



# Spatial and temporal variation of abundance, biomass and diversity within marine reserves in the Philippines

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## ABSTRACT

**Aim** The objective of this study was to investigate the influence of protection duration (years of fishing closure) and location (distance from shore) on reef fish diversity.

**Location** Danajon Double Barrier Reef, Bohol, Philippines.

**Methods** Reef fish abundance and size structure, by species, were obtained monthly using replicated underwater visual belt transects ( $n = 8$ ;  $70 \times 5$ -m belt transects) over 3 years (2002–2005) at eight sites that included six marine reserves and two unprotected reef areas. We analysed species accumulation curves, diversity indices and abundance–biomass comparison (ABC) curves within and across the study sites to assess the influence of protection duration and location.

**Results** Analyses showed that longer protection duration impacted reef fish diversity at both inshore and offshore sites by shifting ABC curves from higher abundance than biomass curves at fished sites to higher biomass than abundance curves at most of the protected sites. Protection duration did not significantly influence either the rate of species accumulation within sites or the 12 diversity indices measured across the study sites. The offshore sites consistently showed higher rates of species accumulation and diversity indices values than inshore sites with similar protection duration. One protected offshore young marine reserve site that has been assessed as the least well-managed showed patterns more consistent with the fished sites.

**Main conclusions** Analyses showed that protection duration mainly impacted diversity by increasing the dominance of large-bodied species and enhancing total biomass. Besides protection duration, reserve location influenced species accumulation curves and diversity indices.

## Keywords

Biodiversity, conservation, marine protected areas, no-take zones, overfishing, small-scale fisheries.

## INTRODUCTION

Understanding spatio-temporal patterns and scale dependence of biodiversity is important for effective biodiversity conservation strategies (Roberts & Gilliam, 1995). Globally, the high diversity in tropical regions appears related to higher temperature, which accelerates genetic divergence and speciation (Briggs, 2007). Regionally, diversity research focuses on dispersal and speciation, which relate to species interactions, adaptation and local extinction (Cornell & Lawton, 1992). The variety of diversity concepts are mirrored by a proliferation of diversity indices that can be grouped as: (i) measures of species

accumulation sampled across space or time (Colwell *et al.*, 2004); (ii) measures of richness, diversity, and evenness (Kempton, 1979); and (iii) measures of dominance, i.e. abundance–biomass comparison (ABC) curves (Clarke & Gorley, 2006). Despite difficulties in interpretation of the numerous diversity measures (Hurlbert, 1971), they remain the most common metrics to quantify diversity (Hill, 1973; Clarke & Warwick, 2001).

Tropical coral reefs are highly diverse ecosystems, and thus ideally suited for advancing our understanding of diversity patterns. The centre of global coral reef diversity is the Western Pacific Coral Triangle, spanning an area that includes the

Philippines and parts of Indonesia, Malaysia, Papua New Guinea and the Solomon Islands (Paulay, 1997). Processes thought to drive fish diversity in coral reefs include dispersal (Mora *et al.*, 2003), habitat complexity (Roberts & Ormond, 1987), niche partitioning (Knowlton & Jackson, 1994) and total reef area (Galzin *et al.*, 1994). In addition, human-induced disturbances such as fishing (Pauly *et al.*, 2002) and global warming (Jones *et al.*, 2004) impact reef diversity and threaten coral reefs (McClanahan, 2002). Variations in the intensity of processes influencing local reef diversity likely contribute to the observed spatio-temporal heterogeneity in reef communities (Nanami & Nishihira, 2003).

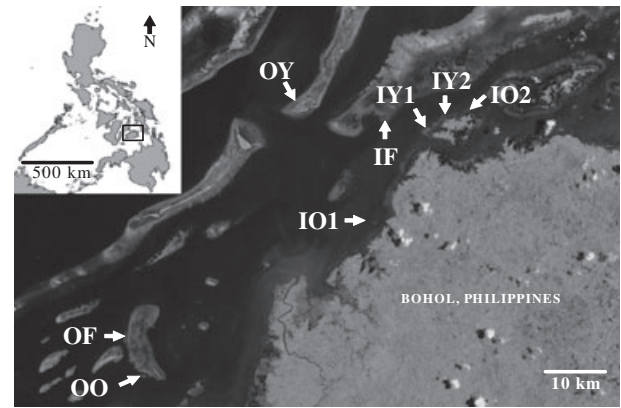
Marine reserves are a major tool for protecting reef diversity (Lubchenco *et al.*, 2003), but our understanding of how diversity changes within reserves remains limited (Sale *et al.*, 2005). While meta-analyses suggest that marine reserves rapidly restore depleted diversity (Halpern & Warner, 2002), long-term empirical studies suggest that the recovery of fish diversity may take substantially longer, depending on a given species' life history dynamics (Russ & Alcala, 2004; McClanahan *et al.*, 2007). Thus, the current intense focus on the establishment of marine reserves in the Philippines offers unique opportunities to improve our understanding of spatio-temporal dynamics of reef fish diversity in relation to the duration of protection and spatial factors such as distance from terrestrial environments (Alcala & Russ, 2006; Wood & Dragicvic, 2007).

Here, we present the results of a 3-year study, where we monitored the changes in spatio-temporal patterns of reef fish diversity on a monthly basis at eight coral reef sites with different protection duration (0–10 years of protection) and site location (inshore vs. offshore).

## METHODS

### Study sites

We selected eight study sites within the Danajon Bank double barrier reef system in the central Philippines, six of which were established marine reserves and two were open to fishing (Fig. 1; Table 1). The sites had different starting dates of protection enforcement (reserve establishment) and were categorized based on the duration of enforcement during the 3-year study period as fished sites (F; zero years reserve enforcement;  $n = 2$ ), younger marine reserves (Y; between 1 and 3 years of enforcement;  $n = 3$ ) or older marine reserves (O; between 3 and 10 years enforcement;  $n = 3$ ) (Table 1). In addition, sites were categorized as inshore (I; between 4 and 12 km from shore;  $n = 5$ ) or offshore (O; between 22 and 30 km from shore;  $n = 3$ ) based on distance from the mainland (Table 1). Unfortunately, time (monthly sampling schedule), manpower and resource restrictions did not allow us to sample a properly balanced design with sufficient and balanced replication of treatments (e.g. several control sites in inshore and offshore environments).



**Figure 1** Location of the study sites on Danajon Bank, off the northwest coast of Bohol in the central Philippines (image source: <http://oceancolor.gsfc.nasa.gov/cgi/landsat.pl>). See Table 1 for site codes and details.

### Field sampling protocol and data treatment

We used underwater belt transects to sample fish communities at each site on a monthly basis between June 2002 and February 2005. One day prior to each monthly sampling period, eight 70-m transects were laid haphazardly at each site along the reef slope parallel to the reef crest. On census day, two divers swam parallel along each side of the transect line to identify, count and estimate the total length of all non-cryptic fish species that were encountered within 2.5 m of each transect side (total transect width: 5 m). Following the method described by Bellwood & Alcala (1988), the first 50 m of each transect was devoted to sampling fishes greater than 10 cm in total length (TL), and the last 20 m of each transect was devoted to fishes between 1 and 10 cm TL. Splitting transects into two sections enabled us to count the abundant but more sedentary small fish more accurately, while not missing the less abundant but more mobile larger fish while doing so. Taxonomic identification was based on FishBase (<http://www.fishbase.org>, Froese & Pauly, 2003), taxonomic literature (e.g. Randall *et al.*, 1997; Lieske & Myers, 2001) and other internet sources (e.g. <http://www.zipcode-zoo.com>). Each census diver was extensively trained prior to the start of the surveys, and retrained every 6 months for consistency in taxonomic identification, visual detection and size estimation. The visual census method and approaches to training and retraining were modified from Bell *et al.* (1985), Fowler (1987), St. John *et al.* (1990), English *et al.* (1997) and Samoily & Carlos (2000).

Count data (abundance estimates) were converted to density (abundance  $m^{-2}$ ), while length estimates were converted to weight ( $g m^{-2}$ ) using standard length–weight relationships obtained from FishBase (<http://www.fishbase.org>). In a few cases with no species-specific length–weight relationships, the length–weight relationships of the closest and most similar shaped congeners were used.

Benthic habitat structure was sampled every 2–4 months using a line intercept technique (LIT) on the first 20 m of each

**Table 1** Study sites on Danajon Bank, their management status and distance relative to the mainland of Bohol, Philippines. Source for management rating in 2004: Coastal Conservation Education Foundation (CCEF) in the Philippines, which adopts a point rating for marine reserve management (see <http://www.coast.ph/>), with a maximum score of 38. Rating categories are as follows: 6 points = pass; 12 points = fair; 20 points = good; 25 points = very good and 30+ = excellent.

Site code	Starting year of enforcement	Management rating in 2004	Protection-duration categories	Shortest distance from mainland of Bohol (km)	Location categories
IF	Unprotected	–	Fished (F)	12	Inshore (I)
OF	Unprotected	–	Fished (F)	30	Offshore (O)
IY1	2002	19	Young marine reserves (Y)	5	Inshore (I)
IY2	2002	19	Young marine reserves (Y)	8	Inshore (I)
OY	2002	12	Young marine reserves (Y)	30	Offshore (O)
IO1	1999	25	Older marine reserves (O)	4	Inshore (I)
OO	1999	28	Older marine reserves (O)	22	Offshore (O)
IO2	1995	34	Older marine reserves (O)	10	Inshore (I)

transect line (English *et al.*, 1997). Hard corals were categorized as massive, branching, foliose, knobby, encrusting, digitate, mushroom or columnar, while anemones, bivalve shells, sponges, ascidians, soft corals, fire corals, *Sargassum*, algal turf, dead hard coral, including rubble and sand/silt were recorded separately. As sand and silt comprised only 5.3% ( $\pm 2.8$  SE) and 5.1% ( $\pm 1.2$  SE), respectively, of the total benthic cover within each site, these two categories were not presented in Fig. S1. Changes in benthic cover at each site over time were examined using linear regression. Further, two-way analysis of variance (Model 1 Fixed Factors ANOVA) tested the effects of protection duration and site location on (i) the mean benthic cover estimates for each site during the last year of sampling and (ii) the slope of the benthic regression line for each site. Throughout this study, we tested the statistical assumptions underlying the analysis of variance (for details, see Anticamara, 2009, <https://circle.ubc.ca/handle/2429/7916>). As we did not detect any significant influence of protection duration and site location on either measure (Figs S1 and S2), we did not include benthic habitat as a factor in our assessment of reef fish diversity.

### Species accumulation curves

We plotted the species accumulation curve (Clarke & Gorley, 2006) for each site, using the mean monthly count of species recorded during the 3-year sampling period (Clarke & Gorley, 2006), and fitted a logarithmic model to these data. We used two-way analysis of variance (Model 1 Fixed Factors ANOVA) to test the effects of protection duration and site location on the slope of each logarithmic model within each site.

### Diversity indices

We initially examined 12 different diversity indices, calculated for mean monthly abundance estimates at each site during the 3-year period: species richness, Hill's  $N_1$ ,  $N_2$ ,  $N_{\infty}$ ,  $N_{10}$ ,  $N_{21}$ ,  $N_{10'}$ ,  $N_{21'}$ , Pielou's  $J$ , Shannon–Weiner's  $\ln(H')$ , Simpson's

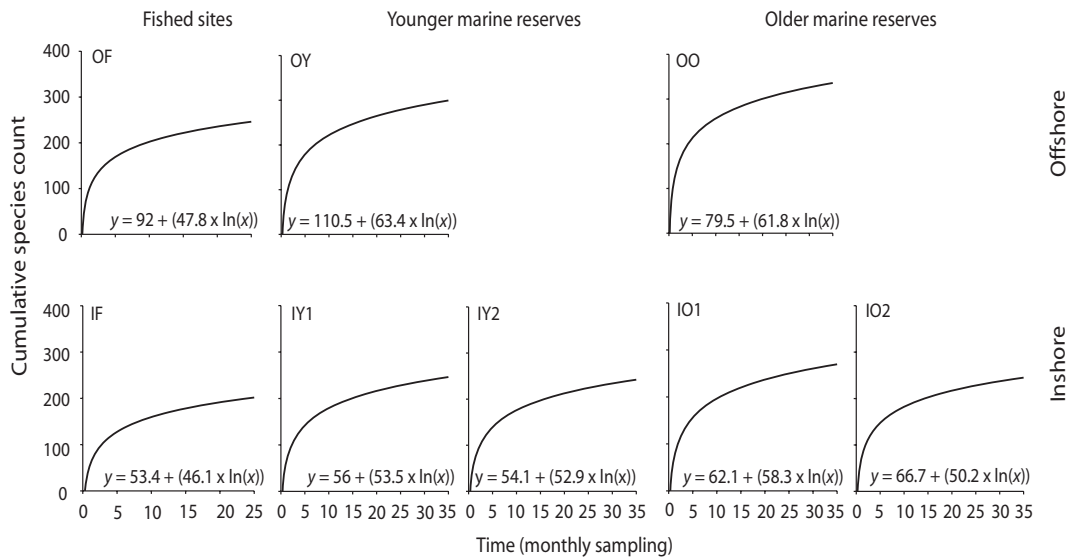
1-lambda and lambda (Clarke & Gorley, 2006). However, 11 of the 12 indices correlated positively with each other, while Simpson's 1-lambda correlated negatively with the other indices. Thus, we decided to present only the results for species richness and the four most widely recognised and used indices (Hill's  $N_1$ , Pielou's  $J$ , Shannon–Weiner's  $\ln(H')$  and Simpson's 1-lambda). As the four later indices are all measures of evenness, lower values imply higher dominance by a small number of species in the assemblage (Clarke & Warwick, 2001). We used linear regression to examine whether there were significant changes in species richness and the four diversity indices within sites over time.

### Abundance–biomass comparison (ABC) curves

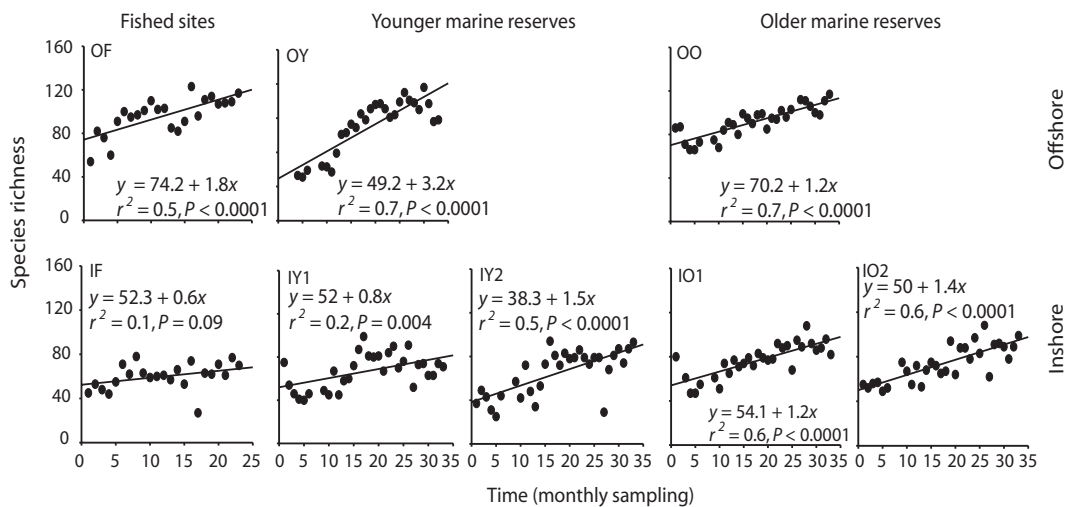
Our ABC curves were based on the average monthly abundance and biomass estimates for all species at each site during the last year of the study (Clarke & Gorley, 2006). These curves present the cumulative abundance and cumulative biomass plots for each site against species rank (i.e. species rank on the  $x$ -axis and the cumulative contribution of species abundance or biomass on the  $y$ -axis). The general prediction of ABC curves is that in protected areas, large-bodied species would dominate the community, and therefore, the cumulative biomass curve would be higher than the cumulative species abundance curve (Clarke & Gorley, 2006). The  $W$ -statistic associated with ABC curves measures the distance between the abundance and biomass curves, i.e. a  $W$ -statistic of +1 for cases with complete biomass dominance (higher biomass than abundance curves) and an even abundance distribution across all species, and a  $W$ -statistic of –1 for the reverse case (Clarke & Gorley, 2006).

### Design issues and statistical assumptions

While we present a data-intensive and species comprehensive analysis of reef fish diversity changes associated with marine reserves, the limited availability of enforced marine reserves



**Figure 2** Logarithmic curve fitted to the cumulative species count based on monthly sampling of species found within study sites over the 3-year sampling period. Also presented is the model of each curve (all:  $r^2 = 0.9$  and  $P < 0.0001$ ).



**Figure 3** Regression of species richness against time (monthly sampling from 2002 to 2005) for each site. Also presented are the model,  $r^2$  and  $P$  values of the regression.

within Danajon Bank during our study led to an un-balanced and poorly replicated study design in terms of protection duration and site location. This imbalance was further aggravated by the time and logistical constraint (monthly sampling) that limited us to two control (fished) sites. Despite this substantial imbalance, we decided to apply two-way ANOVAs to test the influence of protection duration and site location. We cautiously relied on the robustness of ANOVA to these limitations (Zar, 1999). However, we tested the main effects of protection duration and site location only, and conducted no formal tests of the interaction term. Although we did not statistically test interaction terms, we decided to present potential interaction trends in graphical form. We

examined homogeneity of variance (Spearman rank correlation between residuals and observed values of the independent variable), autocorrelation (Durbin–Watson test) and normality (Kolmogorov–Smirnov test) of all data (see Anticamara, 2009, <https://circle.ubc.ca/dspace/handle/2429/7916>).

## RESULTS

### Species accumulation curves

This study identified 320 reef fish species belonging to 44 families (see Table S1). The cumulative number of species per site recorded over the 3-year period fitted logarithmic models

well (Fig. 2). The species accumulation curves reached maxima at the end of all sampling periods without reaching clear asymptotic patterns. However, the trends were moving towards such asymptotes at approximately 200–250 species for fished sites and between approximately 300–400 species for marine reserves (Fig. 2). There was a trend towards higher species accumulation in younger and older marine reserves compared to fished sites (Fig. 2). However, two-way ANOVA did not detect a statistically significant influence of protection duration and site location on the rate of species accumulation within study sites.

**Species diversity indices**

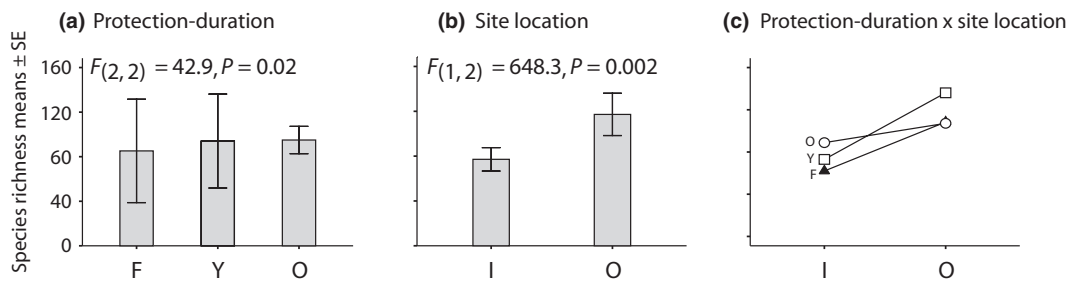
Of all the diversity indices that we examined, only species richness showed a consistent significant increase within sites over time (Fig. 3, all:  $P \leq 0.09$ ; see Fig. S3). Species richness within sites for the last year of sampling differed significantly with protection duration (2-way ANOVA,  $F_{2,7} = 42.9$ ,  $P = 0.02$ , Fig. 4a) and was higher in offshore sites than in

inshore sites (2-way ANOVA,  $F_{1,7} = 648.3$ ,  $P = 0.002$ , Fig. 4b). Interestingly, graphical presentation suggested the possibility of an interaction (not testable because of unbalanced design) between protection duration and site location, possibly driven by lower than expected species richness in the older offshore MPAs (Fig. 4c).

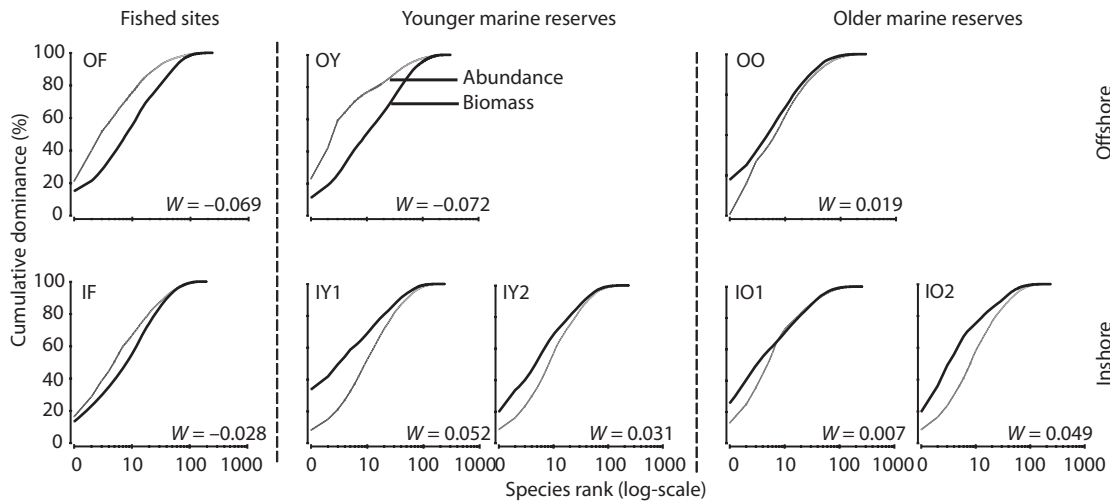
The additional four commonly used diversity indices were considered in detail (Hill's  $N_1$ , Pielou's  $J$ , Shannon–Weiner's  $\ln(H')$  and Simpson's 1-Lambda) suggested some site-specific changes over time (although not statistically significant), with fished sites suggesting some declines, and younger and older marine reserves showing some indications of increases in some of the indices (see Fig. S3).

**Abundance–biomass comparison (ABC) curves**

The abundance–biomass comparison (ABC) curves showed the most interesting pattern. All fished sites showed higher cumulative abundance than biomass curves, while all but one of the protected sites showed higher biomass than abundance



**Figure 4** Two-way ANOVA testing the influence of a) protection duration (F = fished sites, Y = young marine reserves and O = older marine reserves), b) location (I = inshore and O = offshore) and c) the statistically non-testable interaction between these two factors on the mean species richness ( $\pm$  SE) within sites during the last year of sampling. The unbalanced nature of the sampling design did not permit testing of interactions. Also presented are the  $F$  and  $P$  values.



**Figure 5** Abundance–biomass comparison (ABC) curves based on the mean monthly abundance and size-derived biomass of all fish species found within each site during the third year of sampling. Also presented are the  $W$ -statistics, a measure of the closeness of each pair of curves.



curves (Fig. 5). The only exception was the offshore young marine reserve site (OY in Fig. 5), which behaved more like a fished site (OF, IF in Fig. 5). This pattern indicated that the protected sites (except OY) were dominated by large-bodied species (i.e. higher cumulative biomass curves than abundance curves, positive *W*-statistic, Fig. 5) compared with the fished sites, which were dominated by highly abundant small-bodied fishes (i.e. higher cumulative abundance curves than biomass curves, negative *W*-statistic; Fig. 5).

## DISCUSSION

The most interesting finding of our study examining spatio-temporal patterns in reef fish diversity associated with marine reserves in the central Philippines related to the shifting of the abundance–biomass comparison (ABC) curves from higher abundance than biomass curves in fished sites to higher biomass than abundance curves for essentially all protected sites. These results suggested that the primary effect of protection on diversity patterns in heavily impacted ecosystems (at least for the first 10 years of protection) relates more to the increase in large-bodied species than the number and relative abundance of species. Hence, protection-duration-permitted populations to grow in body size and biomass undisturbed by fishing. In turn, this increase in body size and biomass can influence surrounding unprotected areas through adult spill-over effects and recruitment-effects (Zeller *et al.*, 2003; Abesamis & Russ, 2005).

Our results also suggest that offshore sites (22–30 km from land) maintained higher species richness than inshore sites (4–12 km from land) regardless of protection duration (years of protection from fishing). These findings accord with other studies on inshore-offshore patterns in diversity from other coral reef areas (Williams, 1991). In general, species richness has been related to available reef area (Knowlton, 2001), and Pichon (1977) documented that offshore reefs on Danajon Bank have larger and better developed reef areas compared to inshore reefs. Furthermore, higher sedimentation in inshore areas has been suggested as an additional factor lowering the habitat quality of inshore reefs (Cornell & Karlson, 2000). Overall, our study supported the current understanding of patterns of reef diversity in relation to distance from shore, and this pattern was consistent, regardless of protection duration.

Protection duration (up to 10 years of protection designation) had a relatively weak influence on the spatio-temporal trends of observed reef fish diversity. However, we noticed that the potential interaction trends (un-testable in our design) between protection duration and location as possible factors influencing reef fish diversity. Our data suggested that diversity in the fished (control) sites may not have been affected by fishing, since diversity indices did not differ greatly from older marine reserves. This is consistent with Russ & Alcala (1989, 1998), who showed that species richness only declined in an intensely and destructively fished site, but not in three other fished sites where fishing intensity was more or less constant. We concluded that reef fish species richness in our sites is

relatively stable and not detectably depleted at fished sites compared to the relatively small marine reserves protected for about 10 years. However, an important caveat to this conclusion is that all our sites had been subjected to intense fishing for a long time before any reserve establishment, and have already lost many of the top predatory species (e.g. large carangids, groupers, sharks and snappers). This likely applies to essentially all coral reefs in the Philippines and likely to much of the rest of the world's coral reefs (Stevenson *et al.*, 2007).

The rapid changes in species accumulation with increased sampling over the first 10+ months of this study was because of the sensitivity of this index to sampling effort. This response suggests that high diversity systems such as coral reefs require intensive sampling over time to establish reliable diversity baseline data. Hence, studies with short-term data sets with limited sampling may be biased for high diversity systems such as coral reefs (e.g. MacNeil *et al.*, 2008).

In summary, our study suggested, through the use of ABC curves, that the primary effect of protection (up to 10 years) on diversity patterns in heavily impacted coral reef ecosystems relates more to the increase in large-bodied species than the number and relative abundance of species. Hence, protection duration permitted populations to grow in body size and biomass undisturbed by fishing. We did not find strong quantitative differences in diversity patterns between fished sites and marine reserve sites whose protection duration ranged from 1 to 10 years, despite intensive sampling over 3 years. However, our data did support the previously demonstrated inshore-offshore patterns in diversity for coral reef fish communities (Williams, 1991). Thus, one could conclude that at the levels of fishing intensity and quality of protected area enforcement occurring in the Danajon Bank area (Samoilys *et al.*, 2007), basic diversity patterns (such as species richness and other diversity indices) appear to be relatively little affected by exploitation. A caveat to this statement relates to large predatory reef fish and highly mobile reef-associated species that have essentially disappeared from the highly exploited Philippine reef systems and were not found in our study area.

Our results support the notion that if marine reserves are to contribute to conservation goals for improving historically depleted diversity patterns, then the design and scale of marine reserve networks must take into account proper representations of spatial biodiversity distributions at a regional scale (Hastings & Botsford, 2003).

## ACKNOWLEDGEMENTS

This is a contribution from Project Seahorse. We especially thank the numerous field assistants who helped collect the data. We thank L. Lavkulich, M. Mulrennan, M. Samoilys, C. Scott and J. Shurin for comments on the study. This study was made possible by the support of local communities, the local government units of Bohol and the Project Seahorse team members. We acknowledge funding by the John D. and

Catherine T. MacArthur Foundation, the International Development and Research Centre of Canada (IDRC), Guylian Chocolates, Belgium and the John G. Shedd Aquarium (Chicago, USA) through its partnership for marine conservation with Project Seahorse. D. Zeller acknowledges support from the *Sea Around Us* Project, a scientific partnership between the Pew Environment Group and the University of British Columbia. We thank the three anonymous reviewers for giving us very helpful comments that greatly improved this manuscript.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Mean percentage benthic cover ( $\pm$  SE) within sites during the last year of sampling.

**Figure S2** Regression of percentage cover of live benthic habitat against sampling time (monthly sampling interval from 2002–2005).

**Figure S3** Regression of the four most commonly used diversity indices against sampling time (monthly sampling 2002–2005).

**Table S1** Number of species per family recorded at each site.

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## BIOSKETCHES

All authors have interests in marine conservation, diversity, ecological processes and fisheries management. This article forms part of the PhD dissertation of Jonathan Anticamara, which was completed under the supervision of Amanda Vincent.

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Author contributions: J.A.A., D.Z., and A.C.J.V. developed the concepts and structure of the article, and A.C.J.V. secured the funding. J.A.A. collected the data and undertook the analysis and writing. All authors contributed to the revisions and completion of the article.

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Editor: Omar Defeo