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Community structure and size-frequency distribution of soft corals in a heavily disturbed reef system in northwestern Philippines

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ABSTRACT

Soft corals in the Philippines have received little attention. In this study, community structure and size-frequency distribution of soft corals were assessed via quantitative surveys in a heavily disturbed reef system in northwestern Philippines. Relationships between selected environmental parameters and benthic components were also investigated. Results reveal that soft coral cover, density, and taxa richness were lowest at stations nearest a fish farming area, characterized by the poorest water quality. Differences in dominance of taxonomic groups may indicate differences in environmental preference or tolerance. Exposure to waves and water clarity were determined to have high correlations with the distribution of different taxa. Symmetrical size distributions of selected alcyoniids were indicative of healthy populations. However, the negative skewness of *Lobophytum* may indicate an eventual population decline caused by unfavorable environmental conditions. The study's findings suggest the need to conduct a detailed analysis of the different soft coral variables during coral reef surveys to improve data interpretations necessary for coral reef management in the Philippines.

1. Introduction

Coral reefs are one of the most diverse ecosystems in the world (Connell, 1978). Despite their importance, coral reef health is declining due to various disturbances, both natural and anthropogenic (Hughes et al., 2003; Hughes et al., 2010; Heery et al., 2018). Natural disturbances include storms and increased sea surface temperature (SST), while anthropogenic threats are mainly derived from pollution and overfishing (Baum et al., 2015; Yang et al., 2015; Zaneveld et al., 2016; Glynn et al., 2017). For the Philippines, an archipelagic country, these reefs contribute billions of US dollars annually to the economy through fisheries, tourism, and other ecosystem services (Tamayo et al., 2018). A recent nationwide assessment of coral reefs in the Philippines revealed a continuing decline in coral cover (Licuanan et al., 2019) partially attributed to pollution and overfishing (Gomez et al., 1994; Nañola et al., 2011).

Soft corals are major benthic components of Indo-Pacific coral reefs and are highly abundant in many regions (Fabricius and Alderslade, 2001). As major benthic components, they contribute to coral reef complexity by providing habitats to various organisms (Depczynski and Bellwood, 2004; Poulus et al., 2013; Ferrari, 2017) and constituting part of the diet of various organisms (e.g., Van Alstyne et al., 1994; Yesson et al., 2012; Epstein and Kingsford, 2019; Garra et al., 2020). Soft corals also contribute to reef formation through the deposition of their calcite skeletal material, sclerites (Jeng et al., 2011; Shoham et al., 2019). However, the ecological roles of soft corals and their responses to changing environmental conditions, potentially leading to shifts in community structure, which affect the entire reef ecosystem and its services, are still not yet fully explored.

Soft coral distribution and contribution to coral reef community structure has been thoroughly studied in some regions in the Indo-Pacific, such as in the Red Sea, Great Barrier Reef (Australia), and Hong Kong (e.g., Benayahu and Loya, 1981; Dinesen, 1983; Yeung et al., 2014). One study of note that highlighted the major contributions of different soft coral taxa to coral reef community structure is that by Ninio and Meekan (2002), which demonstrated that among three distinct coral reef groups in the Great Barrier Reef, one group was characterized by a high abundance of soft corals of the family Alcyoniidae with hard corals, while another one was mainly characterized by Xeniidae soft corals. However, there is a large gap in the data pertaining to soft corals in the Coral Triangle, despite this region being known as the center of marine biodiversity (e.g., Carpenter and Springer, 2005;

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Sanciangco et al., 2013). In many reef surveys, soft corals are often categorized as a single group with no lower taxonomic differentiation, unlike scleractinians, which are usually identified to the generic level (e.g., Licuanan et al., 2019). This limits the interpretation of coral reef benthic data, which is crucial for management purposes.

One of the best-studied reef systems in the Philippines is the Bolinao-Anda Reef Complex (BARC), covering an area of 200 km^2 of fringing reef along a coastline of 37 km (Cruz-Trinidad et al., 2011). BARC contributes at least 38 million US dollars annually to the economy of Lingayen Gulf directly from reef services, as well as indirectly from shoreline protection (Cruz-Trinidad et al., 2009). However, BARC has experienced various disturbances in the past decades, including increased sea surface temperature (SST), storms, and overfishing, which have led to ecosystem degradation (Arceo et al., 2001; Nañola Jr. et al., 2002; Shaish et al., 2010). A recognized threat to the coral reefs in BARC is the presence of fish farms, which have resulted in increased nutrient concentrations and sedimentation, and consequently decreased water clarity in the adjacent waters. This environmental impact has resulted in a series of fish mortality episodes due to algal blooms, the deterioration of soft bottom macroinfaunal communities, and reduced seagrass diversity (Azanza et al., 2005; Nacorda et al., 2012; Tanaka et al., 2014). The benthic communities on adjacent reefs have been negatively impacted, as shown by the reduced settlement and growth and increased mortality of hard corals, along with increased algal cover (Villanueva et al., 2005, 2006; Quimpo et al., 2020). Moreover, effluents from the fish farms have become a serious concern since these can reach nearby coral reefs especially during the wet season (Ferrera et al., 2016).

Responses of corals at both community and population levels to environmental conditions, which includes disturbances (i.e., sedimentation, eutrophication, increased SST, storms, ocean acidification) have been well-documented and can be used to indicate coral reef health (Bak and Meesters, 1998; Cooper et al., 2009; Fabricius et al., 2012). At the population level, numerous studies have investigated the influence of environmental conditions on size-frequency distributions of coral populations (e.g., Bak and Meesters, 1998; Adjeroud et al., 2015). Variations of the size-frequency distribution of a species can indicate variations in environmental conditions and can even be useful in indicating historical events when long-term monitoring data is unavailable (Bak and Meesters, 1998). However, studies have only focused on hard corals while patterns of soft coral size-frequency distribution are still unexplored. At the community level, most soft coral studies have focused mainly on the effects of varying water quality to species diversity and composition (e.g., Fabricius and McCorry, 2006; De'ath and Fabricius, 2008; Fabricius et al., 2012) while combined effects of other factors to community structure in relation to coverage of different taxa is relatively unexplored. Thus, effects of varying environmental conditions to soft coral size-frequency distribution and community structures have yet to be fully understood.

The goals of this study were (1) to assess and compare soft coral community structures at different spatial scales, (2) to investigate the influence of selected benthic components and environmental parameters (i.e., wave exposure, water clarity) to the distribution of different soft coral taxonomic groups, and (3) to determine the size-frequency distribution of selected soft corals in BARC. To the best of our knowledge, this is the first study to quantitatively examine the contribution of different soft coral taxa in Philippine coral reefs and is also the first to look at patterns in soft coral size-frequency distribution. The insights from this study may also help us better understand the influence of varying environmental conditions on coral reef benthic community structure. In general, this can help improve our capacity in the interpretation of the reef benthic community structure, which is necessary for coral reef management.

2. Materials and methods

2.1. Study sites and sampling design

Seven sites were established in BARC (N 16.3 E 119.9), Pangasinan, northwestern Philippines (Fig. 1). These sites were selected based on the presence of shallow-water coral communities indicated by previous studies in the area (e.g., Villanueva et al., 2005, 2006; Villanueva et al., 2012). A hierarchical sampling (nested) design was applied to study the benthic communities of BARC on different spatial scales (Green et al., 2011). Sites were at least 1 km distant from one another and each site comprised two stations at least 100 m distant from one another. Each sampling station covered a 75 m × 25 m area at 3–5 m depth following the protocols of van Woesik et al. (2009). This design allowed us to compare soft coral communities at different spatial scales– among-sites,

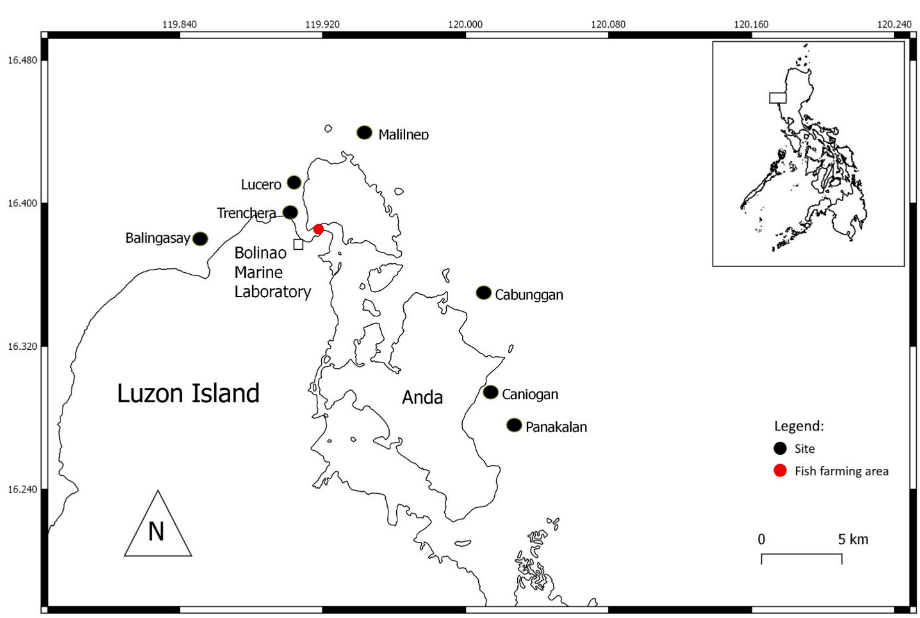

Fig. 1. The seven study sites established in the Bolinao-Anda Reef Complex (BARC), Pangasinan, northwestern Philippines.

within-sites, and among-stations.

2.2. Survey methods

Coral reef surveys were carried out through SCUBA diving. Five 50-m line transects were deployed inside each station, following the reef contour. Photoquadrats were taken for each meter of the shallow side of the transect using a camera (Sony Cyber Shot DSC RX100) inside an underwater housing with a wide-angle lens attached to a tetrapod to ensure that a 1 m^2 area of the reef surface was covered in each photo. To facilitate soft coral identification during image analysis, close-up photos of colonies representing different morphologies were also taken and the positions were recorded of colonies along the transects. The presence of very small (<5 cm) soft coral colonies along a transect, which might not be clearly visible in the photoquadrats, was also recorded.

2.3. Image analysis

Fifty photoquadrats per transect were analyzed using the Coral Point Count with Excel extensions (CPCe) (Kohler and Gill, 2006). The area analysis feature of the CPCe was used to record the surface areas of all soft coral colonies observed in the quadrats. Soft corals were identified to the lowest taxonomic level possible. Due to the challenges in identification, it was more practical to use coral taxonomic amalgamation units (TAUs). Coral TAUs are used to represent different species that are hard to differentiate, referred to hereafter as "taxonomic groups" (e.g., Zvuloni et al., 2010). The taxonomic groups used in this study are listed in Table S1. For the current study, each taxonomic group represented either a genus or a family. It is also worth mentioning that prior to image analysis, the personnel who analyzed the images conducted numerous SCUBA dives in the study sites to document soft corals with different morphologies and was trained by a taxonomic expert in identification. These activities provided us with confidence in identifying soft corals in the images using the taxonomic resolution mentioned. The circumference of each soft coral colony in the photoquadrats was traced to calculate the surface area (cm^2). Surface areas of the colonies were then summed to obtain the total area covered by the soft corals per transect. These values were then converted to percentage cover (% cover = (Taxonomic group cover (cm^2)/500,000 cm^2) × 100%) to represent the percentage cover of the different taxonomic groups in a transect. Percentage cover of the non-soft coral benthic components, such as hard corals, macroalgae, crustose coralline algae, and abiotic components (i.e., sand, silt, rocks, rubble, dead coral) were also analyzed using 10 randomly placed points in each 1 × 1 m frame using the CPCe (Kohler and Gill, 2006). Percentage covers of the non-soft coral benthic components were used as predictor variables for the canonical correspondence analysis (CCA).

Patterns of the size-frequency distribution of *Lobophytum*, *Sarcophyton*, and *Sinularia* were analyzed. The surface areas (cm^2) of the colonies of these taxonomic groups were used for the analysis. Number of colonies under these groups inside the photoquadrats were also counted to generate density data (no. of colonies per 50 m^2). The chosen taxonomic groups are considered appropriate for population structure studies since they are known to be slow-growing and their sizes are related to different life stages (Benayahu and Loya, 1986; Fabricius, 1995; Fan et al., 2005). Also, individual colonies of these taxonomic groups can be easily differentiated, unlike several other soft coral taxa which have mat-like growth forms.

2.4. Environmental parameters

Physical and chemical parameters were measured to characterize the environmental conditions at all seven sites. Water samples were collected to measure nutrient concentrations (i.e. Nitrate (NO_3), Nitrite (NO_2), Phosphate (PO_2), Ammonium (NH_4), and Silicate (SiO_2)), salinity, total alkalinity (TA), and pH. Chemical parameters were analyzed adopting the protocols of Strickland and Parsons (1972). Total alkalinity and pH were measured through potentiometric titration using the Kimoto ATT-05 Total Alkalinity titrator. Chemical parameters were mainly analyzed by the Biogeochemistry laboratory of the Marine Science Institute of the University of the Philippines (UP MSI). Secchi depth of each site was monitored to determine water clarity (Preisendorfer, 1986). Collection of water samples and measurements of Secchi depth were conducted once in February and again in August of 2019. Secondary data of the Relative Exposure Index (REI) values of the different sites collected by the Physical Oceanography laboratory of UP MSI (http://mandaragat.org/midas/exposure/) were also considered in this study. REI represents the level of exposure of a site to wind and waves. The REI was calculated using the wave exposure model developed by Malhotra and Fonseca (2007) using Philippine coastline, bathymetry, and wind data.

2.5. Statistical analyses

The nested sampling design of the study allowed us to compare the different soft coral variables (i.e., cover, taxa richness, and community assemblages) at two spatial scales: (1) among-sites and (2) within-sites. Additionally, variability among-stations, regardless of the sites, were also investigated. Shapiro-Wilk's test for normality and Bartlett's test for homogeneity were performed for all the datasets. A dataset was log-transformed if it was not normally-distributed or non-homogenous. For normally-distributed and homogenous datasets, an analysis of variance (ANOVA) was used to compare the mean values in the soft coral cover and taxa richness at the two spatial scales. The Tukey's HSD post-hoc test was then performed for datasets with significant (*p-value* < 0.05) results from the ANOVA to determine which stations or sites significantly differed from each other. The non-parametric Kruskal-Wallis test and the Mann-Whitney pairwise comparisons test were used for non-normally-distributed and non-homogenous datasets. Water chemistry parameters, Secchi depths, and pooled average densities of selected soft coral genera (*Lobophytum*, *Sarcophyton*, and *Sinularia*) were compared among-sites using the same tests. The univariate tests applied were performed using the PAST software (Hammer et al., 2001).

Multivariate analyses were performed to examine the differences in the soft coral community structure among-sites and within-sites. Soft coral percentage cover datasets were square root-transformed. The analysis of similarity (ANOSIM) was then performed using the Bray-Curtis similarity index to detect significant differences in the community compositions at the two spatial scales (Clarke and Warwick, 1994). The similarity percentages (SIMPER) analysis was then performed to determine the contribution of the different taxonomic groups to the similarities and differences among- and within-sites (Clarke and Warwick, 1994). The ANOSIM and SIMPER analysis were performed using PRIMER-E v6.0 (Clarke and Gorley, 2006).

The Canonical Correspondence Analysis (CCA) was also performed to relate the soft coral community composition to known variation in a set of environmental factors (Ter Braak, 1986). The CCA is an ordination method used to analyze spatial distribution of different taxonomic groups in relation to biotic and abiotic factors. For this analysis, % covers of the taxonomic groups were square root transformed and outliers were not included in the analysis; taxonomic groups which had less than 3 sample points were considered outliers (i.e., rare groups) (Maliao et al., 2008). In this analysis, the Relative Exposure Index (REI) values, Secchi depths, and percentage covers of selected non-soft coral benthic components were used as site descriptors. The CCA was performed using the PAST software (Hammer et al., 2001).

Descriptive statistic parameters (i.e., skewness, kurtosis, coefficient of variation, mode) and histograms of the colony areas of the *Lobophytum*, *Sinularia*, and *Sarcophyton* of the 7 sites were generated to visualize the size-frequency distributions of each taxa, following other coral population structure studies (e.g., Adjeroud et al., 2007; Adjeroud et al., 2015). The colonies of each taxonomic group for the 2 stations of each

Table 1
Test for significance (ANOVA/Kruskal-Wallis test/Tukey's test/Mann-Whitney test) results of the comparisons of total soft coral cover and taxa richness at different spatial scales (Amongsites, among-stations, and within-stations).

Spatial scale	*p-Value*
Total soft coral cover	
Among sites	0.10
Among stations	1.29^{-8}
Balingasay1 × Balingasay2	0.01
Cabunggan1 × Cabunggan2	0.01
Caniogan1 × Caniogan2	0.02
Lucero1 × Lucero2	0.21
Malilnep1 × Malilnep2	0.30
Panakalan1 × Panakalan2	0.01
Trenchera1 × Trenchera2	0.24
Taxa richness	
Among sites	0.08
Among stations	6.23^{-16}
Balingasay1 × Balingasay2	0.91
Cabunggan1 × Cabunggan2	0.23
Caniogan1 × Caniogan2	0.91
Lucero1 × Lucero2	0.12
Malilnep1 × Malilnep2	0.98
Panakalan1 × Panakalan2	0.77
Trenchera1 × Trenchera2	1.00

site were pooled together to have a sufficient sample size. Values of the areas of the colonies were log 10-transformed to normalize size-frequency distributions and increase resolution among smaller sizes (Bak and Meesters, 1998; Adjeroud et al., 2015). The 2-sample Kolmogorov-Smirnov (KS) test was also performed to compare the size-frequency distributions of the colonies among-sites. The R and PAST software were used to perform the different tests (Hammer et al., 2001; R Core Team, 2018).

3. Results

3.1. Soft coral community structure

A total of 14 stations with 70 transects and 3500 photoquadrats were analyzed. From all seven sites, a total of 15 taxonomic groups representing nine coral families were recorded (Table S1). Trenchera had the lowest mean taxa richness among the sites (Fig. 2a). However, among-site differences on mean taxa richness were not significant (Kruskal-Wallis *p-value* = 0.08) (Table 1). Significant differences were observed among-stations (ANOVA *p-value* = 6.23^{-23}) with Trenchera having the lowest values. Azooxanthellate octocorals of the families Nidaliidae and Paraplexauridae were also found in Trenchera (Table S1). The azooxanthellate genus *Dendronephthya* (Nephtheidae) was noted at the station in Lucero nearest to Trenchera. Despite observed differences among-stations, pairwise comparisons revealed insignificant differences between the stations within-sites (Tukey's test *p-value* > 0.05) (Table 1).

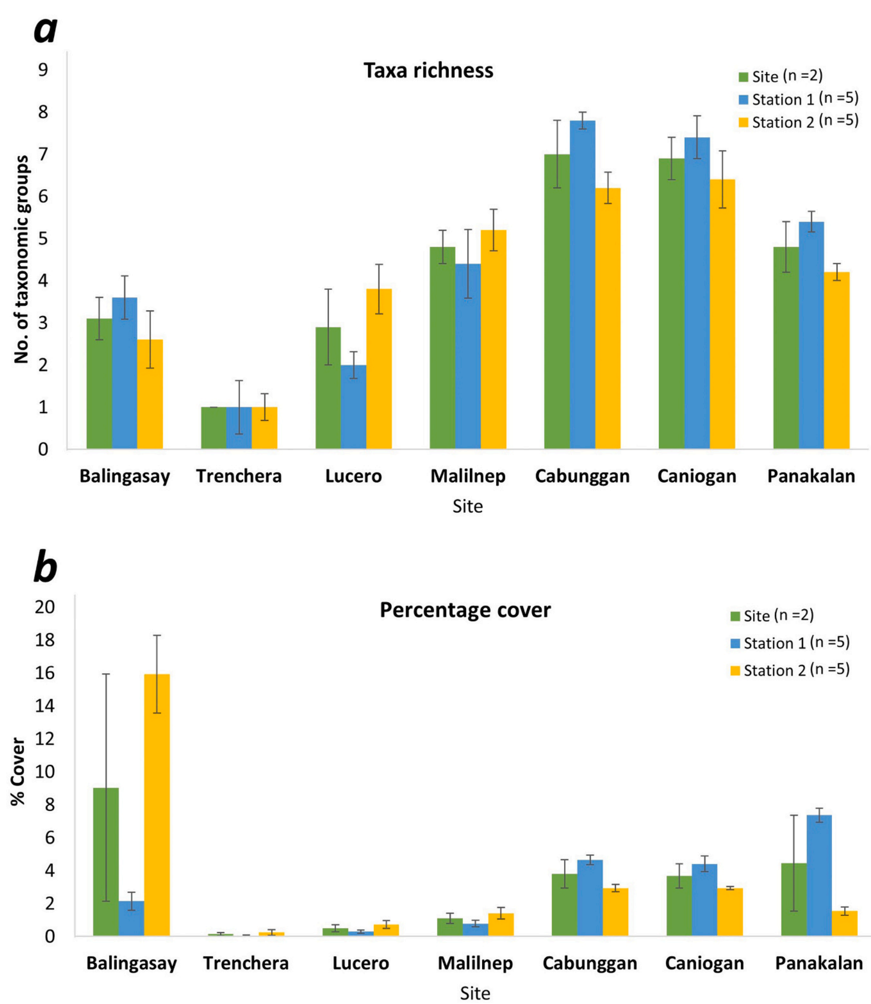

Fig. 2. Soft corals of the Bolinao-Anda Reef Complex (BARC) (a) mean taxonomic richness (±SE) and (b) percentage cover (±SE) at each of the seven study sites and their respective two stations.

In terms of mean soft coral cover among-sites, Trenchera had the lowest and Balingasay had the highest cover (Fig. 2b). Despite big differences between mean soft coral cover, there was no significant difference among-sites (Kruskal-Wallis *p-value* > 0.05). However, overall significant difference was noted among-stations (Kruskal-Wallis *p-value* $= 1.29^{-8}$). Among the stations, the stations in Trenchera had the lowest values. Unlike taxa richness, pairwise comparisons of the mean soft coral covers revealed significant differences between stations within Balingasay, Cabunggan, Caniogan, and Panakalan. Within-site differences of mean soft coral covers were not significant for Trenchera, Lucero, and Malilnep.

The ANOSIM, which takes into consideration the taxonomic groups present and their covers, revealed an overall significant difference in the community structure among-sites (ANOSIM $R = 0.61$, *p-value* = 0.001) and among-stations (ANOSIM $R = 0.66$, *p-value* = 0.001). However, pairwise comparisons revealed no difference between Cabunggan and Caniogan (ANOSIM R = 0–0.05, *p-value* = 0.77). Except for Lucero and Trenchera, soft coral community structures within-sites significantly differed (Table 2).

The SIMPER analysis revealed differences in the taxonomic groups which dominated each site (Table 3). Balingasay was mainly dominated by *Clavularia* (SIMPER % contribution = 83.43%) while Trenchera was dominated by both *Lobophtyum* (SIMPER % contribution = 50.74%) and *Briareum* (SIMPER % contribution = 49.26%). Lucero and Malilnep were mainly dominated by *Lobophytum* (SIMPER % contribution >60%). Cabunggan, Caniogan, and Panakalan were dominated by 4 groups: *Isis*, *Lobophytum*, *Sinularia*, and *Sarcophyton* (SIMPER cumulative % contribution >90%). Among the 4 groups mentioned, *Isis* had the highest contribution to the similarity in each of the 3 sites. Dissimilarity percentages of taxonomic groups which differentiate the sites from one another are shown in Table S4.

Dissimilarity percentages of taxonomic groups which differentiated the stations within the sites are shown in Table S5. The difference between the stations within Balingasay was mainly attributed to *Clavularia* (Dissimilarity % contribution = 83.66%). Differences in the cover of *Lobophytum* mainly differentiated the stations within Trenchera, Lucero, Cabunggan, and Caniogan (Dissimilarity % contribution >29%). *Briareum* differentiated the stations within Malilnep (Dissimilarity % contribution = 24.61%) while difference within Panakalan was attributed mainly to *Sinularia* (Dissimilarity % contribution = 29%).

3.2. Non-soft coral benthic components

Table 4 shows the percentage covers of the non-soft coral benthic components in the 7 sites. Balingasay had the highest hard coral cover (22.52 SE ± 2.98), while Trenchera had the lowest (2.94 SE ± 1.07). However, Balingasay also had the highest macroalgal cover among the sites, while Trenchera and Lucero had the lowest (2.16 (SE ± 1.64) & 2.12 (SE ±0.30), respectively). Crustose coralline algae were highest in Lucero (22.71 SE ± 5.73) and absent in Panakalan. Silt cover was highest in Trenchera (21.08 SE ±9.61) and sand cover was highest in Panakalan (32.98 SE ± 6.54).

Table 2
Results of the analysis of similarity (ANOSIM) to compare the differences in the soft coral community assemblages at different spatial scales (among-sites, among-stations, and within-stations). For pairwise comparisons among sites, this table only highlights the values with insignificant difference.

Spatial scale	R	*p*-Value
Among sites	0.61	0.001
Pairwise tests	−0.5-1	>0.05
Among stations	0.661	0.001
Balingasay1 × Balingasay2	0.904	0.008
Cabunggan1 × Cabunggan2	0.82	0.008
Caniogan1 × Caniogan2	0.516	0.008
Lucero1 × Lucero2	0.304	0.056
Malilnep1 × Malilnep2	0.456	0.008
Panakalan1 × Panakalan2	0.996	0.008
Trenchera1 × Trenchera2	−0.048	0.492

3.3. Environmental parameters

Also presented in Table 4 are the values of the different chemical and physical measurements in the different sites. While ammonium (NH_4) level was low at the Cabunggan, Caniogan, and Panakalan, and highest at Malilnep and Lucero, there were no significant differences (Kruskal-Wallis, *p-value* = 0.20). Nitrite (NO_2) level was significantly higher in Trenchera compared to the other sites (Mann-Whitney post hoc tests, *p-value* < 0.05). Nitrate (NO_3) concentrations exhibited significant differences among the sites (Kruskal-Wallis test, $p = 0.009$), which had different patterns from the nitrite concentrations. Trenchera had significantly higher silicate (SiO_2) concentrations compared to the other sites (KW & MW tests, $p < 0.05$). Total alkalinity, salinity, and pH values were similar for all seven sites (Kruskal-Wallis, *p-value* > 0.05). Regarding Secchi depth, Balingasay had the highest value and Trenchera the lowest (Kruskal-Wallis, *p-value* < 0.05). However, only Balingasay and Trenchera significantly differed among the sites (Mann-Whitney test, *p-value* < 0.05). Balingasay also had the highest relative exposure

Table 3
Results of similarity percentages (SIMPER) analysis. This table shows the taxonomic groups which contribute to at least 90% of the cumulative similarity in each site.

	Average abundance	Average similarity	Contribution (%)
Balingasay			
Average similarity: 52.64			
Clavularia	2.71	43.92	83.43
Lobophytum	0.14	3.95	7.51
Trenchera			
Average similarity: 42.79			
Lobophytum	0.16	21.71	50.74
Briareum	0.27	21.08	49.26
Lucero			
Average similarity: 61.25			
Lobophytum	0.64	45.15	73.71
Sarcophyton	0.17	12.54	20.48
Malilnep			
Average similarity: 70.55			
Lobophytum	0.92	42.62	60.41
Sinularia	0.28	7.03	9.97
Tubipora	0.13	6.4	9.07
Clavularia	0.12	4.81	6.82
Cladiella	0.15	3.82	5.41
Cabunggan			
Average similarity: 84.98			
Isis	1.21	27.79	32.71
Lobophytum	1.19	25.01	29.43
Sinularia	0.85	21.61	25.43
Sarcophyton	0.28	5.45	6.42
Caniogan			
Average similarity: 86.97			
Isis	1.14	29.02	33.36
Lobophytum	1.19	23.99	27.58
Sinularia	0.87	22.52	25.9
Sarcophyton	0.28	5.97	6.86
Panakalan			
Average similarity: 60.29			
Isis	1.37	24.69	40.95
Sinularia	1.08	14.43	23.93
Lobophytum	0.75	12.66	20.99
Sarcophyton	0.52	7.84	13

Table 4
The Bolinao-Anda Reef Complex (BARC): Average values of biotic and abiotic parameters (±SE) at each of the seven study sites. CCA here refers to crustose coralline algae.

	Balingasay	Trenchera	Lucero	Malilnep	Cabunggan	Caniogan	Panakalan
NH_4 (μM)	9.99 (SE± 1.67)	13.71 (SE ±4.12)	19.48 (SE ±7.18)	20.61 (SE ± 6.12)	7.34 (SE ± 2.07)	7.81 (SE ±1.49)	11.41 (SE ± 2.66)
NO_2 (μM)	0.06 (SE ± 0.01)	0.31 (SE ± 0.06)	0.12 (SE ± 0.02)	0.13 (SE ± 0.02)	0.10 (SE ±0.02)	0.14 (SE ±0.04)	0.12 (SE ± 0.02)
NO_3 (μM)	0.63 (SE ± 0.12)	3.01 (SE ± 0.95)	2.81 (SE ±1.21)	5.80 (SE ± 3.04)	1.15 (SE ± 0.30)	2.39 (SE ±0.68)	0.78 (SE ± 0.34)
PO_4 (μM)	0.75 (SE ± 0.44)	0.58 (SE ± 0.11)	0.48 (SE ± 0.09)	0.56 (SE ±0.13)	0.53 (SE ± 0.17)	0.37 (SE ±0.07)	0.39 (SE ±0.08)
SiO_2 (μM)	10.14 (SE ±2.44)	19.71 (SE ±3.07)	11.41 (SE ±1.51)	10.41 (SE ± 0.98)	11.07 (SE ± 1.25)	11.39 (SE ± 2.16)	11.18 (SE ± 1.72)
Salinity (ppt)	31.62 (SE± 0.37)	31.82 (SE± 0.41)	31.30 (SE±0.48)	31.64 (SE± 0.41)	32.11 (SE ± 0.25)	32.22 (SE± 0.25)	32.23 (SE± 0.39)
Total alkalinity (μmol/kg)	2151.08 (SE± 16.40)	2172.64 (SE± 21.78)	2176.61 (SE± 12.46)	2135. 50 (SE± 17.19)	2128.82 (SE ±12.49)	2133.74 (SE± 6.00)	2171.25 (SE± 13.96)
DIC (μmol/kg)	1891.82 (SE± 9.58)	1926.18 (SE ± 27.46)	1639.39 (SE ±288.76)	1857.86 (SE± 5.21)	1876.35 (SE ± 20.07)	1880.69 (SE± 1.95)	1922.955 (SE± 12.57)
pH	8.01 (SE± 0.01)	8.00 (SE ±0.03)	7.99 (SE± 0.02)	8.06 (SE± 0.02)	7.99 (SE± 0.04)	8.00 (SE± 0.01)	8.00 (SE± 0.01)
Secchi depth (m)	10 (SE ± 0.00)	3 (SE ± 0.00)	5 (SE ± 0.58)	7.33 (SE ± 0.33)	7.67 (SE ± 0.33)	7.67 (SE ±0.33)	7.67 (SE ± 0.33)
Relative exposure index	6370 (high)	4420 (medium)	2250 (medium)	2320 (medium)	708 (medium)	907 (medium)	876 (medium)
Hard coral cover (%)	22.52 (SE ± 2.98)	2.94 (SE ± 1.07)	21.84 (SE ±5.78)	12.62 (SE ± 0.70)	9.29 (SE ± 1.06)	8.50 (SE ± 1.41)	16.12 (SE ±2.46)
Macroalgae (%)	26.90 (SE ±7.52)	2.16 (SE ± 1.64)	2.12 (SE ±0.30)	4.80 (SE ± 1.85)	5.84 (SE ± 0.65)	22.00 (SE ± 6.99)	9.71 (SE ±9.71)
Dead coral with algae (%)	0.73 (SE ± 0.10)	0.26 (SE ± 0.05)	1.57 (SE ± 0.17)	2.69 (SE ± 0.88)	0.86 (SE ± 0.15)	1.16 (SE ± 0.15)	3.50 (SE ±3.50)
CCA	16.33 (SE ±4.37)	3.40 (SE ±2.56)	22.71 (SE ± 5.73)	14.93 (SE ± 1.16)	1.01 (SE ± 0.31)	1.32 (SE ± 0.30)	2.49 (SE ±2.49)
Dead coral (%)	0 (SE ± 0)	0 (SE ± 0)	0 (SE ± 0)	0.05 (SE ± 0.05)	0.10 (SE ± 0.00)	0 (SE ± 0)	0 (SE ±0)
Silt (%)	0 (SE ±0)	21.08 (SE ±9.61)	0.05 (SE ± 0.05)	1.20 (SE ± 1.20)	0.05 (SE ± 0.05)	0 (SE ± 0)	0.05 (SE ±0.05)
Sand (%)	2.82 (SE± 2.82)	0.92 (SE ±0.29)	2.98 (SE ±1.76)	4.76 (SE ± 3.09)	10.45 (SE ±2.53)	8.11 (SE ± 3.35)	32.98 (SE ± 6.54)

index, a level that is considered to belong to the "high" exposure category, while the rest of the sites had "medium" category exposures.

3.4. *Effects of environmental parameters to soft coral distribution*

The distributions of the different taxonomic groups in relation to the stations are strongly explained by the different predictor variables used in the CCA (Axis 1 = 65.96%) (Fig. 3). Significant values from the permutation tests (p-value <0.05) also revealed robust findings. One of the most obvious patterns was the positive correlation of *Clavularia* to exposure, crustose coralline algae, hard coral, and Secchi depth, which are factors most dominating in Balingasay. The major alcyoniids (*Sarcophyton*, *Lobophytum*, *Sinularia*) and two gorgonians, *Isis* and *Rumphella*, aggregated in sites with high sand cover and were negatively correlated to the factors that *Clavularia* positively correlated to (i.e., wave exposure). Another notable trend is the positive correlation of the Trenchera stations to silt cover and their negative correlations to hard coral cover and Secchi depth.

3.5. *Size-frequency distributions*

A total of 1370 colonies of *Lobophytum*, 226 of *Sarcophyton*, and 1181 of *Sinularia* were recorded and measured. *Lobophytum* featured a mean density of 19.5 (±2.6) colonies per 50 m^2, 3.2 (±0.6) colonies for *Sarcophyton*, and 16.9 (±2.5) colonies for *Sinularia*. There were significant differences in densities among the sites for these three genera (Kruskal-Wallis test: $p < 0.01$), with that of *Lobophytum* being the lowest in Trenchera, where both *Sarcophyton* and *Sinularia* were absent (Fig. 4).

The surface areas of the *Lobophytum* colonies ranged from 0.0069 cm^2 to 4708 cm^2 with a mean size of 179.2 cm^2 (±7.2) (Table S6). For *Sarcophyton*, the sizes ranged from 0.3488 cm^2 to 6313.2 cm^2 with a mean size of 116.3 cm^2 (±28.4) (Table S7). For *Sinularia*, the surface areas of the colonies ranged from 0.8cm^2 to 4175 cm^2 with a mean size of 129.1 cm^2 (±7.7 SE) (Table S8). A significant difference was found between the mean colony size of *Lobophytum* and *Sinularia* (Kruskal-Wallis *p-value* < 0.05), but not for *Sarcophyton*. Among the sites, Balingasay exhibited the smallest mean colony size for all three taxonomic groups.

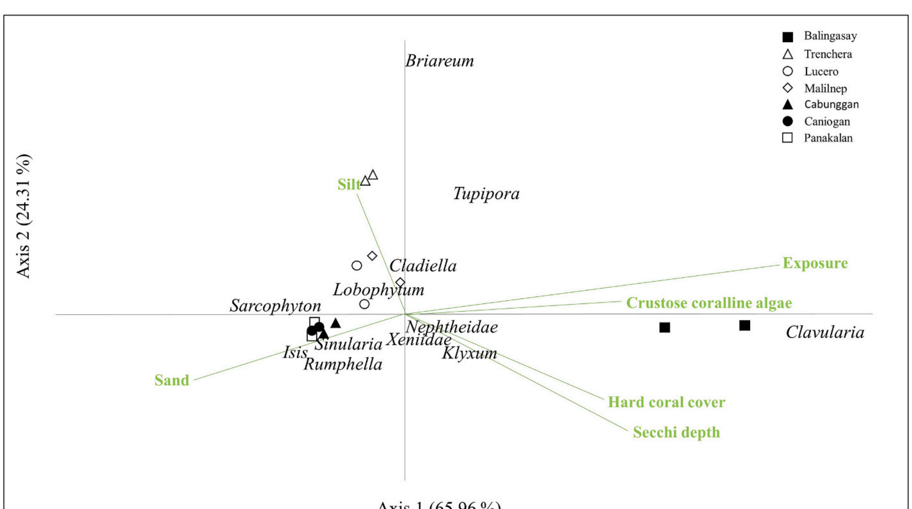

Fig. 3. Ordination plot of the Canonical Correspondence Analysis showing the distribution of the different taxonomic groups and stations (shapes) in relation to the environmental factors (green lines).

Sinularia and *Sarcophyton* had symmetrical distributions, which were slightly positively skewed ($g_1 = 0.08$) and slightly negatively skewed ($g_1 = -0.37$) distributions, respectively (Fig. 5b-c). *Lobophytum* presented a moderately negatively skewed distribution ($g_1 = -0.56$), indicating the dominance of large-sized colonies (Fig. 5a). Details of the size-frequency distributions of the 3 taxonomic groups are presented in Tables S6-S8 and Figs. S1-S3. However, colony counts for *Lobophytum* were very low in Balingasay (14 colonies) and Trenchera (8 colonies). *Sinularia* had low counts in Balingasay and Malilnep (<10 colonies) while *Sarcophyton* had low counts in Balingasay and Lucero (<15 colonies) and both were absent in Trenchera (Tables S6-S8). This prevented a proper comparison of size-frequency distributions between sites with relatively extreme environmental conditions (Table 3). We therefore compared only those sites with sufficient number of colonies. For *Lobophytum* and *Sinularia*, comparisons were possible for all the sites except Balingasay and Trenchera. For *Sarcophyton*, comparisons were only possible for Malilnep, Cabunggan, and Panakalan. Among the three genera, only *Lobophytum* exhibited significant differences (Kolmogorov-Smirnov *p-value* < 0.05) in the size-frequency distributions among the sites. Malilnep differed from Cabunggan and Caniogan, while Panakalan differed from Panakalan.

4. Discussion

This is the first study to engage with the community and population structure of soft corals in the Philippines. Overall, the average soft coral cover of BARC is 3.2% ± 1.2 SE, which is similar to the national average soft coral cover of 3.2% ± 0.6 SE reported by Licuanan et al. (2019). These results resemble those found for the Southern Islands in Singapore (Goh et al., 2009). In contrast, soft coral cover reports were highly variable for Eilat (northern Red Sea), central Great Barrier Reef (Australia), and Papua New Guinea, ranging from 0 to 50% (Benayahu and Loya, 1977, 1981; Dinesen, 1983; Tursch and Tursch, 1982). Comparisons with the soft coral cover reported from other regions indicate that BARC possesses an overall low average soft coral cover.

The findings from this study contribute to the data currently available from taxonomy-oriented studies on Philippine octocorals published decades ago (i.e., Light, 1913, 1914, 1915a, 1915b, 1915c; Roxas, 1932, 1933a, 1933b). Despite BARC being considered a generally disturbed area, its taxa richness in terms of the families and genera observed is comparable to those reported from other studies in other regions (e.g., Benayahu and Loya, 1977; Tursch and Tursch, 1982; Benayahu, 2002; Benayahu et al., 2004; Goh et al., 2009; Mohammad et al., 2016; Ismail et al., 2017). However, the limited taxonomic resolution of the present study highlights the need for assessments to the species level in order to provide more in-depth information on the general biodiversity of the Coral Triangle region (Karlson et al., 2004; Sanciangco et al., 2013).

Differences in both the community structure and mean soft coral cover within-sites indicate stronger variations on smaller spatial scales (several hundred meters) than on a larger one (>1 km) (Tables 1 and 2). The significant difference in the community structure within-sites, despite having insignificant differences in taxa richness, can be explained mainly by the differences in the covers of the taxonomic groups present (see Table S4 for dissimilarity percentages of stations within-sites), and not by what groups were present. This variability may indicate the major contribution of factors operating on a more local scale, such as biological interactions with other organisms and other environmental factors such as water quality. The differences in environmental conditions in BARC even on a small spatial scale (< 1 km) were shown by previous studies. Cardenas et al. (2010) and Senal et al. (2011) found differences in nutrient levels between adjacent stations in BARC. Small spatial scale environmental variability might be the main driver of the differences found here between the stations within-sites. However, the present study was unable to directly identify environmental factors that influenced the differences in soft coral community assemblage and cover at this scale. Thus, a future examination of the environmental differences on a smaller spatial scale is necessary.

High soft and hard coral cover in Balingasay can be explained by the relatively high water clarity in the site (Fig. 3). De'ath and Fabricius (2008) postulated that coral communities are healthier among reefs whose Secchi depth averages at 10 m or greater. In our study, except for Balingasay, all the sites had Secchi depths less than 10 m. This may explain poor coral cover in other sites, especially in Trenchera with Secchi depth less than 5 m. The CCA ordination plot shows the negative correlation of the stations in Trenchera to water clarity and its positive correlation to silt cover, indicating high siltation in these stations (Fig. 3).

High soft coral cover in Balingasay was attributed to the high cover of *Clavularia*. This can be explained mainly by the high positive correlation of *Clavularia* to exposure to waves (Fig. 3). Though Balingasay had the highest hard coral cover among the sites, *Clavularia* mats were observed to overgrow live hard corals which may be detrimental to the overall hard coral community in the site. This dominance by *Clavularia* might have been triggered by a pulse disturbance, such as a sudden runoff of sediments and freshwater derived from a nearby river during the wet season (personal observations). This dominance can also be explained by the life-history strategies and capabilities of *Clavularia* which can be advantageous in highly turbulent areas. As surface-brooders, *Clavularia* planulae settle directly onto nearby substrate and are protected by mucus sheaths while attaching to the colony's hard-

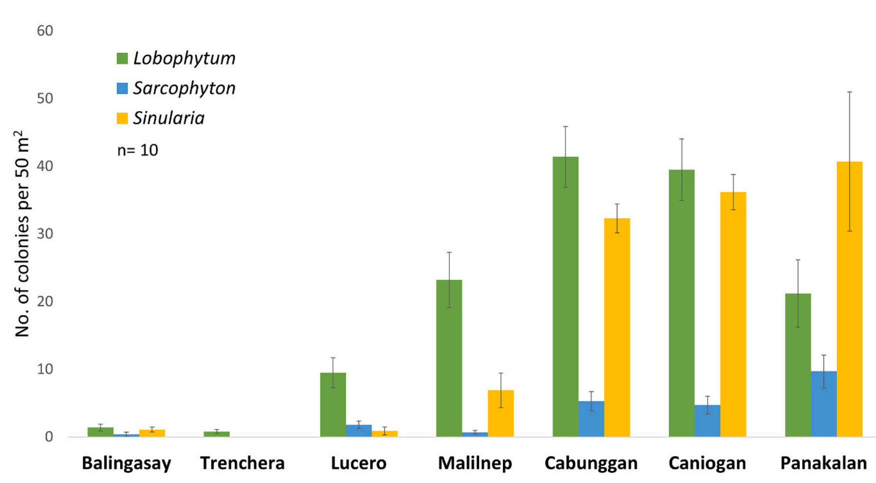

Fig. 4. Soft corals of the Bolinao-Anda Reef Complex (BARC): average density of colonies per 50 m^2 (±SE) of the three studied genera at each of the seven study sites.

coral calyces (Aliño and Coll, 1989). In the Great Barrier Reef, *Clavularia* has been shown to outcompete hard corals during competition for space (Aliño et al., 1992). Indeed, in Brazil, clavulariids were found to dominate the benthic community and led to a drastic change in its structure over time (Mantelatto et al., 2018). The dominance of *Clavularia* may benefit from well-lit and highly exposed areas such as Balingasay. This also shows the importance of long-term coral reef monitoring, to see how *Clavularia* may change benthic community structure in the future.

The low soft coral taxa richness and cover observed at Trenchera, the site nearest the fish farming area, coupled with the lowest hard coral cover value, might have been the result of the poor water quality. Similar conditions at this site have been reported in previous studies (i.e., Villanueva et al., 2005; Ferrera et al., 2016). Only a few studies have investigated the effects of the decline in water quality parameters on soft corals: for example, increased nitrogen levels were shown to result in higher stress metabolites of the soft coral *Sarcophyton* (Fleury et al., 2000); high levels of sedimentation were suggested to decrease productivity due to increased mucus production (Riegl and Branch, 1995); and in hard corals, a decrease in water quality, such as increased sedimentation and nutrient levels, together with reduced light levels, had been widely shown to be detrimental to coral health (Fabricius, 2005). In BARC, the negative environmental effects resulting from fish farming were found to affect the different life stages of hard corals, such as decreased recruitment, fecundity, and survival of both adults and juveniles (Villanueva et al., 2005, 2006; Quimpo et al., 2020). These are probably the same mechanisms that have negatively affected the soft coral community in Trenchera.

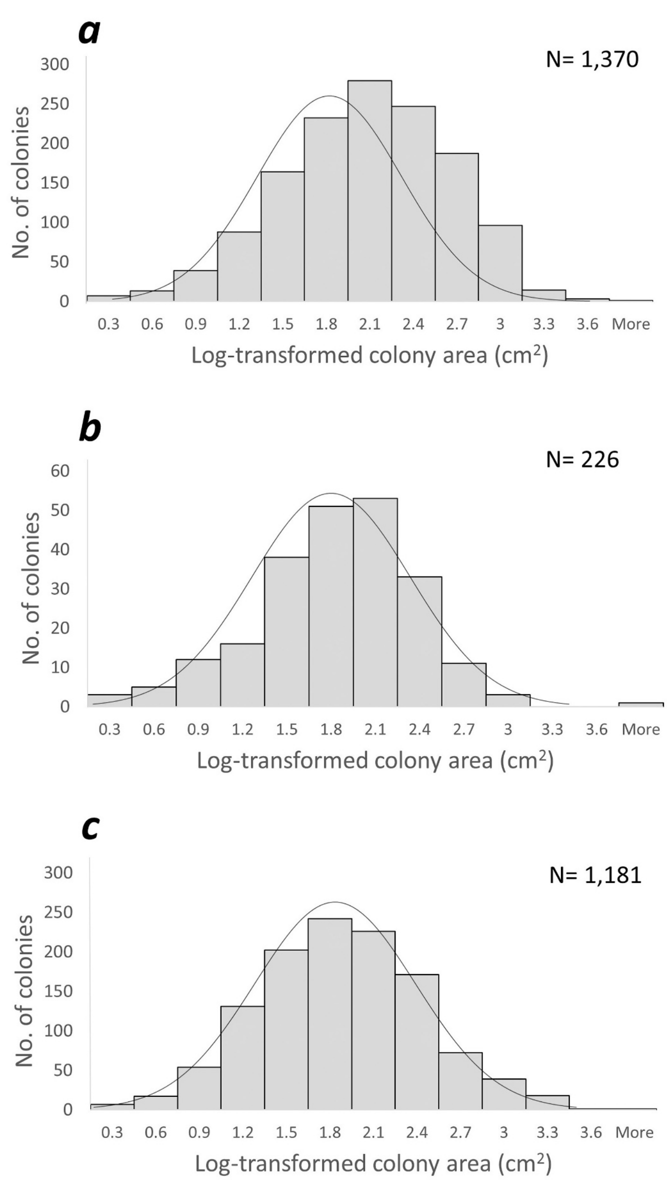

Fig. 5. Soft corals of the Bolinao-Anda Reef Complex (BARC): size-frequency distribution of the genera (a) *Lobophytum*, (b) *Sarcophyton*, and (c) *Sinularia*. Normal distribution bell curves for the datasets are presented for comparison.

The presence of azooxanthellate taxa (families Paraplexauriidae and Nidaliidae and the genus *Dendronephthya*) at Trenchera and Lucero is probably due to low water transparency. The Secchi depth measurements at the sites indicated highly turbid waters (Table 3). In Hong Kong, a similar pattern was noted by Fabricius and McCorry (2006), where zooxanthellate taxa were observed to be restricted to areas with high water clarity. The reduced richness of zooxanthellate taxa and the presence of azooxanthellates in very shallow waters, such as in Trenchera, would therefore appear to indicate low light levels resulting from high turbidity.

Different soft coral taxa may have different preferences and tolerances to environmental conditions (e.g., Riegl and Branch, 1995; Fabricius and Alderslade, 2001; Fabricius and McCorry, 2006; Inoue et al., 2013). Among the taxonomic groups present, *Lobophytum* contributed greatly to the similarities within the 7 sites (Table 3). This indicates *Lobophytum*'s tolerance or resilience to both past and present disturbances in the study region. *Lobophytum* is one of the genera most resilient to sedimentation in a reef in South Africa (Riegl and Branch, 1995). *Sinularia* too contributed to the similarities among most of the sites, possibly due to its similar morphology to *Lobophythum* (Riegl and Branch, 1995). Another finding in this study was that of the relatively high cover of *Briareum* in Trenchera, which comprises most of the soft coral cover at the site (Table 3). This might be due to the increased growth rate or increased competitive ability of *Briareum* driven by the environmental conditions at the site (Aliño et al., 1992). In the Great Barrier Reef, an increased competitive ability of *Briareum* was found when this soft coral was transplanted to inshore reefs with higher nutrient concentrations than offshore reefs (Aliño et al., 1992). Aside from the generally low water quality in BARC, one of the disturbances that might have contributed to the low abundance of the other soft coral groups is that of increased SST which might have led to bleaching. Strychar et al. (2005) found a higher resistance of alcyoniids than of a xeniid species to bleaching during elevated temperatures. However, the effect of the major bleaching events (Arceo et al., 2001) on the community structure of the soft corals in BARC is unknown due to the lack of information regarding coverage of the different soft coral groups in past surveys. This highlights the need for coral reef monitoring that will include detailed analyses of different soft coral groups.

The overall symmetrical size distribution of *Sinularia and Sarcophyton* demonstrates that different size classes of the colonies are well-represented and may indicate a healthy population in BARC (Bak and Meesters, 1998). It further indicates a high tolerance of these genera to disturbances, which may explain their dominance (Table 2). While symmetrical distributions were found for both *Sarcophyton* and *Sinularia*, *Lobophytum* exhibited a moderately-negative skewness ($g_1 = -0.56$), indicating the dominance of large-sized colonies over smaller-sized colonies. The absence of smaller-sized colonies may indicate reef degradation, probably driven by high post-settlement mortality (Bak and Meesters, 1998). Though the dominance of large-sized *Lobophytum* colonies in this study was not as high as other coral size-frequency distributions in other studies done on heavily disturbed areas, it might still indicate reef degradation in BARC. High sedimentation may be one of the major causes of high mortality of recruits in the area (Humanes et al., 2017). In addition to silt coverage, the presence of macroalgae can prevent larval settlement due to lack of space (Tanner, 1995; Webster et al., 2015). The results may indicate differences in the responses of *Lobophytum* from *Sinularia* and *Sarcophyton* to present environmental conditions and possibly to past disturbances. In the reefs of Okinawa, Japan, Loya et al. (2001) have observed the decrease in the cover and abundance of *Lobophytum* while *Sinularia* became more dominant after a bleaching event. Though we cannot presently identify the factors that have influenced soft coral size-frequency distributions in BARC, the dominance of large-sized colonies and the absence of juveniles may have negative implications for the *Lobophytum* population in the future.

Significant differences in *Lobophtyum* size-frequency distribution among a number of sites were noted (Fig. S1). However, the low colony counts in Trenchera and Balingasay prevented us from comparing sites with significant differences in environmental conditions, mainly in terms of water clarity and exposure to waves. Comparisons of size-frequency distributions were only possible for Lucero, Malilnep, Cabunggan, Caniogan, and Panakalan because of adequate number of colonies in these sites. Because these sites did not differ in environmental conditions, at least in regard to the factors that were measured in this study, it was difficult to infer which factors contributed to these differences. The differences may therefore have also been driven by other factors that were not considered in this study, such as species-level differences, interactions with other organisms, and other more localized disturbances (Adjeroud et al., 2015). Again, this highlights the need to study the environmental differences on smaller spatial scales. Although we were not able to compare the size-frequency distributions among all the sites, we were able to compare the densities of the three studied groups among the sites. The low density of *Lobophytum* and the absence of both *Sarcophyton* and *Sinularia* in Trenchera can be explained by the low water quality there, as reflected in the site's poor coral cover and taxa richness (Fig. 2). We also observed relatively low densities for the three groups in Balingasay, which may be a result of unfavorable conditions at the site; mainly high exposure and probable competition with *Clavularia*, which dominated the area.

This study has provided information on the patterns of soft coral community and their population structures in relation to different environmental factors. The obtained results can be used to generate different hypotheses in relation to specific factors which may affect soft corals. However, future studies, designed to investigate specific hypotheses, are still needed to provide data on the effects of specific factors. It is recommended to conduct long-term monitoring that records the benthic communities together with the prevailing environmental parameters. Also, it should be noted that analysis of coral density, which requires counting individual colonies, is often not possible while analyzing photoquadrats. For future studies, it is recommended to adopt in situ surveys to generate data for different coral variables, including density of arborescent octocorals, such as sea fans.

In this study, we have demonstrated the spatial differences in the soft coral community structures and presented the general population structure of the three selected groups in relation to differences in the environmental conditions at the different sites in BARC. We conclude that soft coral variables have the potential to function as indicators of varying environmental conditions, mainly changes in water quality. We therefore recommend the inclusion of soft coral community and population variables in the analysis of benthos data, for application in the different coral reef assessment or monitoring projects. This will contribute to a greater in-depth interpretation of the data necessary for coral reef management. The inclusion of octocoral assemblages during coral reef monitoring will also greatly contribute to a better understanding of the different ecological mechanisms that together affect the future of coral reefs. This study may also serve as a steppingstone for future studies that will further investigate the understudied ecological roles played by octocorals.

CRediT authorship contribution statement

JAAL, YB, MVBR conceived and designed the research.
JAAL, MVBR conducted sampling and field surveys.
JAAL analyzed the data.
YB, MVBR provided supervision.
MVBR provided materials and funds.
JAAL, YB, MVBR wrote and edited the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2020.111871.

References

Adjeroud, M., Pratchett, M.S., Kospartov, M.C., Lejuesne, C., 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.

Adjeroud, M., Mauguit, Q., Penin, L., 2015. The size-structure of corals with contrasting life-histories: a multiscale analysis across environmental conditions. Mar. Environ. Res. 112, 131–139.

Aliño, P.M., Coll, J.C., 1989. Observations of the synchronized mass spawning and post settlement activity of octocorals in the Great Barrier Reef, Australia: biological aspects. Bull. Mar. Sci. 45 (3), 697–707.

Aliño, P.M., Sammarco, P.W., Coll, J.C., 1992. Competitive strategies in soft corals (Coelenterata, Octocorallia). IV. Environmentally induced reversals in competitive superiority. Marine Ecology Progress Series. 81, 129–145.

Arceo, H.O., Quibilan, M.C., Aliño, P.M., Lim, G., Licuanan, W.Y., 2001. Coral bleaching in Philippines reefs: coincident evidences with mesoscale thermal anomalies. Bull. Mar. Sci. 69 (2), 579–593.

Azanza, R.V., Fukuyo, Y., Yap, L.G., Takayama, H., 2005. *Prorocentrum minimum* bloom and its possible link to a massive fish kill in Bolinao, Pangasinan, Northern Philippines. Harmful Algae. 4, 519–524.

Bak, R.P., Meesters, E.H., 1998. Coral population structure: the hidden information of colony size-frequency distributions. Mar. Ecol. Prog. Ser. 162, 301–306.

Baum, G., Januar, H.I., Ferse, S.C.A., Kunzmann, A., 2015. Local and regional impacts of pollution on coral reefs along the thousand islands north of the Megacity Jakarta, Indonesia. PLoS One 10 (9), e0138271. https://doi.org/10.1371/journal.pone.01382712015.

Benayahu, Y., 2002. Soft corals (Octocorallia:Alcyonacea) of southern Ryuku Archipelago: the families Tubiporiidae, Clavulariidae, Alcyoniidae, and Briareidae. Galaxae, JCRS. 4, 11–32.

Benayahu, Y., Loya, Y., 1977. Space partitioning by stony corals, soft corals, and benthic algae in the coral reefs of the northern Gulf of Eilat (Red Sea). Helgol~inder wiss. Meeresunters. 30, 362–382.

Benayahu, Y., Loya, Y., 1981. Competition for space among coral-reef sessile organisms at Eilat, Red Sea. Bull. Mar. Sci. 31 (3), 514–522.

Benayahu, Y., Loya, Y., 1986. Sexual reproduction of a soft coral: synchronous and brief annual spawning of *Sarcophyton glaucum* (Quoy & Gaimard, 1833). Biol. Bull. 170, 32–42.

Benayahu, Y., Jeng, M.S., Perkol-Finkel, S., Dai, C.F., 2004. Soft coral (Octocorallia: Alcyonacea) from southern Taiwan. II. Species diversity and distributional patterns. Zoological Studies. 45 (3), 548–560.

Cardenas, M.B., Zamora, P.B., Siringan, F.P., Lapus, M.R., Rodolfo, R.S., Jacinto, G.S., San Diego-McGlone, M.L., Villanoy, C.L., Cabrera, O., Senal, O., 2010. Linking regional sources and pathways for submarine groundwater discharge at a reef by electrical resistivity tomography, ^{222}Rn, and salinity measurements. Geophys. Res. Lett. 37 (L16401) https://doi.org/10.1029/2010GL044066.

Carpenter, K.E., Springer, V.G., 2005. The center of the center of marine shore fish diversity: the Philippine Islands. Environ. Biol. Fish 72, 467–480.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.

Clarke, K.R., Warwick, R.M., 1994. Changes in Marine Communities: An Approach to Statistical Analyses and Interpretation. Natural Environment Research Council, Plymouth.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science. 199 (4335), 1302–1310.

Cooper, T.F., Gilmour, J.P., Fabricius, K.E., 2009. Bioindicators of changes in water quality on coral reefs: review and recommendations for monitoring programmes. Coral Reefs 28, 589–606.

Cruz-Trinidad, A., Geronimo, R.C., Aliño, P.M., 2009. Development trajectories and impacts on coral reef use in Lingayen Gulf, Philippines. Ocean Coast. Manag. 52 (3–4), 173–180.

Cruz-Trinidad, A., Geronimo, R.C., Cabral, R.B., Aliño, P.M., 2011. How much are the Bolinao-Anda reefs worth? Ocean Coast. Manag. 54, 696–705.

De'ath, G., Fabricius, K., 2008. Water Quality of the Great Barrier Reef: Distributions, Effects on Reef Biota and Trigger Values for the Protection of Ecosystem Health. Final Report to the Great Barrier Reef Marine Park Aothority. Australian Institute of Marine Science, Townsville.

Depczynski, M., Bellwood, D.R., 2004. Microhabitat utilization patterns in cryptobenthic coral reef fish communities. Mar. Biol. 145, 455–463.

Dinesen, Z.D., 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. Coral Reefs 1, 229–236.

Epstein, H.E., Kingsford, M.J., 2019. Are soft coral habitats unfavourable? A closer look at the association between reef fishes and their habitat. Environ Biol Fish. 102, 479–497.

Fabricius, K.E., 1995. Slow population turnover in the soft coral genera *Sinularia* and *Sarcophyton* on mid- and outer shelf reefs of the Great Barrier Reef. Mar. Ecol. Prog. Ser. 126, 145–152.

Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146.

Fabricius, K.E., Alderslade, P., 2001. Soft Corals and Sea Fans: A Comprehensive Guide to the Tropical Shallow-water Genera of the Central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Melbourne, Australia.

Fabricius, K.E., McCorry, D., 2006. Changes in octocoral communities and benthic cover along water quality gradient in the reefs of Hong Kong. Mar. Pollut. Bull. 52, 22–33.

Fabricius, K.E., Cooper, T.F., Humphrey, C., Uthicke, S., De'ath, G., Davidson, J., LeGrand, H., Thompson, A., Schaffelke, B., 2012. A bioindicator system for water quality on inshore reefs of the Great Barrier Reef. Mar. Pollut. Bull. 65 (4–9), 320–332.

Fan, T., Chou, Y., Dai, C., 2005. Sexual reproduction of the alcyonacean coral *Lobophytum pauciliform* in southern Taiwan. Bull. Mar. Sci. 76 (1), 143–154.

Ferrari, R., 2017. The hidden structure in coral reefs. Coral Reefs 36, 445.

Ferrera, C.M., Watanabe, A., Miyajima, T., San Diego-McGlone, M.L., Moromoto, N., Umezawa, Y., Herrera, E., Tsuchiya, T., Yoshikai, M., Nadaoka, K., 2016. Phosphorus as a driver of nitrogen limitation and sustained eutrophic conditions in Bolinao and Anda, Philippines, a mariculture-impacted coastal area. Mar. Pollut. Bull. https://doi.org/10.1016/j.marpolbul.2016.02.025.

Fleury, B.G., Coll, J.C., Tentori, E., Duquesne, S., Figueiredo, L., 2000. Effect of nutrient enrichment on the complementary (secondary) metabolite composition of the soft coral *Sarcophyton ehrenbergi* (Cnidaria: Octocorallia: Alcyonaceae) of the Great Barrier Reef. Mar. Biol. 136, 63–68.

Garra, S., Hall, A., Kingsford, M.J., 2020. The effects of predation on the condition of soft corals. Coral Reefs 39, 1329–1343.

Glynn, P.W., Mones, A.B., Podestá, G.P., Colbert, A., Colgan, M.W., 2017. El Niño-Southern Oscillation: effects on Eastern Pacific coral reefs and associated biota. In: Glynn P., Manzello D., Enochs I. (Eds.), Coral Reefs of the Eastern Tropical Pacific. Coral Reefs of the World, vol 8. Springer, Dordrecht.

Goh, B.P.L., Tan, G.E., Tan, L.T., 2009. Diversity, distribution and biological activity of soft corals (Octocorallia, Alcyonacea) in Singapore. Journal of Coastal Development. 12, 89–98.

Gomez, E.D., Aliño, P.M., Yap, H.T., Licuanan, W.Y., 1994. A review of the status of Philippine reefs. Mar. Pollut. Bull. 29 (1–3), 62–68.

Green, R.H., McArdle, B.A., van Woesik, R., 2011. Sampling state and process variables on coral reefs. Environ. Monit. Assess. 178, 455–460.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1). http://palaeo-electronica.org/2001_1/past/issue1_01.htm (9pp.).

Heery, E.C., Hoeksema, B.W., Browne, N.K., Reimer, J.D., Ang, P.O., Huang, D.H., Friess, D.A., Chou, L.M., Loke, L.H.L., Saksena-Taylor, P., Alsagoff, N., Yeemin, T., Sutthacheep, M., Vo, S.T., Bos, A.R., Gumanao, G.S., Hussein, M.A.S., Waheed, Z., Lane, D.J.W., Todd, P.A., 2018. Urban coral reefs: Degradation and resilience of hard coral assemblages in coastal cities of East and Southeast Asia. Marine Pollution Bulletin. 135, 654–681.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science. 301, 929–933.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology and Evolution. 25 (11), 633–642.

Humanes, A., Fink, A., Willis, B.L., Fabricius, K.E., de Beer, D., Negri, A.P., 2017. Effects of suspended sediments and nutrient enrichment on juvenile corals. Mar. Pollut. Bull. 125 (1–2), 166–175.

Inoue, S., Kayanne, H., Yamamoto, S., Kurihara, H., 2013. Spatial community shift from hard to soft corals in acidified water. Nat. Clim. Chang. 3, 683–687.

Ismail, H.A., Hanafy, M.H., Madkour, F.F., Ahmed, M.I., 2017. Distribution of soft corals in the Egyptian coasts of the Red Sea and Gulf of Aqaba. IJESC. 7 (9).

Jeng, M.S., Huang, H.D., Dai, C.F., Hsiao, Y.C., Benayahu, Y., 2011. Sclerite calcification and reef-building in the fleshy octocoral genus *Sinularia* (Octocorallia: Alcyonacea). Coral Reefs 30, 925–933.

Karlson, R.H., Cornell, H.V., Hughes, T.P., 2004. Coral communities are regionally enriched along an oceanic biodiversity gradient. Nature. 429, 867–870.

Kohler, K.E., Gill, S.M., 2006. Coral point count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32 (39), 1259–1269.

Licuanan, W.Y., Robles, R., Reyes, M., 2019. Status and recent trends in coral reefs of the Philippines. Mar. Pollut. Bull. 142, 544–550.

Light, S.F., 1913. Notes on Philippine Alcyonaria, part I. The Philippine species of the genus *Capnella*. Philippine Journal of Science. 8 (Sec. D): 435-453.3.

Light, S.F., 1914. Notes on Philippine Alcyonaria, Part II. *Lemnaloides kukenthali*, a New Genus and Species of Alcyonaria From the Philippines and Discussion of the Systematic Position of the New Genus. Philippines Journal of Science. 9 (Sec. D): 233-246.

Light, S.F., 1915a. Notes on Philippine Alcyonaria, part III. Two new species of *Lithophytom forskal* from the Philippines. Philippine Journal of Science. 10 (Sec D):1-11.3 figs. 2pls. In: Gomez, E.D., 1980.

Light, S.F., 1915b. Notes on Philippine Alcyonaria, part IV. Notes on Philippine Stolonifera and Xeniidae. Philippine Journal of Science. 10 (Sec. D) 10:155-167.

Light, S.F., 1915c. Notes on Philippine Alcyonaria, part V. *Cornularia minuta*, a new species. Philippine Journal of Marine Science. 10 (Sec. D):103-213.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., van Woesik, R., 2001. Coral bleaching: the winners and the losers. Ecol. Lett. 4, 122–131.

Malhotra, A., Fonseca, M.S., 2007. WEMo (wave exposure model): formulation, procedures and validation. Beaufort, NC, NOAA/National Ocean Service/National Centers for Coastal Ocean Science, (NOAA Technical Memorandum NOS NCCOS, 65).

Maliao, R.J., Turingan, R.G., Lin, J., 2008. Phase-shift in coral reef communities in the Florida Keys Marine Sanctuary (FKNMS), USA. Marine Biology. 154, 841–853.

Mantelatto, M.C., da Silva, A.G., Louzada, T.D., McFadden, C.S., Creed, J.C., 2018. Invasion of aquarium origin soft corals on a tropical rocky reef in the southwest Atlantic, Brazil. Marine Pollution Bulletin. 130, 84–94.

Mohammad, M., Apandi, Z.N., Marican, H.A.W., Kamphol, N., Mubin, N.A.A.A., Salleh, S., Ismail, M.N., 2016. The identification of octocorals from the northern region of Straits of Malacca. Tropical Life Sciences Research. 27 (1), 87–93.

Nacorda, H.M.E., Obliosca, J.M., Tentia, M.C.L., Jacinto, G.S., San diego-McGlone, M.L. C., 2012. Deterioration of soft bottom macroinfaunal communities in a milkfish mariculture zone off Bolinao-Anda, Pangasinan (NW Philippines). In: Kawaguchi, M., Misaki, K., Sato, H., Yokokawa, T., Itai, T., Nguyen, T.M., Ono, J., Tanabe, S. (Eds.), Interdisciplinary Studies on Environmental Chemistry: Environmental Pollution and Ecotoxicology. Terrapub, Tokyo, pp. 387–395 (2012).

Nañola, C.L., Jr., Aliño, P.M., Dantis, A.L., Rañola, M.C.G., Hilomen, V.V., Cabansag, J.P. B., 2002. Understanding Philippine reef fishes: a key to fisheries management and marine biodiversity conservation. In: Aliño, P.M., Miclat, E.F.B., Nañola, C.L. Jr., Roa-Quiaoit, H.A., Campos, R.T. (Eds.), Atlas of Philippine Coral Reefs: Philippine Coral Reef Information (PhilReefs). Goodwill Trading Co., Inc. (Goodwill Bookstore), Quezon City, Philippines, pp. 22-26.

Nañola, C.L., Aliño, P.M., Carpenter, K.E., 2011. Exploitation-related reef fish species richness depletion in the epicenter of marine biodiversity. Environ. Biol. Fish 90 (4), 405–420.

Ninio, R., Meekan, M.G., 2002. Spatial patterns in benthic communities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. Coral Reefs. 21, 95–103.

Poulus, D.A., Harasti, D., Gallen, C., Booth, D.J., 2013. Biodiversity value of a geographically restricted soft coral species within a temperate estuary. Aquat. Conserv. Mar. Freshwat. Ecosyst. 23, 838–849.

Preisendorfer, R.W., 1986. Secchi disk science: visual optics of natural waters. Limnol. Oceanogr. 31 (5), 909–926.

Quimpo, T.J.R., Ligson, C.A., Manogan, D.P., Requilme, J.N.C., Abelda, R.L., Conaco, C., Cabaitan, P.C., 2020. Fish farm effluents alter reef benthic assemblages and reduce coral settlement. Mar. Pollut. Bull. 153, 111025.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Riegl, B., Branch, G.M., 1995. Effects of sediment on the energy of four scleractinian (Bourne 1900) and five alcyonacean (Lamoroux 1816) corals. J. Exp. Mar. Biol. Ecol. 186, 259–275.

Roxas, H.A., 1932. Two new species of *Sarcophyton* Less. from the Philippines. Univ. Philipp. Natur. Appl. Sci. Bull. 4 (1), 73–80.

Roxas, H.A., 1933a. Philippine Alcyonaria: I. The families Cornulariidae and Xeniidae. Philippine Journal of Science. 50, 49–110.

Roxas, H.A., 1933b. Philippine Aclyonaria: II. The families Alcyoniidae and Nephthydae. Philippine Journal of Science. 50, 345–470.

Sanciangco, J.C., Carpenter, K.E., Etnoyer, P.J., Moretzsohn, F., 2013. Habitat availability and heterogeneity and the indo-Pacific warm pool as predictors of marine species richness in the tropical indo-Pacific. PLoS One 8 (2), e56245. https://doi.org/10.1371/journal.pone.0056245.

Senal, M.I.S., Jacinto, G.S., San Diego-McGlone, M.L., Siringan, F., Zamora, P., Soria, L., Cardenas, M.B., Villanoy, C., Cabrera, O., 2011. Nutrient inputs from submarine groundwater discharge on the Santiago flat, Bolinao, Northwestern Philippines. Marine Pollution Bulletin. 63, 195–200.

Shaish, L., Levy, G., Katzir, G., Rinkevich, B., 2010. Coral reef restoration (Bolinao, Philippines) in the face of frequent natural catastrophes. Restor. Ecol. 18 (3), 285–299.

Shoham, E., Prohaska, T., Barkay, Z., Zitek, A., Benayahu, Y., 2019. Soft corals form aragonite-precipitated columnar spiculite in mesophotic reefs. Sci. Rep. 9, 1241. https://doi.org/10.1038/s41598-018-37696-z.

Strickland, J.D.H., Parsons, T.R., 1972. A Practical Handvook of Seawater Analysis. Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

Strychar, K.B., Coates, M., Sammarco, P.W., Piva, T.J., Scott, P.T., 2005. Loss of *Symbiodinium* from bleached soft corals *Sarcophyton ehrenbergi*, *Sinularia* sp. And *Xenia* sp. Journal of Experimental Marine Biology and Ecology. 320, 159–177.

Tamayo, N.C.A., Anticamara, J.A., Acosta-Michlik, L., 2018. National estimates of values of Philippine reef`s ecosystem services. Ecol. Econ. 146, 633–644.

Tanaka, Y., Go, G.A., Watanabe, A., Miyajima, T., Nakaoka, M., Uy, W.H., Nadaoka, K., Watanabe, S., Fortes, M.D., 2014. 17-year change in species composition of mixed seagrass beds around Santiago Island, Bolinao, the northwestern Philippines. Mar. Pollut. Bull. 88, 81–85.

Tanner, J.E., 1995. Competition between scleratinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. J. Exp. Mar. Biol. Ecol. 190 (2), 151–168.

Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology. 67 (5), 1167–1179.

Tursch, B., Tursch, A., 1982. The soft coral community on a sheltered reef quadrat at Laing Island (Papua New Guinea). Mar. Biol. 68, 321–332.

Van Alstyne, K.L., Wylie, C.R., Paul, P.J., 1994. Antipredator defenses in tropical Pacific soft corals (Coelenterata: Alcyonacea) II. The relative importance of chemical and structural defenses in three species of *Sinularia*. Journal of Experimental Marine Biology and Ecology. 178, 17–34.

van Woesik, R., Gilner, J., Hooten, A.J., 2009. Standard Operating Procedures for Repeated Measures of Process and State Variables of Coral Reef Environments. Coral Reef Targeted Research and Capacity Building for Management Program. The University of Queensland, Melbourne (34p).

Villanueva, R.D., Yap, H.T., Montaño, M.N.E., 2005. Survivorship of coral juveniles in a fish farm environment. Mar. Pollut. Bull. 51, 580–589.

Villanueva, R.D., Yap, H.T., Montano, M.N.E., 2006. Intensive fish farmng in the Philippines is detrimental to the reef-building coral *Pocillopora damicornis*. Mar. Ecol. Prog. Ser. 316, 165–174.

Villanueva, R.D., Baria, M.V.B., dela Cruz, D.W., 2012. Growth and survivorship of juvenile corals outplanted to degraded reef areas in Bolinao-Anda Reef Complex, Philippines. Marine Biological Research. 8, 877–884.

Webster, F.J., Babcock, R.C., Van Keulen, M., Loneragan, N.R., 2015. Macroalgae inhibits larval settlement and increases recruit mortality at Ningaloo Reef, Western Australia. PLoS One 10 (4), e0124162. https://doi.org/10.1371/journal.pone.0124162.

Yang, H., Yu, K., Zhao, M., Shi, Q., Tao, S., Yan, H., Chen, T., Liu, G., 2015. Impact on the coral reefs at Yongle Atoll, Xisha Islands, South China Sea from a strong typhoon direct sweep: Wutip, September 2013. J. Asian Earth Sci. 114, 457–466.

Yesson, C., Taylor, M.L., Tittensor, D.P., Davies, A.J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J.M., Rogers, A.D., 2012. Global habitat suitability of cold-water octocorals. J. Biogeogr. 39 (7), 121–126.

Yeung, C.W., Cheang, C.C., Lee, M.W., Fung, H.L., Chow, W.K., Ang, P., 2014. Environmental variabilities and the distribution of octocorals and black corals in Hongkong. Mar. Pollut. Bull. https://doi.org/10.1016/j.marpolbul.2013.12.043.

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.A., Ryan, McMinds, Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat. Commun. 7 (11833) https://doi.org/10.1038/ncomms11833.

Zvuloni, A., van Woesik, R., Loya, Y., 2010. Diversity partitioning of stony corals across multiple spatial scales around Zanzibar Island, Tanzania. PLoS One 5 (3), e9941. https://doi.org/10.1371/journal.pone.0009941.