REPORT

Trajectories and magnitude of change in coral reef fish populations in Philippine marine reserves: a meta-analysis

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Abstract Marine reserves are widely implemented worldwide to meet both conservation and fisheries management goals. This study examines the efficacy of Philippine marine reserves using meta-analysis by comparing variations in fish density (1) between reserves and adjacent fished reefs (spatial comparison), (2) within reserves before establishment relative to years following the establishment (temporal comparison), and (3) among reserves classified based on size, age, and enforcement capacity. A grand (total) mean of nineteen 22.3 ha coral reef reserves, protected for a mean duration of 8.2 years, were included in the meta-analyses. The overall density of fishes was higher in the reserves compared with the fished reefs and this difference was largely accounted for by exploited fishes. However, the overall density of fishes within the same reserves remained similar from the period before its establishment to several years following its establishment.

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Only the density of nonexploited fishes increased significantly during years subsequent to the establishment of the reserves. Neither age nor size of reserves correlated with pattern of change in fish density following the establishment of the reserves; however, fish density was consistently higher in larger and older reserves relative to smaller and younger reserves in the spatial comparison. Furthermore, well-enforced reserves had higher density of exploited fishes relative to less-enforced reserves in both spatial and temporal comparisons. In general, the magnitude and trajectory of change in fish density following the establishment of Philippine marine reserves are influenced by (1) functional groups of fishes under consideration, (2) size and age of the reserve, and (3) level of enforcement of the regulatory mechanisms necessary to sustain a marine reserve.

Keywords Marine-protected area · Marine conservation · Coastal resource management · Fishing impact · Overfishing · Ecological synthesis

Introduction

Global fisheries show signs of severe overexploitation, with global landings falling and several fish stocks experiencing a decline in size or are threatened with extinction (Roberts 1997; Pauly et al. 1998; Hutchings 2000). Marine reserves, a no fishing spatial management zone, are increasingly being used as fisheries management and conservation tool worldwide (Jennings 2001; Gell and Roberts 2003; Sale et al. 2005; Russ 2006; Christie and White 2007). Reserves are expected to protect and enhance the biotic structures within their borders, and then augment the adjacent fisheries through adult spillover and larval subsidy

(Gell and Roberts 2003; Sale et al. 2005; Alcala et al. 2005; Russ 2006).

The recovery process of fish assemblages in reserves is complex and is influenced by a wide range of factors (Jennings 2001). These include the population size and species composition at the onset of protection and the life history characteristics of the fish species under consideration (Hutchings 2000; Jennings 2001), reserve age, size, spacing and habitat structural complexity (Botsford et al. 2003; Hastings and Botsford 2003; Russ et al. 2005; Claudet et al. 2008; Graham et al. 2008), and the magnitude of reduction of fishing mortality in the reserve as a function of enforcement (Russ 2006; Guidetti et al. 2008). Top-trophic level species (e.g., piscivores) are preferentially fished, and thus expected to respond positively with protection because of the elimination (or reduction) of fishing mortality in the reserves (Roberts 1997; Jennings 2001; Russ 2006). The pattern of response (i.e., reserve effects) of top-trophic level species is expected to correlate positively with the age, size, and enforcement capacity of the reserves under consideration (Hastings and Botsford 2003; Russ 2006; Guidetti et al. 2008; Claudet et al. 2008). On the contrary, nonexploited prey species in the reserves are expected to have minimal response or even respond negatively due to concomitant increase in predation pressure (Pinnegar et al. 2002; Graham et al. 2003).

The establishment of reserves has become a major conservation and fisheries management tool in the Philippines under the banner of community-based coastal resource management (White et al. 2000; Alcala and Russ 2006; Christie and White 2007; Maliao et al. 2009). Aside from more pressing economic reasons (White et al. 2000), fisheries conservation and management are particularly urgent in the Philippines because the country is considered as the epicenter of global marine biodiversity (Carpenter and Springer 2005). Currently, the Philippines has implemented $\sim 1,169$ marine reserves (Arceo et al. 2008). Thus, it is critical to evaluate the effectiveness of these reserves to allow continuous feedback of information necessary for adaptive management (Pomeroy et al. 2005; Maliao et al. 2009).

Meta-analysis, commonly used in the medical sciences to synthesize results from disparate studies (Fazey et al. 2004), has recently received wide application in summarizing results of marine reserves across multiple spatial and temporal scales (e.g., Mosquera et al. 2000; Côté et al. 2001; Halpern and Warner 2002; Halpern 2003; Guidetti and Sala 2007; Claudet et al. 2008; Maliao et al. 2009). Meta-analysis provides a rigorous statistical framework for the synthesis of results from disparate studies that may have used different designs, sample sizes, or taxa to test similar questions (Hedges and Olkin 1985; Fernandez-Duque 1997). However, the majority of previous meta-analytical studies evaluating the efficacy of reserves are based on the comparative analyses between reserves and fished reefs. Conclusions about the efficacy of reserves based on such spatial comparisons have to be interpreted with caution because of patterns that may be considered as artifacts of the criteria for selecting coral reefs that are designated as reserves (Edgar et al. 2004; Willis et al. 2003a; Russ 2006). The skepticism associated with the conclusions about the efficacy of reserves drawn from spatial comparisons may be ameliorated by examining the performance of the same set of reserves over time (e.g., Before–After and Control-Impact [BACI] design; Underwood 1994; Edgar et al. 2004; Russ et al. 2005; Russ 2006).

This study examines the efficacy of Philippine reserves using meta-analysis by comparing variations in fish density (1) between reserves and adjacent fished reefs (spatial comparison), (2) within reserves before establishment relative to years following establishment (temporal comparison), and (3) among reserves classified based on size, age, and enforcement capacity. It is hypothesized that fish density, particularly those species that are exploited by fishing (1) is higher in reserves than in adjacent fished reefs, (2) increases in reserves following years of protection, and (3) is higher in larger, older, and well-enforced reserves. This study is one of the more comprehensive studies of marine reserves to date because it simultaneously examines both spatial and temporal effects of reserve protection, as well as the effects of reserve size, age, and enforcement.

Methodology

Data screening

Studies that examined fish assemblages in the Philippine marine reserves were rigorously searched from both the gray (research reports of different research institutions in the Philippines) and scientific literature (using Aquatic Sciences and Fisheries Abstracts and Biological Abstracts). Studies were selected based on the following criteria: (1) enforcement capacity of the reserves is at least a level 2 based on the management rating system implemented by the Coastal Conservation and Education Foundation, Inc., (CCEF) and its partners in the Philippines (White et al. 2004; see Table 1 for the details of this criterion); (2) fish density values were simultaneously collected from coral reef reserves and adjacent fished reefs, and the same reserve had been monitored for fish density before and after its establishment, in order to conform with the BACI design (Underwood 1994; see Table 1 for the details of the sampling methodology); and (3) the study reported the

Reserve name ^a	Town	Province	Reserve	Year	Year monitored	nitored	Replica	Replicate transects ^c	cts ^c	Enforcement rating ^e	Source ^f
				cstautisticu	Before	After	Before	After	Fished reefs ^d		
Apo IFS	Dauin	Negros Oriental	22.5	1985	1985	2002	4	9	6	5	White et al. (2002)
Arthur's Rock MS	Mabini	Batangas	25	1991	1991	2005	4	4	10	2	White et al. (2005)
Balicasag IFS	Panglao	Bohol	5.4	1986	1986	2007	9	9	4	3	White et al. (2003, 2007)
Balingasay MPA	Balingasay	Pangasinan	14.8	1999	1999	2003	5	5	5	2*	Arceo et al. (2005a)
Batalang Bato FS	Tingloy	Batangas	2.5	2002	2001	2005	9	9	15	3	White et al. (2005)
Cabacongan FS	Loon	Bohol	11.8	1997	1997	2003	5	5	9	3*	Arceo et al. (2005b)
Carot MS	Anda	Pangasinan	13.3	1999	2000	2003	4	4	4	2*	Salmo et al. (2005)
Doljo FS	Panglao	Bohol	7.32	1998	1999	2007	2	9	9	2	White et al. (2003, 2007)
Gawi MS	Oslob	Cebu	12.5	2003	2003	2006	4	3	3	2	Apistar et al. (2006)
Gilutongan MS	Cordova	Cebu	14.9	1999	1999	2003	10	4	4	4*	Arceo et al. (2005c)
Granada FS	Boljoon	Cebu	9.4	2002	2002	2007	9	9	9	3	Raymundo (2008)
Kawasihan MS	Candijay	Bohol	20	2001	2001	2005	2	4	3	3*	PROCESS (2003)
Nalusuan MS	Cordova	Cebu	83	2002	2003	2007	ю	З	3	4	Apistar et al. (2007)
Pamilacan MS	Panglao	Bohol	11.9	1985	1985	2007	б	9	5	4	White et al. (2007)
Port Barton MP	SanVicente	Palawan	123	1999	1999	2003	9	ю	n	3*	Nanola et al. (2005)
Sibulan MR	Sibulan	Negros Oriental	9	1997	1997	2003	2	4	4	2*	Arceo et al. (2005d)
Sumilon IFS ^b	Oslob	Cebu	37.5	2001	2002	2006	9	б	2	2	White et al. (2002); Apistar et al. (2006)
Tawala MS	Panglao	Bohol	5.4	1998	1999	2007	2	3	3	2	White et al. (2003, 2007)
Twin Rocks MS	Mabini	Batangas	15	1991	1991	2005	2	S	10	2	White et al. (2005)
Enforcement capac	sity of sites w	Enforcement capacity of sites with asterisk (*) was rated by the	rated by th	ne authors based on the descriptions of each study	sed on th	e descript	tions of	each stu	dy		
^a FS fish sanctuary	y, IFS island f	fish sanctuary, MS n	narine sanc	stuary, MPA	marine-pı	otected a	rea, <i>MP</i>	marine	park, all these	FS fish sanctuary, IFS island fish sanctuary, MS marine sanctuary, MPA marine-protected area, MP marine park, all these terms signified 'no-take' management	ke' management
^c First reserve im	plemented in t	he Philippines. It w	as first est: 2	ablished in 1	974 but h	as compl	ex prote	ction his	stories thereaft	er. Protection resumed	First reserve implemented in the Philippines. It was first established in 1974 but has complex protection histories thereafter. Protection resumed in 2001(see Alcala and Russ 2006)
All studies used Replicate transects used SCUBA (self-	were approxi- contained bre-	(equivalent to 2000 mately 10–20 m ap; athing apparatus) ge	m) uransed art and wer ars. In case	et in the fish e generally la s where sam	visual ce aid out at pling was	6–10 m (rv taken in	() surve (deep sta both dee	tions) or the sec r tions) or p and sh	n reef flat, reef allow stations	Crest, or reef slope par (1-4 m by snorkel), av	All succes used a DV × 10 m (equivation to DOU m.) transfer in the list visual census (FVC) survey (see English of at. 1971). Each transfer was evaluated by one list counter at a time. Replicate transfer were approximately 10–20 m apart and were generally laid out at 6–10 m (deep stations) on reef flat, reef crest, or reef slope parallel to the shore. Surveys at deep stations used SCUBA (self-contained breathing apparatus) gears. In cases where sampling was taken in both deep and shallow stations (1–4 m by snorkel), average density in the two stations were used
in the analyses. Fit	sh monitoring	in the analyses. Fish monitoring in the fished reets was done concurrently in reserves post-establishment	was done c	concurrently :	in reserve	s post-es	tablishm	ent			
^d Fished reefs wer a nearby reserve is	e surveyed at] undetectable	least 300 m away fr at \sim >250 m and, th	om the borc nerefore, fis	thers of reserves shed reefs fro	es. This w m this dis	vas based stance fro	primaril in the re	y on the serve ca	findings of Ru n be used to ru	iss and Alcala (1996) a spresent a control site.	^d Fished reefs were surveyed at least 300 m away from the borders of reserves. This was based primarily on the findings of Russ and Alcala (1996) and Russ et al. (2003) that an adult fish from a nearby reserve is undetectable at $\sim >250$ m and, therefore, fished reefs from this distance from the reserve can be used to represent a control site. Aside from the distance criterion, the main
factor in the select	tion of fished	factor in the selection of fished reefs as a control was based primarily on having relatively similar habitat characteristics as the reserve reefs	as based p	rimarıly on h	aving rel.	atively si.	mılar ha	bitat ché	aracteristics as	the reserve reets	

^e CCEF rated marine reserves in the Philippines in 5 levels: 1 initiated/passing; 2 established/fair; 3 enforced/good; 4 sustained/very good; and 5 institutionalized/excellent (see White et al. 2004 for details of the reserve rating system)

f CCEF data available at www.coast.ph, while data from PHILREEF reports available at http://www.msi.upd.edu.ph/midas

number of replicate transects surveyed, which was necessary for weighting of density estimates by sample sizes (Hedges and Olkin 1985). Fish density was used as the metric of reserve effect because it is the common variate reported in the studies included in the meta-analyses.

Based on the aforementioned criteria, a total of 16 studies covering 19 coral reef reserves in 13 municipalities in six Philippine provinces were selected (Fig. 1; Table 1). These reserves ranged in size from 2.5 to 83 ha (mean: 22.3) and were protected from 3 to 22 years (mean: 8.2).

Meta-analysis

For temporal comparisons, fish density in the reserves before and after their establishment served as the control and experimental values, respectively. In reserves where multiple year data on fish density values were available, the fish density estimated around reserve establishment was used as the control and the latest fish density was used as the experimental values, respectively, in order to avoid analytical problems associated with autocorrelation. For

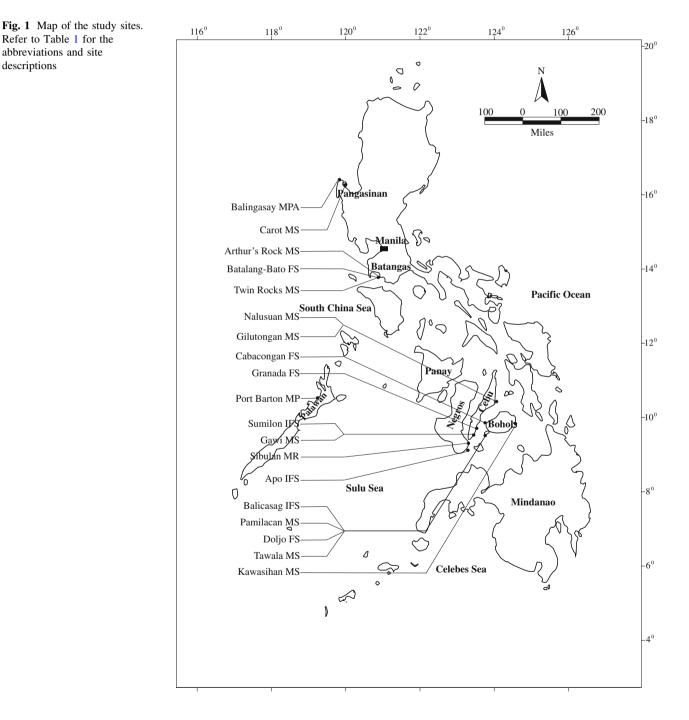


 Table 2
 Fish
 families
 and
 their
 trophic
 and
 exploitation

 classifications

Family	Exploitation category	Trophic group				
Carangidae (jack)	Exploited	Piscivores				
Lutjanidae (snapper)	Exploited	Piscivores				
Serranidae (grouper)	Exploited	Piscivores				
Scaridae (parrotfish)	Exploited	Herbivores				
Siganidae (rabbitfish)	Exploited	Herbivores				
Acanthuridae (surgeonfish)	Exploited	Omnivores				
Pomacanthidae (angelfish)	Nonexploited	Omnivores				
Pomacentridae (damselfish)	Nonexploited	Omnivores				
Anthiinae (fairy basslet)	Nonexploited	Planktivores				
Caesonidae (fusilier)	Exploited	Planktivores				
Balistidae (triggerfish)	Nonexploited	Invertivores				
Labridae (wrass)	Nonexploited	Invertivores				
Lethrinidae (emperor)	Exploited	Invertivores				
Mullidae (goatfish)	Exploited	Invertivores				
Haemulidae (sweetlips)	Exploited	Invertivores				
Nemipteridae (coral bream)	Exploited	Invertivores				
Zanclidae (moorish idol)	Nonexploited	Invertivores				
Chaetodontidae (butterfly fish)	Nonexploited Corallivor					

spatial comparisons, the latest fish density estimated for the reserves was used as the experimental value (i.e., experimental value in the temporal comparisons) and the fish density concurrently estimated for the adjacent fished reefs was used as the control value. Each pair of reserve and fished reef and pre- and post-reserve comparison was treated as an independent study.

The analyses were limited to 18 fish families known to occupy coral reefs (Table 2). These fishes were classified into two fish groups. First, fishes were classified into trophic guilds (Froese and Pauly 2008); this classification scheme was used as the functional units in the analyses. Fishing disproportionately exploit species in high trophic levels; thus, any difference in the density of each trophic guild between reserves and fished reefs, as well as among years may be viewed as evidence for reserve effects on the functional relationships among fishes. These six trophic guilds are planktivores, herbivores, omnivores, invertivores, corallivores, and piscivores (Table 2). Second, to further test the heterogeneity of fish responses to protection, fishes were further classified into either 'exploited' (if they were deliberately fished) or 'nonexploited'(if they were not deliberately fished; Table 2).

In the meta-analysis, the effect size refers to the magnitude of reserve effect (i.e., magnitude of change in fish density) (Fernandez-Duque 1997) and is measured as the natural logarithm of the response ratio ($\ln RR$; Hedges and Olkin 1985; Rosenberg et al. 2000). Since there were cases where density was reported as zero, 0.0001 was added to all density values to be able to calculate the $\ln RR$ (Molloy et al. 2007). The $\ln RR$ for each fish group was calculated as:

$$\ln RR = \ln\left(\frac{X^e}{X^c}\right)$$

where X^e and X^c are the mean experimental and control density values, respectively. The mean effect $(\overline{\ln RR})$ of each fish group was calculated based on the individual $\ln RR$ values of that particular fish group across studies (i.e., sites). $\overline{\ln RR}$ values were weighted with more weight given to studies with lower variance (i.e., more precise that is a function of 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 that fish group $(w_i = \frac{1}{v_i})$. Since most studies included in the analyses did not report v_i values, v_i was approximated based on sample sizes as (Hedges and Olkin 1985):

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

where N_i^e and N_i^c are the study sample sizes for the experimental and control, respectively. Finally, the weighted $\overline{\ln RR}$ of each fish group was calculated as (Hedges and Olkin 1985):

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

where *n* is the number of studies. The confidence interval (CI) values of each $\overline{\ln RR}$ were based on the 95% biascorrected confidence limits around the mean calculated by bootstrapping after 999 iterations (Rosenberg et al. 2000). Back-transformed values of $\overline{\ln RR}$ and CI were reported. The \overline{RR} was considered significantly different from 0 when its CI did not overlap with 1 (Rosenberg et al. 2000). The heterogeneity of responses among fish groups across sites was determined using the total heterogeneity (Q_T) statistic as (Hedges and Olkin 1985):

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

Categorical meta-analysis was conducted between fish groups to determine whether the intragroup responses were significantly different. To determine the correlates of reserve effects, reserves were categorized according to reserve age ($\leq 5:\geq 6$ years), reserve size ($\leq 10:\geq 11$ ha), and enforcement capacity ($2:\geq 3$) and conducted categorical meta-analyses using these categories. The significance of the difference between fish groups and between categories was determined using the statistic Q_b as (Hedges and Olkin 1985):

$$Q_b = \sum_{j=1}^n \sum_{i=1}^{k_j} w_{ij} (\ln RR - \overline{\ln RR})^2$$

where *n* is the number of categories, k_j is the number of studies in the *j*th group, and w_{ij} is the weight for the *i*th study in the *j*th group.

The significance of Q_T and Q_b was tested against the χ^2 distribution with n - 1 degrees of freedom. The metaanalyses were conducted using the categorical fixed-effects model in MetaWin version 2.1 (Rosenberg et al. 2000).

Results

Spatial comparison

The overall density of fishes in reserves was 1.64 times higher than in fished reefs ($\overline{RR} = 1.64$, CI = 1.30–2.07) and this pattern was homogenous among sites (Fig. 2a; Table 3). The higher density of fishes in reserves was largely accounted for by exploited fishes relative to nonexploited fishes ($Q_b = 5.96$, df = 1, P = 0.01). Nevertheless, densities of both exploited ($\overline{RR} = 2.53$, CI = 1.70–3.49) and nonexploited ($\overline{RR} = 1.47$, CI = 1.14–1.91) fishes were significantly higher in reserves than in fished reefs and this trend was consistent across sites. Responses to protection among trophic guilds were significantly different ($\underline{Q_b} = 12.23$, df = 5, P = 0.03). Densities of piscivores ($\overline{RR} = 2.13$, CI = 1.05–2.50), herbivores ($\overline{RR} = 2.15$, CI = 1.38–3.27), omnivores ($\overline{RR} = 1.39$, CI = 1.08–1.80), and planktivores ($\overline{RR} = 1.92$, CI = 1.30–2.93) were significantly higher in reserves. On the other hand, densities of corallivores ($\overline{RR} = 1.17$, CI = 0.87–1.54) and invertivores ($\overline{RR} = 1.25$, CI = 0.92–1.72) in reserves were not significantly different from those in fished reefs. Responses to protection of piscivores, planktivores, herbivores, and corallivores were significantly heterogeneous among sites while that of invertivores and omnivores were consistent (Table 3).

In general, the above pattern of reserve effects remained consistent across age or size of reserves; however, fish density was consistently higher in older and larger reserves (Fig. 3a–d). The only exception was that the density of corallivores in larger reserves was significantly higher $(\overline{RR} = 1.54, \text{CI} = 1.16-2.16)$ than that in smaller reserves $(\overline{RR} = 0.79, \text{CI} = 0.55-1.31)$. Similarly, density of fishes appeared consistently higher in well-enforced reserves (Fig. 3e–f; Table 3). In particular, density of exploited fishes in well-enforced reserves was significantly higher $(\overline{RR} = 3.74, \text{CI} = 2.54-5.20)$ than that in less-enforced reserves ($\overline{RR} = 1.64, \text{CI} = 1.00-2.66$). Density of herbivores was also significantly higher in well-enforced reserves ($\overline{RR} = 2.99, \text{CI} = 1.62-4.70$) than that in less-enforced reserves ($\overline{RR} = 1.40, \text{CI} = 0.64-2.83$).

Temporal comparison

The overall fish density in reserves slightly increased (but not statistically significant) following reserve establishment $(\overline{RR} = 1.19, \text{ CI} = 0.84\text{--}1.65; \text{ Fig. 2b})$, and this pattern

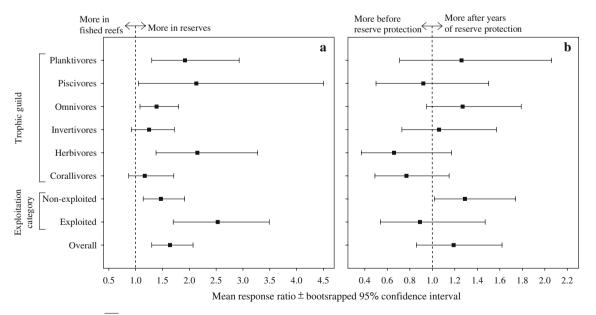


Fig. 2 Mean response ratio (\overline{RR}) of fish groups indicating how fish density varies (a) between reserves and adjacent fished reefs (spatial comparison) and (b) within reserves from the time the reserve is

established to the years following its establishment (temporal comparison). Statistics are given in Table 3

Table 3 Summary statistics of meta-analyses for both spatial and temporal comparisons

Biotic group	Spatial	compari	ison						Temporal comparison							
	Overall analysis (DF =	5	Categ	orical n	neta-ana	alysis			Overal analys (DF =		Categ	orical m	neta-ana	alysis		
						= 6,	Enforce capacities $\leq 2 = 2 = 2 = 3 = 2 = 2 = 2 = 2 = 2 = 2 =$	ty (DF: 8,			Reserve age in years (DF: $\leq 5 = 8$, $\geq 6 = 9$)			= 6,	Enforce capacite $\leq 2 = 3$ $\geq 3 = 9$	y (DF: 8,
	Q_T	Р	Q_b	Р	Q_b	Р	Q_b	Р	Q_t	Р	Q_b	Р	Q_b	Р	Q_b	Р
Overall	12.68	0.81	0.85	0.36	0.06	0.80	0.06	0.77	19.60	0.36	0.29	0.59	0.89	0.35	0.06	0.81
Exploited	28.45	0.06	1.92	0.17	0.04	0.84	6.47	0.01	47.79	0.001	1.60	0.21	1.41	0.23	11.35	0.001
Nonexploited	16.21	0.58	0.93	0.33	0.09	0.74	0.19	0.64	18.12	0.45	0.01	0.99	0.11	0.74	0.45	0.51
Corallivores	32.86	0.02	0.01	0.98	4.43	0.02	0.18	0.68	50.30	0.01	2.99	0.29	1.60	0.38	0.01	0.95
Herbivores	43.94	0.001	1.34	0.25	3.21	0.07	5.27	0.02	55.76	0.001	7.55	0.01	1.10	0.29	1.66	0.19
Invertivores	18.44	0.43	2.45	0.12	1.86	0.21	0.34	0.56	33.27	0.02	0.67	0.41	0.46	0.50	0.21	0.64
Omnivores	15.55	0.62	0.68	0.41	0.03	0.86	0.25	0.87	18.98	0.39	0.01	0.92	0.57	0.45	0.03	0.87
Piscivores	126.7	0.001	0.03	0.85	0.07	0.78	0.65	0.42	93.99	0.001	1.03	0.31	1.56	0.21	0.01	0.90
Planktivores	55.80	0.001	0.79	0.37	1.35	0.24	0.18	0.67	68.10	0.001	5.11	0.02	1.48	0.22	3.23	0.07

The Q_T and Q_b statistics are measures of the difference of $\ln RR$ of each fish group between sites and the difference in $\ln RR$ between categories, respectively (see Meta-analysis section for details). The null hypotheses of these tests are that the $\ln RR$ of each fish group among sites and the $\ln RR$ among categories are equal. P values refer to the significance of both Q_T and Q_b under the χ^2 distribution with n (sites) – 1 degrees of freedom. Bolded text signified that the difference was statistically significant. A significant Q_T implies that the variance among $\ln RR$ is greater than expected by sampling error, while a significant Q_b implies that there are differences in $\ln RR$ among categories

was homogenous among sites (see Table 3). Only nonexploited fishes significantly increased in density since the establishment of reserves ($\overline{RR} = 1.29$, CI = 1.02–1.74), and this pattern was homogenous among sites. In contrast, density of exploited fishes, although not significant and heterogeneous among sites, declined by 11% following at least 8.2 years of protection ($\overline{RR} = 0.89$, CI = 0.54–1.47). Nevertheless, responses among exploited and nonexploited fishes were not significant ($Q_b = 2.51$, df = 1, P = 0.20). Responses among trophic guilds were significantly different $(Q_b = 13.03, df = 5, P = 0.02)$; but, on average, fish density values in reserves before their establishment were not significantly different from pre-reserve values. Densities of piscivores ($\overline{RR} = 0.92$, CI = 0.46–1.87), herbivores $(\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ and corallivores } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.37 - 1.17), \text{ core } (\overline{RR} = 0.66, \text{ CI} = 0.166, \text{ CI} = 0.166, \text{ core } (\overline{RR} = 0.166, \text{ CI} = 0.166, \text{ core } (\overline{RR} = 0.166, \text{$ 0.77, CI = 0.49-1.15) declined after years of protection. Invertivores ($\overline{RR} = 1.06$, CI = 0.73–1.57), omnivores $(\overline{RR} = 1.27, \text{ CI} = 0.95 - 1.79)$, and planktivores $(\overline{RR} = 1.27, \text{ CI} = 0.95 - 1.79)$ 1.26, CI = 0.71-2.06) slightly increased in density since the establishment of the reserves. Response of omnivores to protection was consistent among sites while the rest of the trophic groups were variable (Table 3).

Only herbivores and planktivores exhibited significant difference in their responses with reserve age. Density of herbivores in older reserves ($\overline{RR} = 0.38$, CI = 0.19–0.76) was not only significantly lower than those in younger reserves ($\overline{RR} = 1.00$, CI = 0.47–2.05; Fig. 4a–b; Table 3),

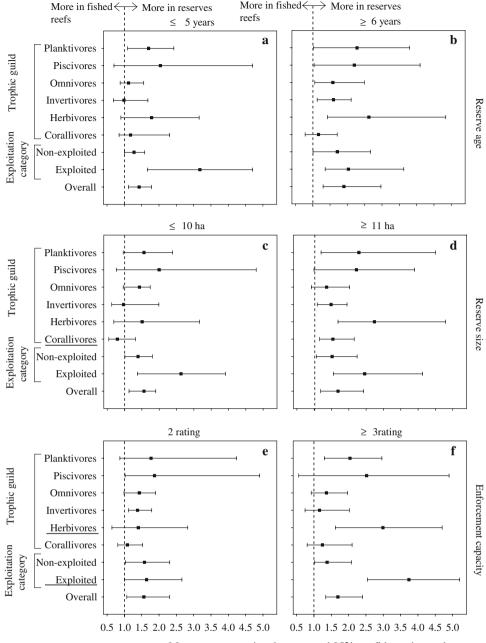
but also had significantly declined as well following several years of protection. Similarly, density of planktivores in older reserves ($\overline{RR} = 0.83$, CI = 0.46–1.70) was significantly lower compared to those in younger reserves ($\overline{RR} = 1.87$, CI = 0.66–3.78). On average, reserve effects appeared consistent regardless of reserve size (Fig. 4c–d). In terms of enforcement capacity, only exploited fishes exhibited significant difference between levels of reserve enforcement (Fig. 4e–f; Table 3). The density of exploited fishes in the less-enforced reserves ($\overline{RR} = 0.44$, CI = 0.27–0.69) significantly declined after years of protection, and this value was <u>significantly</u> lower compared with well-enforced reserves ($\overline{RR} = 1.44$, CI = 0.69–2.83).

Discussion

This meta-analytical synthesis revealed many facets of the performance of Philippine marine reserves in enhancing fish density on coral reefs. In general, response of fish density to protection following reserve establishment is dependent on the (1) functional groups of fishes under consideration, (2) size and age of the reserve, and (3) enforcement capacity.

The higher overall density of fishes in the Philippine reserves relative to fished reefs ($\overline{RR} = 1.64$) is consistent with the findings of previous meta-analyses at global

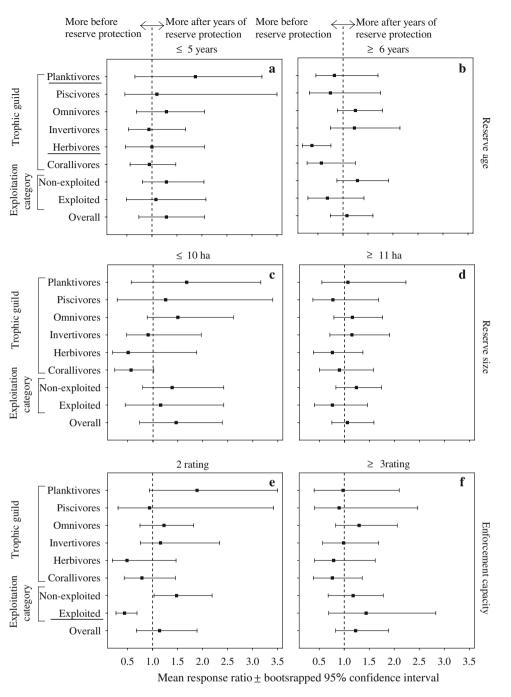
Fig. 3 Mean response ratio (\overline{RR}) of fish groups indicating how fish density varies between reserves and adjacent fished reefs categorized according to **a**-**b** reserve age, **c**-**d** reserve size, and **e**-**f** enforcement capacity. The underlined fish groups had significant density between categories. Statistics are given in Table 3



Mean response ratio ± bootsrapped 95% confidence interval

 $(\overline{RR} = 3.7, \text{Mosquera et al. 2000}; \overline{RR} = 1.9, \text{Halpern 2003})$ and regional levels (Mediterranean: $\overline{RR} = 1.2$, Guidetti and Sala 2007; Europe: $\overline{RR} = 2.5$, Claudet et al. 2008). Although there is a consensus that the overall fish density in reserves is significantly higher relative to fished sites, the magnitude of change following reserve establishment varies depending on the classification of fish under consideration (e.g., functional or taxonomic) and site-specific characteristics of the reserve (e.g., age, size, and habitat structure). An assessment of 81 reserves worldwide, Halpern (2003) revealed that fish density in 30% of these reserves did not differ from that of adjacent fished sites; in 7% of these reserves, fish density was actually lower compared with fished sites. Similarly, Micheli et al. (2004) found that 19% of the 376 species monitored in reserves worldwide have lower abundance relative to the fished sites. It has been hypothesized that the decline in numerical abundance of some fish species following the establishment of the reserves is caused by the cascading effects of subsequent changes in trophic interactions among species in the reserve (Pinnegar et al. 2002; Graham et al. 2003; Micheli et al. 2004).

In this study, it is noteworthy that the density of exploited fishes in the reserves was 2.53 times higher compared with the fished reefs, a conclusion that is consistent with the **Fig. 4** Mean response ratio (\overline{RR}) of fish groups indicating how fish density varies within reserves from the time the reserve is established to the years following its establishment categorized according to **a**-**b** reserve age, **c**-**d** reserve size, and **e**-**f** enforcement capacity. The *underlined* fish groups had significant density between categories. Refer statistics given in Table 3



previous analyses of the Philippine reserves (e.g., Russ and Alcala 2003, 2004; Maliao et al. 2004; Russ et al. 2005; Alcala et al. 2005). This finding is also consistent with the results of previous assessment of reserves on coral reefs elsewhere (Friedlander et al. 2003; Graham et al. 2003; McClanahan et al. 2007; Harborne et al. 2008). Although at the outset it is tempting to attribute the higher density of exploited fishes in the reserves to the absence of fishing, it is conceivable that there are a multitude of factors that contribute to the observed disparity in fish density between reserves and the adjacent fished reefs. Reserves worldwide may be designated in either resource-rich sites (i.e., higher values of biological measures) following the lobbying effort of conservationists and academicians (Edgar et al. 2004; Alcala and Russ 2006) or in resource-poor sites following the demands by local fishers to avoid losing traditionally prime fishing spots (Edgar et al. 2004; Francini-Filho and Moura 2008). Coraldwelling, small-bodied reef fishes (e.g., damselfish and fairy basslet; nonexploited fishes) are more reliant on the reef matrix for protection (Munday and Jones 1998); thus, their higher density in the reserves relative to the fished sites suggests that the Philippine reserves have more complex, resource-rich reef habitats compared with the fished reefs (see Christie et al. 2002; Walmsley and White 2003). If the current inter-reef disparity of habitat conditions reflects those at the time of designation of the reserve, then this may eventually translate into the disparate values for the metrics of performance (e.g., fish density) between reserves and fished reefs, in favor of the reserve. Over time, this difference in baseline fish density could further be magnified by the increased level of fishing in fished reefs as a consequence of the concentration of fishing effort in these locales after the designation of healthy, traditional fishing grounds as reserves (Alcala and Russ 2002; Christie et al. 2002). Fish density in the reserves may also be enhanced by fishes in the neighboring fished reefs immigrating into the reserves because of the presence of more food resources and better habitat quality (re: Ideal Free Distribution Theory of Fretwell and Lucas 1970), similar to the findings of Willis et al. (2003b) in the New Zealand reserves.

The use of BACI design type of analysis isolates the artifacts inherent in the spatial comparisons discussed earlier. However, temporal analyses of fish communities in reserves remain scarce, and results are variable among study sites (Roberts 1995; Wantiez et al. 1997; McClanahan 2000; Galal et al. 2002; Barrett et al. 2007; Kulbicki et al. 2007; also see Russ 2006 for a review). In the Philippines, Russ and Alcala (2003, 2004) reported a sustained increase in density of exploited fishes in Apo and Sumilon Reserves after decades of protection; in contrast, Christie et al. (2002) documented a decline in density of exploited fishes in Balicasag Reserve in Bohol. Results of the metaanalyses conducted in this study revealed that after an average of 8.2 years of protection, the reserves under consideration did not significantly enhance the density of fish populations in all trophic levels, except for nonexploited species. Nonetheless, the overall pattern of change in fish density during the period following the establishment of reserves in the Philippines suggests that on the average reserve age considered in this study, these reserves had been effective in maintaining the status quo of fish assemblages within them. This is similar to the previous reports of Christie et al. (2002) and Walmsley and White (2003) that in the central Philippines, reserves are more effective in enhancing or at least maintaining the biological conditions compared with the fished reefs. Thus, it is likely that the Philippine reserves play a critical role as a buffer against the adverse effects of localized overfishing.

In conducting both spatial and temporal meta-analyses synchronously on the same set of reserves in the Philippines, a contrasting pattern of change in fish density emerges, reflecting the constraints of each analytical approach. On one hand, the results of spatial comparisons share the same conclusion that fish density in the reserves are higher than that in fished reefs as those of Russ and Alcala (2003, 2004), Russ et al. (2005) and Alcala et al. (2005). On the other hand, the results of the temporal comparisons contradicted these findings. It is noteworthy that the works of Russ, Alcala, and colleagues are focused on two small, relatively isolated reserves at Sumilon and Apo Islands in the Philippines. In particular, the apparent success of the Apo Reserve has become an influential template for marine conservation in the country and is often cited as evidence for reserve success worldwide (Russ and Alcala 1996; Alcala and Russ 2006).

Exploited top-trophic level species are considered to be the best indicator of reserve performance (Russ and Alcala 2003, 2004; Russ 2006). When reserves were partitioned according to enforcement capacity in this study, density of exploited fishes was significantly higher in well-enforced reserves than those in less-enforced reserves, similar to the previous findings of Walmsley and White (2003) and Samoilys et al. (2007) in central Philippines and of Guidetti et al. (2008) in Italy. In fact, density of exploited fishes in less-enforced reserves significantly declined after years of protection, suggesting the prevalence of poaching. Poaching, generally cited as the major cause of the widespread failure of reserves in the Philippines (Christie et al. 2002; Walmsley and White 2003; Maliao et al. 2004, 2009; Russ 2006), as well as worldwide (Mora et al. 2006), can quickly negate the long-term and short-term positive effects of establishing the reserve. However, this result is highly variable across sites, which could be linked to the geographical location of the reserve. Mainland reserves are more accessible, thus are more vulnerable to poachers than remote island reserves (e.g., Apo and Sumilon Reserves), where resource stewardship is easier to establish and monitor (White et al. 2000; Maliao et al. 2009). Wellenforced reserves in this study are also on average older and larger compared with less-enforced reserves.

The magnitude of reserve effects have been shown to correlate positively with reserve age (Russ and Alcala 2003, 2004; Micheli et al. 2004; Guidetti and Sala 2007; Molloy et al. 2007; Claudet et al. 2008). However, this study, together with the studies of Mosquera et al. (2000), Côté et al. (2001) and Halpern and Warner (2002), demonstrated that the magnitude of reserve effect was independent of reserve age, although higher density was consistently found in older reserves in the spatial comparison. It is likely that the temporal pattern of response among fish groups was obscured by pooling the responses of fish species with different life histories (Russ et al. 2005). Differences in poaching intensity among reserves of different ages could also confound the pattern of reserve effects observed. In a recent meta-analysis of Philippine reserves based on fishers' perceptions, Maliao et al. (2009) demonstrated that poaching by 'roving bandits' is likely more prevalent in older reserves to maximize profits. Hence, the higher poaching intensity in older reserves relative to younger reserves could homogenize the pattern of reserve effects observed among reserves of different ages.

The structural complexity of coral reefs (e.g., percent live hard coral cover, slope and rugosity) is critical in the recovery of reef fish assemblages (Friedlander et al. 2003; Russ et al. 2005; Maliao et al. 2008; Graham et al. 2008). In this study, a comprehensive analysis of temporal and spatial changes in habitat structure could not be conducted because habitat data were not reported in most of the studies included in the meta-analyses. However, Philippine reserves are usually established on reefs that were formerly fishing grounds, and many suffered from the deleterious effects of overfishing and illegal fishing (e.g., blast fishing) before their establishment as reserves (White et al. 2000; Alcala and Russ 2002). The 1997/1998 El Niño Southern Oscillation (ENSO) further resulted in the massive decline of live coral cover in the Philippines (Arceo et al. 2001) and subsequent decline in reef fish populations in many parts of the world (Graham et al. 2008). A recent report of Marcus et al. (2007) states that based on 28 coral reef fishing grounds examined in central Philippines, the magnitude of coral-reef destruction is alarming; these authors reported that only 12% of the reefs are covered with live coral and the rest is covered with abiotic structures (69%, e.g., coral rubble) and Sargassum (11%). Although only a few fish species are heavily coral dependent, most reef fishes are reliant on the reef matrix for protection at some stage in their life cycle (Graham et al. 2008). Hence, the minimal overall impact of Philippine reserves in enhancing fish density is probably linked to persistent poor habitat condition and past climatic events. It is possible that older reserves in this study have more complex habitat compared with younger reserves, either because of reserve effects (Christie et al. 2002; Walmsley and White 2003), or simply because older reserves are initially designated in more complex reef habitat than those recently established reserves (Russ et al. 2005). The 1997/1998 ENSO possibly resulted to the homogenization of benthic structural complexity between older and younger reserves; hence, the relative magnitude of decline of fish assemblages, particularly for planktivores and herbivores, in older reserves was higher compared with younger reserves.

Finally, although any size of reserves can potentially enhance fish populations, empirical studies demonstrated that the magnitude of reserve effect correlates with reserve size (Edgar and Barrett 1999; Barrett et al. 2007; Claudet et al. 2008). This is consistent with theoretical studies suggesting that larger reserves are more effective in ensuring population persistence (Botsford et al. 2003; Hastings and Botsford 2003). However, this study, together with the meta-analyses of Côté et al. (2001), Halpern and Warner (2002), Halpern (2003), Micheli et al. (2004), and Guidetti and Sala (2007), indicated that the magnitude of reserve effect was independent of reserve size, although higher density was consistently found in larger reserves in the spatial comparison. A caveat here is that larger reserves are more difficult to monitor relative to smaller reserves, and thus more likely to be poached (Webb et al. 2004). In the spatial comparison, density of corallivores represented by chaetodontids was significantly lower in smaller reserves than in larger reserves. Since chaetodontids are generally associated with living corals (thus are often perceived as indicators of coral-reef health), their lower density in smaller reserves is perhaps reflective of the vulnerability of these small-size reserves to habitat disturbances relative to bigger reserves, thus decreasing the chance for healthy coral reefs to be sustained within these smaller reserves.

The strength of this meta-analytical study is the coupling of the results of conventional spatial comparisons with contemporary temporal approach in assessing the efficacy of marine reserves in the Philippines. However, the current analyses may suffer from some valid constraints. First, differences in habitat structure among reserves and fished reefs were not incorporated in the analyses. Second, fish density is considered a less robust metric of reserve effect compared with fish biomass. Fish density is susceptible to stochastic recruitment events and may remain stable or increase even if population biomass has declined due to size-selective poaching or size-dependent ontogenetic migrations. Finally, the density comparisons were based on a single, snapshot data set; thus, the analysis may have not accounted for stochastic sources of variation (see Kulbicki et al. 2007; Harborne et al. 2008). Despite these apparent weaknesses, the integration of spatial and temporal analyses on the same sets of data provides valuable, holistic information that increases our understanding of the utility and performance of marine reserves in the Philippines.

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