

Preliminary observations of macrobenthic invertebrates and megafauna communities in the upper mesophotic coral ecosystems in Apo Reef Natural Park, Philippines

Timothy Joseph R. Quimpo, Patrick C. Cabaitan*, Ronald Dionnie D. Olavides, Edwin E. Dumalagan, Jr., Jeffrey Munar and Fernando P. Siringan

Abstract. The Philippines is located within an area of high reef biodiversity. However, it is vulnerable to the overexploitation of marine resources, which has reduced the abundance of many species, particularly large reef fish and marine turtles in the shallow reef areas (< 30 m). There is a need to assess the populations of these marine animals in the mesophotic coral ecosystems (> 30 m). The objectives of the study were (1) to determine the macrobenthic invertebrates and megafauna communities across the different reef type and depth; (2) compare species composition of macrobenthic invertebrates and megafauna communities across reef type and depth; and (3) to determine the benthic cover across reef type and depth. Macrofauna invertebrates and megafauna communities in the upper mesophotic zone (30–40 m) in Apo Reef Natural Park, Philippines were sampled using 15 min Underwater Visual Census (UVC). We observed ‘regionally’ rare macroinvertebrates and megafauna such as *Holothuria fuscogilva*, *Thelenota ananas*, *Bolbometopon muricatum*, *Cheilinus undulatus*, *Alopis pelagicus*, *Triaenodon obesus*, and *Eretmochelys imbricata*, which may be attributed to the long term (21 years) protection provided by Apo Reef. Interestingly, there were no significant differences in species richness, abundance and species composition across reef types and depths, probably because of horizontal and vertical movement of megafauna and the relatively similar benthic composition. This study provides one of first quantification of macrobenthic invertebrate and megafauna communities in mesophotic reefs, which is data deficient in the coral triangle; thus, contributing to the budding mesophotic research program in the region.

Key words. macrobenthos, megafauna, mesophotic coral ecosystems, Philippines

INTRODUCTION

The Philippines is considered the center of marine biodiversity (Carpenter & Springer, 2005; Veron et al., 2008); however, overexploitation has greatly reduced the abundance of many reef associated invertebrates, reptiles, and fishes in the country (Shanker & Pilcher, 2003; Nañola et al., 2011; Erikson & Clarke, 2015; Lavides et al., 2016). Particularly more vulnerable to exploitation are large bodied benthic and nektonic animals, which exhibit slow growth rates and reproductive maturity (Banse & Moser, 1980; Jennings et al., 1994; Brey, 1999). These large bodied animals may be referred to as ‘macrobenthos’ (for sessile and mobile invertebrates) and ‘megafauna’ (for nektonic fish, reptiles, and mammals) (Warwick & Clarke, 1993; Blanchard et al., 2004; Lewison et al., 2004; Lewison et al., 2013). Currently, there is no consensus as to the exact size requirement for an animal to be categorised as a ‘macrobenthos’ and a ‘megafauna’; hence, in this study, we defined macrobenthos

as invertebrates that reached a size of > 30 cm while megafauna were fish and reptiles that reached a size of > 50 cm. Majority of macrobenthos and megafauna communities are threatened in developing countries, such as the Philippines because of unregulated fishing and socioeconomic demands (e.g., overpopulation, market infrastructures, to name a few) that have contributed to their decline (Lavides et al., 2016). However, these findings were based predominantly on observations from shallow fringing reefs, with minimal observations in atoll reefs and no observations on deep reef ecosystems, such as the mesophotic coral reef ecosystems.

Majority of the coral reefs in the Philippines are fringing, consequently, most of the reef assessments were confined to nearshore shallow fringing reefs (see Gomez et al., 1994; Nañola et al., 2004, 2011; Go et al., 2015). Few studies have been conducted on offshore atoll reefs, such as Apo Reef Natural Park and Tubbataha Reef Natural Park. These atoll reefs have distinct communities because of less exposure to impacts by disturbances associated with nearshore reefs, e.g., sedimentation, pollution (Dygico et al., 2013; Licuanan et al., 2017). However, differences in reef communities between fringing and atoll reef types and between depths are not well understood.

The Marine Science Institute, College of Science, University of the Philippines, Diliman, Quezon City, 1101, Philippines; Email: pcabaitan@msi.upd.edu.ph
(*corresponding author)

Apo Reef

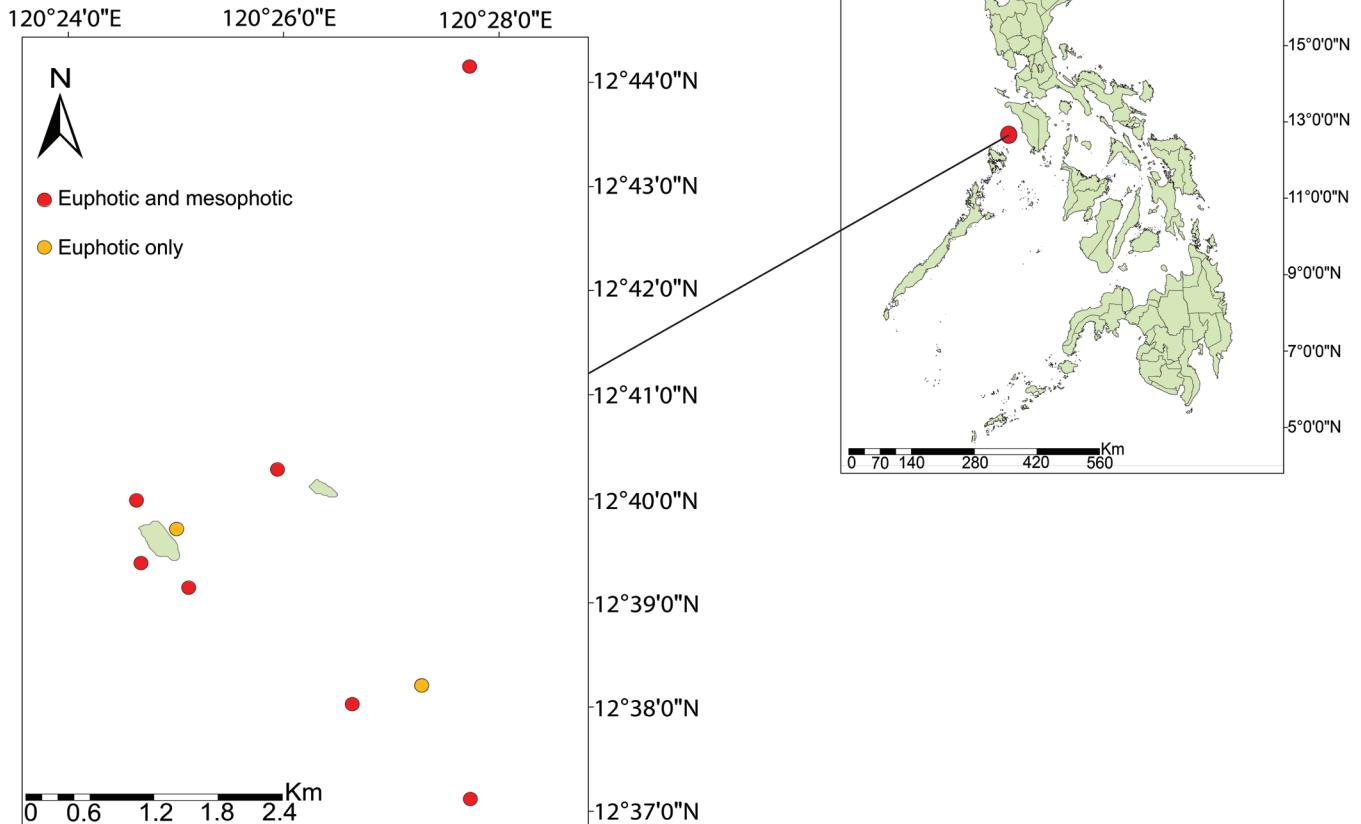


Fig. 1. Map showing the location of Apo Reef Natural Park in the Philippines, as well as, the study sites that were surveyed in March 2016.

to 150 m, and are characterised by a photosynthetically active radiation (PAR) of 1% (Lesser et al., 2009; Kahng et al., 2010). Attributed to their depth, MCEs experience lower levels of disturbances (e.g., bleaching, fishing, to name a few), which may potentially protect many reef associated species (Bongaerts et al., 2010; Bridge et al., 2013). MCEs may also serve as nursery habitats, as well as sites for ontogenetic migrations and mass spawning events, highlighting the interconnectivity between shallow and mesophotic reefs (Brokovich et al., 2007; Slattery et al., 2011; Holstein et al., 2016). However, most of these observations are limited to the Caribbean, with minimal observations in the Indo-Pacific (Kahng et al., 2010) and only one observation in the Philippines (Ross & Hodgson, 1981; reviewed in Turner et al., 2017).

In the present study, we determined the community structure of macrobenthic invertebrate and megafauna communities in Apo Reef Natural Park (ARNP) across different reef types and depths. First, we determined dissimilarities in species composition across depths and reef types (fringing versus atoll). Second, we examined the spatial and depth variability in species richness and abundance of macrobenthic invertebrate and megafauna communities. Lastly, we quantified the benthic composition across depths and reef

types. Given the capability of most marine megafauna to move along a wide range of distances between depths and sites (Papastamatiou et al., 2015; Khan et al., 2017), we hypothesise that there may be less variability in the structure of megafauna communities between depths and reef types. However, it is not well understood whether the differences in the structure of benthic communities will influence the differences in megafauna community structure between euphotic and upper mesophotic reefs, and between reef types. The initial quantification of macrobenthic invertebrate and megafauna communities in mesophotic reefs in the Philippines will help to unravel the biodiversity of this relatively unexplored ecosystem in the coral triangle.

MATERIAL & METHODS

Study site. The study was conducted in Apo Reef Natural Park (ARNP) in Sablayan Occidental Mindoro (Fig. 1). ARNP is one of the largest Marine Protected Areas (MPAs) in the Philippines, covering a total area of 11,667 ha. The spatial coverage of ARNP is sufficiently larger than the other MPAs in the Philippines, which mostly cover an area of less than 20 ha (Cabral et al., 2014). The MPA size of ARNP is second only to Tubbataha Reefs Natural Park (97,030 ha), the largest MPA in the country. It is a no-take MPA, which

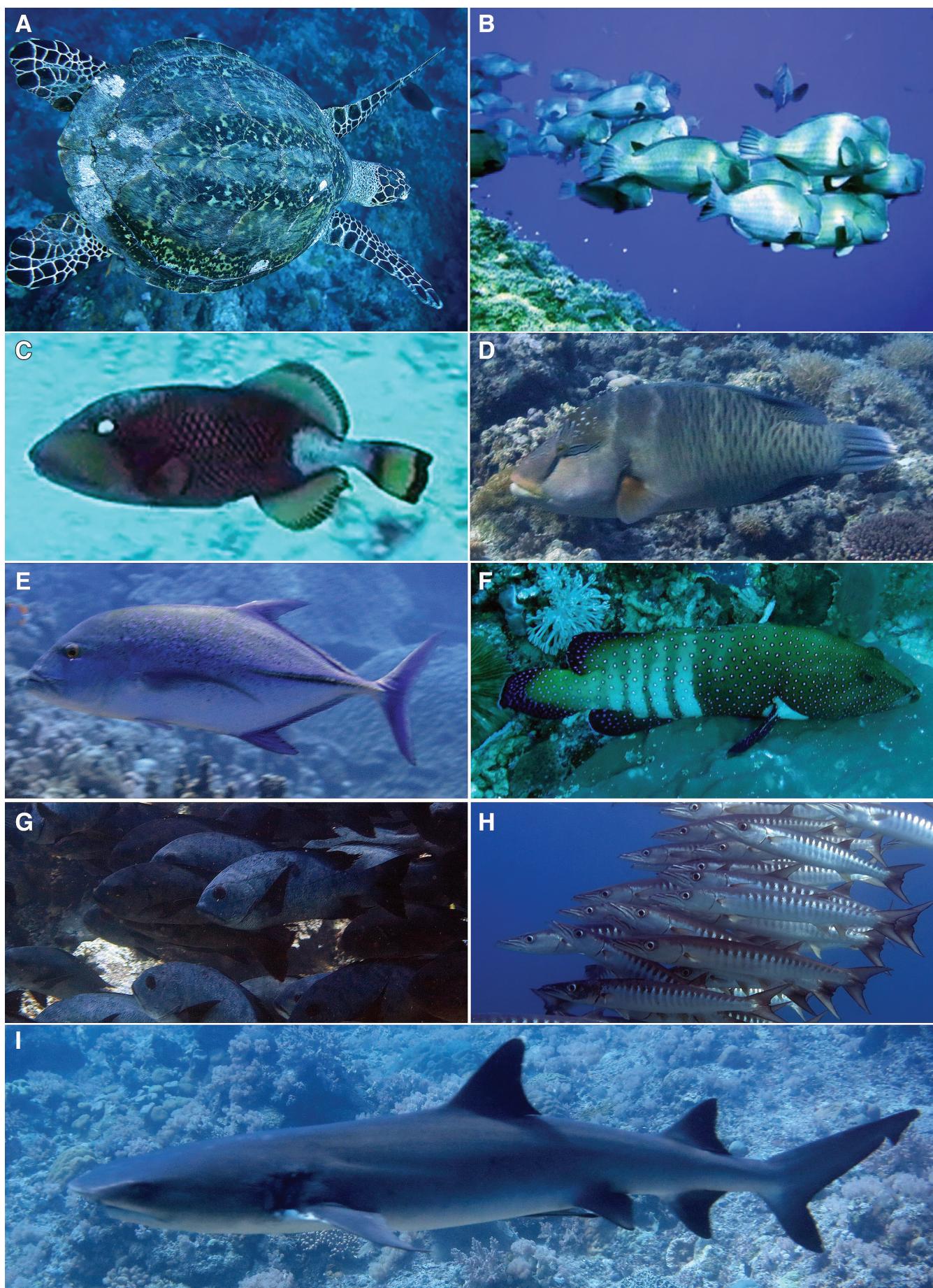


Fig. 2. Reef fish and marine reptile megafaunal species in Apo Reef Natural Park. A, *Eretmochelys imbricata*; B, *Bolbometopon muricatum*; C, *Balistoides viridescens*; D, *Cheilinus undulatus*; E, *Caranx melampygus*; F, *Cephalopholis argus*; G, *Macolor niger*; H, *Sphyraena genie*; I, *Triaenodon obesus*.

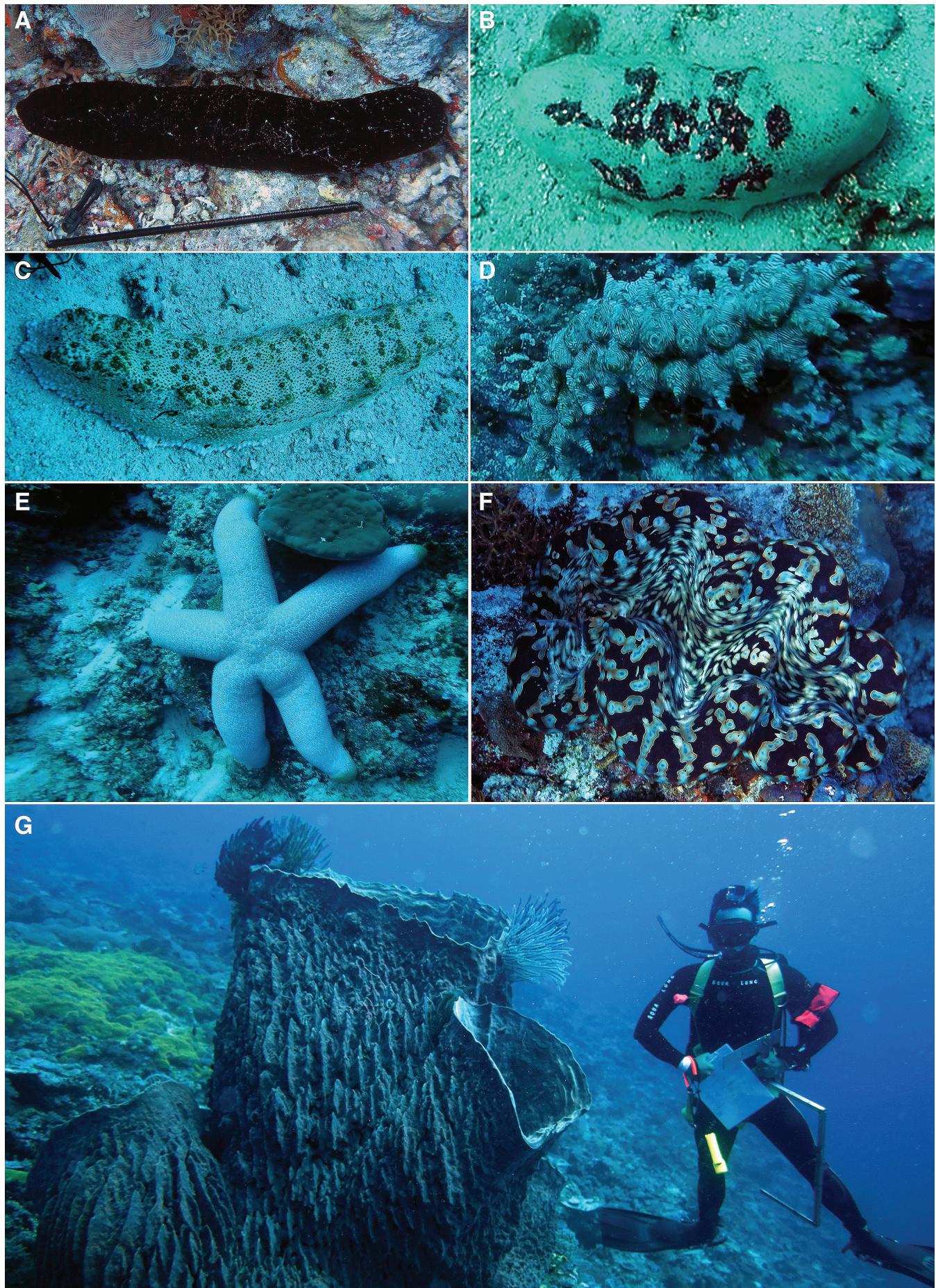


Fig. 3. Macrofauna invertebrates in Apo Reef Natural Park. A, *Holothuria atra*; B, *Holothuria fuscogilva*; C, *Thelenota anax*; D, *Thelenotarubra lineata*; E, *Thromidia catalai*; F, *Tridacna* sp.; G, *Xetospongia* sp.

has been protected since 1996; although, recreational diving activities are allowed in some areas within ARNP. ARNP is also one of the well managed MPAs in the country based on MPA Effectiveness Assessment Tool (MEAT) scores (Cabral et al., 2014). MEAT is used to evaluate governance and management of MPAs based on indicators such as existence of a consistent monitoring program, sustained enforcement, funding support, and others (White et al., 2004).

Nine (9) survey sites were established in ARNP, which covered Apo Island, and the northwest and southwest atoll systems. The distances between the sites ranged from 0.5 km to \sim 3 km (Fig. 1). Here, Apo Island refers to the island inside the ARNP in the Western Philippine Sea, which should not be confused with the smaller (74 ha) Apo Island in the Visayan Sea. Four (4) sites were located in the fringing reefs within the main island, while five sites were located in the atoll reefs. Euphotic surveys were conducted in all 9 sites, while mesophotic surveys were conducted in 7 sites. All of the surveys were conducted in March 2016 as ARNP is exposed to calmer weather condition around this time.

Sampling design. Timed underwater visual census (UVC; White et al., 2015) was conducted to survey the macrobenthic invertebrate and megafauna communities in two depths, euphotic (7–15 m) and upper mesophotic (30–40 m). This method is ideal for the assessment of large animals, which are difficult to sample using conventional visual census methods that cover only small areas, because these animals have large territories and exhibit behaviors that limit their sightings (Richards et al., 2011). Moreover, this method may also be advantageous to surveying relatively cryptic animals (e.g., sea cucumbers) that hide in the holes, nooks and crannies of limestone reefs (Shepherd et al., 2003).

Fifteen minute observations were conducted in each euphotic and mesophotic station. The 15 min observation time was conducted to standardise the assessment per depth, since mesophotic surveys were limited to a maximum time of 15 min because of safety limitations using open-circuit SCUBA. Macrofauna invertebrates and megafauna observed during the assessments were identified to species level along with recordings of their abundance. One diver censused the megafauna within a 10 m width area, while the macrofauna survey was conducted by another diver that censused within a 2 m width area. The macrofauna invertebrates and megafauna were categorised according to their trophic levels, namely: detritivore, suspension feeder, herbivore, omnivore, piscivore and planktivore. The categorisation was based on their predominant diets that were gleaned from Froese & Pauly (2017) and Palomares & Pauly (2017).

To determine the benthic cover in each site, a modified photo-quadrat method was used. Images were taken at \sim 1 m intervals haphazardly within the area where the UVC was conducted. The sampling time for this method was also 15 min, which yielded \sim 25 images per dive. The images obtained were subsequently analysed using Coral Point Count with excel extensions (CPCe; Kohler & Gill, 2006). In each CPCe image, 25 (5 \times 5 uniform grid) points were

overlaid. The benthic categories were classified as hard coral (C), octocorals (OCT), algae assemblages (ALG), small invertebrates (< 30 cm; INV), dead coral (DC) and abiotic components (e.g., sand; ABI).

Statistical analyses. The abundance data was square-root transformed and visually inspected using an unconstrained, non-metric multidimensional scaling (nMDS), with the ordination distances based on Bray-Curtis similarity. To determine differences in species composition across reef types and depths, analysis of similarity (ANOSIM) test was conducted. Species that contributed to the similarities and dissimilarities in the macrobenthic and megafauna communities were determined using similarity percentage (SIMPER) test.

The differences in macrobenthic and megafauna abundance across reef types (fixed factor, two levels: atoll and fringing) and depth (fixed factor, two levels: euphotic and mesophotic) were tested using multiple t-tests. The assumptions of the t-test were tested using residual analysis (data normality) and Levene's test (data homogeneity). The raw data for macrofauna and megafauna were log10 transformed to improve data normality. Similarly, t-test was used to determine differences in arcsin percentage cover of the benthic categories across reef types and depth. To test for differences in cumulative species richness across reef type and depth, a permutation test was conducted (Rossi, 2011). The permutation test is based on the difference between community one and two (referred to as d) compared to n differences in d_{random} obtained after permutating the samples between communities (Rossi, 2011). A total of 499 permutations were conducted wherein p-values were generated. We considered significant differences in species richness between communities if p-values were below 0.05. All statistical analyses were conducted using R software, with the univariate analyses conducted using stats and rich packages, and the multivariate analyses conducted using vegan (R Core Team, 2017; Rossi, 2011; Oksanen et al., 2017).

RESULTS

Overall, 38 macrobenthic invertebrate and megafauna species were observed, with a total abundance of 528 individuals (Table 1, Figs. 2, 3). Remarkable species that were observed included the vulnerable *Eretmochelys imbricata* (hawksbill turtle), *Alopias pelagicus* (pelagic thresher shark), *Bolbometopon muricatum* (bumphead parrotfish), and *Holothuria fuscogilva* (white teeth), as well as the nearly threatened *Triaenodon obesus* (whitetip reef shark), and the endangered *Cheilinus undulatus* (bumphead wrasse) and *Thelenota ananas* (prickly red fish).

Species composition of macrobenthic invertebrates and megafauna were not significantly different across depths (Fig. 4A) and reef types (Fig. 4B). The top 10 species that contributed to the similarities and dissimilarities across depths and reef types are summarised in Table 2. For instance, *Triaenodon obesus*, *Macolor macularis*, and *Cheilinus*

Table 1. Macrofaunal and megafauna species observed in Apo Reef along with their trophic groupings and IUCN status: O (Omnivore), C (Carnivore), H (Herbivore), D (Detritivore) and P (Planktivore); NE (Not Evaluated), DD (Data Deficient), LC (Least Concern), NT (Near Threatened), VU (Vulnerable), EN (Endangered) and CE (Critically Endangered).

| Species | Trophic groups | IUCN Status | Number of individuals recorded | |
|---------------------------------------------------------|----------------|-------------|--------------------------------|------------|
| | | | Euphotic | Mesophotic |
| Marine Reptiles | | | | |
| <i>Eretmochelys imbricata</i> (Linnaeus 1766) | O | CE | 10 | 1 |
| <i>Laticauda colubrina</i> (Schneider 1799) | C | LC | 1 | 0 |
| Marine fishes | | | | |
| <i>Balistoides viridescens</i> (Bloch & Schneider 1801) | C | NE | 1 | 0 |
| <i>Bolbometopon muricatum</i> (Valenciennes 1840) | H | VU | 44 | 0 |
| <i>Chelinus undulatus</i> (Ruppell 1835) | C | EN | 15 | 4 |
| <i>Caranx ignobilis</i> (Forsskal 1775) | C | NE | 1 | 0 |
| <i>Caranx lugubris</i> (Poey 1860) | C | NE | 2 | 5 |
| <i>Caranx melampygus</i> (Cuvier 1833) | C | NE | 1 | 3 |
| <i>Caranx sexfasciatus</i> (Quoy & Gaimard 1825) | C | NE | 0 | 9 |
| <i>Cephalopholis argus</i> (Schneider 1801) | C | LC | 1 | 4 |
| <i>Epinephelus howlandi</i> (Gunther 1873) | C | LC | 0 | 1 |
| <i>Plectropomus leopardus</i> (Lacepede 1802) | C | NT | 2 | 0 |
| <i>Lutjanus bohar</i> (Forsskal 1755) | C | NE | 1 | 0 |
| <i>Macolor macularis</i> (Fowler 1931) | C | NE | 12 | 17 |
| <i>Macolor niger</i> (Forsskal 1755) | C | NE | 115 | 0 |
| <i>Pinjalo lewisi</i> (Randall, Allen & Anderson 1987) | C | NE | 0 | 2 |
| <i>Naso brevirostris</i> (Cuvier 1829) | P | LC | 8 | 0 |
| <i>Naso hexacanthus</i> (Bleeker 1855) | P | LC | 2 | 44 |
| <i>Naso vlamingii</i> (Valenciennes 1835) | P | LC | 2 | 0 |
| <i>Gymnosarda unicolor</i> (Ruppell 1836) | C | LC | 1 | 37 |
| <i>Sphyraena barracuda</i> (Edwards 1771) | C | LC | 13 | 0 |
| <i>Sphyraena qenie</i> (Klunzinger 1870) | C | NE | 79 | 0 |
| Shark | | | | |
| <i>Alopias pelagicus</i> (Nakamura 1935) | C | VU | 0 | 1 |
| <i>Triaenodon obesus</i> (Ruppell 1837) | C | NT | 29 | 19 |
| Macrofaunal invertebrates | | | | |
| <i>Holothuria atra</i> (Jaeger 1833) | D | LC | 3 | 1 |
| <i>Holothuria edulis</i> (Lesson 1830) | D | LC | 5 | 0 |
| <i>Holothuria fuscogilva</i> (Cherbonnier 1980) | D | VU | 1 | 0 |
| <i>Pearonothuria graeffei</i> (Semper 1868) | D | LC | 1 | 0 |
| <i>Thelenota ananas</i> (Jaeger 1833) | D | EN | 0 | 1 |
| <i>Thelenota anax</i> (Clark 1921) | O | DD | 8 | 0 |
| <i>Thelenota rubralineata</i> (Massin & Lane 1991) | O | DD | 2 | 1 |
| <i>Choriaster granulatus</i> (Lutken 1869) | D | NE | 1 | 0 |
| <i>Thromidina catalai</i> (Pope & Rowe 197) | D | NE | 0 | 2 |
| <i>Culcita novaeguineae</i> (Muller and Troschel 1842) | D | NE | 1 | 0 |
| <i>Tridacna crocea</i> (Lamark 1819) | O | LC | 2 | 0 |
| <i>Tridacna maxima</i> (Roding 1798) | O | LC | 2 | 1 |
| <i>Xetospongia</i> sp. | O | NE | 2 | 7 |
| Total | | | 368 | 160 |

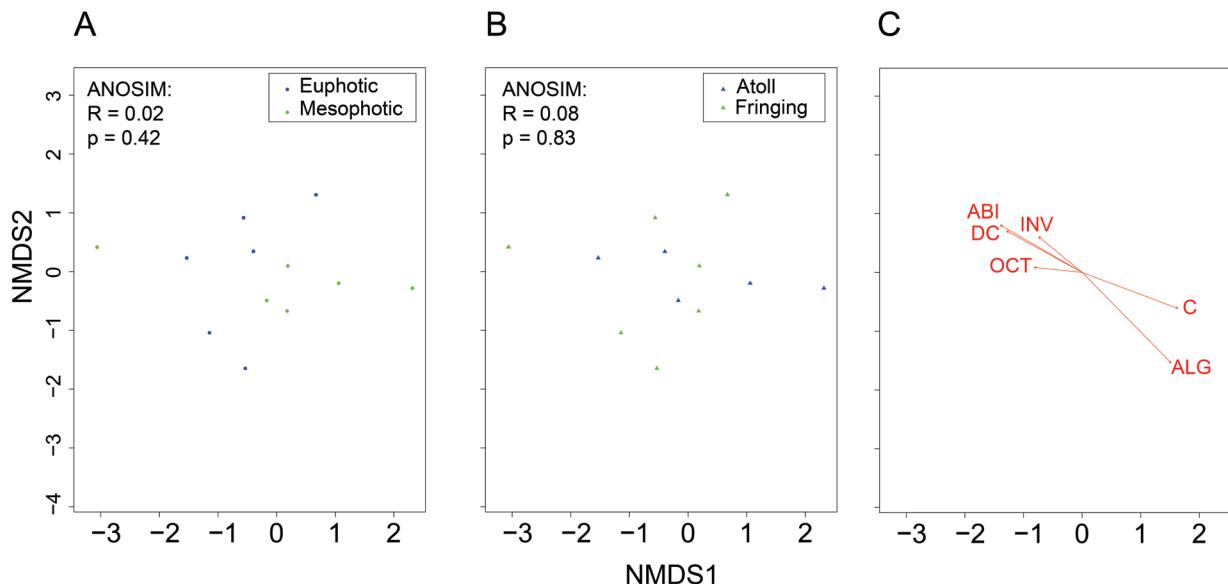


Fig. 4. Results of the non-metric multidimensional scaling (nMDS) across depths (A) and reef types (B). Analysis of similarity (ANOSIM) results along with the corresponding p values are included in the plots (A and B). Vectors showing the influence (direction and magnitude) of the different benthic cover on the species composition (C).

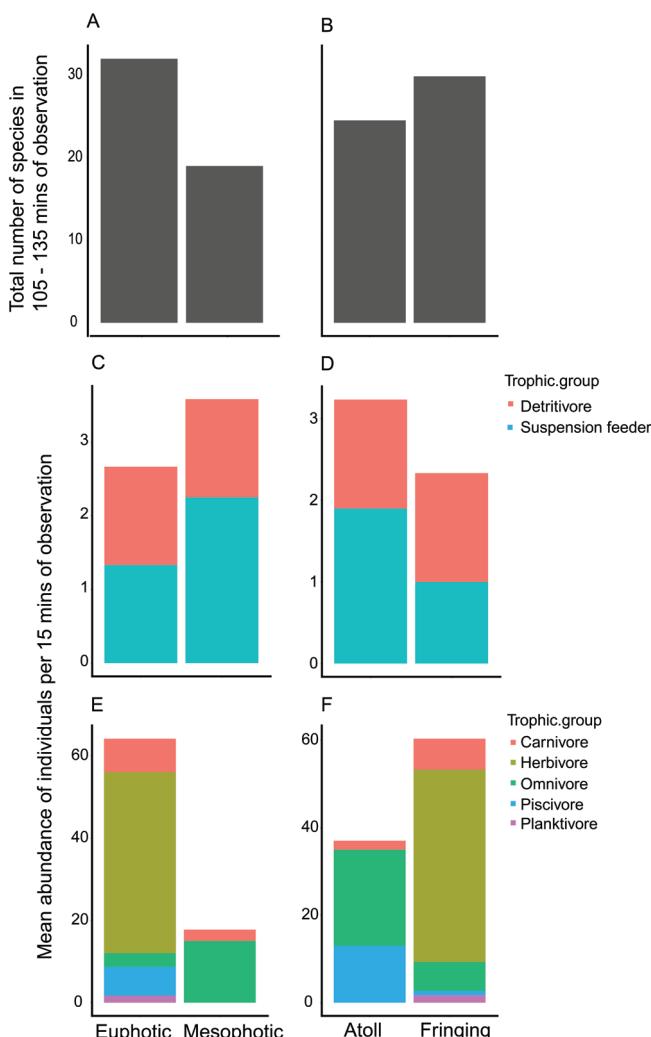


Fig. 5. Barplots represent the total species richness across the depths (A) and reef types (B). C and E show the abundance of macrobenthic invertebrates and megafauna, respectively, with their corresponding trophic groups across depths. D and F show the abundance of macrobenthic invertebrates and megafauna, respectively, with their corresponding trophic groups across reef types.

undulatus had comparable mean abundances between the fringing and atoll reef types. The vector plot (Fig. 4C) across the two depths indicate that corals and algae had a higher cover in euphotic relative to mesophotic reefs. In contrast, the vector plot across the two reef types had no distinct patterns, i.e., there were sites in the atolls and in the fringing reefs that had high coral cover and high abiotic cover.

Total species richness was higher in the euphotic (32) than in the mesophotic (19) zone, and was higher in the fringing (28) relative to atoll reefs (23) (Fig. 5A, B). However, both of these differences were not statistically significant (depth: $d = 13$, $p = 0.19$; reef type: $d = 5$, $p = 0.46$). The mean abundance in the mesophotic zone for the macrobenthic invertebrates was higher relative to the euphotic zone (Fig. 5C), however, the opposite was true for the megafauna wherein abundance was higher in the euphotic than in the mesophotic zone (Fig. 5E). Atoll reefs had a slightly higher mean abundance compared to fringing reefs for the macrobenthic invertebrates (Fig. 5D); whereas, the abundance of the megafauna was higher in the fringing than in the atoll reefs (Fig. 5F). Yet, these differences across depths were not significant for macrobenthic invertebrates ($t = 0.60$, $p = 0.56$) and for megafauna ($t = 0.11$, $p = 0.91$). Similarly, differences in abundance across reef types for macrobenthos ($t = 1.52$, $p = 1.34$) and megafauna ($t = 0.58$, $p = 0.56$) were not statistically significant.

The macrobenthic invertebrates were represented by only two trophic groups, i.e., detritivores and suspension feeders, which did not vary across depths and reef types (Fig. 5C, D). In contrast, megafauna had a more diverse set of groups in the euphotic relative to the mesophotic reefs (Fig. 5E). However, between the atoll and fringing reefs, there were only slight differences in the number of megafauna trophic groups (Fig. 5F).

Table 2. Summary of the SIMPER results showing the top 10 species that contributed to the similarities/dissimilarities in species composition.

| Species | % Contribution | Abundance | |
|-------------------------------|----------------|-----------|------------|
| | | Euphotic | Mesophotic |
| <i>Naso hexacanthus</i> | 10.45 | 3.67 | 3 |
| <i>Triaenodon obesus</i> | 10.31 | 4 | 3 |
| <i>Macolor niger</i> | 8.78 | 19.16 | 0 |
| <i>Bolbometopon muricatum</i> | 8.56 | 7.33 | 0 |
| <i>Gymnosarda unicolor</i> | 7.62 | 6.16 | 0.12 |
| <i>Xetospongia</i> sp. | 6.36 | 0.33 | 0.86 |
| <i>Sphyraena qenie</i> | 6.03 | 13.17 | 0 |
| <i>Macolor macularis</i> | 5.4 | 3 | 1.38 |
| <i>Chelinus undulatus</i> | 3.28 | 1.67 | 1.12 |
| <i>Eretmochelys imbricata</i> | 2.29 | 1.33 | 0.37 |
| | | Fringing | Atoll |
| <i>Naso hexacanthus</i> | 11.98 | 6.28 | 0.28 |
| <i>Triaenodon obesus</i> | 10.83 | 4.14 | 2.71 |
| <i>Xetospongia</i> sp. | 7.26 | 0.42 | 0.85 |
| <i>Macolor niger</i> | 7.15 | 0 | 16.42 |
| <i>Bolbometopon muricatum</i> | 6.6 | 6.28 | 0 |
| <i>Gymnosarda unicolor</i> | 6.1 | 5.42 | 0 |
| <i>Macolor macularis</i> | 5.42 | 2.57 | 1.57 |
| <i>Sphyraena qenie</i> | 4.91 | 0 | 11.28 |
| <i>Chelinus undulatus</i> | 3.46 | 1.28 | 1.42 |
| <i>Sphyraena barracuda</i> | 2.34 | 0 | 1.85 |

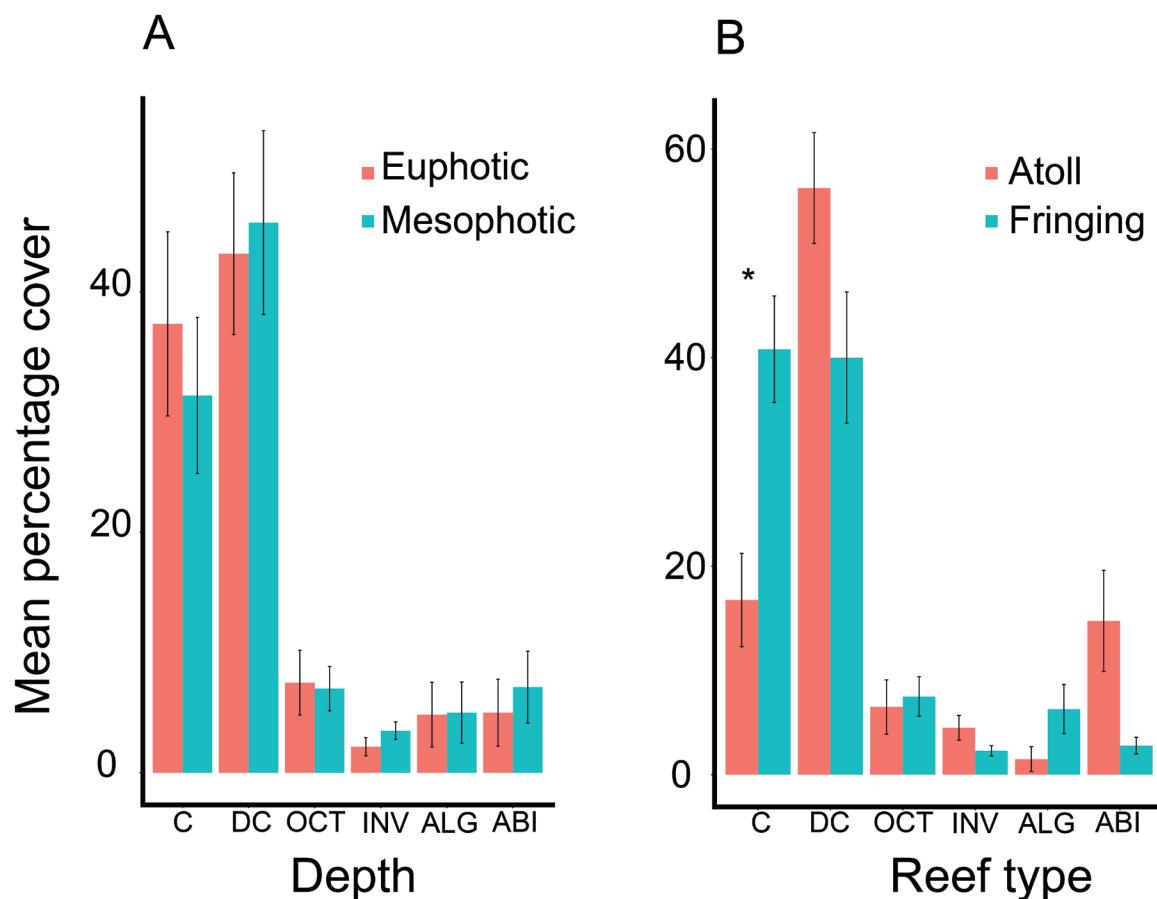


Fig. 6. Mean percentage cover of the benthic categories across depths (A) and reef types (B). Abbreviations of the benthic categories are as follows: C – hard coral, DC – dead coral, OCT – octocoral, INV – small invertebrates, ALG – algae assemblages and ABI – abitoic. Significant differences are denoted by an asterisk (*) sign.

Benthic cover across depths and reef types were dominated by dead and hard corals, with the remaining cover occupied by the 5 other benthic categories (Fig. 6). Significant differences in benthic cover were only observed across reef types (Fig. 6B). Specifically, coral cover was higher in the fringing reefs relative to the atoll reefs ($t = 3.40$, $p < 0.001$).

DISCUSSIONS

Five remarkable megafauna species (*E. imbricata*, *A. pelagicus*, *B. muricatum*, *T. obesus*, and *C. undulatus*) and two macrobenthic invertebrates (*H. fuscogilva* and *T. ananas*) were observed during the surveys in Apo Reef. The occurrence of these species may be attributed to MPA protection. Apo Reef is a strict no-take MPA that has been functioning since 1996 (21 years of protection), which may have protected these fishery-targeted species for decades. Although, we were unable to sample non-MPA sites near Apo Reef, indirect evidence suggests that *B. muricatum* and *C. undulatus* are now rarely observed in the Philippines because of overexploitation (Lavides et al., 2016). Similarly, sea turtles and sharks are still heavily exploited in the Philippines despite management interventions, with their current population status in the region relatively unknown (Shanker & Pilcher, 2003; Erikson & Clarke, 2015). However, based solely on their traits (e.g., slow maturity and large body size) these animals may also be on the decline (Jennings et al., 1994; Cheung et al., 2005). Fortunately, MPAs in other regions have showed improvement of their megafauna populations such as *Chelonia mydas* (green sea turtle), *B. muricatum*, and *T. obesus* because of MPA protection (Muñoz et al., 2012; Scott et al., 2012; White et al., 2015).

There were no differences in community structure of megafauna across reef types and depths. The similarity in the community structure between reef types was attributed to the comparable mean abundances of *Triaenodon obesus*, *Macolor macularis*, and *Cheilinus undulatus* between the fringing and atoll reef types. Moreover, the mean abundances of *Naso hexacanthus*, *T. obesus*, *M. macularis*, and *C. undulatus* contributed to the similarity in community structure between depths. A common trait among these species is they attain large maximum lengths that range from 50 to 200 cm (Kuiter & Tonozuka, 2004). Although, we were unable to directly track individual movements, studies show that large bodied carnivorous megafauna exhibit horizontal and vertical movements, wherein they may travel an area of 15 km wide and a depth of 70 m (Papastamatiou et al., 2015; Khan et al., 2017). The daily movement of individuals is attributed to foraging (Krumme, 2009), thermoregulation (Papastamatiou et al., 2015), and seeking shelter (Khan et al., 2017); whereas seasonal movement is due to spawning (Papastamatiou et al., 2015; Holstein et al., 2016; Khan et al., 2017).

Concordant with the multivariate results, univariate analyses also indicate that there were no significant differences in species richness and abundances across depths and reef types. Again, this may be attributed to the movement of individuals. Alternatively, the relatively similar benthic composition,

especially between depths, may also have contributed to the similarity in species richness and abundances. Benthic composition, specifically coral cover, is positively correlated with the species richness and abundance of reef-associated fauna (Bell & Galzin, 1984).

The macrobenthic invertebrates were only represented by two trophic groups, namely: detritivores and suspension feeders. There were no apparent differences in macrobenthic trophic groups across the two depths and reef types. Megafauna, on the other hand, had a more diverse trophic group in the euphotic relative to the mesophotic reefs. A large portion of this variability was attributed to the herbivore group. Rarely does algae grow at a high rate in mesophotic reefs to support herbivorous fishes because of low light levels; hence the herbivore group is limited to shallow reefs (Kahng et al., 2010). In contrast, mesophotic reefs had higher abundances of omnivores and carnivores. The higher abundances of these groups may be attributed to prey availability, which has also been reported in other studies that the prey items of these trophic groups increase with depth (Kahng et al., 2010; Pinheiro et al., 2015). Across the two reef types, there were only minimal differences in the trophic groups for the megafauna.

In conclusion, we observed 'regionally' rare megafauna species, together with other vulnerable animals across the different reef types and depths in Apo Reef. Interestingly, we found no differences in species richness, abundance and species composition across reef types and depths, which may be attributed to the movements of megafauna and/or the similarity in benthic composition. This study provides, to our knowledge, the first preliminary quantification of macrobenthic invertebrates and megafauna communities in mesophotic reefs in the Philippines; thus, contributes to the budding mesophotic research in the data deficient coral triangle.

ACKNOWLEDGEMENTS

We are grateful to the Biodiversity Management Bureau of the Department of Environment and Natural Resources and the Apo Reef Protected Area Management Board. We thank the Municipal Government of Sablayan, A. Vallejo of Sablayan Tourism Office, F. Magno of DENR-PAMB, and F. Sabban for their assistance in the field surveys. This manuscript was greatly improved with the suggestions provided by the anonymous reviewers. This work was funded by the Philippine Council for Agriculture, Aquatic and Natural Resources Research and Development, Department of Science and Technology. This is UPMSI contribution no. 453.

LITERATURE CITED

Banse K & Moser S (1980) Adult body mass and annual production/biomass relationships of field populations. Ecological Monographs, 50: 355–379.
 Bell JD & Galzin R (1984) Influence of live coral cover on coral-reef fish communities. Marine Ecology Progress Series, 15: 265–274.
 Blanchard F, LeLoc'h F, Hily C & Boucher J (2004) Fishing effects on diversity, size and community structure of the benthic

invertebrate and fish megafauna on the Bay of Biscay coast of France. *Marine Ecology Progress Series*, 280: 249–260.

Bongaerts P, Ridgway T, Sampayo, EM & Hoegh-Guldberg O (2010) Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral Reefs*, 29: 309–327.

Brey T (1999) Growth performance and mortality in aquatic macrobenthic invertebrates. *Advances in Marine Biology*, 35: 153–223.

Bridge TCL, Hughes TP, Guinotte JM & Bongaerts P (2013) Call to protect all coral reefs. *Nature Climate Change*, 3: 528–530.

Brokovich E, Einbinder S, Kark S, Shashar N & Kiflawi M (2007) A deep nursery for juveniles of the zebra angelfish *Genicanthus caudovittatus*. *Environmental Biology of Fishes*, 80: 1–6.

Cabral RB, Aliño PM, Balingit ACM, Alis CM, Arceo HO, Nañola CL Jr., Geronimo RC & MSN Partners (2014) The Philippine Marine Protected Area (MPA) database. *Philippine Science Letters*, 7: 300–308.

Carpenter KE & Springer VG (2005) The center of the center of marine shore fish biodiversity: the Philippines Islands. *Environmental Biology of Fishes*, 72: 467–480.

Cheung WWL, Pitcher TJ & Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities marine fishes to fishing. *Biological Conservation*, 124(1): 97–111.

Dygico M, Songco A, White AT & Green SJ (2013) Achieving MPA effectiveness through application of responsive governance incentives in the Tubbataha reefs. *Marine Policy*, 41: 87–94.

Erikson H & Clarke S (2015) Chinese market responses to overexploitation of sharks and seacucumbers. *Biological Conservation*, 184: 163–173.

Froese R & Pauly D (2017) FishBase. World Wide Web Electronic Publication. www.fishbase.org. (Accessed 20 June 2016).

Go KTB, Anticamara JA, de Ramos JJJ, Gabona SF, Agao DF, Herrera EC & Bitara AU (2015) Species richness and abundance of non-cryptic fish species in the Philippines: a global center of reef fish diversity. *Biodiversity Conservation*, 24(10): 2475–2495. doi: 10.1007/s10531-015-0938-0.

Gomez ED, Aliño PM, Yap HT & Licuanan WY (1994) A review of the status of Philippine reefs. *Marine Pollution Bulletin*, 29: 62–68.

Holstein D, Smith TB & Appeldorn RS (2016) Ecosystem services provided by mesophotic coral ecosystems. In: Baker EK, Puglise KA & Harris PT (eds.) *Mesophotic Coral Ecosystems - A Lifeboat for Coral Reefs?* The United Nations Environmental Programme and GRID - Arendal, Nairobi and Arendal. Pp. 63–66.

Jennings S, Pinnegar JK, Polunin NV & Boon TW (1994) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70(6): 934–944.

Khan JA, Goatley CHR, Brandl SJ, Tebbett SB & Bellwood DR (2017) Shelter use by large reef fishes: long-term occupancy and the impacts of disturbance. *Coral Reefs*, 36: 1123–1132.

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil, Hinderstein L & Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*. doi: 10.1007/s00338-010-0593-6.

Kohler KE & Gill SM (2006) Coral Point Count with excel extensions: a visual basic program for determination of coral and substrate coverage using random point count methodology. *Computer and Geosciences*, 32: 1259–1269.

Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Ivan Nagelkerken (ed.) *Ecological Connectivity among Tropical Coastal Ecosystems*. Springer Dordrecht Heidelberg London New York. Pp. 271–324.

Kuiter RH & Tonozuka T (2004) *Pictorial Guide to Indonesian Reef Fishes*. PT Dive & Dive’s, Bali, Indonesia, 440 pp.

Lavides MN, Molina EPV, de la Rosa GE Jr., Mill AC, Rushton SP, Stead SM & Polunin NVC (2016) Patterns of coral-reef finfish disappearances inferred from fishers’ knowledge in global epicentre of marine shorefish diversity. *PLoS ONE*, 11(5): e0155752. doi: 10.1371/journal.pone.0155752.

Lesser MP, Slattery M & Leichter JJ (2009) Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, 35: 1–8.

Lewison RL, Crowder LB, Read AJ & Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution*, doi:10.1016/j.tree.2004.09.004.

Lewison RL, Crowder LB, Wallace BP, Moore JE, Cox T, Zydelis R, McDonald S, DiMatteo A, Dunn DC, Kot CY, Bjorkland R, Kelez S, Soykan C, Stewart KR, Sims M, Boustany A, Read AJ, Halpin P, Nichols WJ & Safina C (2013) Global patterns of marine mammal, seabird, and seaturtle bycatch reveal taxa-specific and cumulative megafauna hotspots, *PNAS* 11(4): 5271–5276.

Licuanan AM, Reyes MZ, Luzon KS, Chan MAA & Licuanan WY (2017) Initial findings of the nationwide assessment of Philippine coral reefs. *Philippine Journal of Science*, 146(2): 177–185.

Muñoz RC, Zgliczynski BJ, Laughlin JL & Teer BZ (2012) Extraordinary aggressive behaviour from the giant coral reef fish, *Bolbometopon muricatum*, in a remote marine reserve. *PLoS ONE*, 7(6): e38120. doi: 10.1371/journal.pone.0038120.

Nañola CL Jr., Aliño PM & Carpenter KE (2011) Exploitation-related reef fish species richness depleted in the epicenter of marine biodiversity. *Environmental Biology of Fishes*, 90(4): 405–420. doi: 10.1007/s10641-010-9750-6.

Nañola C Jr., Aliño PM, Arceo H, Licuanan W, Uychiaoco A, Quibilan M, Campos W, Alcala A, White A & Gomez E (2004) Status report on coral reefs of the Philippines. *Proceedings of the 10th International Coral Reef Symposium*, 1055–1061.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E & Wagner H (2017) *vegan: Community Ecology Package*. R Package Version 2.4.3. <https://CRAN.R-project.org/package=vegan>. (Accessed 23 June 2016).

Palomares MLD & Pauly D (2017) SealifeBase. World Wide Web Electronic Publication. www.sealifebase.org. (Accessed 25 June 2016).

Papastamatiou YP, Meyer CG, Kosaki RK, Wallsgroove NJ & Popp BN (2015) Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Marine Ecological Progress Series*, 521: 155–170.

Pinheiro HT, Goodbody-Gringley G, Jessup ME, Sheperd B, Chequer AD & Rocha LA (2015) Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, 35(1): 139–151. doi 10.1007/s00338-015-1381-0.

R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. (Accessed 6 December 2017).

Richards BL, Williams ID, Nadon MO & Zgliczynski BJ (2011) A towed-diver survey method for mesoscale fishery-independent assessment of large-bodied reef fishes. *Bulletin of Marine Science*, 87(1): 55–74. doi: 10.5343/bms.2010.1019.

Ross MA & Hodgson G (1981) A quantitative study of hermatypic coral diversity and zonation at Apo Reef, Mindoro, Philippines. *Proceedings of the 4th International Coral Reef Symposium*, Manila, 2: 281–291.

Rossi JP (2011) rich: An R package to analyse species richness. *Diversity*, 3: 112–120. doi: 10.3390/d3010112.

Scott R, Hodgson DJ, Witt MJ, Coyne MS, Adnyana W, Blumenthal JM, Broderick AC, Canbolat AF, Catry P, Ciccione S, Delcinox E, Hitipeuw C, Luschi P, Pet-Soede L, Pendoley K, Richardson

PB, Rees AF & Godley BJ (2012) Global analysis of satellite tracking data shows that adult green turtles are significantly aggregated in Marine Protected Areas. *Global Ecology and Biogeography*, 21: 1053–1061.

Shanker K & Pilcher NJ (2003) Marine turtle conservation in South and Southeast Asia: hopeless cause of cause for hope? *Marine Turtle Newsletter*, 100: 43–51.

Shepherd SA, Toral-Granda V & Edgar GJ (2003) Estimating the abundance of clustered and cryptic marine macro-invertebrates in the Galapagos with particular reference to seacucumbers. *Noticias de Galapagos*, 62: 36–39.

Slattery M, Lesser MP, Brazeau D, Stokes MD & Leichter JJ (2011) Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, 408: 32–41.

Turner JA, Babcock RC, Hovey R & Kendrick GA (2017) Deep thinking: a systematic review of mesophotic coral ecosystems. *ICES Journal of Marine Science*, 74(9): 2309–2320. doi: 10.1093/icesjms/fsx085.

Veron JEN, Devantier LM, Turak, E, Green AL, Kininmonth S, Stafford-Smith M & Peterson N (2008) Delineating the coral triangle. *Galaxea*, 11: 91–100.

Warwick RM & Clarke KR (1993) Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Marine Ecology Progress Series*, 92: 221–231.

White AT, Meneses AT & Ovenden MF (2004) Management rating system for marine protected areas: an important tool for management. In: DA-BFAR (Department of Agriculture-Bureau of Fisheries and Aquatic Resources) (ed.) In *Turbulent Seas: The Status of Philippine Marine Fisheries*. Coastal Resource Management Project of the Department of Environment and Natural Resource, Cebu City, Philippines. Pp. 226–232.

White ER, Myers MC, Flemming JM & Baum JK (2015) Shifting elasmobranch community assemblage at Cocos Island – an isolated marine protected area. *Conservation Biology*, 29: 1186–1197.