

Reef-wide beneficial shifts in fish population structure following establishment of marine protected areas in Philippine coral reefs

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ABSTRACT: Marine protected areas (MPAs) have become critical components of fisheries management programs worldwide. Despite their widespread usage, the performance of MPAs in sustaining fisheries remains debated, partially due to inconsistent results across studies. Here, we aim to standardize conclusions regarding MPA performance throughout the Philippines using a 'reef-wide' meta-analysis. This analysis uses pooled visual census data from 39 matched pairs of MPAs and fished reefs surveyed twice over a mean period of 3 yr, allowing for the comparison of abundance and demographic structure of fishes across both protected and fished areas over time. The meta-analysis revealed that (1) although fish density was higher inside MPAs within individual sampling periods, reef-wide fish density generally either increased or remained stable over time, and (2) reef-wide increases in large-bodied fish were evident between survey periods, indicating positive demographic shifts within both MPAs and adjacent areas. These results suggest that, over relatively few years of protection, MPAs in the Philippines are able to promote beneficial shifts in fish population structure throughout entire reef systems rather than simply maintaining stable populations within their borders. Demonstrating such benefits to adjacent reefs is critically important to the success of MPAs in the Philippines because compliance with closures of fishing grounds increases with realized benefits to fishing communities. The reef-wide framework of MPA assessment demonstrated in this study presents the advantages of including adjacent fisheries as integrated components when quantifying MPA performance, revealing trends that are indistinguishable when using spatial comparisons between MPAs and fished reefs.

KEY WORDS: MPA · Marine reserve · Spillover · Fisheries management · Coral-reef fish · Meta-analysis

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INTRODUCTION

Overfishing and destructive fishing practices represent 2 of the most critical challenges facing global food security and marine conservation efforts. Exploitative human fishing practices have increased the percentage of overfished stocks worldwide from 10% in 1974 to 29% in 2011 (FAO 2014), significantly reducing biodiversity throughout marine food-webs (Pauly et al. 1998, 2002) and threatening the continued integrity of marine ecosystems (Dayton et al.

1995, Botsford et al. 1997, Lauck et al. 1998, Pauly et al. 1998, Hodgson 1999, Worm et al. 2006). Marine reserves or marine protected areas (MPAs) have become one of the most widely utilized tools for managing declining marine fisheries, with >9000 MPAs established globally, covering 2.65% of the total ocean surface, and with 6% of MPAs (0.2% of ocean surface) being fully 'no-take' areas (Costello & Ballantine 2015). The rapid proliferation of MPAs has been driven by the failures of traditional stock-management strategies (i.e. size and catch limits) as

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well as a lack of viable alternative management options, especially in developing nations where artisanal fisheries are the norm and demand for fishery yields is extraordinarily high (Russ 2002). The efficacy of MPAs in achieving their fisheries-management and biodiversity goals, however, remains contentious (Sale et al. 2005, Halpern et al. 2009).

Attempts to quantify the ability of MPAs to promote sustainable fisheries have most often focused on comparisons of metrics such as reef-fish abundance, biomass, and species richness between MPAs and adjacent, fished reefs in order to quantify MPA 'success' (Russ 2002). Studies analyzing individual or groups of MPAs using these metrics have often found beneficial shifts in fish biomass (Polunin & Roberts 1993, Johnson et al. 1999, Mosqueira et al. 2000, Paddock & Estes 2000, Roberts et al. 2001, Christie 2004, Maliao et al. 2009), fish density and overall species richness (Lester et al. 2009), and size-frequency distributions (Fidler et al. 2014) within MPAs compared to adjacent, fished reefs following MPA establishment. The reported magnitude of response of reef-fishes to protection, however, is often highly variable and dependent on a multitude of factors, including the taxonomic group under consideration (Jennings 2000, Micheli et al. 2004, Babcock et al. 2010) and the characteristics of the MPAs being studied, most notably age, size, and enforcement capability (Russ et al. 2005, Claudet et al. 2008, Maliao et al. 2009, Fidler et al. 2014). Consequently, results from studies on a single MPA are often difficult, if not impossible, to extrapolate to neighboring areas.

Paradoxically, 2 of the most critical processes by which MPAs have been hypothesized to promote sustainable fisheries—spillover and recruitment subsidy—may be partially responsible for the lack of consistency across results of MPA assessments. Spillover occurs when individuals from within an MPA emigrate into adjacent areas open to fishing, while recruitment subsidy is the process by which larvae produced by large and fecund populations within MPAs are exported to neighboring reefs (Boersma & Parrish 1999, Russ et al. 2004, Gaines et al. 2010). Numerous studies have detected these processes occurring in reefs surrounding MPAs (Russ & Alcala 1996, McClanahan & Mangi 2000, Russ et al. 2003, 2004, Abesamis & Russ 2005, Alcala et al. 2005, Abesamis et al. 2006), albeit often on spatial scales ranging only in the 100s of meters (Harmelin-Vivien et al. 2008, Halpern et al. 2009). The potential of MPAs to promote increased abundance of fishery populations outside of their borders complicates the assessment of MPAs using adjacent reefs as contrast-

ing experimental units because these areas are inherently altered by the establishment of nearby MPAs (Caselle et al. 2015). As a result, spatial comparisons may mask shifts in populations within MPAs and adjacent fisheries if changes occur simultaneously in both areas. In addition, similar to the impact of MPAs on populations within their borders, the rate and magnitude of spillover from MPAs to adjacent fished areas also appear to be dependent on taxonomic groups and MPA characteristics (Caselle et al. 2015), which is likely a contributing factor in the highly variable and site-specific quantitative impacts of MPAs across studies using spatial comparisons as metrics of performance.

A second critical, but less understood, phenomenon that can complicate assessments of MPA performance involves the evolutionary repercussions of overfishing. Declines in the sizes and stability of worldwide fisheries have been accelerated by shifts in life-history traits within exploited populations (Hsieh et al. 2010), driven by the overwhelming tendency of fishing effort to selectively remove the largest individuals from any given population (Myers & Hoenig 1997, Birkeland & Dayton 2005, Fukuwaka & Morita 2008). Sustained and extensive size-selective harvesting has been shown to induce an intense directional-selection pressure favoring individuals with smaller terminal body-sizes within exploited populations (Law 2000, 2007, Heino & Godø 2002, Hawkins & Roberts 2004, Kuparinen & Merilä 2007, Swain et al. 2007, Heino & Dieckmann 2009, Swain 2011). The strength of artificial selection in exploited fisheries is often extreme, having demonstrated the capacity to promote significant shifts in body-size frequency distributions within contemporary time-scales (Conner 2003, de Roos et al. 2006). A higher prevalence of small-bodied individuals within a fishery experiencing intense harvest pressure can have serious consequences for population viability, as decreased adult body-size in mature females has been demonstrated to cause reduced larval size-at-hatch, growth rate, viability, feeding rate, and even vertebral number in offspring (Haugen & Vøllestad 2001, Walsh et al. 2006). Shifts in the demographic composition of harvested populations, therefore, can significantly accelerate the decline of fisheries stocks, necessitating the inclusion of changes in population structure in analyses of MPA efficacy.

The majority of studies on the impact of MPAs in the Philippines have been conducted on a single locale or a limited number of MPAs, with only a few investigations involving region-wide assessments of MPA performance (Maliao et al. 2009). Additionally,

previous studies often utilized conventional techniques involving pairwise comparisons of fish density between MPAs and adjacent, fished reefs. This investigation aims to advance our understanding of the propensity of MPAs to promote beneficial shifts in fish density and population demographic structure across both protected and exploited populations over time. To accomplish this, we conduct a meta-analysis of 39 paired MPAs and adjacent, fished reefs in the Philippines using a 'reef-wide' approach. This reef-wide framework alleviates concerns regarding spatial analyses as described above by comparing pooled data from MPAs and adjacent, fished reefs between replicate surveys of overall and body-size-specific fish density. Meta-analyses have proven to be effective statistical tools for synthesizing results across disparate studies, as they are able to standardize the magnitude of impact of multiple MPA studies despite differences in statistical variance and metrics of performance (Mosqueira et al. 2000, Halpern 2003, Claudet et al. 2008).

By examining the magnitude of temporal changes in abundance and demographic structure of coral-reef fish populations across both protected and fished reefs resulting from the establishment of MPAs, this meta-analysis framework allows for the detection of shifts in the density and structure of interconnected populations that would be indistinguishable when using spatial comparisons alone. Such analyses are especially important in the Philippines because the country is considered the global epicenter of marine biodiversity (Carpenter & Springer 2005) and has established a country-wide system of MPAs as its primary conservation and fisheries management tool (Alcala & Russ 2006, Christie & White 2007). Studies that assess how well these MPAs achieve their biodiversity and fisheries management objectives not only within protected areas, but throughout the entirety of coastal marine ecosystems, will be critical to the long-term sustainability of coastal resources in the country.

MATERIALS AND METHODS

Visual census data

To determine the effect of MPAs on fish density, results of visual surveys of 18 fish families (Table 1)

Table 1. Fish families included in fish-visual censuses and the trophic and harvest category of each fish family

Family	Trophic group	Harvest category
Acanthuridae (surgeonfish)	Herbivores	Target
Anthiinae (fairy basslet)	Planktivores	Non-target
Balistidae (triggerfish)	Zoobenthivores	Non-target
Caesionidae (fusilier)	Planktivores	Target
Carangidae (jack)	Piscivores	Target
Chaetodontidae (butterflyfish)	Zoobenthivores	Non-target
Haemulidae (sweetlips)	Zoobenthivores	Target
Labridae (wrass)	Zoobenthivores	Non-target
Lethrinidae (emperor)	Zoobenthivores	Target
Lutjanidae (snapper)	Piscivores	Target
Mullidae (goatfish)	Zoobenthivores	Target
Nemipteridae (coral bream)	Zoobenthivores	Target
Pomacanthidae (angelfish)	Omnivores	Non-target
Pomacentridae (damselfish)	Omnivores	Non-target
Scaridae (parrotfish)	Herbivores	Target
Serranidae (grouper)	Piscivores	Target
Siganidae (rabbitfish)	Herbivores	Target
Zanclidae (moorish idol)	Omnivores	Non-target

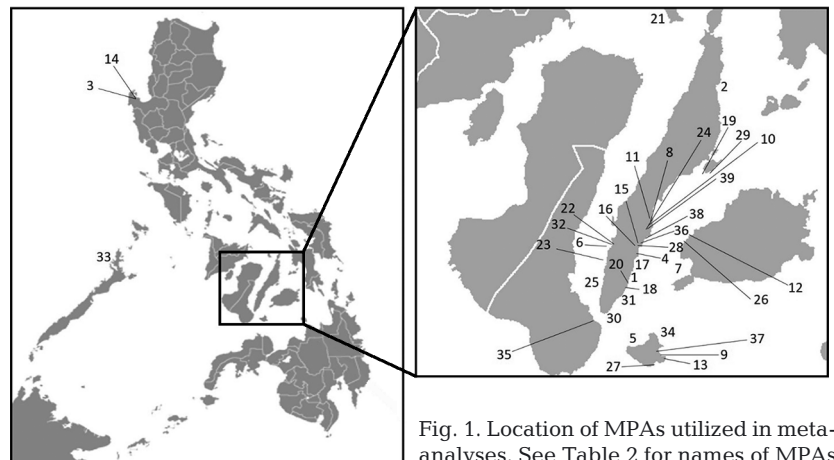


Fig. 1. Location of MPAs utilized in meta-analyses. See Table 2 for names of MPAs

across 39 pairs of no-take MPAs and fished reefs in the Philippines, primarily from the Visayas region, performed between 1997 and 2009 (Fig. 1, Table 2) were subjected to a categorical meta-analysis. MPAs ranged in size from 5 to 123 ha (mean: 25.0 ± 15.4 ha) and were considered 'well-enforced' at the time of surveys by the Coastal Conservation and Education Foundation (CCEF). Individual surveys were conducted primarily by CCEF, with additional data being derived from studies presented by Miclat et al. (2005). Surveys consisted of 3 to 8 replicate transects both inside and outside of each MPA, with surveys in fished reefs taking place 200 to 1000 m outside MPA borders in similar habitat. In order to assess the body-size frequency distributions of fishes within MPAs and fished reefs, the results of size-specific fish-

Table 2. List of MPAs included in meta-analyses concerning fish density and size-frequency distributions between MPAs and fished reefs across the Philippines, including the location, size, and data of establishment of each protected area. 'First survey' and 'second survey' indicate the years in which replicate surveys were conducted, with the first date being surveys utilizing overall density (D) and the second date being surveys utilizing size-specific densities (SF) where both types of data were available. Single years indicate only overall density data was present. 'Map #' refers to the location of each MPA as shown on Fig. 1

Marine reserve	Province	Size (ha)	Year established	First survey (D/SF)	Second survey (D/SF)	Map #
Arbor Marine Sanctuary	Cebu	8.99	2001	2002/2005	2008/2008	1
Bagacay Fish Sanctuary	Cebu	23.61	2002	2005/2005	2008/2008	2
Balingasay MP Replacement Area	Pangasinan	14.77	1999	2001	2003	3
Balud-Consolacion Marine Park and Sanctuary	Cebu	12.6	2002	2003/2003	2007/2008	4
Banban-Luyang Marine Sanctuary	Siquijor	10	2006	2007	2008	5
Bato Seagrass and Fish Sanctuary	Cebu	25	2003	2005/2005	2007/2007	6
Bil-isan Fish Sanctuary	Bohol	7.76	1998	2003	2007	7
Binlod Marine Sanctuary	Cebu	12	2003	2005	2008	8
Bogo Marine Sanctuary	Siquijor	10	2003	2007	2009	9
Bogo Marine Sanctuary	Cebu	12	2002	2005	2008	10
Bulasa Marine Sanctuary	Cebu	12	2003	2006	2008	11
Cabacongan Fish Sanctuary	Bohol	11.8	1997	1997	2003	12
Candaping B Marine Sanctuary	Siquijor	20.42	2003	2005	2008	13
Carot Marine Sanctuary	Pangasinan	13.3	1998	2000	2003	14
Casay Marine Park and Sanctuary	Cebu	5	2002	2002/2003	2008/2008	15
Cawayan Marine Sanctuary	Cebu	12.61	2006	2007/2007	2008/2009	16
Daan-Lungsod and Guiwang Marine Sanctuary	Cebu	22.71	2002	2002	2008	17
Gawi Marine Sanctuary	Cebu	12.54	2003	2005/2005	2008/2009	18
Gilutongan Island Marine Sanctuary	Cebu	14.89	1999	2001	2003	19
Granada Fish Sanctuary	Cebu	9.35	2002	2002/2004	2008/2008	20
Guiwanon Marine Sanctuary	Cebu	12	2003	2005	2009	21
Hinablan Marine Sanctuary	Cebu	12	2003	2005/2005	2007/2007	22
Lambog Seagrass and Fish Sanctuary	Cebu	25	2003	2005/2005	2007/2007	23
Langtad Marine Sanctuary	Cebu	12	2002	2005/2005	2008/2008	24
Legaspi Marine Sanctuary	Cebu	10.35	2002	2006	2007	25
Lomboy-Kahayag Fish Sanctuary	Bohol	8.6	1995	1997	2003	26
Lower Cabancalan Marine Sanctuary	Siquijor	8.23	2003	2005	2008	27
Matutinao Marine Sanctuary	Cebu	15	2003	2006/2006	2007/2007	28
Nalusuan Marine Sanctuary	Cebu	83	2002	2006	2007	29
Pasil Marine Sanctuary	Cebu	10.45	2002	2003/2003	2008/2008	30
Poblacion Marine Sanctuary	Cebu	6.38	2002	2007	2008	31
Poblacion-Argaon Marine Sanctuary	Cebu	12	2003	2005/2005	2008/2008	32
Port Barton Marine Park	Palawan	123	1998	1999	2003	33
Sandugan Marine Sanctuary	Siquijor	13.38	2003	2005	2008	34
Sibulan Marine Reserve	Negros	6	1997	1998	2003	35
Talaga Marine Sanctuary	Cebu	12	2002	2005/2005	2008/2008	36
Talayong Marine Sanctuary	Siquijor	6.68	2003	2005	2008	37
Talo-ot Marine Sanctuary	Cebu	12	2002	2005/2005	2008/2008	38
Tulic Marine Sanctuary	Cebu	12	2002	2005/2005	2008/2008	39

visual surveys conducted by CCEF from 2003 to 2009 across a subset of 17 MPAs (Fig. 1, Table 2) were analyzed. These surveys were conducted as a function of size, with each fish observed being placed into 1 of 4 body-size classes (1–10 cm; 11–20 cm; 21–30 cm; >30 cm). All divers conducting body-size-specific surveys were trained by CCEF using consistent methods and were tested against controls to ensure reliability between surveys.

At each site, surveys of fish density, size-frequency distributions, or both measurements were conducted at 2 periods after MPA establishment. To determine

the impact of MPAs on fish density and size-frequency over time, 3 analyses were conducted. Comparisons were made between (1) the disparity in overall or body-size specific density of fishes between MPAs and adjacent reefs from visual censuses conducted closest to MPA establishment (hereafter referred to as 'first'); (2) the disparity in overall or body-size specific density of fishes between MPAs and adjacent reefs from the second censuses (hereafter referred to as 'second'); and (3) the disparity in average total or body-size specific density of fishes recorded simultaneously inside and outside of MPAs

between the first and second surveys for each MPA (hereafter referred to as 'reef-wide analysis').

For census data in which surveys used overall density as a metric, the age of MPAs at the time of the first surveys ranged from >1 to 5 yr (mean \pm SD = 2.1 \pm 1.3 yr), the age of MPAs at the time of second surveys ranged from 2 to 9 yr (mean = 5.3 \pm 1.3), and the gap between replicate surveys ranged from 1 to 6 yr (mean = 3.2 \pm 1.6 yr). For census data in which body-size specific densities were recorded, the age of MPAs at the time of first surveys ranged from 1 to 4 yr (mean = 2.2 \pm 0.9 yr), the age of MPAs at the time of second surveys ranged from 3 to 7 yr (mean = 5.4 \pm 1.1 yr), and the gap between replicate surveys ranged from 1 to 5 yr (mean = 3.1 \pm 1.2 yr).

Meta-analysis

The protocol for meta-analysis was modified from that of Maliao et al. (2009). For spatial comparisons, surveys within MPAs and in adjacent, fished reefs were considered 'experimental' and 'control' groups, respectively. In reef-wide analyses (i.e. temporal changes in populations across MPAs and adjacent reefs), fish density was averaged across surveys conducted inside and outside of an MPA in a given year. The average fish density recorded in the first survey was considered the control variable, while average fish density from the second survey was considered the experimental variable. Each pair of MPA/fished-reef and first/second comparisons was treated as an independent study. Analyses utilized fish density (per 500 m²) of 18 reef-resident families (Table 1) either overall or based on body-size class (1–10 cm; 11–20 cm; 21–30 cm; >30 cm). Fish were classified in 2 levels. First, fish families were separated into trophic guilds (Froese & Pauly 2016) consisting of herbivores, omnivores, piscivores, planktivores, and zoobenthivores. Second, fish families were classified in terms of fishing pressure, as either 'target' (directly targeted by fishermen) or 'non-target' (not directly targeted by fishermen).

The magnitude of the effect of MPAs on fish density was measured via 'effect size', calculated as the natural logarithm of the response ratio (lnRR; Hedges & Olkin 1985). This calculation results in non-real numbers when 'zero' values are included in analyses; therefore, fish density values that were reported as zero were treated in 1 of 2 ways. First, in both overall density and body-size specific analyses, all values of a given fish family were removed from replicate surveys if that family was present in one survey but

reported as absent from the other. For size-specific analysis, removal only occurred if zero values were reported for all 4 body-size classes within a survey. This process removed 'extinction' (i.e. present in the first survey but not in the second survey) and 'colonization' (present in the second survey but not in the first) events, which produced extreme lnRR values despite often relatively small changes in absolute density. Alternatively, in body-size specific analyses where density values were present within one body-size class but not another, 0.01 was added to all values in order to calculate lnRR (Molloy et al. 2007), as zero values for individual body-size classes did not represent 'extinction' or 'colonization' events. To retain consistency across calculations, 0.01 was added to all values within size-specific analyses regardless of whether zero values were present within any given survey. The lnRR for each group was then calculated as follows:

$$\ln RR = \ln \left(\frac{X^E}{X^C} \right) \quad (1)$$

where X^E and X^C are the experimental and control fish densities, respectively. The mean response ratio (\overline{RR}) of each fish classification (i.e. trophic or harvest category) was calculated based on the individual lnRR values of that fish group across sites. lnRR values were weighted more heavily when studies had lower variance as a function of larger sample size (Rosenberg et al. 2000). Weight (w_i) for each study was defined as the inverse of the variance (v_i) of the mean density of each fish group ($w_i = 1/v_i$). Because variance values are often not reported, v_i was approximated based on sample size (Hedges & Olkin 1985):

$$v_i = \left[\frac{N_i^e + N_i^c}{N_i^e N_i^c} \right] + \left[\frac{(\ln RR_i)^2}{2(N_i^e + N_i^c)} \right] \quad (2)$$

where N_i^e and N_i^c are the sample sizes for the experimental and control variables, respectively. Here, sample size represents the number of replicate transects conducted in a census within a given year, within either an MPA or adjacent reef, or the average number of transects conducted across an MPA and adjacent reef at a given time period for reef-wide analyses. The weighted \overline{RR} of each fish group was then calculated as:

$$\overline{RR} = \frac{\sum_{i=1}^n w_i \ln RR_i}{\sum_{i=1}^n w_i} \quad (3)$$

where n is the number of studies. Confidence interval (CI) values of each \overline{RR} were based on 95% confidence limits around the mean calculated by bootstrapping after 999 iterations. Response ratio values

were considered significantly different from 0 when their respective CIs did not overlap with 1. The heterogeneity of responses among fish groups across sites was determined using the total heterogeneity statistic (Q_T) (Hedges & Olkin 1985):

$$Q_T = \sum_{i=1}^n w_i (\ln RR_i - \overline{RR})^2 \quad (4)$$

All statistical analyses were conducted using Meta-Win 2.0 software (Rosenberg et al. 2000), and conducted using a fixed- rather than random-effects model to remain consistent with previous studies on Philippine MPAs (Maliao et al. 2009).

RESULTS

Overall density

The total density of fishes in MPAs was consistently higher than in adjacent reefs, being 27 and 47% greater in MPAs compared to adjacent fished reefs in the first (F) and second (S) surveys, respectively (F: $\overline{RR} = 1.27$, CI = 1.04–1.60; S: $\overline{RR} = 1.47$, CI = 1.18–1.81; Fig. 2a,b). Increases in fish density over time were not limited to populations inside MPAs, however, as the reef-wide (RW) analysis demonstrated a 16% greater total density across both MPAs and fished reefs between the 2 survey periods ($\overline{RR} = 1.16$, CI = 1.02–1.32; Fig. 2c). Target fishes exhibited a markedly different pattern, with no significant disparity in density in either the first surveys ($\overline{RR} = 1.13$, CI = 0.93–1.40) or reef-wide analysis ($\overline{RR} = 0.98$, CI = 0.82–1.21), but 43% higher density within MPAs compared to fished reefs in the second surveys ($\overline{RR} = 1.43$, CI = 1.09–1.90; Fig. 2a–c). Non-target fishes

demonstrated a similar pattern to that of total fish density, with significantly higher densities within MPAs in both spatial surveys, but no significant increase in density in the temporal reef-wide analysis (F: $\overline{RR} = 1.29$, CI = 1.02–1.60; S: $\overline{RR} = 1.51$, CI = 1.19–2.01; RW: $\overline{RR} = 1.17$, CI = 0.96–1.39; Fig. 2a–c).

Within trophic guilds, the relative densities of fish between MPAs and fished reefs tended to remain static over time, with significantly higher densities of fish inside MPAs compared to adjacent reefs in both spatial analyses, and no temporal differences in abundance in reef-wide analysis between replicate surveys for herbivores (F: $\overline{RR} = 1.47$, CI = 1.18–1.92; S: $\overline{RR} = 1.68$, CI = 1.20–2.29; RW: $\overline{RR} = 0.96$, CI = 0.76–1.19), omnivores (F: $\overline{RR} = 1.34$, CI = 1.05–1.70; S: $\overline{RR} = 1.44$, CI = 1.15–1.83; RW: $\overline{RR} = 1.19$, CI = 0.99–1.45), and piscivores (F: $\overline{RR} = 1.49$, CI = 1.01–2.22; S: $\overline{RR} = 2.44$, CI = 1.67–3.60; RW: $\overline{RR} = 1.01$, CI = 0.60–1.60; Fig. 2a–c). Planktivores demonstrated a similar pattern, with the exception that no spatial disparity in density was observed in the first surveys (F: $\overline{RR} = 0.95$, CI = 0.65–1.45; S: $\overline{RR} = 1.55$, CI = 1.06–2.33; RW: $\overline{RR} = 1.31$, CI = 0.93–1.72). Zoobenthivores appeared to be either unaffected or negatively impacted by MPA establishment, with reef-wide analysis revealing an overall reduction in density (F: $\overline{RR} = 1.25$, CI = 1.02–1.55; S: $\overline{RR} = 1.24$, CI = 0.93–1.66; RW: $\overline{RR} = 0.80$, CI = 0.63–0.98). Summary statistics for total fish density are provided in Table 3.

Size-specific densities

Across the 17 MPAs surveyed using census techniques that classified fish by body-size, the population structure of total and target fish groups followed

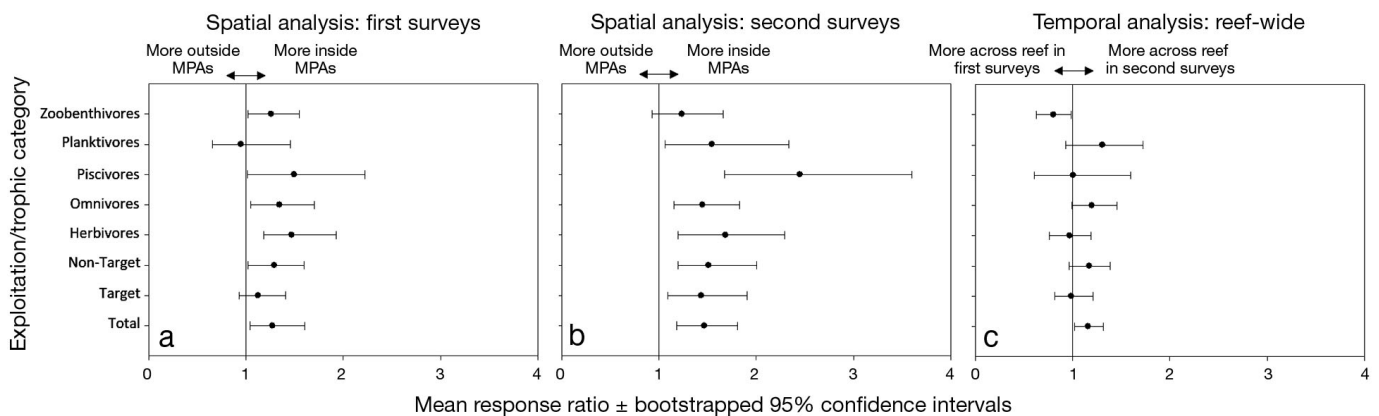


Fig. 2. Mean response ratio (\overline{RR}) of fish groups illustrating how fish density varies between MPAs and fished reefs in the (a) first surveys and (b) second surveys, as well as (c) in the reef-wide analysis (changes in both MPAs and fished reefs over time between replicate surveys)

Table 3. Summary statistics of meta-analysis for total fish density. The Q_T statistic measures the difference in $\ln RR$ of each fish group between sites, with the null hypothesis being that the $\ln RR$ of each group among sites are equal. The p values indicate the significance of Q_T under the chi-squared distribution. A significant Q_T indicates that the variance among $\ln RR$ values between sites is higher than expected by sampling error. Significant values in **bold**

Biotic group	First surveys			Second surveys			Reef-wide analysis		
	Q_T	df	p	Q_T	df	p	Q_T	df	p
Total	32.90	38	0.704	38.96	38	0.427	10.86	38	1.000
Target	32.02	38	0.742	55.75	38	0.032	29.67	38	0.831
Non-Target	41.88	38	0.306	42.77	38	0.274	23.04	38	0.973
Herbivores	40.13	38	0.376	59.56	36	0.008	35.51	34	0.397
Omnivores	38.94	38	0.427	40.86	38	0.346	24.86	38	0.950
Piscivores	68.64	28	<0.001	45.43	25	0.007	43.06	18	<0.001
Planktivores	77.90	29	<0.001	69.90	30	<0.001	29.28	22	0.137
Zoobenthivores	34.91	38	0.613	57.38	38	0.023	30.23	38	0.811

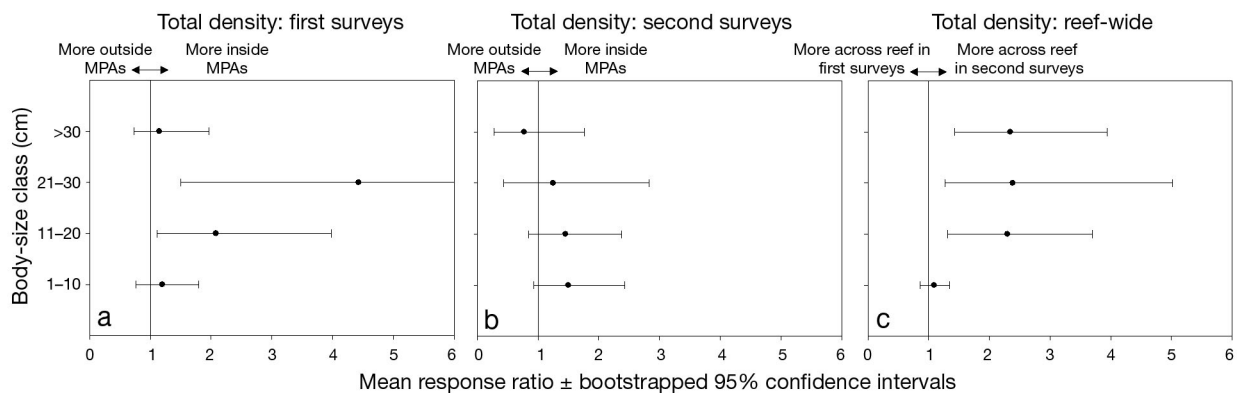


Fig. 3. Mean response ratio (\overline{RR}) of all fish families illustrating how body-size specific fish density varies between MPAs and fished reefs in the (a) first surveys and (b) second surveys, as well as (c) in the reef-wide analysis (changes in both MPAs and fished reefs over time between replicate surveys)

similar patterns. For both groups, fish densities were higher within MPAs at the 11–20 cm and 21–30 cm size classes compared to adjacent reefs in the first surveys ([Total: 11–20 cm: $\overline{RR} = 2.08$, CI = 1.11–3.98; 21–30 cm: $\overline{RR} = 4.43$, CI = 1.50–19.03; Fig. 3a]; [Target: 11–20 cm: $\overline{RR} = 4.88$, CI = 1.50–21.41; 21–30 cm: $\overline{RR} = 2.01$, CI = 1.01–4.07; Fig. 4a]). No significant disparities in density for either group were observed in any size class in the second surveys (Figs. 3b & 4b). In the reef-wide analysis, however, significant increases in density were evident for total fish density within the largest 3 size-classes, and for target families in the largest 2 size-classes across both MPAs and fished reefs over time ([Total: 11–20 cm: $\overline{RR} = 2.30$, CI = 1.31–3.70; 21–30 cm: $\overline{RR} = 2.38$, CI = 1.27–5.02; >30 cm: $\overline{RR} = 2.35$, CI = 1.43–3.94; Fig. 3c]; [Target: 21–30 cm: $\overline{RR} = 2.38$, CI = 1.17–5.10; >30 cm: $\overline{RR} = 2.73$, CI = 1.63–4.91; Fig. 4c]). For non-target fish families, the 11–20 cm range was the only size-class to demonstrate significantly higher density inside MPAs, occurring in the first surveys ($\overline{RR} = 2.27$,

CI = 1.53–3.91) and reef-wide analysis ($\overline{RR} = 2.88$, CI = 1.20–8.40), while fish density in the largest size class (>30 cm) was significantly greater in fished reefs compared to MPAs in the second surveys ($\overline{RR} = 0.66$, CI = 0.42–0.89; Fig. 5).

Among trophic categories, there was substantial variation in responses to protection across body-size classes (Figs. 6–10). General trends included a lack of significant disparities in size-specific density between MPAs and fished reefs in either spatial survey. Notable exceptions include omnivores, which demonstrated significantly higher densities inside MPAs in the first surveys within the 11–20 cm size-class ($\overline{RR} = 1.68$, CI = 1.16–2.80; Fig. 7a) and significantly lower densities inside MPAs compared to adjacent reefs in second surveys within the largest size-class (>30 cm: $\overline{RR} = 0.72$, CI = 0.46–0.93; Fig. 7b). Higher fish densities were also observed within MPAs at the first survey period within specific body-size groups herbivores (11–20 cm: $\overline{RR} = 2.88$, CI = 1.36–6.09; Fig. 6a), for planktivores (21–30 cm: $\overline{RR} =$

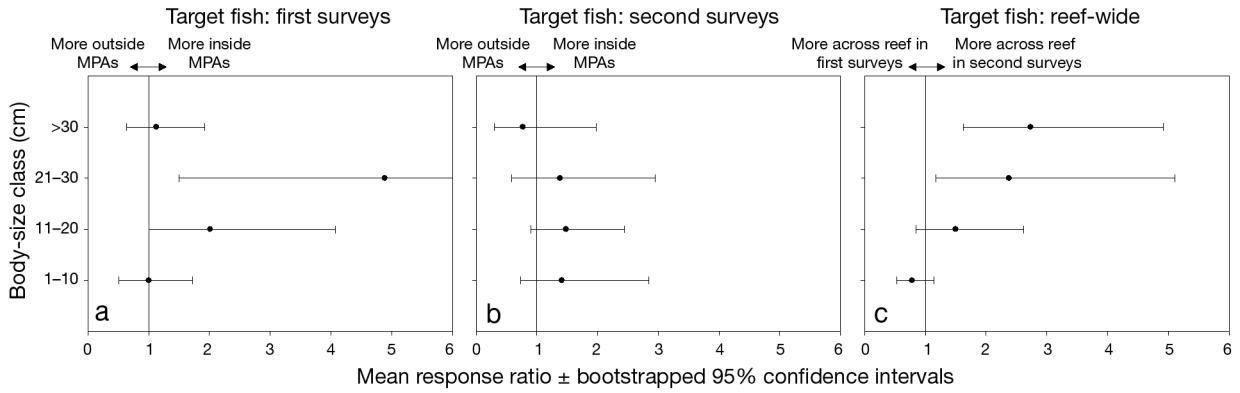


Fig. 4. As in Fig. 3 but for target fish families

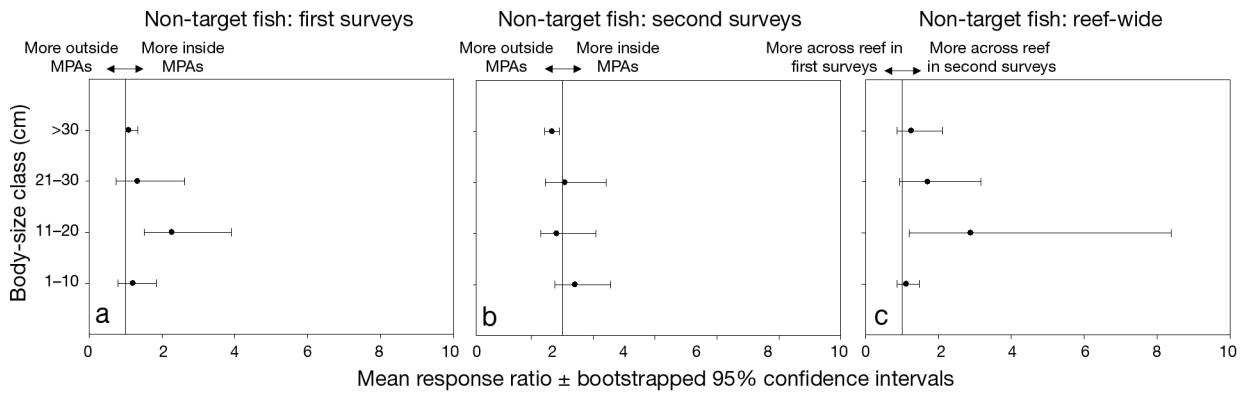


Fig. 5. As in Fig. 3 but for non-target fish families

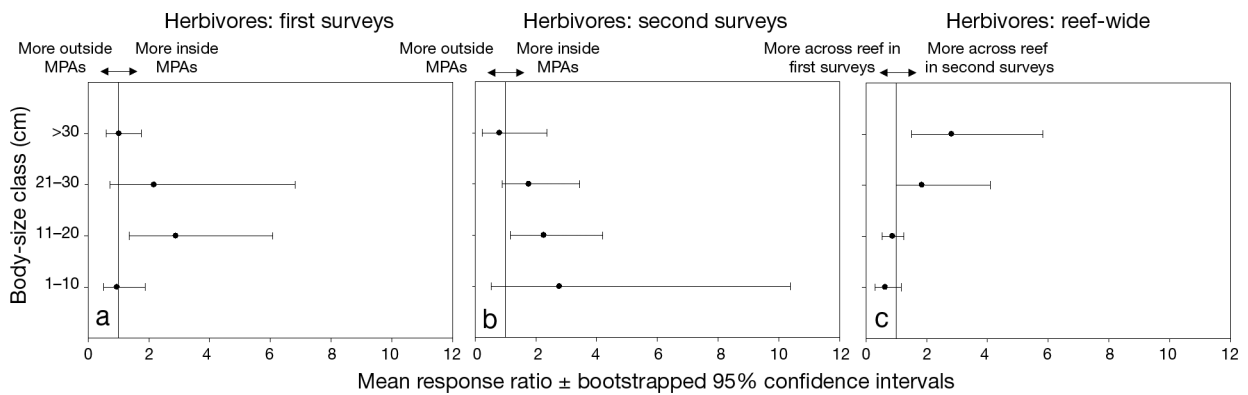


Fig. 6. As in Fig. 3 but for herbivorous fish families

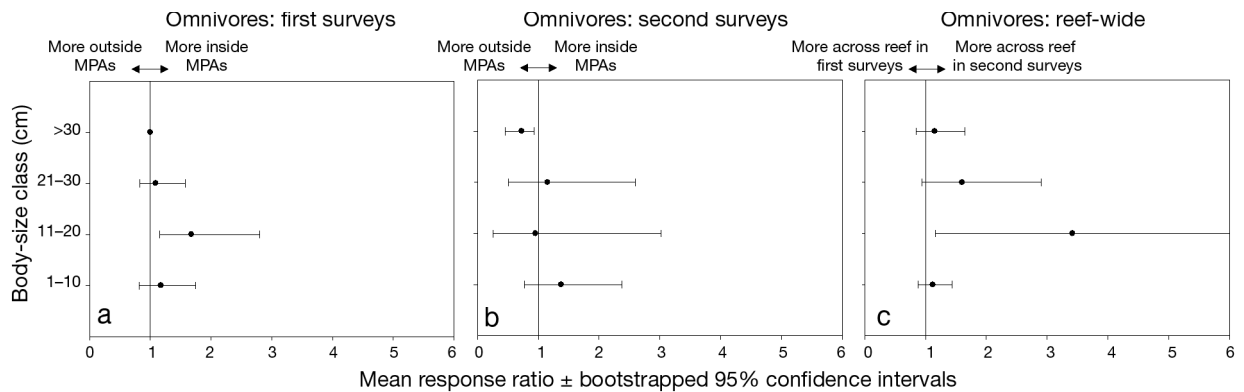


Fig. 7. As in Fig. 3 but for omnivorous fish families

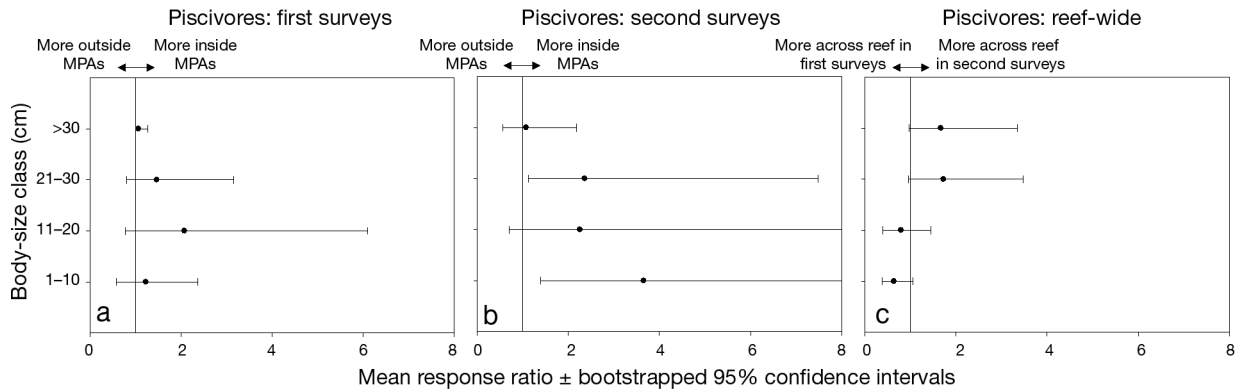


Fig. 8. As in Fig. 3 but for piscivorous fish families

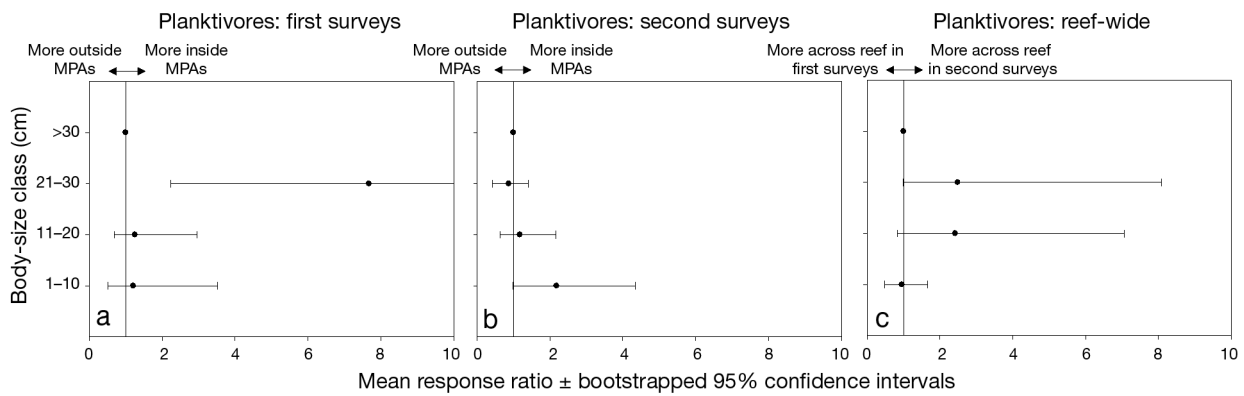


Fig. 9. As in Fig. 3 but for planktivorous fish families

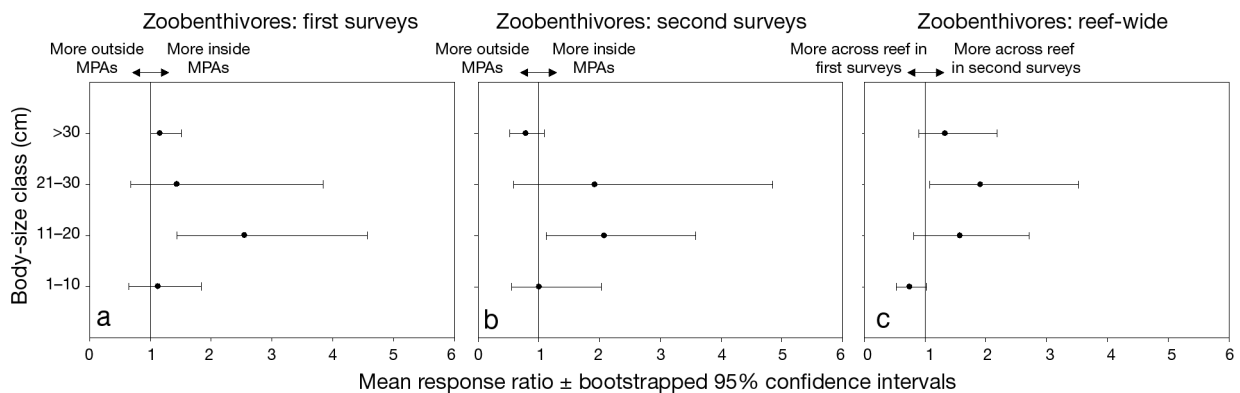


Fig. 10. As in Fig. 3 but for zoobenthic-feeding fish families

7.70, CI = 2.23–68.37; Fig. 9a), and zoobenthivores (11–20 cm: \overline{RR} = 2.55, CI = 1.43–4.56; Fig. 10a), and in the second surveys for herbivores (11–20 cm: \overline{RR} = 2.26, CI = 1.17–4.20; Fig. 6b), piscivores (1–10 cm: \overline{RR} = 3.66, CI = 1.39–10.10; 21–30 cm: \overline{RR} = 2.36, CI = 1.13–7.48; Fig. 8b), and zoobenthivores (11–20 cm: \overline{RR} = 2.08, CI = 1.12–3.58; Fig. 10b).

In reef-wide analyses, increases in density both within MPAs and in adjacent fished reefs were observed in at least one of the largest 3 body-size

classes in herbivores, omnivores, and zoobenthivores, while no increases occurred over time in either piscivores or planktivores (Figs. 6c–10c). Increases in the density of 11–20 cm fish occurred across fished and protected populations in omnivores (\overline{RR} = 3.42, CI = 1.16–11.22; Fig. 7c), while increases in 21–30 cm fish were observed for zoobenthivores (\overline{RR} = 1.91, CI = 1.08–3.52; Fig. 10c). Herbivores were the only trophic group to demonstrate a significant increase in the largest body-size class over time (\overline{RR} = 2.82, CI =

1.50–5.82; Fig. 8c). Summary statistics of body-size specific densities are provided in Tables 4–6.

DISCUSSION

The Philippines is considered the global epicenter of marine biodiversity (Carpenter & Springer 2005) and is thus a top priority for marine conservation (Roberts et al. 2002). Philippine coral reefs contain >1700 species of reef fishes (Carpenter & Springer

2005) and represent roughly 9% of the global coral reef area (Spalding et al. 2001). Coastal marine resources including coral reefs support over 120 million people, >2 million of whom are fishermen (Veron et al. 2009, Goreau 2010), and provide 70% of the animal protein intake of the country (State of the Coral Triangle Report 2014). The Philippines has also been consistently on the front-line of MPA establishment (Christie et al. 2002, White et al. 2006). At least 985 MPAs were established in the Philippines between 1970 and 2008, covering 14 943 km² (4.9% of coastal

Table 4. Summary statistics of meta-analysis for body-size specific fish density in first surveys. An explanation of the Q_T statistic can be found in the description of Table 3. Significant values in **bold**

Biotic group	1–10 cm			11–20 cm			21–30 cm			>30 cm		
	Q_T	df	p	Q_T	df	p	Q_T	df	p	Q_T	df	p
Total	17.06	16	0.382	43.32	16	<0.001	73.37	16	<0.001	34.35	16	0.005
Target	36.81	16	<0.001	45.47	16	<0.001	77.80	16	<0.001	39.24	16	0.001
Non-Target	16.81	16	0.398	26.69	16	0.045	52.11	16	<0.001	4.43	16	0.998
Herbivores	37.08	15	<0.001	47.52	15	<0.001	85.76	15	<0.001	43.50	15	<0.001
Omnivores	15.00	16	0.525	24.46	16	0.080	27.06	16	0.041	0.00	16	1.000
Piscivores	45.04	14	<0.001	66.05	14	<0.001	49.80	14	<0.001	5.19	14	0.983
Planktivores	47.69	12	<0.001	40.03	12	<0.001	65.44	12	<0.001	0.00	12	1.000
Zoobenthivores	31.13	16	0.013	36.28	16	0.003	73.21	16	<0.001	8.48	16	0.933

Table 5. Summary statistics of meta-analysis for body-size specific fish density in second surveys. An explanation of the Q_T statistic can be found in the description of Table 3. Significant values in **bold**

Biotic group	1–10 cm			11–20 cm			21–30 cm			>30 cm		
	Q_T	df	p	Q_T	df	p	Q_T	df	p	Q_T	df	p
Total	29.50	16	0.021	31.37	16	0.012	83.11	16	<0.001	78.19	16	<0.001
Target	50.40	16	<0.001	28.53	16	0.027	81.07	16	<0.001	82.27	16	<0.001
Non-Target	40.38	16	<0.001	90.75	16	<0.001	76.54	16	<0.001	25.20	16	0.066
Herbivores	109.45	15	<0.001	32.50	15	0.006	60.14	15	<0.001	97.49	15	<0.001
Omnivores	44.20	16	<0.001	113.31	16	<0.001	78.67	16	<0.001	23.05	16	0.112
Piscivores	57.97	13	<0.001	80.87	13	<0.001	58.19	13	<0.001	50.10	13	<0.001
Planktivores	74.30	15	<0.001	58.84	15	<0.001	70.70	15	<0.001	0.00	15	1.000
Zoobenthivores	51.51	16	<0.001	43.40	16	<0.001	92.24	16	<0.001	26.91	16	0.042

Table 6. Summary statistics of meta-analysis for body-size specific fish density in reef-wide analyses. An explanation of the Q_T statistic can be found in the description of Table 3. Significant values in **bold**

Biotic group	1–10 cm			11–20 cm			21–30 cm			>30 cm		
	Q_T	df	p	Q_T	df	p	Q_T	df	p	Q_T	df	p
Total	11.93	16	0.749	46.74	16	<0.001	87.00	16	<0.001	55.25	16	<0.001
Target	34.67	16	0.004	61.62	16	<0.001	102.99	16	<0.001	55.83	16	<0.001
Non-Target	18.50	16	0.295	132.25	16	<0.001	87.06	16	<0.001	54.16	16	<0.001
Herbivores	95.73	16	<0.001	52.65	16	<0.001	102.36	16	<0.001	85.30	16	<0.001
Omnivores	12.77	16	0.689	162.34	16	<0.001	87.85	16	<0.001	43.96	16	<0.001
Piscivores	84.86	16	<0.001	113.09	16	<0.001	94.15	16	<0.001	80.58	16	<0.001
Planktivores	82.34	14	<0.001	146.68	14	<0.001	154.29	14	<0.001	0.00	14	1.000
Zoobenthivores	28.48	16	0.028	83.42	16	<0.001	82.12	16	<0.001	56.14	16	<0.001

waters) with 1459 km² (0.5%) being designated as no-take zones (Weeks et al. 2010). The availability of a large number of MPAs to examine, the country's vast utilization of coastal resources, and the critical importance of its marine biodiversity make the Philippines the ideal region in which to study the effects of MPAs on exploited fisheries. It is essential that continued assessments of MPA performance be conducted in the Philippines, as the maintenance of fishery stocks is essential for the future of both food security and ecological integrity throughout the country. In light of the growing anthropogenic pressure being placed on marine ecosystems and the increasing use of MPAs as a primary management tool, a more complete understanding of the effects of MPAs on exploited fish populations is critical (Allison et al. 1998, Jameson et al. 2002, Sale et al. 2005).

A categorical meta-analysis of Philippine MPAs revealed that the total density of coral-reef fishes was consistently higher within MPAs than in adjacent fished areas and that the density of large-bodied fish both within and outside of MPA boundaries increased over the first ~5 yr of protection. These results are congruent with theoretical predictions about the effects of MPAs on fish populations within their borders (Baskett & Barnett 2015) and, more importantly, with the proposed benefits of 'spillover' and 'recruitment subsidy' to reefs adjacent to MPAs that remain open to fishing (Russ & Alcala 1996, Boersma & Parrish 1999, Russ et al. 2004). These phenomena appear to have strong influence on fish-population structure across reefs that include MPAs, as significant increases in large-bodied fishes were evident both in protected and fished reefs over time after the establishment of MPAs.

Fish directly targeted by fishermen demonstrated positive responses to protection over time in terms of both spatial distributions and changes to the demographic structure of populations across protected and fished reefs. Although no spatial disparity between MPAs and fished reefs was observed in the first surveys, the density of target species was 43% greater in MPAs compared to adjacent reefs in the second surveys. The shift towards higher densities of targeted fish inside MPAs is likely the result of lowered mortality rates within MPAs, while fished reefs experience sustained or potentially increased mortality rates due to fishing displacement (Halpern et al. 2004). The overall density of target species across reefs remained stable between the 2 surveys, however, indicating that increases in density inside MPAs were able to offset any declines in population sizes in fished reefs. More importantly, reef-wide

analysis revealed that the density of large-bodied individuals increased significantly between the 2 survey periods, with 137% and 173% higher densities within the 21–30 cm and >30 cm categories, respectively. The ability of MPAs to promote higher abundances of large-bodied individuals in adjacent, fished reefs is critical to food security for sustenance fishermen and the sustainability of fish populations, as larval production exponentially increases with fish body-size (Birkeland & Dayton 2005, Walsh et al. 2006, Hixon et al. 2014). Despite reef-wide population sizes of target families remaining static, the higher prevalence of large-bodied individuals observed here indicates that MPAs were able to increase fish biomass across both protected and fished reefs. Additionally, due to the exponential relationship between body-size and fecundity, larger average body-sizes within fisheries, even without increases in population density, are more likely to promote population expansion over successive years of protection than higher densities of small-bodied individuals.

The density of non-target fishes remained unchanged in most categories across spatial surveys as well as in temporal reef-wide analyses. Interestingly, in spatial analyses, non-target species demonstrated significantly higher overall densities in both the first and second surveys inside MPAs compared to adjacent reefs. This result is somewhat unexpected, as the lack of anthropogenic mortality outside of reserves has previously resulted in fairly equivalent densities across protected and exploited reefs for these species (Mosqueira et al. 2000). Such disparities could be the result of a variety of factors, including MPAs being preferentially placed in areas with higher fish densities at their inception, or decreased mortality of non-target species within MPAs due to collateral damage as bycatch in highly efficient collection gear and from destructive fishing practices such as the use of dynamite. Body-size specific densities also indicated that non-target fishes were able to maintain a more robust population structure in the presence of MPAs. At the 11–20 cm size class, non-target fish density was 127% higher inside MPAs for non-target fishes compared to adjacent reefs in the first surveys and 188% higher in reef-wide analyses between the first and second surveys. As the families included in the 'non-target' category tend to achieve much smaller terminal adult body-sizes, positive shifts within this size-class may indicate that similar to target species, non-target fish are able to reach their 'maximum' terminal adult body-sizes both within and outside of MPAs after the initiation of protec-

tion. Further investigation is needed to determine if these shifts are indeed the direct result of MPAs and, if so, what mechanisms underlie benefits to taxa that are not directly targeted by fishermen.

Within trophic categories, responses were variable among groups, but at both survey periods, overall population densities were often higher inside MPAs than in adjacent reefs, with no significant increases in densities occurring in reef-wide analyses over time. These results suggest that MPAs were adequate to prevent significant declines in population sizes due to fishing pressure across reefs, but did not provide sufficient refuge to promote population expansion for most trophic groups. A notable exception to this trend was zoobenthivores, which exhibited significantly higher densities inside MPAs in the first surveys, no spatial disparity in the second surveys, and an overall decline in reef-wide density over time. Examination of size-specific changes in density, however, revealed that despite absolute densities remaining static over time, the population structure of several trophic groups shifted towards the predominance of large-bodied individuals across both protected and fished reefs. Significant reef-wide increases in large-bodied fish were evident for herbivores, omnivores, and even zoobenthivores (despite a significant decrease in overall abundance), suggesting that MPAs may be able to reverse age- and size-truncation characteristic of exploited fish populations (Hixon et al. 2014) across a multitude of species. Additional research on the specificity of responses to protection within trophic and taxonomic groups is necessary to advance our understanding of why some taxa recover faster and with greater magnitude from fishing-induced disturbances, and what mechanisms can be put in place to promote similar rates of recovery in other groups.

The strength of the analytical framework used in the assessment of MPA performance presented here is the inclusion of harvested populations in the temporal, reef-wide analyses. Increasing the density of populations in adjacent reefs is absolutely essential for MPAs to achieve their ecological and biodiversity goals (Russ 2002), making empirical evidence supporting the realization of these benefits to sustained support for the establishment of MPAs and compliance to MPA regulations among resource users. The ability of MPAs to promote healthy fisheries resources outside of their borders may indeed be the most crucial factor of MPA success, as compliance to 'no-fishing' regulations by fishermen is tied to personal beliefs that MPAs within traditional fishing grounds have direct eco-

nomic benefits (Cinner et al. 2014). Compliance, in turn, has been identified as a critical factor in MPA performance (Kritzer 2004, Samoilys et al. 2007), as poaching inside protected areas can quickly negate both the ecological and fishery benefits of MPAs (Sanchirico 2000, Sale et al. 2005, Gaines et al. 2010). Although enforcement ratings for the MPAs included in this study indicated high levels of compliance, country-wide estimates of enforcement in Philippine MPAs are generally low, with recent investigations suggesting that roughly 35% of MPAs in the country are enforced and only 12% are enforced on a consistent and ongoing basis (Weeks et al. 2010). As a result, it is possible that this analysis may include MPAs that have been subjected to considerable levels of poaching. Despite challenges in implementation and practice often faced in developing nations with widespread artisanal fisheries, the improvement in the quality and quantity of exploited-fish populations across both protected and fished reefs observed here is a remarkable indicator of the potential contribution of MPAs to the sustainability of coral-reef fisheries.

The results of this reef-wide meta-analysis, therefore, should be encouraging to both conservation managers and resource users. Although overall densities of fish were consistently higher within MPAs compared to fished reefs, the overall density of fish across both populations remained stable over time, indicating that the establishment of MPAs was sufficient to prevent continued declines in fish-population size and structure often observed in response to sustained, heavy fishing pressure common in subsistence fisheries in the Philippines. Additionally, the density of large-bodied individuals increased throughout both MPAs and fished reefs, suggesting that total harvestable fish biomass was increased by the establishment of MPAs despite population sizes remaining static over time. Shifts in the demographic structure of harvested populations towards the predominance of large-bodied individuals are beneficial not only in the short term for fisheries yields but also for long-term sustainability, as a higher prevalence of large-bodied fish increases the capacity of populations to replenish individuals lost to fishing pressure (White et al. 2013). The reef-wide shifts in both population size and structure over time demonstrated here illustrate the potential of juxtapositions between MPAs and adjacent fished reefs to mask the benefits of MPAs, as shifts within exploited fisheries are likely to occur simultaneously both inside and outside of protected zones after MPA establishment.

Further studies are necessary, however, to determine whether similar reef-wide shifts occur for additional taxonomic groups not included in this analysis, and how spatial patterns of density and abundance shift over time scales beyond the 3 yr temporal period utilized in this investigation. Recent research has indicated that fish biomass may take 20 to 60 yr to fully recover in areas around MPAs (McClanahan 2014, MacNeil et al. 2015), and that beneficial alterations to life-history traits including growth and maturation patterns may take even longer to stabilize (McClanahan & Humphries 2012, McClanahan & Graham 2015). Although the increases in overall fish density inside MPAs compared to adjacent reefs observed here occurred at faster rates ($\sim 10\% \text{ yr}^{-1}$) than in previous meta-analyses ($\sim 5\% \text{ yr}^{-1}$; Molloy et al. 2009), reef-wide increases in density occurred at half the rate ($\sim 5\% \text{ yr}^{-1}$). Given that reef-fish populations in the Philippines are estimated to be as low as 10% of their baseline levels (Stobutzki et al. 2006), this rate of increase across protected and fished populations, were it to remain stable, would require 18 yr to reach full recovery. However, as the magnitude of increases in fish density and biomass tend to be highly variable after the first 5 yr of protection (Babcock et al. 2010), the increases observed here are not likely to continue linearly with subsequent years of protection, making much longer time-scales for full recovery more realistic. In addition, no significant reef-wide increases in density were observed for any trophic or exploitation group, indicating that the recovery of individual fish populations are likely to require longer time periods than analyzed here. Reef-wide analyses encompassing extended time periods are needed to determine when equilibrium points are reached at which reef-wide population sizes and spatial distributions stabilize. Finally, although MPA size is often cited as a significant factor in efficacy, the largest MPAs in this study (Nalusuan Marine Sanctuary [83 Ha] and Port Barton Marine Park [123 Ha]) did not demonstrate consistently higher response ratios compared to smaller MPAs.

Simultaneous changes in the density and demographic structure of fish populations inside and adjacent to MPAs, as evident in this analysis, may be the result of the interaction of a number of different processes. First, it is possible that spillover may occur across Philippine reefs faster than previously detected (~ 5 yr [this study], compared to 9–11 yr [Russ & Alcala 1996], 8 yr [Russ et al. 2004], or 14 yr [Russ & Alcala 2011]) and does so at low but consistent levels, resulting in the migration of large-bodied individuals at a sufficient rate to pre-

vent fishing pressure outside of MPA borders from depleting populations still exposed to harvest (Green et al. 2015). This is slightly different than the classical description of the spillover phenomenon, in which populations increase almost exclusively inside MPA borders until density-dependent processes force individuals into adjacent reefs. Second, recruitment subsidy from an abundance of large-bodied, highly-fecund individuals within MPAs may supply an excess of recruits to adjacent fished reefs, promoting population densities that are sufficient to not only withstand fishing pressure but also allow some individuals to survive long enough to achieve large body-sizes that confer greater fecundity. Additionally, it is possible that recruits being exported from MPAs may not be of significantly greater quantity, but rather quality, as large-bodied females are able to invest more into egg provisioning in the absence of increased mortality from fishing pressure (Walsh et al. 2006). These individuals are more likely to be larger at settlement and demonstrate faster growth rates (Vigliola & Meekan 2002), reducing early-life mortality rates from predation (Searcy & Sponaugle 2001) and increasing the average size-at-age of cohorts throughout their lifespan (Berkeley et al. 2004). Finally, as recent modelling and empirical tests have indicated that MPAs can potentially buffer against the impacts of fisheries-induced evolution (Trexler & Travis 2000, Baskett et al. 2005, Dunlop et al. 2009, Miethe et al. 2010, Fidler et al. 2014), it is conceivable that the absence of fishing pressure inside MPA borders has favored the proliferation of individuals that carry phenotypes that confer higher fitness (i.e. larger terminal-body size and later sexual maturation; Walsh et al. 2006). The development of these traits within MPAs would not only lead to increased export of larvae to adjacent reefs but could potentially also transport beneficial life-history traits to populations within fishing grounds (Baskett et al. 2005). Because the expected impact each of these mechanisms would have on the long-term viability of fisheries stocks varies significantly, it is critical that further studies be conducted to quantify the relative contribution of each of these phenomena to the reef-wide shifts in abundance and demographics observed here.

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