Short communication

Size-frequency distributions of scleractinian coral (*Porites* spp.) colonies inside and outside a marine reserve in Leyte Gulf, central Philippines

Authors:

Sheldon Rey Boco^{1,2,5*}, Jerome Benedict P. Cabansag^{1,3}, Emmeline A. Jamodiong⁴, Victor S. Ticzon^{1,5}

Affiliation:

¹Coral Reef Visualization and Assessment (CoRVA) Program, University of the Philippines Visayas Tacloban College, Magsaysay Blvd., Tacloban City, the Philippines

²Present Address: School of Environment and Science and Australian Rivers Institute – Coasts and Estuaries, Gold Coast Campus, Griffith University, QLD 4222, Australia

³Division of Natural Sciences and Mathematics, University of the Philippines Visayas Tacloban College, Magsaysay Blvd., Tacloban City, the Philippines

⁴Mackeough Marine Center, Xavier University – Ateneo de Cagayan, Cagayan de Oro City, the Philippines

⁵Institute of Biological Sciences, College of Arts and Sciences, University of the Philippines Los Baños, Laguna, the Philippines

*Corresponding author: Sheldon Rey Boco

Email address: sheldonrey.boco@griffithuni.edu.au

Telephone number: +61 452 419 914

ORCID ID: 0000-0002-8967-3521 (Sheldon Rey Boco), 0000-0001-9483-1531 (Emmeline Jamodiong)

Abstract

Coral colony size-frequency distributions (SFDs) can elucidate demographic differences among coral species and their responses to environmental drivers. However, studies on species-specific demography of coral colonies in the Coral Triangle are rare despite knowledge on the regional variability of reef conditions. Coral reefs in the Southern Philippine Sea biogeographic zone (SPS) frequently experience natural (e.g. typhoons) and anthropogenic disturbances. Coral colony sizes in the SPS may vary with depth within a small-distance (< 1 km) scale and with the presence of marine protected areas (MPA) but studies rarely demonstrate this variability in Indo-Pacific coral reefs. Here, we examined the colony density, SFDs and the extent of partial mortality of scleractinian coral species *Porites cylindrica* and *P. rus* in Leyte Gulf, SPS. Field surveys were conducted within and outside (locations) the Bagonbanua Marine Reserve and Fish Sanctuary, SPS and between depths (3 m and 8 m) of each location. High densities of colonies of both species occur at shallow depths. We found that SFDs and colony sizes were similar between depths and between locations (inside and outside of the MPA). The percent partial mortality of only *P. cylindrica* colonies was significantly different between depths and between locations with low mortality at 3 m inside the MPA. Our study showed small-sized colonies that could indicate high colony recruitment, fragmentation and potential recovery from disturbances.

Keywords Poritidae, coral abundance, marine reserve, size-frequency distributions, depth variability

1. Introduction

Reef-building corals shape coral reef ecosystems, which are areas of immense ecological and economic importance. However, disturbances such as destructive fishing, sedimentation, pollution and strong waves and currents limit coral reefs (Fabricius *et al.* 2008; Kipson *et al.* 2014; Maynard *et al.* 2015). These disturbances can alter the reproductive activity, physiology and morphology of corals (Fabricius *et al.* 2008) and may impede their recovery mechanisms, i.e. recruitment of coral planulae and growth (Mumby *et al.* 2007; Gilmour *et al.* 2013). Information about mechanisms that allow coral colonies to persist are needed to manage coral reefs (Graham *et al.* 2011; Mumby *et al.*, 2011).

Size-frequency distributions (SFDs) of corals can help examine coral recruitment, growth and mortality since these demographic processes depend on colony size (Soong 1993; Adjeroud *et al.* 2015; Grimsditch *et al.* 2017). Coral SFDs can be derived from surface areas of approximate geometric shapes of colonies to determine ecological and physical attributes of the coral

(Grimsditch *et al.* 2017). For example, shape-based SFDs of coral colonies were examined in French Polynesia to determine the variation of coral colony sizes and conditions of corals between few kilometers and large regional distances (Adjeroud *et al.* 2007; 2015). Moreover, coral SFDs can be used to infer the influence of marine reserves on coral reefs (McClanahan *et al.* 2008). For example, some reefs with nutrient pollution from urban settlement and severe fishing pressure have colonies with relatively large sizes but these reefs are associated with low coral recruitment (Meesters *et al.* 2001). In contrast, small-sized colonies, with negatively skewed frequency distribution, may dominate reef areas with high fishing pressure and prevalent partial mortality (McClanahan *et al.*, 2008). Therefore, coral ecological processes and conditions can be examined using coral SFDs to overcome challenges with the use of coral cover or species composition data alone (Meesters *et al.* 2001; Grimsditch *et al.* 2017).

The Southern Philippine Sea biogeographic zone (SPS) sits in the epicenter of coral diversity (Roberts *et al.* 2002; Carpenter and Springer 2005; Anticamara and Go 2017). It encounters intense ocean waves, frequent typhoons (Aliño and Gomez 1994; Roeber and Bricker 2015; Anticamara and Go 2017), coral bleaching and direct anthropogenic threats (e.g. blast fishing) (Aliño *et al.* 2002; Mcleod *et al.* 2010), all of which can reduce coral cover, composition and colony sizes. Although coral SFD studies were conducted in other reef locations (Caribbean, Meesters *et al.* 2001; Indian Ocean, Grimsditch *et al.* 2017; Mediterranean, Serrano *et al.* 2018), their results may not explain the conditions influencing Philippine corals due to differences in the species examined and regional variability of reef conditions (Hughes *et al.* 2017). Hence, information on the demography of coral colonies in the SPS is needed.

Coral colony sizes may vary with depth and between the marine protected area (MPA) and nearby (< 1 km) unprotected reefs since MPAs can mitigate the effects of local anthropogenic stressors on coral reefs and associated biota (Adjeroud *et al.* 2007; Edgar *et al.* 2014; Mellin *et al.* 2016). Indeed, a meta-analysis that examined the effectiveness of MPAs in the Philippines indicated higher coral cover inside MPAs compared to the outside of the reserves (Magdaong *et al.* 2014). An MPA may have higher coral colony growth rates compared to adjacent fished reefs due to drastic increase of fish grazers that prevent harmful algal phase shifts (Hughes *et al.* 2007; Mumby and Harborne 2010; Mellin *et al.* 2016), differences in disturbance history, partial and whole-colony mortality, and energy allocation (Pisapia *et al.* 2014). In addition, swell and wave energy decrease with increasing depth (Adjeroud *et al.* 2007), thus depth also influences coral population dynamics.

We examined the coral colonies in Bagonbanua Marine Reserve and Fish Sanctuary and in fished reefs (< 1 km distance from the MPA) in the SPS. This no-take (all types of fishing is prohibited) MPA was established in year 1990 and, since then, policies against fishing in the MPA have been successfully enforced (Kuhlman 2002; see West *et al.* 2011). The MPA and nearby unprotected reefs face natural stressors such as siltation and frequent cyclones (Aliño *et al.* 2002;

Kuhlman 2002) and they may reveal local variability of coral colony conditions. We selected *Porites cylindrica* and *P. rus*, coral species that have contrasting growth forms and different life-history strategies (Bak and Meesters 1998). *P. cylindrica* colonies, here, exhibited cream to yellow branching growth forms whereas *P. rus* colonies were bluish brown to purple and occurred as submassive and/or columnar colonies. These species have variable growth responses to environmental disturbances (Dizon and Yap 2005; Dizon and Yap 2006).

Here, colony populations of *P. cylindrica* and *P. rus* were examined inside and outside a marine reserve in Leyte Gulf, SPS. We hypothesized that there is significant variation in the colony abundance, size structure and partial mortality of the two coral species between depths and between locations (inside or outside MPA). We also hypothesized that coral colonies are larger and more abundant inside the MPA than the outside.

2. Materials and methods

2.1 Study area

Data were collected in the reefs inside and outside the marine protected area (MPA) of Bagonbanua Marine Reserve and Fish Sanctuary in the province of Eastern Samar, central Philippines (Fig. 1). Four stations were established using GPS device (Garmin eTrex 10): two stations inside (In) and outside (Out) the MPA and each station at 3 m (shallow) and 8 m (deep) (Fig. 1). Each station has five replicate belt (10 x 2 m) transects parallel to the nearest land area. Bagonbanua Island is the nearest land area of the MPA while the nearby sandbar is close to the outside stations. Each station and transect has at least 30 m distance from one another.

2.2 Data Collection

Initial surveys conducted on 7 May and 3 June 2015 to determine presence of the target coral species showed the abundance of *Porites cylindrica* and *P. rus* in the study areas. Collection of colony size data were conducted from 4 to 6 June 2015. By swimming and SCUBA diving, all colonies with their centers present in the belt transects were examined, following Zvuloni *et al.* (2008). Identification of a “coral colony” was based on Bak and Meesters (1998). Colonies resulting from fission or fragmentation were carefully distinguished by tracing patterns of growth and orientation, and form of colony calyces (Traçon *et al.* 2013). Juvenile corals of < 2 cm in diameter were not examined due to logistical considerations and difficulty in spotting them in the field. The longest diameter (*L*), perpendicular diameter (*I*) and maximum height (*h*) of each colony were measured using a metal tape measure. Partial mortality (bare or algal-covered skeleton on

each colony) was observed. The percentage of partial mortality of each colony was carefully estimated *in situ* by recording the approximate percentage of dead skeleton from the live sections of the colony. Transects were randomly examined to avoid observer bias.

2.3 Data Analysis

Measurements of the linear dimensions (L , l , and h) were used in the appropriate geometric formulae [were used] to calculate approximate colony surface areas (Meesters *et al.* 2001; Adjerooud *et al.* 2007). A hemisphere is the most appropriate shape for *P. cylindrica* that usually form dome-shaped branching colonies while cylinder with a circle top for *P. rus* (based on Veron 2000, Meesters *et al.* 2001 and Adjerooud *et al.* 2007). Hence, colony sizes (cm^2) were calculated using the formulae: $2\pi [(L+l+h)/6]^2$ for *P. cylindrica* and $2\pi [(L+l)/4]^2 + 2\pi [(L+l)/4]h$ for *P. rus*. SFDs were constructed based on estimates of the total recognizable live colony surface areas of each species. We selected fixed intervals of SFDs to compare sizes of colonies among stations. Log-transformation of colony size prevented accurate interpretation of frequency distributions, thus untransformed size data were analyzed.

Kruskal-Wallis (K-W) H and Mann-Whitney (M-W) U tests with Bonferroni correction ($\alpha = 0.025$) were used to determine the variation of the dependent variables (colony density, size and partial mortality) between the factors (depths and locations: inside (In) or outside (Out) the MPA), since the distribution of dependent variable data did not satisfy normality (Shapiro-Wilk test) even after transformation. When at least one of the factors showed significant difference, we used K-W test with Dunn's pairwise post-hoc test to compare the four levels of data (In MPA-3 m, In MPA-8 m, Out MPA-3 m, Out MPA-8 m) of each dependent variable. Overall shapes of the SFDs (interval: 5 to > 100) of each species were compared between depths and locations using the independent samples Kolmogorov-Smirnov (K-S) test. The single K-S test was used to determine the normality of each size-frequency distribution.

The percentage of average partial mortality for each size class and prevalence (percentage of colonies with partial mortality) in each station were calculated to determine the extent of colony mortality. Correlation between log-transformed partial mortality averages and average colony sizes was shown using Pearson correlation analysis. The geometric mean, coefficient of variation (CV), skewness (g_1) or asymmetry ($g_1 > 0$ have values toward smaller size classes) and kurtosis (g_2) or peakedness were used to compare the variation of the size-structure of the colonies (Bak and Meesters 1998). All statistical tests were conducted in SPSS v. 20 (IBM).

3. Results

3.1 Colony density

P. cylindrica and *P. rus* colonies were counted in the study sites. *P. cylindrica* had mean ($\pm$ SD) density of 8.4 ± 5.97 colonies per transect (20 m^2) and there were 4.1 ± 5.7 *P. rus* colonies per 20 m^2 (Table 1). The abundance of the colonies of both species varied between depths (K-W test, $H = 10.7, p = <0.01$; M-W test $U=7, p = <0.01$ for *P. cylindrica*) (K-W $H = 6.7, p = 0.01$; M-W $U = 16.5, p = 0.009$ for *P. rus*) but not between locations (Fig. 2, Table 1). Specifically, there were more colonies of *P. cylindrica* at 3 m in the MPA than at 8 m outside the MPA (K-W test, $H = 12.3, p = <0.01$; Dunn $p = <0.01$) (Fig. 2a). More colonies of *P. rus* were found at 3 m than at 8 m depths, regardless of location (Fig. 2b, Table 1).

3.2 Surface area (size) and size frequency distribution

Surface area sizes of *P. cylindrica* ranged between 21 cm^2 to $164 \times 10^2 \text{ cm}^2$ (equivalent to the longest diameters (L) of $0.04 - 3.53 \text{ m}$) whereas *P. rus* sizes ranged from 124 cm^2 to $110 \times 10^2 \text{ cm}^2$ (or $L = 0.05 - 0.88 \text{ m}$). Colony sizes for both species were not significantly different between depths (K-W test, $H = 0.32, p = 0.570$ for *P. cylindrica*) (K-W $H = 0.572, p = 0.45$ for *P. rus*) and locations (K-W test, $H = 3.25, p = 0.071$ for *P. cylindrica*) (K-W $H = 0.033, p = 0.855$ for *P. rus*). The shapes of the SFD graph of the species between depths and between locations were similar (K-S $p > 0.05$) (Fig. 3). Species SFDs for the reef areas (In MPA-3 m, In MPA-8 m, Out MPA-3 m, Out MPA-8 m) were positively skewed ($g_1 > 0$, colony sizes appear in smaller size classes (5 to $15 \times 10^2 \text{ cm}^2$)) and generally highly leptokurtic ($g_2 > 0$, aggregating toward the mean) except in Out MPA-8 m of *P. rus* (Fig. 3, Table 1).

3.3 Partial mortality

Significant variation of percent partial mortality of *P. cylindrica* colonies exists between depths (K-W test, $H = 8.65, p = 0.003$; M-W $U = 712, p = 0.002$) and locations (K-W $H = 6.497, p = 0.011$; M-W $U = 1933, p = 0.003$) (Fig. 4). *P. cylindrica* at the shallow depth inside the MPA had the lowest partial mortality (K-W $H = 17.2, p = 0.001$) among the reef areas (versus In MPA-8 m, Out MPA-3 m, and Out MPA-8 m) (Fig. 4). *P. rus* partial mortality, however, did not vary between depths (K-W test, $H_1 = 0.842, p = 0.359$) and locations ($H_1 = 0.548, p = 0.459$) but its slightly increasing trend of partial mortality follows this order of study areas: In MPA-3 m < in MPA-8 m < Out MPA-3 m < Out MPA-8 m (Fig. 4). The partial mortality of both species was highly prevalent ($\sim 70\%$ to 100%) but the prevalence was similar between depths (K-W test, $H = 0.157, p = 0.692$ for *P. cylindrica*; K-W $H = 0.112, p = 0.738$ for *P. rus*) and locations (K-W $H = 0.353, p = 0.552$ for *P. cylindrica*; K-W $H = 0.925, p = 0.336$ for *P. rus*) (Fig. 4). Furthermore, we

found strong positive overall (species combined) correlation between the averages of log colony sizes and percent partial mortality ($r = 0.64$, $p = < 0.01$) and both species contributed to the strong correlation (*P. cylindrica* $r = 0.832$, $p = < 0.01$; *P. rus* $r = 0.526$, $p = 0.04$) (Fig. 5).

4. Discussion

This study presents the first information about colony size frequency distributions of *Porites cylindrica* and *P. rus* in the Philippines. Our results showed that colonies of the two coral species were more abundant at shallow depths and there was minimal variability of their abundance between the inside and outside of the MPA. The results also oppose our hypotheses and showed lack of difference of the shapes of SFDs and colony sizes of both species between depths and between locations relative to the MPA. Percent partial mortality *P. cylindrica* colonies, only, varied between depths and between locations.

P. cylindrica and *P. rus* colonies were abundant at shallow depths. The abundance of *P. cylindrica* varied minimally between the inside and outside of the MPA. We could not link the influence of depth and associated factors such as light intensity and turbulence on their abundance since we lack ground data to support this claim. Colonies of both species in northwestern Philippines (Pangasinan waters) have higher growth rates at shallow depths compared to deep areas (Yap *et al.* 1998; Dizon and Yap 2005). If depth indeed influenced the abundance of these species, then the abundance and survival of the colonies depend on strong light exposure and zooxanthellae photosynthesis, which can enhance coral reef condition including coral growth and high recruitment rate (Pratchett *et al.* 2015). In addition, colony population conditions can vary with depth even within local reefs ($< 1 \text{ km}^2$) (Adjeroud *et al.* 2015).

The study areas have either more recruits or more fragments of existing colonies since $g_l > 0$. This observation matches with the geometric mean, a metric that allows estimates of overall colony size or size ‘central tendency’ while considering outliers (Anderson and Pratchett, 2014). Indeed, we found smaller GMs of *P. cylindrica* sizes compared to *P. rus* sizes with low positive skewness of SFDs ($g_1 = \sim 1.2$) (versus *P. cylindrica* $g_1 = \sim 3$). Small-size colony distributions are common among *Porites* spp. and congeneric species from French Polynesia showed small-sized colonies at shallow stations (Adjeroud *et al.* 2007; Adjeroud *et al.* 2015). The positive skewness here matches the size distributions of coral colonies in reefs with large-scale disturbance histories (i.e. high mortality and fragmentation) (Linares *et al.* 2011; Adjeroud *et al.* 2015). Moreover, the highly leptokurtic SFDs of colonies across the study areas (except on Out MPA- 8 m) could match with the SFDs of other tropical corals (e.g. *Acropora* and *Isopora* spp. in Heron Is., Australia) with peaked SFDs that indicate high mortalities across colony sizes, i.e. small or large size classes, despite high growth rates (Anderson and Pratchett, 2014).

Severe storms and cyclones could be linked to the size-structure of corals here since these weather events can increase the proportion of small colonies through fragmentation and mortality of large colonies (Hughes 1989; Harmelin-Vivien 1994; Fabricius et al. 2008). Frequent typhoons in the SPS including the super typhoon Haiyan (November 2013) and more recent typhoon Hagupit (6 December 2014) presumably prevented large colonies to persist in the study areas (Anticamara and Go 2017; Stephenson et al. 2018). In fact, typhoon Haiyan released maximum sustained winds of 315 kph that can carry boulders, overturn corals and fragment colonies (Reyes *et al.* 2015; May *et al.* 2016; Soria *et al.* 2016). However, our dataset cannot suggest that typhoons mainly caused the occurrence of small colony sizes and lack of difference of SFDs since other ecological (e.g. colony resilience) or abiotic factors (e.g. siltation and fishing) possibly influence our study areas.

The pattern of partial mortality of the colonies here could be linked to species-specific responses of corals to agents of mortality (*sensu* Darling *et al.* 2012). However, this pattern deserves examination in future work. Indeed, *P. cylindrica* is more sensitive to disturbances than *P. rus* in shallow depths (Yap *et al.* 1998; Dizon and Yap 2005, 2006). Unlike *P. cylindrica*, *P. rus* can acclimatize in turbid environments by increasing chlorophyll concentrations in their colonies (Padilla-Gamiño *et al.* 2012). This physiological mechanism may have presumably supported the recovery of this species in this study from injuries at different depths and ultimately influenced the lack of variation of partial mortality. Furthermore, we found strong correlation between the extent of partial mortality and colony sizes. This trend exists in other studies that examined partial mortality of coral colonies (Babcock 1991; Bak and Meesters 1998; Anderson and Pratchett 2014). Colony partial mortality increases as the probability of encountering agents of mortality elevates with increasing colony size (Hughes and Jackson 1985; Pratchett *et al.* 2015). The data here could be used to support the hypothesis that the condition of the corals with prevalent partial mortality leans towards degradation due to disturbances such as typhoons, siltation, predation and destructive fishing such as use of fishing lines and small metal fish traps (Anticamara and Go 2017). This proposition needs to be examined in future work.

In conclusion, coral colonies were abundant at shallow depths and, to some extent, *P. cylindrica* colonies were more abundant at shallow areas in the MPA than the outside of the MPA at 8 m. SFDs and colony sizes were similar between depths and between locations (inside or outside a marine reserve). Partial mortality of colonies was prevalent but only *P. cylindrica* showed high partial mortality at deep locations, which link possible species-specific responses to agents of colony injury. Anthropogenic stressors and frequent typhoons threaten the SPS, but our study showed small-sized colonies that possibly link to high coral recruitment or fragmentation and potential recovery from disturbances. Long term monitoring on coral colony SFDs and other metrics such as density and mortality of these species and other scleractinian corals in the SPS is necessary to better understand the resilience of corals in this biogeographic region of the Coral Triangle.

Declarations of interest: none

Acknowledgments

This study was funded by the Philippine Department of Environment and Natural Resources. We acknowledge the Regional Environmental Information System of the University of the Philippines Visayas Tacloban College (UPVTC), Prof. M. T. dela Cruz, UP Los Baños, and Guiuan Development Foundation, Inc. for the support. L. C. Manguilimotan, T. J. Quimpo and our boat operators are acknowledged for the assistance in the field. Dr. N. Kongjandtre of Burapha University, Thailand and Prof. A. H. Baird of James Cook University, Australia provided comments on coral species identification. Dr. Patrick C. Cabaitan provided comments about the study. We sincerely thank the three anonymous reviewers for the very helpful comments on this study.

References

- Adjeroud, M., Pratchett, M. S., Kospartov, M. C., Lejeusne, C., and Penin, L., 2007. Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. *Hydrobiologia* **589**, 117-126.
<http://dx.doi.org/10.1007/s10750-007-0726-2>
- Adjeroud, M., Mauguit, Q., & Penin, L. (2015). The size-structure of corals with contrasting life-histories: A multi-scale analysis across environmental conditions. *Marine environmental research*, 112, 131-139.
- Anderson, K. D., and Pratchett, M. S., 2014. Variation in size-frequency distributions of branching corals between a tropical versus sub-tropical reef. *Marine Ecology Progress Series* **502**, 117-128. <http://dx.doi.org/10.3354/meps10697>
- Aliño, P. M., and Gomez, E. D., 1994. Philippine coral reef conservation: Its significance to the South China Sea. In 'Development and conservation in the Asia-Pacific Region. Proceedings of the Regional Conference of East-West Center Association: Regional Development in the 21st Century, Think Globally, Act Locally: 1993'. (Eds K. Yamazato, S. Ishijima, S. Sakihara, H. Taira, Z. Shimabukuro, F. Teruya and F. Nishihira) pp. 222-229. (Okinawa, Japan: The East-West Center Association Okinawa Chapter.)

- Aliño, P. M., Miclat, E., Nañola, Jr. C. L., Roa-Quiaoit, H. A., and Campos, R. T., 2002. 'Atlas of Philippine coral reefs.' (Quezon City, Philippines: Goodwill Trading Company, Incorporated.)
- Anticamara, J. A., and Go, K. T. B., 2017. Impacts of super-typhoon Yolanda on Philippine reefs and communities. *Regional Environmental Change* **17**, 703-713.
<http://dx.doi.org/10.1007/s10113-016-1062-8>
- Babcock, R. C., 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecological Monographs* **61**, 225e244.
<https://doi.org/10.2307/2937107>
- Bak, R. P., and Meesters, E. H., 1998. Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series* **162**, 301-306.
- Carpenter, K. E., and Springer, V. G., 2005. The center of the center of marine shorefish biodiversity: the Philippine Islands. *Environmental Biology of Fish* **72**, 467-480.
<https://doi.org/10.1007/s10641-004-3154-4>
- Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., Côté, I. M., 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* **15**, 1378–1386.
<https://doi.org/10.1111/j.1461-0248.2012.01861.x>
- Dizon, R. M., and Yap, H. T., 2005. Coral responses in single- and mixed-species plots to nutrient disturbance. *Marine Ecology Progress Series* **296**, 165-172.
<http://dx.doi.org/10.3354/meps296165>
- Dizon, R., Yap, H., 2006. Effects of multiple perturbations on the survivorship of fragments of three coral species. *Marine Pollution Bulletin* **52**, 928-934.
- Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T. F., Berkhout, J., Buxton, C. D., Campbell, S. J., Cooper, A. T., Davey, M., Edgar, S. E., Försterra, G., Galván, D. E., Irigoyen, A. J., Kushner, D. J., Moura, R., Ed Parnell, P., Shears, N. T., Soler, G., Strain, E. M. A., Thomson, R. J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216-220. <https://doi.org/10.1038/nature13022>
- Fabricius, K. E., De'Ath, G., Puotinen, M. L., Done, T., Cooper, T. F., and Burgess, S. C., 2008. Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography* **53**, 690-704.
<http://dx.doi.org/10.4319/lo.2008.53.2.0690>

360 Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H., and Pratchett, M. S., 2013. Recovery of
 361 an isolated coral reef system following severe disturbance. *Science* **340**, 69-71.
 362 <http://dx.doi.org/10.1126/science.1232310>

363 Graham, N. A. J., Nash, K. L., and Kool, J. T., 2011. Coral reef recovery dynamics in a changing
 364 world. *Coral Reefs* **30** (2): 283-294. <http://dx.doi.org/10.1007/s00338-010-0717-z>

365 Grimsditch, G., Pisapia, C., Huck, M., Karisa, J., Obura, D., and Sweet, M., 2017. Variation in size
 366 frequency distribution of coral populations under different fishing pressures in two
 367 contrasting locations in the Indian Ocean. *Marine Environmental Research* **131**, 146-155.
 368 <http://dx.doi.org/10.1016/j.marenvres.2017.09.017>

369 Harmelin-Vivien, M. L. 1994. The effects of storms and cyclones on coral reefs: a review. *Journal*
 370 *of Coastal Research* 211-231.

371 Hughes, T. P., and Jackson, J. B. C. 1985. Population dynamics and life histories of foliaceous
 372 corals. *Ecological Monographs* **55**, 141-166. <https://doi.org/10.2307/1942555>

373 Hughes, T. P. 1989. Community structure and diversity of coral reefs: The role of history. *Ecology*
 374 **70**, 275-279. <http://dx.doi.org/10.2307/1938434>

375 Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook,
 376 L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., and Willis, B., 2007. Phase
 377 shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**,
 378 360–365. <https://doi.org/10.1016/j.cub.2006.12.049>

379 Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C.,
 380 Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes,
 381 E. H., and Scheffer, M., 2017. Coral reefs in the Anthropocene. *Nature* **546**, 82-90.
 382 <https://doi.org/10.1038/nature22901>

383 Kipson, S., Linares, C., Čížmek, H., Cebrian, E., Ballesteros, E., Bakran-Petricioli, T., and
 384 Garrabou, J., 2014. Population structure and conservation status of the red gorgonian
 385 *Paramuricea clavata* (Risso, 1826) in the Eastern Adriatic Sea. *Marine Ecology* **36**, 982-
 386 993. <https://doi.org/10.1111/maec.12195>

387 Kühlman, K. J., 2002. Evaluations of marine reserves as basis to develop alternative livelihoods in
 388 coastal areas of the Philippines. *Aquaculture International* **10**, 527-549.
 389 <https://doi.org/10.1023/A:1023955626357>

390 Linares, C., Pratchett, M. S., & Coker, D. J. (2011). Recolonisation of *Acropora hyacinthus*
 391 following climate-induced coral bleaching on the Great Barrier Reef. *Marine ecology*
 392 *Progress series*, 438, 97-104.

393 Magdaong, E. T., Fujii, M., Yamano, H., Licuanan, W. Y., Campos, W. L., Alcalá, A. C., White,
 394 A. T., Maypa, A., Apistar, D., Martinez, R. 2014. Long-term change in coral cover and the
 395 effectiveness of marine protected areas in the Philippines: a meta-analysis. *Hydrobiologia*
 396 **733**, 5-17. <http://dx.doi.org/10.1007/s10750-013-1720-5>

397 May, S. M., Engel, M., Brill, D., Cuadra, C., Lagmay, A. M. F., Santiago, J., Suarez, J. K., Reyes,
 398 M., and Brückner, H., 2015. Block and boulder transport in Eastern Samar (Philippines)
 399 during Supertyphoon Haiyan. *Earth Surface Dynamics Discussion* **3**, 739-771.
 400 <http://dx.doi.org/10.5194/esurfd-3-739-2015>

401 Maynard, J., van Hooidonk, R., Eakin, C. M., Puotinen, M., Garren, M., Williams, G. et al., 2015.
 402 Projections of climate conditions that increase coral disease susceptibility and pathogen
 403 abundance and virulence. *Nature Climate Change* **5**, 688–694.
 404 <https://doi.org/10.1038/nclimate2625>

405 McClanahan, T. R., Ateweberhan, M., and Omukoto, J. 2008. Long-term changes in coral colony
 406 size distributions on Kenyan reefs under different management regimes and across the
 407 1998 bleaching event. *Marine Biology* **153**, 755-768. [http://dx.doi.org/10.1007/s00227-](http://dx.doi.org/10.1007/s00227-007-0844-4)
 408 [007-0844-4](http://dx.doi.org/10.1007/s00227-007-0844-4)

409 Mcleod, E., Moffitt, R., Timmermann, A., Salm, R., Menviel, L., Palmer, M. J., Selig, E. R.,
 410 Casey, K. S., and Bruno, J. F., 2010. Warming seas in the Coral Triangle: coral reef
 411 vulnerability and management implications. *Coastal Management* **38**, 518-539.
 412 <https://doi.org/10.1080/08920753.2010.509466>

413 Meesters, E. H., Hilterman, M., Kardinaal, E., Keetman, M., de Vries, M., and Bak, R. P. M.,
 414 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and
 415 interspecific variation. *Marine Ecology Progress Series* **209**, 43-54.
 416 <http://dx.doi.org/10.3354/meps209043>

417 Mellin, C., MacNeil, M., Cheal, A. J., Emslie, M. J., Julian Caley, M., 2016. Marine protected
 418 areas increase resilience among coral reef communities. *Ecology Letters* **19**, 629-637.
 419 <https://doi.org/10.1111/ele.12598>

420 Mumby, P. J., Hastings, A., and Edwards, H. J. 2007. Thresholds and the resilience of Caribbean
 421 coral reefs. *Nature* **450**, 98-101. <https://doi.org/10.1038/nature06252>

422 Mumby, P. J., and Harborne, A. R., 2010. Marine reserves enhance the recovery of corals on
 423 Caribbean reefs. *PLoS One* **5**, e8657. <https://doi.org/10.1371/journal.pone.0008657>

424 Mumby, P. J., Elliott, I. A., Eakin, C. M., Skirving, W., Paris, C. B., Edwards, H. J., ... & Stevens,
 425 J. R. (2011). Reserve design for uncertain responses of coral reefs to climate change.
 426 *Ecology letters*, 14(2), 132-140.

427 Padilla-Gamiño, J. L., Hanson, K. M., Stat, M., and Gates, R. D., 2012. Phenotypic plasticity of the
 428 coral *Porites rus*: acclimatization responses to a turbid environment. *Journal of*
 429 *Experimental Marine Biology and Ecology* **434**, 71-80

430 Pisapia, C., Anderson, K., and Pratchett, M. S. 2014. Intraspecific variation in physiological
 431 condition of reef-building corals associated with differential levels of chronic disturbance.
 432 *PLoS One* **9**, e91529. <https://doi.org/10.1371/journal.pone.0091529>

433 Pratchett, M. S., Anderson, K. D., Hoogenboom, M. O., Widman, E., Baird, A. H., Pandolfi, J. M.,
 434 Edmunds, P. J., and Lough, J. M. 2015. Spatial, temporal, and taxonomic variation in coral
 435 growth—implications for the structure and function of coral reef ecosystems. In
 436 ‘Oceanography and Marine Biology - An Annual Review’. (Eds R. Hughes, D. Hughes, I.
 437 Smith, A. Dale) pp. 215-296. (Taylor and Francis Group, Boca Raton)

438 Reyes, M., Engel, M., May, S. M., Brill, D., and Brueckner, H., 2015. Life and death after super
 439 typhoon Haiyan. *Coral Reefs* **34**, 419. <http://dx.doi.org/10.1007/s00338-015-1259-1>

440 Roberts, C., McClean, C., Veron, J., Hawkins, J., Allen, G., McAllister, D., Mittermeier, C.,
 441 Schueler, F., Spalding, M., Wells, F., Vynne, C., and Werner, T. 2002. Marine biodiversity
 442 hotspots and conservation priorities for tropical reefs. *Science* **295**, 1280-1284.
 443 <https://doi.org/10.1126/science.1067728>

444 Roeber, V., and Bricker, J. D. 2015. Destructive tsunami-like wave generated by surf beat over a
 445 coral reef during Typhoon Haiyan. *Nature Communications* **6**, 7854.
 446 <https://doi.org/10.1038/ncomms8854>

447 Serrano, E., Ribes, M., and Coma, R., 2018. Demographics of the zooxanthellate coral *Oculina*
 448 *patagonica* along the Mediterranean Iberian coast in relation to environmental parameters.
 449 *Science of the Total Environment* **634**, 1580-1592.
 450 <http://dx.doi.org/10.1016/j.scitotenv.2018.04.032>

451 Soong, K. (1993). Colony size as a species character in massive reef corals. *Coral reefs* 12(2), 77-
 452 83.

- Soria, J. L. A., Switzer, A. D., Villanoy, C. L., Fritz, H. M., Bilgera, P. H. T., Cabrera, O. C., Siringan, F. P., Yacat-Sta. Maria, Y., Ramos, R. D., and Fernandez, I. Q., 2016. Repeat storm surge disasters of Typhoon Haiyan and its 1897 predecessor in the Philippines. *Bulletin of the American Meteorological Society* **97**, 31-48. <https://doi.org/10.1175/BAMS-D-14-00245.1>
- Stephenson, V., Finlayson, A., & Miranda Morel, L. (2018). A risk-based approach to shelter resilience following flood and typhoon damage in rural Philippines. *Geosciences* **8** (2): 76.
- Trapon, M. L., Pratchett, M. S., and Hoey, A. S., 2013. Spatial variation in abundance, size and orientation of juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef, Australia. *PloS One* **8**, e57788. <http://dx.doi.org/10.1371/journal.pone.0057788>
- Veron, J. E. N. 2000. 'Corals of the World.' Vol. 1–3 (Australian Institute of Marine Science, Townsville.)
- West, R. J., Palma, M. A., Barut, N., Garvilles, E., and Ayanan, D., 2011. 'Preliminary assessment of the handline (banca) fisheries in the Philippines.' (Australian Centre for International Agricultural Research, Canberra.)
- Yap, H. T., Alvarez, R. M., Custodio, H. M., Dizon, R. M. 1998. Physiological and ecological aspects of coral transplantation. *Journal of Experimental Marine Biology and Ecology* **229**, 69-84. [http://dx.doi.org/10.1016/S0022-0981\(98\)00041-0](http://dx.doi.org/10.1016/S0022-0981(98)00041-0)
- Zvuloni, A., Artzy-Randrup, Y., Stone, L., van Woesik, R., and Loya, Y. 2008. Ecological size-frequency distributions: how to prevent and correct biases in spatial sampling. *Limnology and Oceanography: Methods* **6**, 144-153. <https://doi.org/10.4319/lom.2008.6.144>

Figure captions

Figure 1 Map of the study area and data collection sites inside and outside a marine protected area (MPA) in Leyte Gulf, Southern Philippine Sea biogeographic zone.

Figure 2 Average densities of colonies/ 20 m² transect “T” with standard deviation as error bars. Lines above error bars indicate reef areas in this study with significant difference at $p < 0.05$.

Figure 3 Size-frequency distributions of *Porites cylindrica* (a-d) and *Porites rus* (e-h) colonies at different depths (3 and 8 m) inside and outside a marine protected area (MPA) at the Southern Philippine Sea biogeographic zone.

Figure 4 Colony partial mortality. Averages (a-b) and prevalence (c-d) of partial mortality of *Porites cylindrica* and *P. rus* at different depths and locations relative to a marine protected area in the Southern Philippine Sea biogeographic zone. Error bars are standard deviations. The lines above error bars indicate significant difference at $p < 0.05$ between In MPA – 3 m and other reef areas: In MPA - 8 m, Out MPA - 3 m, and Out MPA - 8 m.

Figure 5 Relationship between colony sizes (log averages) and partial mortality (log mean %) of the colonies examined.

Table caption

Table 1 Summary of values from the size-frequency distribution parameters examined among the colonies of *Porites cylindrica* and *P. rus* inside and outside a marine reserve (MPA) in the Southern Philippine Sea biogeographic zone (sample size, n; density, No. per 20 m²; average colony sizes, Mean; geometric mean, GM; coefficient of variation, CV; skewness, g1; kurtosis, g2; single Kolmogorov-Smirnov test p-value, p).

Table

Table 1 Summary of values from the size-frequency distribution parameters examined among the colonies of *Porites cylindrica* and *P. rus* inside and outside a marine reserve (MPA) in the Southern Philippine Sea biogeographic zone (sample size, n; density, No. of individuals per 20 m²; average colony sizes, Mean; geometric mean, GM; coefficient of variation, CV; skewness, g1; kurtosis, g2; single Kolmogorov-Smirnov test p-value, *p*).

Parameter	Inside MPA		Outside MPA	
	3 m	8 m	3 m	8 m
<i>P. cylindrica</i>				
n	74	31	50	13
No. per 20 m ²	14.8	6.2	10	2.6
Mean ($\times 10^2$)	35.51	27.02	27.56	10.43
GM ($\times 10^2$)	12.1	15.4	11.9	6.5
CV	2.1	1.25	1.58	1.25
g1	5.61	2.37	0.06	2.76
g2	38.4	5.49	3.47	8.67
<i>p</i>	<0.01	<0.01	<0.01	<0.01
<i>P. rus</i>				
n	45	9	21	7
No. per 20 m ²	9	1.8	4.2	1.4
Mean ($\times 10^2$)	44.61	43.55	46.57	74.07
GM ($\times 10^2$)	24.5	27.4	27.1	36.8
CV	0.95	0.94	1.00	0.88
g1	1.06	1.64	1.63	0.27
g2	0.04	3.24	2.97	-2.38
<i>p</i>	<0.01	>0.05	>0.05	>0.05