, browsers, excavators and scraping herbivores), corals (total, branching, massive and tabular) and algae (total, foliose and filamentous). We estimated the effects and interactions of the five key MPA attributes identified by Edgar et al. (2014): >10 years old, well-enforced, no-take and isolated on each functional group, separately. We then

tested the direct versus indirect pathways by which no-take MPA protection can potentially enhance coral cover.

2 | METHODS

2.1 | Fish and benthic data

All data were collected through the Reef Life Survey Program (Edgar & Stuart-Smith, 2014), an ongoing global cooperative effort conducted by researchers and trained volunteer divers (Edgar & Stuart-Smith, 2009). Divers survey fishes in two blocks along a 50 m line transect. Each transect is set along a depth contour, with two or more depth contours generally surveyed at each site. Divers count all fishes (≥ 2.5 cm) observed within 5 m each side of the 50 m transect, and estimate their lengths. Digital photographs are then taken every 2.5 m along the transect line ($n = 20$), each photoquadrat covering approximately 0.25 m^2 of the benthos. All surveys were individual events, undertaken between 2006 and 2012.

All photographs are labelled and archived in a publicly-accessible database (www.reeflifesurvey.com). Five random points were scored on each image (100 per transect) by technicians and trained volunteers. These points were classified into 16 functional or morphological categories of corals and algae (Supporting Information Table S1), which are aligned with an Australian image classification standard, CATAMI (Althaus et al., 2015). Previous research has found that this number of points is sufficient for estimating the cover of broad functional groups, providing that the cover of rare species or species richness is not the main goal (Cresswell et al., 2017).

Fish counts and lengths were converted to biomass per transect using length-weight relationships provided for each fish species (genera or family) in FishBase (<http://www.fishbase.org>). The bias in divers' perceptions of fish size underwater was also corrected (Edgar et al., 2014). Fishes were classified into trophic groups (Stuart-Smith et al., 2013), with members of the genera *Chlorurus*, *Bolbometopon* and *Cetoscarus* distinguished as excavators (Supporting Information Table S2).

Fish biomass and benthos cover data were averaged to the site level (465 sites). All sites were located at least 0.2 km apart. Sites were classified as "tropical" based on the realms defined by Spalding et al. (2007). Sites used in analyses were located inside and outside (but within 10 km) of the boundaries of 30 tropical MPAs from 28 ecoregions (Supporting Information Table S3). We compared sites from within and around MPAs with different characteristics (i.e., no-take vs. fished) to minimize the biases associated with MPA site selection and to ensure all sites inside and outside the MPAs experienced similar environmental conditions (Supporting Information Table S3). The analyses were run at the ecoregion, rather than the realm or province level, because of the high variability in the cover of coral and algae and biomass of fishes at this scale (Supporting Information Table S4). All analyses were conducted on four functional groups

of coral (total, branching, tabular, massive), three functional groups of algae (total, foliose and filamentous), and 258 species of fishes belonging to four functional groups (higher carnivores, excavators, browsers and scrapers).

2.2 | Environmental covariates

Six environmental covariates were collected in order to account for regional and local variation between sites. Mean sea surface temperature (SST) was collected from satellite data and nitrate levels from interpolated in situ measurements. The index of population pressure was obtained from Edgar et al. (2014). The presence of a cyclone (within 10 years and 150 km of a survey) was derived from the publicly available IBTrACS dataset (Knapp, Kruk, Levinson, Diamond, & Neumann, 2010). Wave exposure and structural complexity were estimated at 173 sites using standard categories applied by divers, or estimated for the remaining sites using a machine learning (random forest) technique (Edgar et al., 2017). The population index, SST and nitrate environmental covariates were selected from a list of 25 potential variables because of their high explanatory power and low collinearity (Duffy, Lefcheck, Stuart-Smith, Navarrete, & Edgar, 2016). Data sources for the various environmental variables are described in Supporting Information Table S5.

2.3 | Analyses

We assessed the effects of the five MPA planning and management attributes from Edgar et al. (2014) using penalized quasi-likelihood generalized linear models for (a) age (old: >10 years vs. ≤ 10 years); (b) level of compliance (well-enforced vs. ineffective); (c) degree of protection from fishing (no-take vs. open access or restricted fishing); (d) isolation (isolated: reef fully surrounded by deep water >25 m or large expanses of sand vs. connected: shallow reef habitat extending across boundary into fished area allowing unconstrained movement of fishes); and (e) size (large: $>100 \text{ km}^2$ vs. $\leq 100 \text{ km}^2$). The effects of each of the five attributes were assessed separately for each functional group of coral, algae and fish. Models used the quasibinomial distribution (which generalizes the binomial distribution by allowing for overdispersion) with a logit link for cover data or the Gaussian distribution for $\log(\text{biomass} + 0.5)$ data. Effect sizes were reported as response ratios of sites within high categories relative to sites in the low category, from the exponent of the beta coefficients.

All analyses were weighted by the available coral habitat, calculated as proportion of observed reef substratum (i.e., that was not sand or pebbles). The models also included the effects of ecoregion (random) and the fixed effects of four environmental variables (recent cyclone passage <10 years and within 150 km of the site, mean nitrate, sea surface temperature and human population index). For the coral and algae functional groups, the generalized linear models also included the fixed effects of wave exposure and structural complexity. We did not test the effects of wave exposure and structural complexity on fish biomass (Edgar et al., 2017) because the effects

were confounded. The inclusion of a random effect of ecoregion allowed for large-scale region-specific dependencies. Such a hierarchical modelling framework is a common approach for analysis of large spatial-scale data sets, with advantages, disadvantages and alternative approaches previously discussed in relation to this dataset (Bird et al., 2014). Covariates were included in the model to account for spatial autocorrelation and to reduce influences associated with the natural variability at the site level and at the larger scales (ecoregion). The residuals from the regression models did not exhibit

any positive spatial autocorrelation in the variogram (Supporting Information Figure S6).

We used a model comparison technique to assess which combination of the five MPA attributes had the greatest effect on the different fish, coral and algal functional groups. The models included all combinations of the five MPA attributes, and an additional composite model composed of the total number of attributes observed at the highest level. All models included the six environmental covariates for coral and algae cover analyses; the other functional group

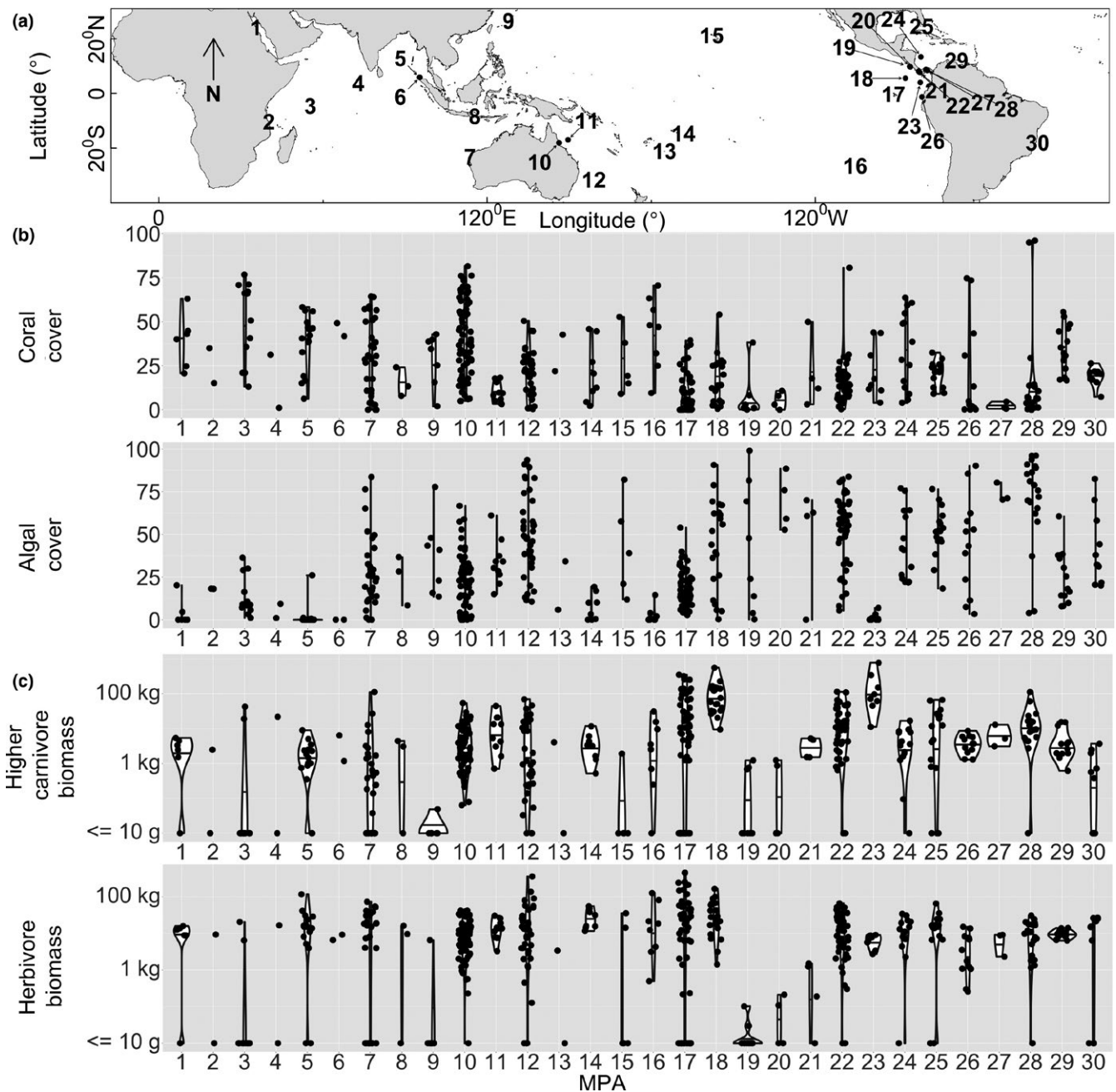


FIGURE 1 (a) Map of MPAs, and violin plots overlaid with scatter plots of (b) total coral cover and total algal cover, and (c) herbivorous and higher carnivore fish biomass at sites inside and outside each MPA. Herbivore biomass represents the sum of excavator, scraper and browser groups considered separately in analyses. Medians are marked by horizontal lines. Percent cover data range from 0%–100% and biomass data are on the log-scale. The numbers on the maps correspond to the MPA names listed in Supporting Information Table S3

analyses all included the same environmental covariates except for wave exposure and structural complexity, as discussed above. The model with the lowest Akaike information criterion (AIC) was deemed the best fit if it was >2 values lower than the next model. The Bayesian information criterion (BIC), deviance and R^2 (for fish biomass only) are also provided.

A structural equation model (SEM) was fitted to explore the direct effects (through reduced disturbance from fishing gear) and indirect effects (enhancing the biomass of herbivorous fish via the removal of fishing pressure) of no-take MPA protection in reducing the algal cover and increasing the coral cover. SEMs provide an approach to propose a causal hypothesis in a statistical framework that can then yield causal interpretations conditional on the model assumptions and data. The R package piecewise SEM was used to estimate the coefficients that describe the strength of the causal pathways in the SEM, as it allowed the use of mixed effects models (Lefcheck, 2016). Two SEMs were considered: a model that included total coral and algal cover, and another model that partitioned coral and algae into functional groups. For each SEM, coral and algal proportions were arcsine transformed and fish biomass $\log_{10}(X + 1)$ transformed to meet assumptions of normality, with a linear mixed effect model applied for all outcome variables. The four fish groups were assumed to have correlated errors as local effects that were introduced by unmeasured covariates can result in similar variation

in the biomass of all groups at a site ($p < 0.05$, for all comparisons, Supporting Information Tables S13 and S14). Wave exposure and structural complexity were also assumed to have correlated errors, with each other and with fish biomass as they were derived from the same dataset ($p < 0.05$, for some comparisons, Supporting Information Tables S13 and S14). In this study, we focused on testing the direct and indirect benefits of no-take MPAs for coral cover, rather than any positive association between total coral cover/structural complexity and fish biomass. We evaluated whether the direct effects were stronger than the indirect effects by comparing the effects of MPAs on coral cover, with the effects via the fish and algae. The strengths of the effects were estimated by multiplying the coefficients along the respective pathways (Bollen, 1987). The significance of the direct and indirect effects were evaluated using the conservative Sobel test (Sobel, 1982).

3 | RESULTS

Across the 30 tropical MPAs investigated, those with the highest total coral cover were located in the Western Indian Ocean, Southeast Pacific Ocean and the Coral Sea (Figure 1, Supporting Information Table S3). The MPAs with the lowest total algal cover were also found in the Western Indian Ocean and the Southeast

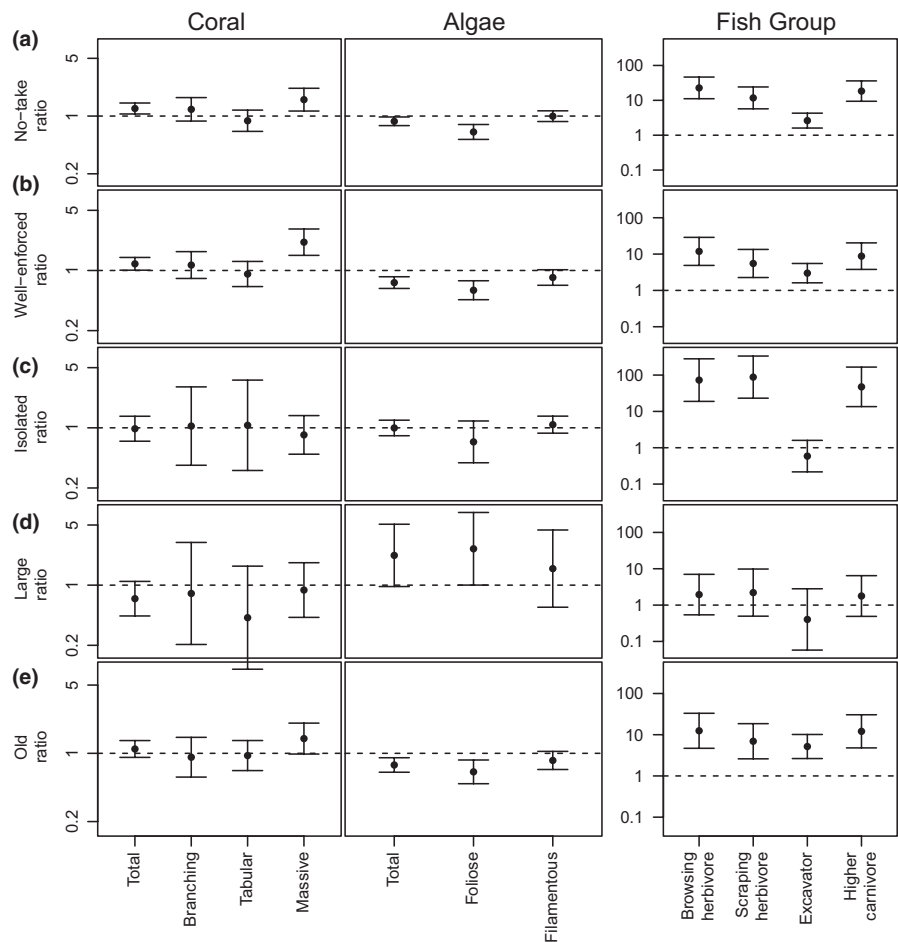


FIGURE 2 Response ratios (95% confidence intervals) for MPA sites (inside and outside but within 10 km) which were (a) no-take vs. fished (restricted fishing or open access); (b) well-enforced vs. ineffective; (c) isolated vs. connected; (d) large (>100 km²) vs. small (≤100 km²); and (e) old (>10 years) vs. young (≤10 years). Ratios are plotted separately for each functional group: (a) coral cover (total, branching, massive, tabular), (b) algal cover (total, filamentous, foliose) and (c) fish biomass (higher carnivore, browsing herbivore, scraping herbivore and excavator)

Pacific Ocean (Figure 1, Supporting Information Table S3). In contrast, the highest biomass of herbivore and higher carnivore fishes were identified in the Eastern Pacific Ocean, East Indian Ocean and the Caribbean (Figure 1, Supporting Information Table S3).

Four of the five attributes of MPAs assessed were significantly related to the cover of corals and algae (Figure 2, Supporting Information Tables S3, S7–S12). MPA sites that were older than 10 years had slightly, but not significantly, higher total (response ratio = 1.08 \times) and significantly higher massive coral cover (1.34 \times) (Figure 2, Supporting Information Tables S7 and S12). In contrast, MPA sites older than 10 years had significantly lower total (0.78 \times) and foliose (0.70 \times) algal cover, and increased biomass of browsing (11.5 \times), scraping (7.29 \times), excavating (5.40 \times) and higher carnivore (11.45 \times) fishes (Figure 2, Supporting Information Tables S7 and S12).

Well-enforced and no-take MPA sites had significantly higher total (1.17 \times and 1.19 \times) and massive (2.06 \times and 1.51 \times) coral cover, and lower total (0.74 \times and 0.88 \times) and foliose (0.62 \times and 0.67 \times) algal cover relative to sites that were not well-enforced or fished (Figure 2, Supporting Information Tables S8, S9 and S12). These sites also had significantly higher biomass of browsing (11.35 \times and 23.37 \times), scraping (5.82 \times and 12.82 \times), and excavating (2.98 \times and 2.64 \times) fishes and higher carnivores (8.7 \times and 20.01 \times) (Figure 2, Supporting Information Tables S8, S9 and S12). No-take MPA sites also had significantly lower filamentous algal cover (Figure 2, Supporting Information Tables S9 and S12). Conversely, isolated MPAs only had significantly higher biomass of browsing (79.32 \times) and scraping (89.37 \times) herbivores and higher carnivores (52.72 \times) (Figure 2, Supporting Information Tables S10 and S12). MPA size showed no clear influence on fish biomass, coral cover or algal cover (Figure 2, Supporting Information Tables S11 and S12), and none of the five planning and management attributes significantly affected the cover of branching or tabular coral (Supporting Information Tables S7–12).

Analyses also revealed associations between the environmental covariates and the functional groups. The structural complexity of the reef showed a significant positive association with total coral cover and a negative correlation with algal cover (Supporting Information Tables S7–S11). Wave exposure and the presence of a cyclone (within 10 years and 150 km of a survey) showed a significant negative association with total coral and branching coral cover (Supporting Information Tables S7–S11). In contrast, mean temperature had a significant positive association with massive coral cover and the biomass of scraping herbivores but a negative association with the foliose algal cover (Supporting Information Tables S7–S11). Human population density had a significant negative association with the biomass of browsing and scraping herbivorous fishes, and higher carnivores (Supporting Information Tables S7–S11).

The model comparison showed that importance of the five MPA attributes differed between the functional groups considered (Tables 1 and 2). The no-take sites from 23 MPAs had higher total coral cover and lower filamentous algal cover relative to fished sites (Table 1). Well-enforced and old (>10 years) sites from 13 MPAs had higher cover of massive coral. Well-enforced sites from 13 MPAs also had lower total and foliose algal cover. In contrast, no-take sites

TABLE 1 The top five models that predict coral and algal cover

Model	AIC	BIC	Deviance
Total coral cover			
No-take	-72.1	-30.7	-92.1
Composite	-71.8	-30.3	-91.8
No-take + Old	-71.7	-26.1	-93.7
No-take + Large + Old	-71.4	-22.6	-95.4
No-take + Isolated	-70.8	-25.2	-92.8
Massive coral cover			
Well-enforced + Old	-536	-490.4	-558
Well-enforced	-534.7	-493.3	-554.7
Well-enforced + Isolated + Old	-534.1	-484.4	-558.1
Composite	-533.1	-491.6	-553.1
Well-enforced + Isolated	-532.7	-487.1	-554.7
Total algal cover			
Well-enforced	102.7	144.1	82.7
No-take	111.9	153.3	91.9
Composite	113.5	155	93.5
Filamentous algal cover			
No-take	-310	-268.6	-330
No-take + Isolated	-309.4	-263.8	-331.4
Well-enforced + Isolated	-309.3	-263.7	-331.3
Well-enforced	-309.1	-267.7	-329.1
No-take + Old	-308.8	-263.2	-330.8
Foliose algal cover			
Well-enforced	90.3	131.7	70.3
No-take	95.4	136.8	75.4
Composite	95.4	136.8	75.4

Note. The models are ordered from lowest AIC to highest AIC. The models include the random effect of ecoregion and the fixed effects of six environmental variables listed in methods. The composite model tests the effects of the number of MPA attributes at the highest level (i.e., old; well-enforced; no-take; isolated, large) as a linear predictor. Models that generated negative coefficients for coral or positive coefficients for algal cover were not included. Models for branching and tabular coral were also not included as there were no detectable effects of the five attributes on these functional groups.

from 12 large MPAs had greater scraper, browser and higher carnivore fish biomass (Table 2). The sites with all five attributes from two MPAs had enhanced excavator biomass (Table 2).

The structural equation model (SEM) corroborated that no-take MPA protection resulted in significantly higher biomass of all fish groups and massive coral cover (Figure 3, and Supporting Information Tables S12 and S13). Excavators had a strong negative effect and the browsers a weak negative effect on the total, foliose and filamentous algal cover (Figure 3, Supporting Information Tables S13 and S14). However, scrapers showed no significant negative effect on either the total or filamentous algal cover (Figure 3, Supporting Information Tables S13 and S14). The direct effect of

TABLE 2 The top four models that predict the herbivore and higher carnivore fish biomass

Model	AIC	BIC	Deviance	R ² (%)
Higher carnivores				
No-take + Large	2,174.5	2,219.3	2,152.5	60.4
No-take + Well-enforced + Large	2,175.7	2,224.5	2,151.7	60.4
No-take + Size + Old	2,176.5	2,225.3	2,152.5	60.4
No-take + Well-enforced + Large + Old	2,177.7	2,230.6	2,151.7	60.4
Well-enforced + Isolated + Large	2,181.3	2,230.1	2,157.3	59.9
Browsers				
No-take + Large	2,238.8	2,283.6	2,216.8	55.3
No-take + Well-enforced + Large	2,240.1	2,288.9	2,216.1	55.3
Well-enforced + Large	2,248.3	2,293	2,226.3	54.4
Large	2,262.7	2,303.3	2,242.7	52.7
Large + Old	2,264.7	2,309.4	2,242.7	52.7
Excavators				
Composite	2,142	2,183.5	2,122	58.2
No-take + Old	2,152.4	2,198	2,130.4	57.4
Well-enforced + Old	2,152.5	2,198.1	2,130.5	57.4
No-take + Well-enforced + Old	2,152.8	2,202.5	2,128.8	57.6
No-take	2,153.1	2,194.6	2,133.1	57.2
Scrapers				
No-take + Large	2,258.5	2,303.2	2,236.5	54.8
No-take + Well-enforced + Large	2,259.6	2,308.3	2,235.6	54.9
No-take + Large + Old	2,259.9	2,308.6	2,235.9	54.9
Well-enforced + Old	2,260.3	2,305	2,238.3	54.6
No-take + Well-enforced + Large + Old	2,261	2,313.9	2,235	55

Note. The models are ordered according to lowest AIC. The models include the random effect of ecoregion and the fixed effects of five environmental variables listed in methods. The composite model tests the effects of all the MPA attributes at the highest level (i.e., old; well-enforced; no-take; isolated, large) as a linear predictor. Models that generated negative coefficients for fish biomass were not included.

no-take MPAs on total coral cover had a standardized coefficient of $B_{\text{direct}} = 0.058$ ($SE = 0.040$), while the indirect effect via the herbivorous fish biomass and algal cover was $B_{\text{indirect}} = 0.035$ ($SE = 0.012$). The difference between them was not statistically significant (Difference = 0.023, $p = 0.29$). These results suggest the presence of both direct effects of no-take MPA regulations on the benthos, and indirect effects through the herbivorous fishes.

4 | DISCUSSION

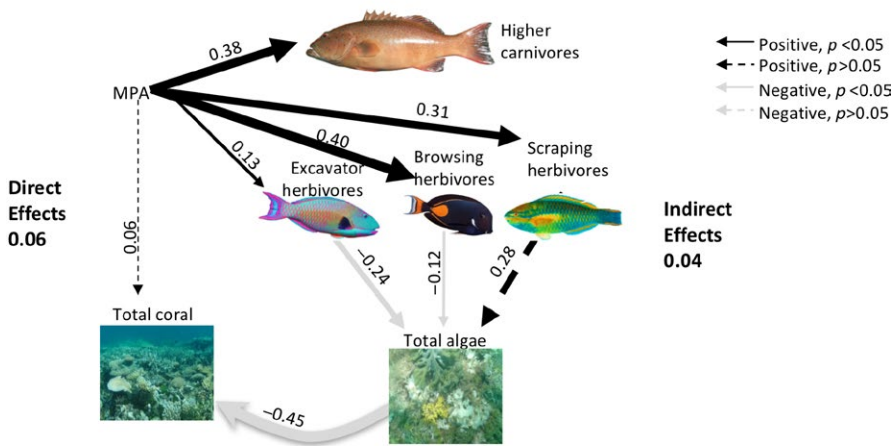
Worldwide, MPAs are one of the most widely used tools in marine conservation. Unsurprisingly, we found MPA protection had greater benefits for enhancing the biomass of carnivorous and herbivorous fishes, which are often targeted by local fisheries, than for the cover of live corals (Coelho & Manfrino, 2007; Cox et al., 2017; McClanahan, Graham, Wilson, Letourneur, & Fisher, 2009). However, our results extend findings from previous global studies

(Cinner et al., 2016; Selig & Bruno, 2010; Soler et al., 2015) and meta-analyses (Babcock et al., 2010; Claudet et al., 2008; Micheli et al., 2004) by demonstrating that specific MPA planning and management attributes are important for protecting different components of coral reefs. In particular, well-enforced, no-take and >10-year-old MPAs sites were associated with slightly higher total (response ratio 1.08–1.19 \times) and massive coral cover (1.34–2.06 \times), while well-enforced, no-take, isolated and >10 years old sites had substantially higher biomass of higher carnivorous (8.7–52.72 \times) and herbivorous fishes (1.54–89.37 \times) relative to other sites inside MPAs and outside but near MPAs (within 10 km).

4.1 | Effects of the MPA attributes on coral reefs

Effects of MPA protection on nontarget taxa on corals reefs may be difficult to detect because of complex food webs and high functional redundancy (Micheli et al., 2004; Selig & Bruno, 2010). However, our study reveals that MPAs sites that were >10 years old, well-enforced

(a) Total coral and algal cover and fish biomass



(b) Coral and algal cover and fish biomass by functional groups

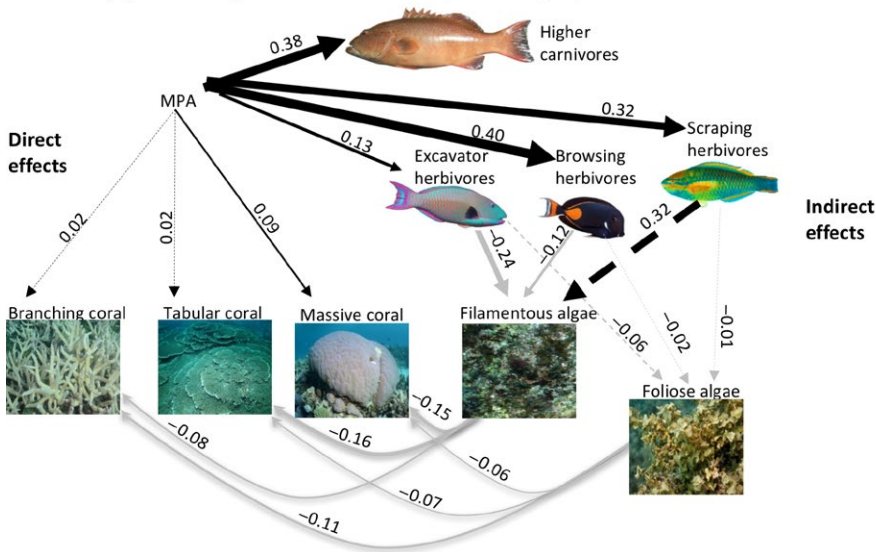


FIGURE 3 Results of structural equation model exploring the direct and indirect effects of no-take MPAs on the (a) higher carnivore and herbivorous fish biomass, and total coral and algal cover and (b) higher carnivore and herbivorous fish biomass, and branching, massive and tabular coral cover and foliose and filamentous algal cover. The boxes represent the variables measured at a site; the arrows show relationships between the variables (black/gray arrows for positive/negative relationships, respectively); and the numbers show standardized coefficients. The thickness of the arrows has been scaled based on the magnitude of the standardized regression coefficient for putative causative relationships. The type of line denotes the significance of a 1-tailed test (solid: $p < 0.05$; dotted: p -value > 0.05). Correlation coefficients and effects of environmental covariates are not shown for ease of interpretation (see Supporting Information Tables S12 and S13 for full results)

and no-take had slightly higher total coral cover ($>1.08\times$) and lower total algal cover ($>0.74\times$). This result is consistent with other broad-scale studies which have demonstrated that old (~ 30 years), highly compliant and unfished MPA sites had marginally higher total coral cover than unprotected sites (Claudet et al., 2008; Selig & Bruno, 2010). Conversely, other studies, particularly at local scales, have found no clear benefits of the same MPA attributes for coral cover (Coelho & Manfrino, 2007; Cox et al., 2017; McClanahan et al., 2009; Wenger et al., 2016). This discrepancy may relate to differences in the level of replication of sites between local and global studies (Carassou, Léopold, Guillemot, Wantiez, & Kulbicki, 2013; Selig & Bruno, 2010), highlighting strong context dependency in mechanisms and key pathways for MPA effects. Alternatively, our results could be driven by bias in site selection because some MPAs may be located in areas where there was initially greater coral cover and/or lower algal cover (Carassou et al., 2013; Selig & Bruno, 2010). To address this potential bias, we only compared MPA sites to reference sites inside and within <10 km outside of the MPA boundary. The strength of this study, therefore, lies in understanding the net

effects of these locally-variable responses to protection, when examined at the scale at which general patterns emerge. Although we found that differences in total coral cover were relatively subtle, the cumulative benefits could be quite substantial in some MPAs.

We demonstrated that >10 years old, no-take and well-enforced MPAs had significantly higher massive coral cover ($1.34\text{--}2.06\times$), and slightly higher (but not significant) branching ($1.13\text{--}1.16\times$) coral cover. Following MPA protection, coral regrowth at degraded sites commences with the colonization of fast-growing branching and tabular species and the regrowth of branching fragments, and continues over longer time-scales, with eventual increases in slower-growing species of massive morphologies (McManus, Rodolfo, Reyes, Cleto, & Nanola, 1997). Massive corals are more resistant to thermal stress than tabular or branching corals (Hughes et al., 2017), so are more likely to remain after extreme events which reduce the cover of other morphologies (Darling, McClanahan, & Côté, 2010). Bleaching events and rising temperatures can result in greater mortality of corals (in particular those of tabular and branching forms) in protected than unprotected sites (Darling et al., 2010; Graham et al., 2008). We

suggest that >10 years old, well-enforced and no-take MPA sites can promote coral cover (of all forms), but the increasing frequency and scale of bleaching events (Baker et al., 2008; Hughes et al., 2017; Stuart-Smith et al., 2018) indiscriminately reduces the cover of non-massive groups (e.g., branching and tabular corals), leaving primarily massive corals as the key difference (Loya et al., 2001; Marshall & Baird, 2000). However, further monitoring of MPAs with particular characteristics before and after bleaching events is required to confirm these findings.

Contrary to our expectations, sites in large (>100 km²) or isolated (surrounded by deep water >25 m or large expanses of sand) MPAs showed no clear differences in coral or algal cover. Even small reserves such as Baie Ternay in the Seychelles (0.863 km²) had higher coral cover than other larger MPAs in the same ecoregion and sites in the surrounding area (outside but within 10 km of the MPA). Our results support the idea that even small reserves can maintain higher total coral cover and lower total algal cover than fished locations (Halpern & Warner, 2002). These results are encouraging for MPA areas that seek to protect specific habitat features and/or species. However, smaller reserves could have several disadvantages, including reduced protected areas for larger and more mobile species, decreased potential for larval exchange (and therefore lower connectivity with surrounding areas), increased MPA-wide impacts from noncompliance, high susceptibility to catastrophic events, and limited habitat niches for rarer species, which all must be considered when a management goal is to safeguard biodiversity (Halpern & Warner, 2002).

In contrast to the benthos, all five attributes contributed significantly to greater biomass of herbivore and higher carnivore fish groups. MPA sites that were >10 years old, no-take and well-enforced, and sites in well-enforced and large MPAs, had more than double the biomass of all fish groups than sites in and around MPAs without these attributes. Similar to related global studies (Campbell et al., 2017; Edgar et al., 2014; Soler et al., 2015), sites isolated from other shallow reef habitats at the MPA boundary possessed the highest fish biomass of browsers, scrapers and higher carnivores (50.72–79.32×), but not excavators (0.57×). These isolated MPA sites could provide a natural refuge from fishing, and their clearly marked boundaries enable more effective policing of fishing regulations (Edgar et al., 2014; McClanahan et al., 2009).

4.2 | Direct vs. indirect MPA effects

Across the 30 reserves examined, no-take MPA sites were directly associated with slightly higher (but not significant) total and massive coral cover. In our dataset, five MPAs were located in regions in which destructive fishing practises such as blast or dynamite fishing are still regularly used, and all thirty MPAs were found in regions that use trawling or net fishing (Campbell et al., 2017). These results suggest that MPA sites which ban all fishing gear could potentially provide increased protection for specific coral functional groups from the chronic physical disturbances linked with a range of fishing gear, and the associated negative effects of shifting rubble and increased sedimentation (Munro et al., 1987).

Similar to other global studies, no-take MPA protection had positive effects on the biomass of all fish groups examined (Cox et al., 2017; Emslie et al., 2015; Stockwell, Jadloc, Abesamis, Alcala, & Russ, 2009). We demonstrated that no-take MPA sites had increased biomass of higher carnivores, browsers, scrapers and excavators relative to restricted or open access sites. There was, however, a greater difference in the biomass of higher carnivores, browsers and scrapers than the excavators. These results could imply that trophic cascades are weak in no-take coral reef MPAs, or that the effects of higher carnivores on herbivorous fishes are limited to specific species, size classes and/or locations (Campbell et al., 2017; Edgar et al., 2014; Soler et al., 2015). Regardless, the combined outcomes presented here suggests the impacts of fishing are often underestimated across trophic food webs, especially in MPAs that allow some form of fishing (Edwards et al., 2014; Pauly & Palomares, 2005).

No-take MPA protection can also enhance the biomass of the dominant herbivorous fish groups that consume filamentous or foliose algae that repress the recruitment, survival and fecundity of corals (Mumby et al., 2006; Selig & Bruno, 2010). Herbivores are usually considered the most important functional group of all fishes on coral reefs with respect to their role in maintaining ecosystem structure (Bellwood et al., 2004; Hughes, Bellwood, et al., 2007). Indeed, we demonstrated that high biomass of excavators and browsers (including parrotfishes, rabbitfishes and surgeonfishes) were associated with significantly lower total and foliose algal cover, and slightly lower filamentous algal cover, while the scrapers had an unexpected positive association with total and foliose algal cover and negative effect on filamentous algal cover. These results could be spurious, driven by the wide variation in fish diet within this group, or a reflection of scraper attraction to specific algal habitats. Further study is required to distinguish between these possibilities.

Overall, we found that no-take MPA sites were associated with substantially higher fish biomass but only slightly higher total and massive coral cover. No differences were detected in the direct (ban on destructive fish gear, standardized coefficient = 0.06) and indirect (via enhancement of fish biomass and reduction of algal cover, standardized coefficient = 0.04) benefits of no-take MPA protection for benthic cover, with both pathways significant. The effects of no-take MPA protection on coral cover were not particularly strong, which could reflect the differences in the initial state of the MPAs and/or differences in the strength and nature of their trophic webs. Ideally, the effects of no-take MPAs could be tested by looking at the processes involved, from both the management perspective (e.g., protection of healthy reef vs. recovery of damaged reefs) or ecology (predation and herbivory rates), and how these translate to changes in benthic cover. Exploration of processes was beyond the scope of this study, however, but represents an important avenue for future research.

The MPAs were also located in a range of ecoregions including the Caribbean Sea, where sea urchins have been reported as the main agent structuring benthos (Coelho & Manfrino, 2007; Huntington et al., 2011; Newman, Paredes, Sala, & Jackson, 2006). Regardless of these important but complicating factors, we found

that MPA sites from a range of ecoregions that ban the use of fishing gears in the Floridian, Maldives, Samoa Islands, Central and Southern Great Barrier Reef, and Torres Strait Northern Great Barrier Reef ecoregions were associated with much higher fish biomass, slightly reduced algal cover and marginally increased coral cover, relative to fished sites within and around but within 10 km of these MPAs.

5 | CONCLUSIONS

Aichi Target 11 of the Convention of Biological Diversity includes a goal of 10% global coverage of MPAs by 2020. Our results add further evidence that well-managed MPAs are important tools for sustaining multiple ecological components of coral reefs. However, these areas need to be well-enforced, no-take, and with long-term (>10 years) protection to be associated with higher coral cover. In our dataset, twelve MPAs met these criteria: Tulamben (Indonesia), Ningaloo, Great Barrier Reef, and Lord Howe Island (Australia), Rose Atoll (American Samoa), Hanauma Bay and Florida Keys (USA), Galapagos (Ecuador), Cocos (Costa Rica), Malpelo (Colombia), Ponta da Baleia-Abrolhos (Brazil) and Mushi Mas Mingili Thila (Maldives). The proportion of tropical MPAs in this study with these three attributes (40%) is likely to be higher than the global proportion with these attributes, as our reef surveys tended to focus more on the well-known, old and well-regarded MPAs, rather than small, obscure and less well-documented MPAs.

Coral reefs are subject to a wide range of anthropogenic pressures that operate on multiple spatial and temporal scales (Ban, Graham, & Connolly, 2014; Halpern et al., 2008). Such pressures include overfishing, declining water quality, eutrophication, sedimentation, and climate-related stressors such as acidification, warming, bleaching events and extreme weather events (Hughes & Connell, 1999). Previous studies have produced mixed conclusions as to whether MPAs can enhance the resilience of corals to stressors (Cinner et al., 2009; Darling et al., 2010; De'ath, Fabricius, Sweatman, & Puotinen, 2012; Diaz-Pulido et al., 2009; Hughes, Bellwood, et al., 2007; Selig & Bruno, 2010). Our global analysis supports the paradigm (Cinner et al., 2016; Kroeker, 2016) that well-managed MPAs with clear limits on fishing practices can not only substantially increase the biomass of functionally-important reef fishes, but can also slightly increase total coral cover and massive coral cover relative to nearby fished sites. Further research is required, however, to better understand whether well-managed MPAs can enhance the resilience of coral communities to other anthropogenic stressors through indirect mechanisms associated with ecological interactions.

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DATA ACCESSIBILITY

All data used in this study are freely available online, and are accessible through the Reef Life Survey website (<https://reeflifesurvey.com>).

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BIOSKETCH

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Author contribution: E.S., R.T. and G.E. conceived and designed the study. All authors contributed to synthesizing published data, analyses, interpreting the results and writing and revising the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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