



FEATURE ARTICLE

Trophic and benthic responses to no-take marine reserve protection in the Philippines

Brian Stockwell^{1,*}, Claro Renato L. Jadloc¹, Rene A. Abesamis^{1,2}, Angel C. Alcala¹, Garry R. Russ^{1,2}

¹Silliman University — Angelo King Center for Research and Environmental Management (SUAKCREM), Bantayan, Dumaguete City, Negros Oriental 6200, Philippines

²School of Marine and Tropical Biology and ARC Centre for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

ABSTRACT: No-take marine reserves are expected to enhance coral reef resilience indirectly through suppression of algal growth and thus maintenance of coral dominance. The mechanism of such enhancement is protection of functionally important herbivorous fishes from harvest. We provide indirect (inferred) evidence of reserves performing this role. We used data on herbivorous fishes, macroalgae and corals collected at one point in time in 15 reserves (range of duration of protection: 0.5 to 11 yr) and at 15 fished sites in the Philippines. Results inferred a 9- and 15-fold increase in density and biomass, respectively, of herbivorous fishes, which coincided with a 13-fold decrease in macroalgal cover inside reserves after 11 yr of protection. The inferred decline in macroalgal cover was more rapid during the first 5 yr of protection. No significant trends in fish abundance or macroalgal cover were detected among fished sites. Biomass of herbivorous fishes was 8 times higher, and cover of macroalgae 25 times lower, on average, inside older (8 to 11 yr) reserves than at fished sites. Parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) had markedly different inferred trajectories of population recovery. Recovery of parrotfish was more rapid than that of surgeonfish in the first 5 yr of protection, suggesting that the functional role of parrotfish was important in reducing macroalgal cover. The inferred relationships of hard coral cover with duration of reserve protection and with herbivore biomass were non-significant. Even at fished sites, coral cover (mostly >25%) was much higher than macroalgal cover (mostly <15%). Thus, there was no evidence that the current levels of fishing of herbivores on these reefs have led to 'benthic phase shifts'.

KEY WORDS: Coral reefs · Herbivorous fish · Macroalgae · Marine reserves · Phase shifts · Resilience · Trophic responses

Resale or republication not permitted without written consent of the publisher



Bleeker's parrotfish *Chlorurus bleekeri*, a dominant herbivore in Philippine marine reserves.

Photo: B. Stockwell

INTRODUCTION

Coral reefs worldwide have suffered extensive degradation throughout human history, due to the direct and indirect effects of overfishing and land-based human activities (Jackson et al. 2001, Pandolfi et al. 2003). More recently, global climate change has amplified threats to coral reefs by causing episodes of coral bleaching, which impact reefs at regional scales (Hoegh-Guldberg 1999, Hughes et al. 2003, 2007). On many reefs, reduced herbivory due to overfishing, destructive fishing, excess nutrients, coral bleaching and

*Email: brianstockwell@gmail.com

disease outbreaks have impaired the capacity of corals to recover, resulting in coral reefs dominated by algae (Hughes 1994, Wilkinson 2008, Graham et al. 2006). As a consequence, algal-dominated reefs provide less ecosystem goods and services to humans than healthy coral reefs (Moberg & Folke 1999).

No-take marine reserves, or areas permanently closed to fishing, have become an increasingly popular approach to managing coral reefs, especially in poorer countries where few reef management options are feasible (Russ 2002, Sale et al. 2005). Although they are not a panacea to the problems faced by coral reefs, reserves are expected to increase resilience of reefs (i.e. the ability of reefs to withstand recurrent disturbances and to rebuild coral-dominated systems; Hughes et al. 2007) by allowing recovery of overfished herbivore populations (Pinnegar et al. 2000, Hughes et al. 2003, Micheli et al. 2004, Bellwood et al. 2004). Increased density, biomass and diversity of exploited species within reserves has been demonstrated many times (Roberts & Hawkins 2000, Russ 2002, Halpern 2003). Moreover, reserves are expected to benefit areas beyond their boundaries by becoming net exporters of adults and juveniles of target species (Russ 2002, Gell & Roberts 2003, Sale et al. 2005).

A few field studies have shown evidence of reduced macroalgal cover associated with increases in herbivore abundance in reserves and fisheries management zones (McClanahan et al. 2001, Williams & Polunin 2001, Mumby et al. 2006). No studies have demonstrated that enhanced grazing on macroalgae due to recovery of reef herbivores inside reserves can facilitate coral recovery. It is not clear whether coral recovery is an inevitable outcome of reduction of macroalgal cover by herbivores (Newman et al. 2006, Mumby et al. 2007). Interactions between reef herbivores, macroalgae and corals are complex, and the expected outcomes of these interactions may be modified by disturbances (McCook et al. 2001, Ledlie et al. 2007, Mumby et al. 2007).

The majority of studies on the interaction of herbivore and algal community dynamics within marine reserves have been done in the Caribbean and in Kenya. Except for the field experiment by Hughes et al. (2007) in a no-take zone on an inshore island fringing reef of Australia's Great Barrier Reef, no other example of the relationship between herbivores, algae and corals within reserves is available in the western Pacific, where coral reef biodiversity is highest (Veron 2000, Carpenter & Springer 2005). While greater species diversity may not necessarily enhance reef resilience (but see Burkepile & Hay 2008), there is emerging consensus that greater functional diversity does (Nyström 2006). Bellwood et al. (2004)

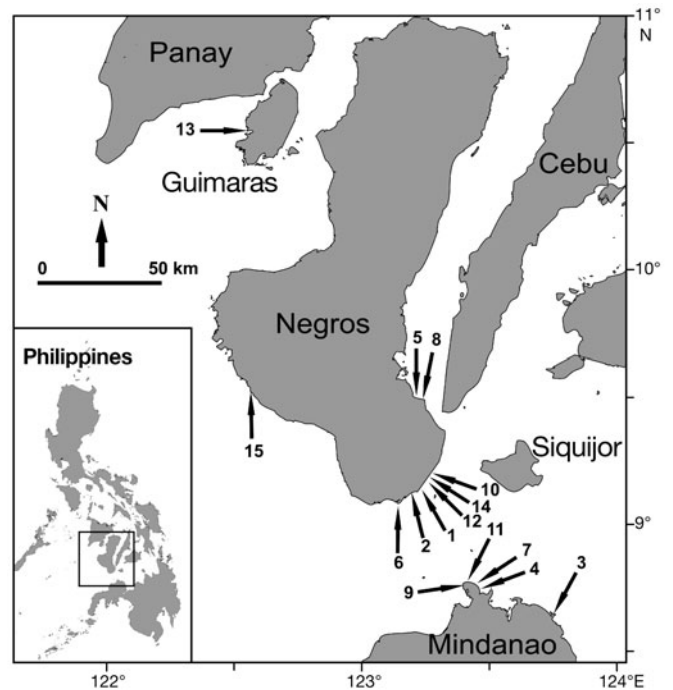


Fig. 1. Reserves and their municipalities, in order of increasing duration of protection when surveys were done—see Table 1 for descriptions. Reserves had at least 1 nearby fished site that was surveyed at the time the reserve was surveyed; exceptions to this were Tandayag and the 3 reserves in Dauin municipality (see 'Materials and methods')

argued that reefs in the western Pacific have a higher degree of 'ecological insurance' than reefs in the Caribbean because of higher functional diversity. However, reefs in the western Pacific, especially in Southeast Asia, are also some of the most damaged by human activities. The few remaining reefs in good condition in this region are still at high risk of further degradation (Gomez et al. 1994, McManus 1997, Burke et al. 2002, Wilkinson 2008). More investigations into herbivore–algal community dynamics within marine reserves in the western Pacific are thus warranted.

Can greater abundance of herbivorous fish in no-take marine reserves reduce algal cover and therefore promote recovery of corals? Here we show indirect evidence that reserves can reduce macroalgal cover, by examining data on abundance of herbivorous reef fishes and benthic attributes inside and outside reserves that have been protected from fishing for 0.5 to 11 yr. Using data from 1-point-in-time assessments of fish populations and benthic communities in reserves of different ages and at control sites open to fishing, we inferred the dynamics of herbivorous fish, macroalgae (fleshy algae and erect calcareous algae) and coral communities.

MATERIALS AND METHODS

Study sites. We studied 15 no-take marine reserves and 15 fished sites (controls) on fringing reefs along large islands located in the central Philippines (Fig. 1, Table 1). The sites were distributed among 8 municipalities in 4 provinces. The reserves were relatively small (6 to 30 ha) and were managed by local communities (see Alcala & Russ 2006). All reserves had an adjacent fished site that was also surveyed, except for Tandayag and the 3 reserves in the municipality of Dauin (where

reserves occupied most of the town's reef area). Adjacent fished sites were typically <500 m away from the reserve. Of the 11 reserves that had an adjacent fished site, 7 (3, 4, 6, 7, 9, 11, 15; Fig. 1, Table 1) were situated on the same stretch of continuous reef as the adjacent fished site and 4 (1, 2, 5, 13) had their adjacent fished site located on a separate patch of reef. In addition to the control sites adjacent to reserves, additional fished sites within 2 km of the reserve were also surveyed for 2 reserves (Baobaon and Andulay). Typical of many reefs in the Philippines, the reserve sites prior to protection,

Table 1. Reserve and fished sites surveyed in the present study and their mean (\pm SE) herbivore biomass, macroalgal cover and coral cover. YE: year when reserve was established; DOP: duration of protection of the reserve when surveys were done. Protection of 4 reserves (Bio-os, Andulay, Tandayag and Bongalonan) was not constant; hence, DOP values for these reserves were equal to the number of consecutive years of effective protection prior to the year of survey. Adjacent fished sites were typically <500 m away from the reserve. Other fished sites were <2 km from the reserve

YE	DOP (yr)	Size (ha)	Herbivore biomass (kg per 500 m ²)	Macroalgal cover (%)	Coral cover (%)	Fished sites	Herbivore biomass (kg per 500 m ²)	Macroalgal cover (%)	Coral cover (%)	
1. Basak, Zamboanguita	2006	0.5	8	0.7 \pm 0.2	9.6 \pm 1.4	17.8 \pm 3.9	Adjacent site	0.6 \pm 0.4	13.7 \pm 2.6	22.8 \pm 3.8
2. Lutoban, Zamboanguita	2006	1	12	3.8 \pm 1.2	13.2 \pm 0.3	30.7 \pm 2.6	Adjacent site	0.4 \pm 0.2	17.7 \pm 1.9	10.8 \pm 3.2
3. Baobaon, Plaridel	2003	3	30	6.3 \pm 2.4	4.7 \pm 1.0	47.8 \pm 4.0	Adjacent site Osokan	4.9 \pm 0.5 3.0 \pm 1.2	8.2 \pm 1.5 2.5 \pm 0.8	40.3 \pm 3.0 52.2 \pm 3.3
4. Baylimango, Dapitan	2003	3	10	7.5 \pm 0.9	13.5 \pm 2.9	52.8 \pm 4.5	Adjacent site	4.0 \pm 0.9	12.2 \pm 1.9	8.7 \pm 2.2
5. Bio-os, Amlan	1999	3	9	5.9 \pm 0.9	2.2 \pm 0.9	39.8 \pm 4.3	Takot Dako	8.6 \pm 1.7	11.7 \pm 2.6	32.7 \pm 3.9
6. Andulay, Siaton	1993	4	6	14.3 \pm 4.5	1.7 \pm 0.5	37.3 \pm 3.9	Adjacent site Tongo Pt. Kuku's Nest Antulang	7.1 \pm 2.1 3.5 \pm 1.7 7.9 \pm 3.4 3.5 \pm 1.6	6.0 \pm 2.7 17.8 \pm 1.0 26.2 \pm 0.5 6.5 \pm 1.0	30.0 \pm 2.9 5.7 \pm 2.0 36.8 \pm 2.9 29.5 \pm 2.3
7. Karang, Dapitan	2001	5	12	12.8 \pm 2.9	4.5 \pm 1.9	30.7 \pm 4.3	Adjacent site	3.1 \pm 1.3	16.7 \pm 4.4	52.5 \pm 3.4
8. Tandayag, Amlan	1996	5	6	20.1 \pm 10.5	1.7 \pm 0.8	41.7 \pm 5.0	–	–	–	–
9. Canlucani, Dapitan	2000	6	9	8.5 \pm 1.6	3.5 \pm 1.3	18.7 \pm 2.2	Adjacent site	0.7 \pm 0.4	14.5 \pm 1.8	26.0 \pm 2.3
10. Poblacion I, Dauin	2000	6	9	22.1 \pm 3.0	0.3 \pm 0.3	67.3 \pm 3.6	–	–	–	–
11. Guimputlan, Dapitan	1999	7	13	29.7 \pm 4.9	0.01 \pm 0.02	50.5 \pm 4.2	Adjacent site	1.0 \pm 0.3	7.2 \pm 1.8	54.3 \pm 4.1
12. Masaplod Sur, Dauin	1999	8	6	32.7 \pm 4.5	0.8 \pm 0.7	33.0 \pm 4.2	–	–	–	–
13. Ave Maria, Guimaras	1999	9	10	32.4 \pm 1.6	0.3 \pm 0.2	40.2 \pm 2.7	Villa Igang	1.5 \pm 0.7	3.7 \pm 0.5	43.0 \pm 2.5
14. Masaplod Norte, Dauin	1995	10	6	28.8 \pm 6.2	0.2 \pm 0.2	26.7 \pm 4.4	–	–	–	–
15. Bongalonan, Basay	1985	11	20	32.4 \pm 10.8	1.2 \pm 0.8	33.3 \pm 2.5	Adjacent site	3.3 \pm 1.6	26.3 \pm 1.0	30.0 \pm 2.5
Overall				15.7 \pm 1.6	3.8 \pm 1.2	37.9 \pm 4.4		3.9 \pm 0.5	12.7 \pm 1.9	31.7 \pm 4.2

and all of the fished sites surveyed, were heavily fished by fishers exploiting a wide range of species using a variety of fishing gears (Alcala & Russ 2002). During site selection, care was taken to ensure that fished sites had habitats that were as similar as possible to nearby reserve sites. Durations of protection (DOP) when reserves were surveyed ranged from 6 mo to 11 yr. All reserves were well protected since their establishment, except for 4 reserves (Tandayag, Bio-os, Bongalanan and Andulay). For these 4, DOP was equal to the number of consecutive years of effective protection (i.e. maintenance of 'no-take' status with minimal poaching) prior to the year when the reserve was surveyed. Estimates of DOP for these 4 reserves were determined with the help of information from locals. Poaching in all reserves during years of effective protection was probably minimal, as there were only infrequent reports of such incidents from locals.

Surveys of reef fish and benthic composition. Visual census of reef fishes was carried out by 1 diver (B. Stockwell) inside and outside marine reserves along 50 m × 10 m transects (500 m² area transect⁻¹). Surveys were done on 3 transects along the reef slope (depth of 10 to 12 m) and 3 transects along the reef flat (depth of 2 to 3 m), resulting in 6 replicate transects per study site or 180 transects surveyed for the entire study. Adults and juveniles of all non-cryptic, diurnally active reef fish species were counted, and their total body length (TL) was estimated to the nearest centimetre. Fishes appeared to be the dominant herbivores at all sites. Sea urchins were not recorded because they were rare, especially on the reef slope. Benthic composition was estimated along the same transects used in the fish visual census by recording the type of substrate at every 0.5 m point intercepted by the 50 m long transect (100 points transect⁻¹). Substrate types included hard corals, macroalgae, soft corals, crustose coralline algae, dead coral, rock, sand and other sessile invertebrates (e.g. sponges, clams, etc.). Macroalgae included all fleshy brown algae (of the genera *Sargassum*, *Turbinaria*, *Dictyota*, *Hormophysa*), green algae (*Caulerpa*, *Enteromorpha*, *Ulva*) and red algae (*Euclima*, *Kappaphycus*, *Gracilaria*), as well as erect calcareous algae belonging to the genera *Halimeda* and *Padina*. However, all fleshy algae and erect calcareous algae were recorded under a single category (macroalgae [MA]) during the survey. Mean reef steepness and rugosity were estimated visually according to a 5-point scale for every 10 × 10 m area along the transects (see Russ et al. 2005). The main objective of the fish and benthic surveys was to monitor and compare fish biomass and coral cover inside versus outside reserves and not specifically to investigate relationships between herbivorous fish and macroalgal communities. Surveys were conducted between February 2006 and May 2008.

Data analyses. Analyses of the fish community data were limited to 47 species of larger-bodied herbivores belonging to 5 families: the surgeonfishes (Acanthuridae), parrotfishes (Scaridae), rabbitfishes (Siganidae), rudderfishes (Kyphosidae) and batfishes (Ephippidae) (Table 2). These herbivores were further classified into 4 functional groups: scrapers (shallow bites that only remove material from the surface), excavators (deep bites that remove portions of the substratum), browsers (feed on portions of plants, mostly macroscopic algae) and grazers (feed on the entire plant, mostly algal turfs). Classification of all species into functional groups was based on primary literature (Bellwood & Choat 1990, Clements & Choat 1995, Choat et al. 2002, 2004), except for batfishes (2 species), the classifications of which followed FishBase (Froese & Pauly 2003). Smaller-bodied herbivorous species — e.g. damselfishes (Pomacentridae), and angelfishes (Pomacanthidae) in the genus *Centropyge* — that were unlikely to benefit from reserve protection because they are not targeted by fishers, were excluded. Biomass of herbivores was estimated using length–weight relationships available from FishBase (Froese & Pauly 2003). When the length–weight relationship for a species was unknown, the relationship available for a closely related species was used.

Benthic habitat for each site was described as percent cover of each substrate type, which was equivalent to the number of points recorded per substrate type along each transect (since there were 100 points per transect). In addition, benthic habitat for each site was described as a single habitat complexity index (HCI) modified from a study done in the same region (Abesamis et al. 2006): $HCI = (\text{mean rugosity} + 1) \times (\text{hard coral cover} + 1)$. For this index, coral cover was expressed as a proportion (0 to 1), with 100% cover = 1. This index ranges from 1 to 10. Higher values indicated reefs with high hard coral cover and rugosity. Lower values indicated relatively flat expanses of sand, rubble, or rock with low hard coral cover. The original HCI proposed by Abesamis et al. (2006) included values for mean reef steepness and ranged from 1 to 50. In the present study, mean reef steepness was excluded in the computation of HCI, since all sites were inshore reefs with very gradual reef slopes.

We inferred changes in the herbivore fish community by plotting density, biomass and species richness of fish groups in reserves and fished sites against duration of reserve protection. The same was done for percent cover of each benthic substrate type and HCI to infer changes in benthic habitat. In analysing data from fished sites, we used the duration of protection values of their respective neighbouring reserve. Analyses of percent cover data focused on macroalgae and hard corals. Inferred changes in these benthic components

Table 2. Species list and mean biomass (kg per 500 m²) of all herbivorous fishes recorded in each of the 15 no-take marine reserves and fished sites. Data from fished sites were pooled. DOP: duration of protection; FG: functional group; B: browser; E: excavator; S: scraper; G: grazer; in parentheses: reserve number (see Table 1)

Family	Species	FG	Fished sites	Reserves																
				(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)		
Kyphosidae	<i>Kyphosus cinerascens</i> ^a	B											1.10				3.63			
	<i>K. vaigiensis</i> ^a	B															1.86			
	<i>Platax orbicularis</i>	B											0.73						1.27	
Ephippidae	<i>P. tetra</i> ^a	B											0.02							
	<i>Cetoscarus bicolor</i> ^a	E											0.02							
	<i>Chlorurus bleekeri</i> ^a	E											0.02							
Scaridae	<i>C. bowersi</i> ^a	E											0.02							
	<i>C. microrhinos</i>	E											0.02							
	<i>C. sordidus</i>	E											0.02							
	<i>Scarus chameleone</i> ^a	S											0.02							
	<i>S. dimidiatus</i> ^a	S											0.02							
	<i>S. flavipectoralis</i> ^a	S											0.02							
	<i>S. forsteri</i> ^a	S											0.01							
	<i>S. frenatus</i>	S											0.01							
	<i>S. ghobban</i>	S											0.01							
	<i>S. hypselopterus</i> ^a	S											0.01							
	<i>S. niger</i>	S											0.15							
	<i>S. prasiognathos</i> ^a	S											0.15							
	<i>S. psittacus</i>	S											0.07							
	<i>S. quoyi</i> ^a	S											0.17							
	<i>S. rivulatus</i>	S											0.08							
<i>S. rubroviolaceus</i>	S											0.08								
<i>S. schlegeli</i>	S											0.05								
<i>S. spinus</i> ^a	S											0.03								
<i>S. tricolor</i> ^a	S											0.08								
Siganidae	<i>Siganus argenteus</i>	B											0.03							
	<i>S. canaliculatus</i>	B											0.03							
	<i>S. corallinus</i>	B											0.13							
	<i>S. fuscescens</i>	B											0.15							
	<i>S. guttatus</i> ^a	B											0.13							
	<i>S. javus</i> ^a	B											0.13							
	<i>S. puellus</i> ^a	B											0.01							
	<i>S. punctatissimus</i> ^a	B											0.01							
	<i>S. punctatus</i> ^a	B											0.04							
	<i>S. spinus</i>	B											0.02							
	<i>S. unimaculatus</i> ^a	B											0.02							
	<i>S. virgatus</i> ^a	B											0.02							
	<i>S. vulpinus</i> ^a	B											0.18							
	Acanthuridae	<i>Acanthurus japonicus</i> ^a	G											0.08						
		<i>A. lineatus</i>	C											0.02						
<i>A. nigricans</i>		G											0.61							
<i>A. nigrofuscus</i>		G											0.29							
<i>N. annulatus</i> ^a		B											0.08							
Zebrasomidae	<i>N. lituratus</i>	B											0.18							
	<i>N. unicoloris</i>	B											0.18							
	<i>Zebrasoma scopas</i>	G											0.16							
	<i>Z. veliferum</i>	G											0.15							
	<i>Z. veliferum</i>	G											0.19							
Grand total																				

^aBiomass estimated using length-weight relationships of closely related species

were validated by examining trends in percent cover of hard substrate colonisable by algae and corals (i.e. the sum of percent cover of bare rock and dead coral), soft corals, crustose coralline algae and sponges. We also plotted percent macroalgal cover and percent hard coral cover (separately) against herbivore biomass values from all sites. This was done to validate inferred relationships of macroalgal cover and hard coral cover with duration of reserve protection.

Inferred recovery of herbivorous fish inside reserves was expected to conform to at least 1 of 4 possible models: linear, exponential, s-curve and Ricker. A linear model would suggest recovery at a constant rate without limits. An exponential model would suggest accelerated recovery without limit. The s-curve would indicate an initial phase of rapid recovery before slowing down as abundance approaches carrying capacity. The Ricker model would best describe a 'dome-shaped' recovery trajectory that declines at longer durations of protection, possibly due to increased competition with slow-recovering species or due to predation by slow-recovering predators. Inferred decline of macroalgal cover with increasing duration of reserve protection or herbivore biomass was hypothesized to conform to a linear model (declining at a constant rate)

or a logarithmic model (declining at an accelerated rate). Inferred increase of hard coral cover with increasing duration of reserve protection or herbivore biomass was assumed to conform to a linear model, due to slow growth of corals and the relatively short time frame of reserve protection considered (maximum 11 yr). Fitting of linear, exponential, s-curve and logarithmic models was performed in SPSS. Fitting of Ricker models was performed in MATLAB. The model selected was that with the highest r^2 value.

Statistical comparisons of herbivore density, biomass, macroalgal cover and coral cover at the reserve and fished sites were made separately with a univariate 2-factor ANOVA. The 2 factors in these analyses were a fixed factor Protection status (2 levels: Reserve vs. Fished) and a random factor Duration of protection (11 levels ranging from 0.5 to 11 yr). For total density, total biomass, parrotfish biomass and surgeonfish biomass, a 2-factor ANCOVA was also performed with HCI as the covariate in order to examine whether habitat was a significant predictor of fish biomass. *Post hoc* analyses using Tukey's test were made to infer the year of protection at the first significant difference in total herbivore biomass between reserve and fished sites (Zar 1999). Prior to statistical analyses, density and bio-

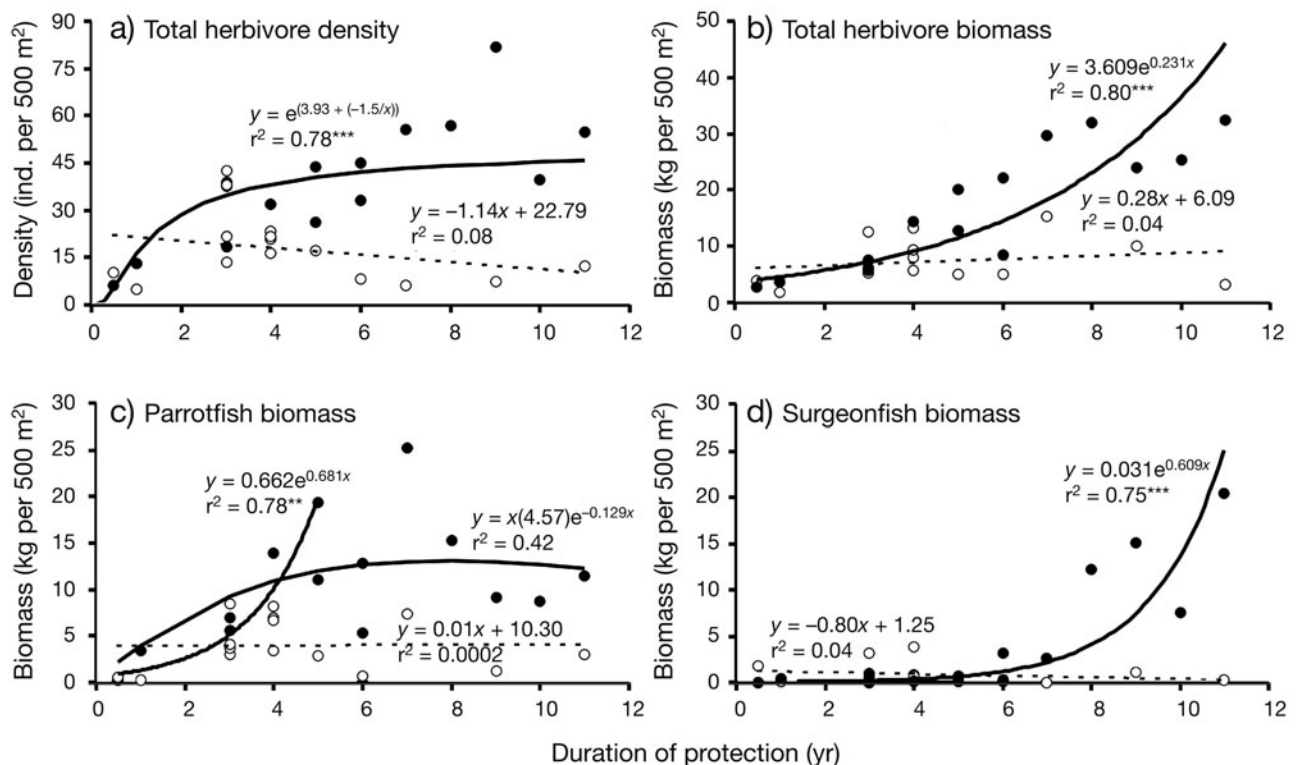


Fig. 2. Mean density and biomass of herbivorous fish plotted against duration of reserve protection. Data from 15 no-take reserves of varying ages (0.5 to 11 yr) and 15 fished sites. ●: reserves; ○: fished sites. Curved lines show regression models fitted to data from reserves: (a) total herbivore density (s-curve); (b) total herbivore biomass (exponential); (c) parrotfish (Scaridae) biomass, 0.5 to 11 yr (Ricker) and parrotfish biomass, 0.5 to 5 yr (exponential); (d) surgeonfish (Acanthuridae) biomass (exponential). *** $p < 0.001$; ** $p < 0.01$. Broken lines show linear model fitted to data from fished sites ($p > 0.05$)

mass values were log (x + 1) transformed, while percent cover values were arcsine transformed.

Principal components analyses (PCA) were used to infer changes in the biomass composition of fish families or functional groups in relation to the duration of reserve protection. Log (x + 1) transformed biomass values of each family or functional group within reserve and fished sites were used. Reserves were classified into 3 arbitrarily defined age groups: younger (0.5 to 4 yr), intermediate (5 to 7 yr) and older (8 to 11 yr). PCAs were run in PRIMER V6 software (Clark & Gorley 2006).

Size frequency histograms of parrotfishes and surgeonfishes were generated using 10 size classes in 5 cm increments (1 to 50 cm TL). Histograms were generated separately for reserves grouped into the same arbitrarily defined age groups as in the PCA. Histograms were also generated for fished sites (data from all fished sites pooled). For surgeonfishes, larger-bodied species (*Acanthurus* spp. and *Naso* spp.) were distinguished from smaller-bodied species (*Zebrasoma scopas* and *Z. velliferum*) within the same histogram. Raw data were converted to percent composition.

RESULTS

Total density and biomass of herbivorous fish in reserves had positive relationships with duration of reserve protection (Fig. 2). The inferred increase in density conformed to an s-curve model, with a rapid increase in density in the first 3 yr of reserve protection, tending to asymptote in succeeding years at about 40 to 45 fish 500 m⁻² (Fig. 2a, Table 3). The inferred increase in biomass was best described by an exponential model (Fig. 2b, Table 3). Total density and biomass in reserves were inferred to have increased by a factor of 9 and 15, respectively, over 11 yr of protection. In contrast, total density and biomass of herbivorous fish at fished sites did not exhibit any significant trends (Fig. 2a,b, Table 3). A highly significant interaction between protection status and duration of protection was detected for herbivore biomass (ANOVA; Table 4). The interaction remained significant when habitat (HCI) was

Table 3. Summary of regression analyses according to: linear (Lin), exponential (Exp), S-curve (S), Ricker (Rick) and logarithmic(Log) models. A linear model ('Lin' in parentheses) is indicated when no significant relationship was detected between variables of interest. DOP: duration of reserve protection; HB: herbivore biomass; HCI: habitat complexity index (see 'Materials and methods')

Regression	Model	r ²	F	df	p
Reserves					
Herbivores vs. DOP					
Total density	S	0.78	45.24	1,13	<0.001
Total biomass	Exp	0.80	50.76	1,13	<0.001
Parrotfish biomass					
DOP: 0.5 to 11 yr	Rick	0.42	338.5 ^a		(Lin)
DOP: 0.5 to 5 yr	Exp	0.78	15.59	1,6	0.008
Surgeonfish biomass	Exp	0.75	39.73	1,13	<0.001
Species richness	(Lin)	0.12	1.80	1,13	0.20
% Macroalgae vs. DOP					
Reef flat and reef slope	Log	0.79	48.67	1,13	<0.001
Reef flat	Log	0.72	32.61	1,13	<0.001
Reef slope	Lin	0.41	8.92	1,13	0.01
% Hard coral vs. DOP					
Reef flat and reef slope	(Lin)	0.007	0.09	1,13	0.77
Reef flat	(Lin)	0.002	0.02	1,13	0.88
Reef slope	(Lin)	<0.001	0.004	1,13	0.95
% Hard substrate (rock + dead coral) vs. DOP					
DOP: 0.5 to 11 yr	(Lin)	0.16	2.53	1,13	0.14
DOP: 0.5 to 5 yr	Log	0.69	13.33	1,6	0.01
HCI vs. DOP	(Lin)	0.02	0.25	1,13	0.62
Fished sites					
Herbivores vs. DOP					
Total density	(Lin)	0.08	1.19	1,13	0.29
Total biomass	(Lin)	0.04	0.52	1,13	0.48
Parrotfish biomass					
DOP: 0.5 to 11 yr	<0.001	0.003	1,13	0.96	
DOP: 0.5 to 5 yr	(Lin)	0.04	0.53	1,13	0.48
Surgeonfish biomass	(Lin)	0.05	0.61	1,13	0.45
% Macroalgae vs. DOP					
Reef flat and reef slope	(Lin)	0.02	0.24	1,13	0.63
Reef flat	(Lin)	0.01	0.06	1,13	0.81
Reef slope	(Lin)	0.03	0.35	1,13	0.56
% Hard coral vs. DOP					
Reef flat and reef slope	(Lin)	0.09	1.34	1,13	0.27
Reef flat	(Lin)	0.01	0.06	1,13	0.81
Reef slope	(Lin)	<0.01	0.02	1,13	0.89
All sites					
Macroalgae vs. HB					
Reef flat and reef slope	Log	0.60	41.78	1,28	<0.001
Reef flat	Log	0.57	36.38	1,28	<0.001
Reef slope	Log	0.50	27.61	1,28	<0.001
Hard coral vs. HB					
Reef flat and reef slope	(Lin)	0.07	2.01	1,28	0.17
Reef flat	(Lin)	0.08	2.55	1,28	0.12
Reef slope	(Lin)	0.01	0.25	1,28	0.62

^a Minimum sum of squared errors in the fitted Ricker model

Table 4. Summary of 2-factor ANOVAs and ANCOVAs. The factors in the ANOVA were: protection status (PS; reserve vs. fished) and duration of reserve protection (DOP). The covariate in the ANCOVA was habitat complexity index (HCI)

ANOVA				ANCOVA			
Source	F	df	p	Source	F	df	p
Total herbivore density							
PS	11.32	1,10	0.01	PS	10.01	1,10	0.01
DOP	0.90	10,160	0.57	DOP	1.03	10,159	0.49
PS × DOP	3.66	8,160	0.03	PS × DOP	3.31	8,159	0.05
				Covariate	1.21	1,159	0.30
Total herbivore biomass							
PS	18.64	1,10	<0.01	PS	19.33	1,10	<0.01
DOP	1.34	10,160	0.33	DOP	1.40	10,159	0.32
PS × DOP	8.10	8,160	<0.001	PS × DOP	7.57	8,159	<0.001
				Covariate	1.76	1,159	0.19
Parrotfish biomass							
PS	11.97	1,10	<0.01	PS	11.80	1,10	<0.01
DOP	0.96	10,160	0.54	DOP	0.90	10,159	0.57
PS × DOP	4.10	8,160	<0.001	PS × DOP	3.96	8,159	<0.001
				Covariate	1.27	1,159	0.26
Surgeonfish biomass							
PS	9.00	1,10	0.02	PS	9.03	1,10	0.02
DOP	1.83	10,160	0.20	DOP	1.85	10,159	0.19
PS × DOP	4.76	8,160	<0.001	PS × DOP	4.84	8,159	<0.001
				Covariate	0.01	1,159	0.93
Macroalgal cover							
PS	9.56	1,10	0.01				
DOP	1.68	10,160	0.23				
PS × DOP	3.58	8,160	<0.001				
Hard coral cover							
PS	1.07	1,10	0.33				
DOP	2.25	10,160	0.13				
PS × DOP	2.10	8,160	0.04				

taken into account as the covariate in the ANCOVA (Table 4). HCI was not a significant predictor of biomass. Furthermore, HCI varied among sites and did not have any significant relationship with duration of protection (Table 3). Herbivore biomass started to differ significantly between reserve and fished sites beginning at 1 yr of reserve protection (Tukey's test, $q_{2,160}$ ranged from 4.93 to 51.50, $p < 0.001$). Herbivore biomass inside reserves compared to fished sites was on average 1.4, 4.8 and 8.1 times higher at 0.5 to 4, 5 to 7 and 8 to 11 yr of protection, respectively (Table 1).

The major families of herbivorous fish that increased in biomass inside reserves with duration of reserve protection were the parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) (Fig. 2c, d). For these 2 families, the ANOVA also detected significant interactions between biomass and duration of protection (Table 4). HCI was not a significant predictor of their biomass (ANCOVA; Table 4). The inferred rates of recovery over time differed markedly between parrotfish and surgeonfish biomass (Fig. 2b,c). The inferred recovery of parrotfishes during 11 yr of protection suggested a 'dome-shaped' relationship of biomass with time

(Fig. 2c). This was best described by a Ricker model with a maximum biomass of about 13 kg per 500 m² achieved at 7 to 8 yr of reserve protection. However, inferred recovery of parrotfish biomass in the first 5 yr of protection was rapid and conformed to an exponential model (Fig. 2c). The inferred accumulation of surgeonfish biomass, on the other hand, was best described by an exponential model, with recovery slow in the first 7 yr of reserve protection, but considerably more rapid in subsequent years (Fig. 2d). Parrotfish and surgeonfish biomass at fished sites plotted against 'duration of reserve protection' (i.e. fished sites paired with adjacent reserves) did not exhibit any significant trends.

Species richness of herbivorous fish inside reserves did not have a statistically significant relationship with duration of protection (Table 3). However, species richness in reserves was often higher than in fished sites, especially in older reserves (Fig. 3a). Biomass of herbivorous fish in reserves 0.5 to 6 yr old was dominated by parrotfishes, while reserves older than 6 yr tended to have a more varied familial composition or was dominated by surgeonfishes (Fig. 3b). Since all of the parrotfishes

were classified as scrapers or excavators, these functional groups dominated younger reserves (Fig. 3c). Grazers and browsers, which were mainly the surgeonfishes and minor groups (i.e. rabbitfishes, rudderfishes and batfishes) made up a significant portion of the herbivore biomass of older reserves.

PCA plots of biomass of herbivorous fish also inferred a change from a parrotfish-dominated to a surgeonfish-dominated herbivore community with increasing age of reserves (Fig. 4, Table 5). The ordinations of biomass of family or functional group indicated that fished sites were difficult to distinguish from younger reserves (0.5 to 4 yr), but were clearly differentiated from intermediate (5 to 7 yr) and older (8 to 11 yr) reserves. Reserves of intermediate age had a higher biomass of parrotfish than fished sites and younger reserves (Fig. 4a). Older reserves were different from all other sites by the presence of higher surgeonfish biomass (Fig. 4a). Rabbitfish, rudderfish and batfish biomass had a marginal influence in distinguishing reserves from fished sites in the biplots (Table 5). Reserves of intermediate age were different from other sites by the presence of much higher biomass of

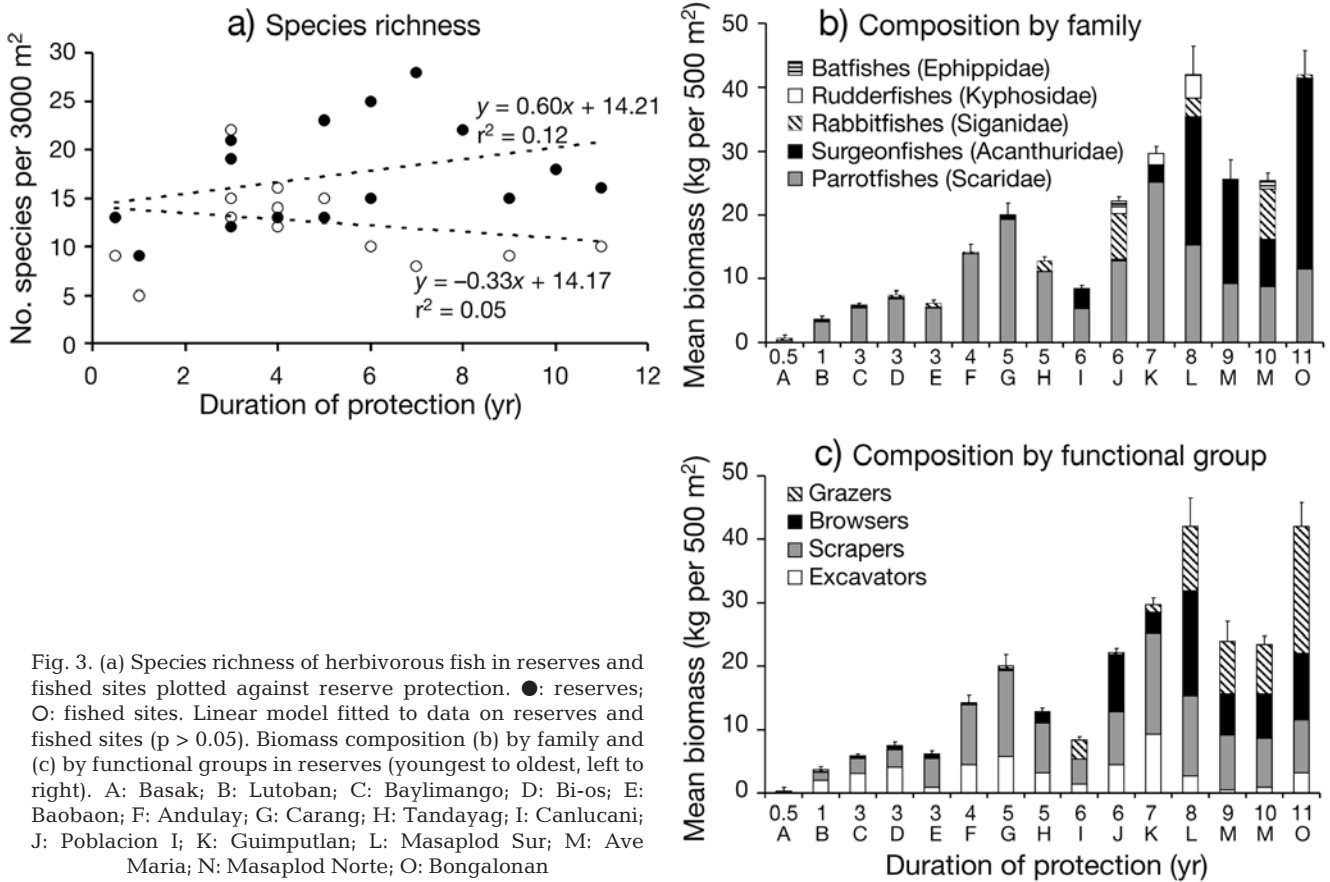


Fig. 3. (a) Species richness of herbivorous fish in reserves and fished sites plotted against reserve protection. ●: reserves; ○: fished sites. Linear model fitted to data on reserves and fished sites ($p > 0.05$). Biomass composition (b) by family and (c) by functional groups in reserves (youngest to oldest, left to right). A: Basak; B: Lutoban; C: Baylimango; D: Bi-os; E: Baobaon; F: Andulay; G: Karang; H: Tandayag; I: Canlucani; J: Poblacion I; K: Guimputlan; L: Masaplod Sur; M: Ave Maria; N: Masaplod Norte; O: Bongalonan

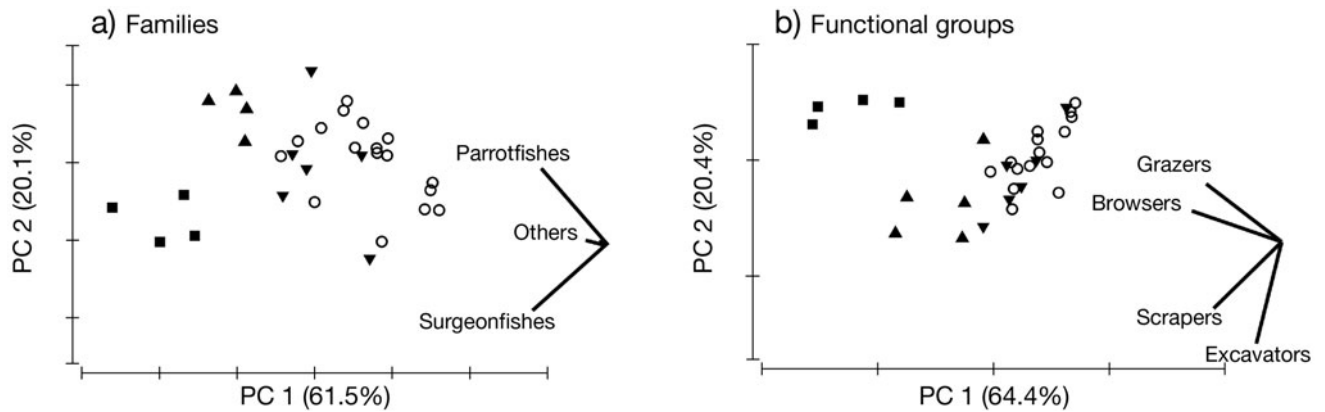


Fig. 4. PCA plots of site scores for reserve and fished sites using biomass of herbivorous fish grouped into (a) families and (b) functional groups. PC1 and PC2 combined explained 81.6% of variability in Panel (a) and 84.8% of variability in Panel (b). Vectors based on fish biomass are shown in the lower right corner of each plot. ○: fished sites; reserves were classified into 3 age groups— younger (▼; 0.5 to 4 yr), intermediate (▲; 5 to 7 yr) and older (■; 8 to 11 yr). Factor loadings are given in Table 5

scrapers and excavators (all parrotfishes), while older reserves formed a distinct group due to the higher biomass of grazers and browsers (mostly surgeonfishes) (Fig. 4b).

The modal size class of parrotfishes at fished sites was identical to that in younger reserves (11 to 15 cm

TL), but smaller compared to that in intermediate and older reserves (both 26 to 30 cm TL) (Fig. 5). In contrast to intermediate and older reserves, no parrotfishes >35 cm TL were found at fished sites and younger reserves. Modal size class of the larger-bodied species of surgeonfish (*Acanthurus* spp. and *Naso* spp.) in

Table 5. Summary of principal components analyses (PCA) using herbivore biomass values in reserve and fished sites. Herbivorous fishes were grouped into families or functional groups (see 'Materials and methods')

	PC 1	PC 2	PC 3	PC 4	PC 5
Families					
Eigenvalue	1.16	0.378	0.264	0.0773	0.00529
Percent variation explained	61.5	20.1	14.0	4.1	0.3
Cumulative percent variation explained	61.5	81.6	95.6	99.7	100.0
Component weights					
Parrotfishes (Scaridae)	-0.648	0.707	-0.265	0.101	-0.009
Surgeonfishes (Acanthuridae)	-0.687	-0.702	-0.176	0.045	0.040
Rabbitfishes (Siganidae)	-0.278	0.052	0.919	0.253	-0.102
Rudderfishes (Kyphosidae)	-0.173	0.054	0.204	-0.961	-0.049
Batfishes (Ephippidae)	-0.015	0.043	0.109	-0.022	0.993
Functional groups					
Eigenvalue	1.62	0.512	0.242	0.14	
Percent variation explained	64.4	20.4	9.6	5.6	
Cumulative percent variation explained	64.4	84.8	94.4	100.0	
Component weights:					
Scrapers	-0.516	-0.433	0.738	-0.031	
Excavators	-0.214	-0.736	-0.593	-0.246	
Browsers	-0.626	0.189	-0.297	0.696	
Grazers	-0.544	0.484	-0.125	-0.674	

younger reserves was slightly larger than that in fished sites (16 to 20 vs. 11 to 15 cm TL), but was identical to that in reserves of intermediate age (Fig. 5). Older reserves had the largest modal size class for the larger-bodied surgeonfishes (26 to 30 cm TL). Only the older reserves had surgeonfishes that were >35 cm TL. Modal size class of the smaller-bodied surgeonfish species (*Zebrasoma* spp.) were the same among fished sites and reserves of all age groups (11 to 15 cm TL).

Macroalgal cover inside reserves had a strong negative relationship with duration of reserve protection (Fig. 6a). The trend inferred a 13-fold reduction in macroalgal cover from a maximum of 13.5% to negligible levels (<1% cover) 11 yr after reserve establishment. This relationship conformed to a logarithmic model, suggesting a more rapid rate of decline of macroalgal cover in the first 5 yr following reserve establishment. The inferred decline of macroalgae with increasing duration of protection was evident on both the reef flat and the reef slope of reserves, but was more rapid on the reef flat (logarithmic, $r^2 = 0.72$) than on the reef slope (linear, $r^2 = 0.41$) (Table 3). In contrast, macroalgal cover in fished sites did not show any significant trends (Fig. 6a). A significant interaction was detected between protection status and duration of protection for macroalgal cover (ANOVA; Table 4). Macroalgal cover in reserves relative to fished sites was on average 1.7, 6.3 and 25.1 times lower at 0.5 to 4, 5 to 7, and 8 to 11 yr of protection, respectively (Table 1). Macroalgal cover plotted against herbivore biomass at all sites (reserve and fished) showed a neg-

ative trend that conformed to a logarithmic model (Table 3, Fig. 6b). There was no significant relationship between hard coral cover in reserves and duration of reserve protection (Fig. 6c). The relationship between hard coral cover and herbivore biomass at all sites was not significant (Fig. 6d). There were no significant relationships between percent cover of other benthic components in reserves (i.e. soft corals, crustose coralline algae and sponges) and duration of reserve protection, except for the variate 'hard substrate'. Although percent cover of hard substrate in reserves showed no significant trends throughout 11 yr of protection, a significant increasing trend was detected for this variate in the first 5 yr of protection. This trend was best described by a logarithmic function (Fig. 6e).

DISCUSSION

Protection provided by Philippine no-take marine reserves has been inferred to result in relatively rapid (within 5 yr) reductions of macroalgae on reefs, due to recovery of exploited populations of larger-bodied herbivorous fishes. Results did not suggest an increase in coral cover given the 'decline' in macroalgal cover with reserve protection. These patterns were inferred by comparing between reserves of different ages with fished sites. We concede that this approach is inferior to before-after-control-impact-pair (BACIP) investigations of the effects of marine reserves, particularly BACIP studies that monitor over long-time periods (Russ 2002, Edgar et al. 2004, Russ et al. 2005). The approach we used can be problematic if habitat differences between reserve and fished sites, and lack of knowledge of poaching histories of reserves, confound the effect of reserve protection on fish abundance and benthic cover (Russ 2002, Edgar et al. 2004, Russ et al. 2005). However, we accounted for the potential confounding effect of habitat, specifically reef rugosity and coral cover, 2 of the most important habitat variables that can influence fish abundance on coral reefs strongly. Our analyses showed that benthic habitat was not a significant predictor of biomass of herbivorous fish. Therefore, the inferred increase in density and biomass of herbivorous fish populations was likely to be a direct effect of reserve protection, while the inferred reduction of macroalgae was likely to be an indirect effect of increased herbivore biomass.

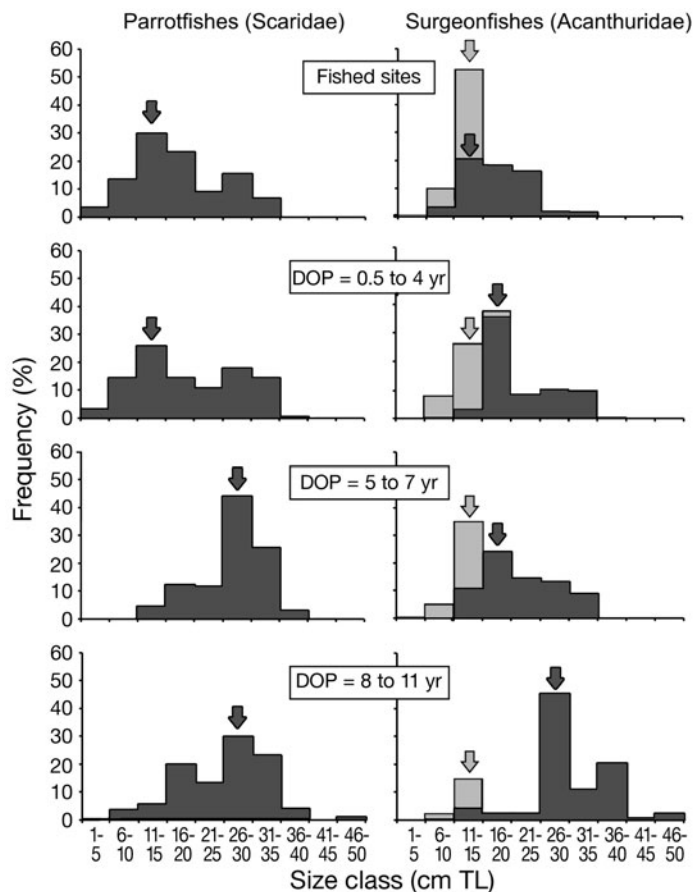


Fig. 5. Size-frequency histograms of parrotfishes (Scaridae; left column) and surgeonfishes (Acanthuridae; right column) for fished sites and reserves of different age groups (top to bottom: younger, 0.5 to 4 yr; intermediate, 5 to 7 yr; older, 8 to 11 yr). Smaller-bodied surgeonfishes (*Zebrasoma* spp.) were distinguished from larger-bodied surgeonfishes (*Acanthurus* and *Naso* spp.), which are denoted by light and dark columns, respectively. ↓ Modal size class: parrotfishes and larger surgeonfishes; ↓ small surgeonfishes. DOP: duration of protection

Differences in larval supply of fish among sites may also confound the effect of reserve protection on the abundance of herbivorous fishes. Furthermore, differences among sites in exposure to nutrients (e.g. from agricultural runoff, sewage outfall) may confound the indirect effect of reserve protection on macroalgal cover. For either or both of these factors to confound the results, the youngest reserves would, on average, have to be in areas with low levels of larval supply and be exposed to high levels of nutrients, and the oldest reserves would, on average, be subject to the opposite conditions. This is very unlikely in the present study. The majority (11 out of 15) of the reserves were 'paired' with nearby control sites (most controls <500 m from reserves, 7 controls <2 km from reserves). Patterns of abundance of herbivorous fishes and macroalgae in

the reserves usually contrasted with those found at nearby control sites. In addition, many of the reserves are situated very close to one another, and neighbouring reserves sometimes differed substantially in DOP (e.g. Reserves 1, 2, 6, 10, 12, 14 in Fig. 1 ranged from 0.5 to 10 yr of protection; see Table 1). For larval supply and nutrient levels to confound the results, both factors would need to vary in a predictable manner according to reserve age over relatively short distances. Preliminary larval dispersal modelling and empirical monitoring of fish recruitment at the relevant spatial scales suggest that this is unlikely (Abesamis et al. unpubl. data). Furthermore, there are no point sources of nutrients (e.g. rivermouths, creeks, densely populated areas) along the stretches of coast occupied by neighbouring reserves that may affect only the younger reserves. Based on our own observations and experience, the more likely possibility is that neighbouring reserves along the same stretch of coast experience similar levels of nutrient exposure, especially during the wet season.

Recovery of exploited reef fish populations after significant durations of protection has been demonstrated by many studies (see reviews by Roberts & Hawkins 2000, Russ 2002, Halpern 2003, Sale et al. 2005). However, few studies have shown that recovery of herbivorous fish inside no-take reserves can lead to reduction of macroalgae. Studies have demonstrated that herbivore (fish and/or urchin) biomass was negatively correlated with macroalgal cover in both protected and fished sites (McClanahan et al. 2001, Williams & Polunin 2001, Newman et al. 2006). Mumby et al. (2006) found that higher densities of large parrotfishes in a marine park in the Bahamas (18 yr of reserve protection) were associated with grazing being twice as high in reserve than in fished sites, which, in turn, was associated with a 4-fold lower macroalgal cover in the reserve. This lower cover of macroalgae did not affect overall coral cover or community structure (Mumby et al. 2007). However, Mumby et al. (2007) detected a 2-fold higher density of coral recruits in the marine park. They argued that the complexities of coral community dynamics probably masked any influence of grazing by herbivores on coral cover and community structure. In the context of our study, no significant relationship of coral cover with duration of reserve protection or with herbivore biomass was observed. This lack of a relationship may be explained in part by the relatively limited range of years of protection (0.5 to 11 yr). Similarly, Newman et al. (2006) did not find any evidence for coral recovery with increased herbivore biomass, which they attributed to the greater generation times of corals compared to fish and algae. An alternative interpretation is that no-take reserve protection in our sites has a relatively weak effect on coral

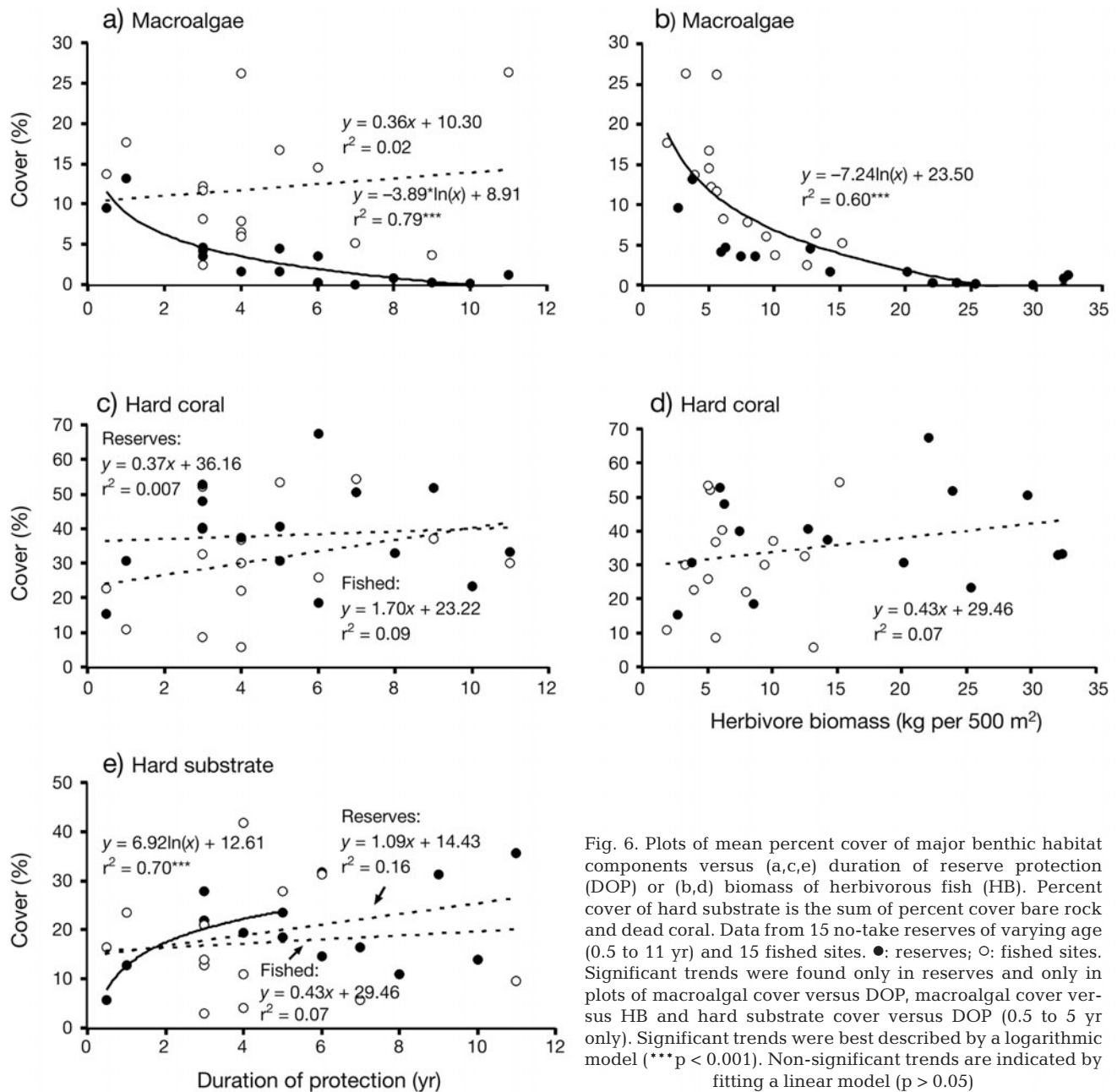


Fig. 6. Plots of mean percent cover of major benthic habitat components versus (a,c,e) duration of reserve protection (DOP) or (b,d) biomass of herbivorous fish (HB). Percent cover of hard substrate is the sum of percent cover bare rock and dead coral. Data from 15 no-take reserves of varying age (0.5 to 11 yr) and 15 fished sites. ●: reserves; ○: fished sites. Significant trends were found only in reserves and only in plots of macroalgal cover versus DOP, macroalgal cover versus HB and hard substrate cover versus DOP (0.5 to 5 yr only). Significant trends were best described by a logarithmic model ($***p < 0.001$). Non-significant trends are indicated by fitting a linear model ($p > 0.05$).

cover, since even on reefs with heavy fishing pressure, coral cover was still relatively high. Hard coral cover was consistently between 25 and 50% in most reserves and fished sites (Fig. 6d), indicating that the reefs studied were not in the most degraded state (<25% coral cover) according to the classification of Philippine reefs by Licuanan & Gomez (2000). On the other hand, the highest density of municipal fishers occurs in the central Philippine islands (Alcala & Russ 2002), where our study took place, and our study reefs were all coastal, usually near fishing villages.

Biomass of herbivorous fishes inside the reserves in the present study was dominated by parrotfishes (Scaridae) and surgeonfishes (Acanthuridae). The inferred recovery rates of the 2 families were very different. A Ricker model fitted to the parrotfish data suggested an initial increase in biomass up to the 7th to 8th year of protection, followed by a gradual decline. In the first 5 yr of protection, however, a strong exponential relationship between parrotfish biomass and duration of protection was detected. In contrast, surgeonfish recovery was exponential throughout 11 yr of

protection, showing a rapid increase in biomass only after the 7th year (Fig. 2). The inferred recovery patterns of these 2 families were similar to the results of a study by McClanahan et al. (2007) in Kenya that included reserves that were much larger (6 to 28 km²) and much older (up to 37 yr of protection) than the small reserves that we studied (0.06 to 0.30 km²). In the Kenyan reserves, the rate of recovery of parrotfish biomass began to slow down after 10 to 12 yr (McClanahan et al. 2007). Our study, as well as that of McClanahan et al., inferred that parrotfish populations can attain carrying capacity after a relatively short period (7 to 12 yr) of reserve protection. Inferences from the present study are also consistent with time-series data collected by Samoily et al. (2007) in newly established marine reserves in the central Philippines. They detected a rapid increase in parrotfish density within the first 3 to 4 yr of protection. The more rapid increase in biomass of parrotfish than surgeonfish in the present study is likely a result of contrasting life history traits (Choat & Axe 1996, Choat et al. 1996, 2002, McClanahan et al. 2007). Parrotfish generally have shorter life-spans, faster growth and generally faster population turnover rates than surgeonfish (Choat & Axe 1996, Choat et al. 1996, Choat & Robertson 2002). This explanation is also supported by the results of the size-frequency distribution analysis. Parrotfishes were inferred to attain a maximum modal size class sooner (within 7 yr) than the surgeonfishes after protection from fishing (Fig. 5). The inferred exponential increase in surgeonfish biomass with duration of reserve protection of up to 11 yr is similar to that measured over time for biomass of large predatory reef fishes in small Philippine reserves (Russ & Alcala 2003, 2004). Biomass of predatory reef fishes increased exponentially for periods of 9 to 18 yr of no-take reserve protection at Sumilon and Apo Islands (Russ & Alcala 2003, 2004).

The only group of herbivorous fish that showed an inferred rapid increase in biomass within the first 5 to 7 yr of reserve protection was the parrotfishes. This increase coincided with the greatest inferred rates of decline of macroalgae. Thus, it is very likely that parrotfishes were largely responsible for reducing macroalgae during the initial years of reserve protection. The parrotfish abundance could have increased through recruitment or migration from fished sites. The former is more likely for 2 reasons. (1) Parrotfish numbers in fished sites were very low due to fishing pressure (see Table 1), so that fished sites were poor sources of migrants into reserves. (2) The increase in modal size in reserves with time (Fig. 5) is consistent with recruitment and subsequent growth of fishes.

Proper temporal monitoring would likely have given us greater insight into mechanisms of interaction between herbivores and macroalgae, particularly the

mechanism by which increased abundance of parrotfishes result in fewer macroalgae (since we presumably would have observed the nature of the interaction over time). Parrotfish do not normally ingest thalli of macrophytic algae (Bellwood & Choat 1990), so the inferred decline in macroalgae in reserves is not likely to be due to a simple process of 'herbivores cropping down macroalgae'. Many macroalgae on coral reefs are ephemeral, sloughing seasonally (e.g. *Sargassum*). It is possible that feeding by parrotfish has 2 effects: (1) keeps short bases of macroalgae (bases remain after the main thallus sloughs seasonally) cropped down, preventing development of large thalli, and (2) reduces recruitment of macroalgae due to incidental ingestion of macroalgal recruits. Seasonal sloughing of macroalgae, plus the 2 cropping mechanisms above, could lead to a fairly rapid reduction of macroalgal cover in reserves as parrotfish populations recover. This is supported by the finding that only hard substrate (among the remaining benthic components) was inferred to have increased with duration of reserve protection (Fig. 6e). We assume here that percent cover of hard substrate accurately represents the amount of habitat uncolonised by macroalgae (or corals). The inferred increase in hard substrate cover occurred during the initial years of reserve protection, and thus at the same time as the inferred declines in macroalgal cover (Fig. 6a,e).

No-take marine reserves may not always prevent a shift from coral to algal dominance following mass mortality of corals. For instance, herbivorous fish populations may not necessarily increase in abundance inside reserves as much as reduced fishing mortality on them would predict, due to trophic interactions between herbivores and their potential predators (Graham et al. 2003, Mumby et al. 2006, McClanahan et al. 2007). Trophic interactions may not have been strong enough to slow down or prevent recovery of herbivores (parrotfishes) for at least 2 reasons. (1) Both the herbivores and their potential predators (e.g. groupers and snappers) are usually fished down prior to reserve establishment in the areas we studied. (2) Recovery rates of the herbivores (inferred from the present study) are more rapid than those of large predators (Russ & Alcala 1998a, b, 2003, 2004). Also, herbivores may only be capable of maintaining a limited amount of benthic space in a cropped state (Mumby 2006, Williams & Polunin 2001), and therefore space occupied by corals and other sessile invertebrates is also a critical factor.

The history and severity of disturbance, as well as the history of reserve protection, need to be taken into consideration when evaluating the efficacy of reserves in promoting reef resilience. In the present study, the main chronic disturbance was intense fishing (before reserve establishment) spanning decades (Carpenter

1977, McManus 1997, Russ & Alcala 1998a, Alcala & Russ 2002). The main acute disturbance was probably coral bleaching in 1998, but we have no specific information on the extent of coral bleaching and mortality at our study sites. There were, however, reports of 'medium' to 'severe' bleaching in the region (Arceo et al. 2001, Raymundo & Maypa 2002). In addition, most of the no-take reserves we studied were established after 1998 (11 of 15 reserves). It is also possible that bleaching may not have been severe in our study sites, as indicated by relatively high coral cover (18 to 67% in reserves, 6 to 54% in fished sites) and low macroalgal cover (10 to 13% in reserves \leq 1 yr old, 3 to 26% in fished sites) 8 to 10 yr after the 1998 El Niño–Southern Oscillation event. Hence, surviving corals may also have been critical in preventing macroalgal dominance, simply through space occupation and through facilitating herbivory by providing sufficient recruitment and juvenile habitat for herbivorous fishes. Results suggest that reserves can facilitate reef resilience in the face of the combined effects of overfishing and bleaching.

In conclusion, the results of the present study support the notion that no-take marine reserves can enhance coral reef resilience by allowing recovery of functionally important populations of herbivorous fishes. We showed indirect evidence for parrotfishes recovering rapidly and reducing macroalgal cover within 5 yr of reserve protection and that this suppression of macroalgae continued in the later years of reserve protection. In contrast, the inferred relationships between hard coral cover and the duration of reserve protection and hard coral cover and herbivore biomass were non-significant. Even in the fished sites, coral cover (mostly >25%) was much higher than macroalgal cover (mostly <15%). Thus, there was no evidence that the current levels of fishing of herbivores on these reefs has led to 'benthic phase shifts' (changes from coral to macroalgal dominance). Competitive interactions between algae and corals when herbivores are heavily fished may not necessarily result in corals losing out to algae (McCook et al. 2001). Such outcomes are likely site-, species- and time-specific (McCook et al. 2001). The results of the present study do, however, highlight the critical role of key groups of herbivorous fishes and the need to conserve these groups not only within reserves but also beyond reserve boundaries through conventional fisheries management. Implementing fisheries management in developing countries is undoubtedly a big challenge, but nevertheless necessary. No-take marine reserves, although apparently effective, are currently being established at a rate that is insufficient to protect ecologically significant proportions of reef area to reverse the trend of coral reef degradation.

Acknowledgements. We thank M. C. Quibilan, L. J. Raymundo and H. O. Arceo and 4 anonymous reviewers for helpful comments on the manuscript. Research was funded in part by a Pew Fellowship in Marine Conservation (1999 to 2002) to A.C.A. and G.R.R. and by an Australian Research Council grant (2006 to 2009) to G.R.R. through the ARC Centre of Excellence for Coral Reef Studies at James Cook University. Additional support was obtained from a USAID-EcoGov II-funded Small Grants Program (2006) and the IUCN-funded Ecosystems, Protected Areas and People (EPP) Project implemented by SUAKCREM. R.A.A. was supported by an International Postgraduate Research Scholarship at James Cook University. We thank M. Inocencio and J. Maypa for assistance during fieldwork. We are grateful to the local government units and people's organizations of the various municipalities where fieldwork was conducted. This is Contribution No. 30 of SUAKCREM.

LITERATURE CITED

- Abesamis RA, Russ GR, Alcala AC (2006) Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. *Aquat Conserv Mar Freshwat Ecosyst* 16:349–371
- Alcala AC, Russ GR (2002) Status of Philippine coral reef fisheries. *Asian Fish Sci* 15:177–192
- Alcala AC, Russ GR (2006) No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. *Ambio* 35:245–254
- Arceo HO, Quibilan MC, Alino PM, Lim G, Licuanan WY (2001) Coral bleaching in Philippine reefs: coincident evidences with mesoscale thermal anomalies. *Bull Mar Sci* 69: 579–593
- Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ Biol Fishes* 28:189–214
- Bellwood DR, Hughes TP, Folke C, Nystroem M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Burke L, Selig L, Spalding M (2002) Reefs at risk in Southeast Asia. World Resources Institute, Washington, DC
- Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function of a coral reef. *Proc Natl Acad Sci USA* 105: 16201–16206
- Carpenter KE (1977) Philippine coral reef fisheries resources. *Philipp J Fish* 15:95–126
- Carpenter KE, Springer VG (2005) The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environ Biol Fishes* 72:467–480
- Choat JH, Axe LM (1996) Growth and longevity in acanthurid fishes; an analysis of otolith increments. *Mar Ecol Prog Ser* 134:15–26
- Choat JH, Robertson DR (2002) Age-based studies. In: Sale PF (ed) *Coral reef fishes dynamics and diversity in a complex ecosystem*. Academic Press, London, p 57–80
- Choat JH, Axe LM, Lou DC (1996) Growth and longevity in fishes of the family Scaridae. *Mar Ecol Prog Ser* 145:33–41
- Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs. I. Dietary analyses. *Mar Biol* 140:613–623
- Choat JH, Robbins WD, Clements KD (2004) The trophic status of herbivorous fishes on coral reefs. II. Food processing modes and trophodynamics. *Mar Biol* 145:445–454
- Clark KR, Gorley RN (2006) PRIMER V6: User manual/tutorial. PRIMER-E, Plymouth
- Clements KD, Choat JH (1995) Fermentation in tropical

- marine herbivorous fishes. *Physiol Zool* 68:355–378
- Edgar GJ, Bustamante RH, Farina JM, Calvopina M, Martinez C, Toral-Granda MV (2004) Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environ Conserv* 31:212–218
- Froese R, Pauly D (2003) Fishbase. Available at: www.fishbase.org
- Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol Evol* 18: 448–454
- Gomez ED, Alino PM, Yap HT, Licuanan WY (1994) A review of the status of Philippine reefs. *Mar Pollut Bull* 29:62–68
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30: 200–208
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci USA* 103:8425–8429
- Halpern BS (2003) The impact of marine reserves: do reserves work and does size matter? *Ecol Appl* 13:117–137
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551
- Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D and others (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360–365
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26: 641–653
- Licuanan WY, Gomez ED (2000) Philippine coral reefs, reef fishes and associated fisheries: status and recommendations to improve their management. Australian Institute of Marine Science, Townsville
- McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380–391
- McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol Appl* 17: 1055–1067
- McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417
- McManus JW (1997) Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. *Coral Reefs* 16:121–127
- Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecol Appl* 14:1709–1723
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecol Econ* 29:215–233
- Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol Appl* 16: 747–769
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV and others (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- Mumby PJ, Harborne AR, Williams J, Kappel CV and others (2007) Trophic cascade facilitates coral recruitment in a marine reserve. *Proc Natl Acad Sci USA* 104:8362–8367
- Newman MJH, Paredes GA, Sala E, Jackson JBC (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecol Lett* 9:1216–1227
- Nyström M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio* 35:30–35
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F and others (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ Conserv* 27:179–200
- Raymundo LJ, Maypa AP (2002) Recovery of the Apo Island Marine Reserve, Philippines, 2 years after the El Nino bleaching event. *Coral Reefs* 21:260–261
- Roberts CM, Hawkins JP (2000) Fully-protected marine reserves: a guide. WWF, Washington, DC, and University of York
- Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. In: Sale PF (ed) *Coral reef fishes dynamics and diversity in a complex ecosystem*. Academic Press, London, p 421–443
- Russ GR, Alcala AC (1998a) Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* 17:383–397
- Russ GR, Alcala AC (1998b) Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* 17:399–416
- Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983–2000. *Ecol Appl* 13:1553–1565
- Russ GR, Alcala AC (2004) Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138:622–627
- Russ GR, Stockwell B, Alcala AC (2005) Inferring versus measuring rates of recovery in no-take marine reserves. *Mar Ecol Prog Ser* 292:1–12
- Sale PF, Cowen RK, Danilowicz BS, Jones GP and others (2005) Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol* 20:74–80
- Samoilys MA, Martin-Smith KM, Giles BG, Cabrera B, Anticamara JA, Brunio EO, Vincent ACJ (2007) Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. *Biol Conserv* 136:584–601
- Veron JEN (2000) *Corals of the world*. Australian Institute of Marine Science, Townsville
- Wilkinson C (2008) *Status of coral reefs of the world, Vol 3*. Australian Institute of Marine Science, Townsville
- Williams ID, Polunin NVC (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19:358–366
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, London