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Cross shelf gradients of scleractinian corals in the Spermonde Islands, South Sulawesi, Indonesia

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Abstract. *Yusuf S, Beger M, Tassakka ACMAR, Brauwer MD, Pricella A, Rahmi, Umar W, Limmon GV, Moore AM, Jompa J. 2021. Cross shelf gradients of scleractinian corals in the Spermonde Islands, South Sulawesi, Indonesia. Biodiversitas 22: 1415-1423.* Coral reef ecosystems around the world have suffered extensive degradation, including the reefs of the Wallacea region within the Coral Triangle global biodiversity hotspot. Anthropogenic and natural threats can reduce the level of coral reef biodiversity differentially across environmental or impact gradients. The purpose of this study was to evaluate the changes in hard coral (Scleractinia) diversity and community structure across an inshore-offshore zonation gradient in the Spermonde Islands, South Sulawesi, Indonesia. Data on coral colony species and abundance as well as live coral cover were collected from 10 m^2 belt transects at a depth of 6 to 8 m. A total of 72 transects were placed around the 12 island stations in three zones: the inner mid-shelf zone, outer mid-shelf zone and outer shelf zone. Data were analyzed to determine the species richness, and three ecological indices for the hard coral communities were calculated: the Shannon Diversity Index (H'), Similarity Index (E), and Dominance Index (C). A total of 310 hard coral species belonging to 62 genera were recorded. The coral communities were dominated by the genera *Fungia*, *Montipora* and *Porites*, and coral cover was in the 'moderate' category. The number of species was directly proportional to the number of colonies within each zone. Live coral cover was higher in the inner mid-shelf zone and outer shelf zone than the outer mid-shelf zone; conversely, the species richness and coral colony abundance were higher in the outer mid-shelf zone. However, the differences were not statistically significant. The indices H', C, and E did not differ significantly between the zones. However, Tambakulu Island in Zone 4 had the lowest values of E and H' and the highest value of C. Findings suggest that most-hard coral communities in the cross-shelf zones of the Spermonde Islands are stable communities characterized by relatively high diversity and low dominance indices.

Keywords: Biodiversity, Coral Triangle, ecological indices, Scleractinia, Wallacea Region

INTRODUCTION

Reef building or stony corals (Scleractinia) are widely distributed throughout the tropical and subtropical regions of the world (Obura 2012). Distribution patterns can be expressed in terms of the numbers of taxa (e.g. genera or sub-generic groups) present in different regions (Wallace et al. 1991). Coral reef ecosystems are a key storehouse of marine biodiversity (Kondo and Hashimoto 2010; Hoegh-guldberg et al. 2018). Wallacea is a terrestrial and marine megadiversity area in the western Indo-Pacific, comprising the region between the Wallace Line which extends from the Philippines through the Makassar Strait to the Lombok Strait to the west and the Lydekker Line to the east (Lohman et al. 2011). The Wallacea Line divides the western (Sunda Shelf) from the eastern Indonesian biodiversity areas. Alfred Wallace concentrated much of his study on the biodiversity of eastern Indonesia, in particular the islands of Sulawesi, Maluku, Halmahera, Nusa Tenggara and the seas around them, undertaking a major voyage of exploration lasting from 1854 to 1862 (Lloyd et al. 2010). Since then there has been considerable amount of research on coral biodiversity in the coral reef ecosystems of Southeast Asia in general, and Wallacea in particular (Moll 1983; Best et al. 1989; Hoeksema 2012a, 2012b; Veron et al. 2015). Geographical variations within the Southeast Asia region affect the level of biodiversity, as reflected in the delineation of the Coral Triangle (Veron et al. 2009), the global epicenter of coral reef biodiversity (Barber et al. 2011), with at least 627 species of coral and many finer-scale ecoregions (Veron et al. 2015).

In addition to their intrinsic biodiversity value, coral reef ecosystems support the livelihoods of millions of people, including through locally and globally important fisheries (Cullen 2010; Burke et al. 2012; Hughes et al. 2014; Rhyne et al. 2014; Cabral and Geronimo 2018), However, as for coral reefs worldwide (Hughes et al. 2014; Weijerman et al. 2018), the coral reef ecosystems in the Wallacea region are not free from anthropogenic disturbances which can reduce the level of biodiversity and ecosystem services (Green et al. 2014). These include destructive fishing, overfishing, land-based and marine pollution, the effects of land-use changes such as run-off, eutrophication and sedimentation, coastal development, anthropogenic climate change and ocean acidification (Burke et al. 2012; Ambo-Rappe and Moore 2018; Heery et al. 2018). Collectively, these stressors are severely degrading the reef ecosystems, threatening sustainable fisheries, tourism, coastal protection, and a myriad of other ecosystem services provided by reefs, in some cases causing irreversible changes to community structure and productivity (Green et al. 2014; Hughes et al. 2014; Hoey et al. 2016). While efforts have been made to reduce some of the more obvious direct impacts such as destructive fishing, the revised regional autonomy law UU 23/2014 has resulted in (hopefully temporary) setbacks (Ambo-Rappe and Moore 2018) and over-fishing remains a pervasive problem (Burke et al. 2012; Ferse et al. 2012; Ferse et al. 2014; Glaser et al. 2018).

Many reefs in the Wallacea region appear to have escaped historical thermal stress and large-scale environmental disturbances. Such reefs are seen as being global importance as potential refugia (Weijerman et al. 2018). Nonetheless, like all tropical coral reef ecosystems, it is predicted that these reefs are or will eventually be imperiled due to predicted climate trends and associated impacts (Burke et al. 2012). Indeed, there are signs that, despite the apparent relatively high resistance or resilience of some reefs to past and current levels of local and climate-related stressors (Heery et al. 2018; Williams et al. 2019), they are also likely to be increasingly vulnerable as global warming accelerates (Oliver et al. 2019; Andradi-Brown et al. 2020). For example, areas that did not bleach in the 1998 or 2010 global coral bleaching events did bleach in 2016 (Moore et al. 2017; Ambo-Rappe and Moore 2018; Moore et al. 2019). Furthermore, bleaching patterns may not always be visible; while shallow reefs typically bleached most in 2010 (Muslihuddin et al. 2012; Yusuf and Jompa 2012), in 2016 bleaching was only observed at depths below 7 m in the Spermonde (Yusuf, unpublished data) and Menui (Ambo-Rappe and Moore 2018) Archipelagos.

Understanding the complex interactions and dynamic responses of coral reef communities to multiple stressors is key to predicting future trends and managing reefs to sustain ecosystem services (Edinger et al. 1998; Hughes et al. 2014; Weijerman et al. 2018; Andradi-Brown et al. 2020). The coral reef ecosystem in the Spermonde Islands, South Sulawesi, offers an example where coral reef ecosystem disruption comes from anthropogenic activities in the sea and land, with an inshore-offshore gradient (Edinger et al. 1998; Hoeksema 2012a; Plass-Johnson et al. 2018a). The Fungiidae are one coral taxon exhibiting ecological differentiation in distribution patterns along cross-shelf environmental gradients in the area (Hoeksema 2012b).

There have been studies on various aspects of reef health and biodiversity across this gradient in the Spermonde Islands over the past decades (Moll 1983; Best et al. 1989; CRITC 2012; Hoeksema 2012b), as well as more recent studies on coral reefs and associated biodiversity (Plass-Johnson et al. 2018a; Plass-Johnson et al. 2018b; Teichberg et al. 2018). However, there is a need for updated and/or complementary data on certain aspects of coral community biodiversity, ecology and health. Molecular biology methods are gaining in popularity for a wide range of biodiversity-related studies in the marine realm (Bourlat et al. 2013; Bowen et al. 2014; von der Heyden et al. 2014; Crandall et al. 2019) including for corals (Gittenberger et al. 2011; Umar et al. 2019; Jompa et al. 2020). In particular, environmental DNA (eDNA) can provide data on the taxonomic groups present (Berry et al. 2019), and in some cases also provide an indication of relative abundance (Kutti et al. 2020). However, there is still a need for ground-truthing, particularly with respect to the abundance of taxonomic groups such as the Scleractinia where eDNA has not been widely used.

This research aimed to estimate the species and genus level biodiversity and abundance of coral colonies and evaluate the interactions between anthropogenic pressures and coral community characteristics across an inshore-offshore gradient using standard ecological indices. An additional objective of the study was to provide data which could be used to evaluate the results of a parallel study on coral community biodiversity using a molecular biology method (eDNA) with respect to both species identified and their relative abundance. The fine-scale taxonomic data generated by this study will contribute to the knowledge on coral biodiversity and biogeography, while the existence of historical (time series) data should make the ecological data particularly valuable to both managers and researchers.

MATERIALS AND METHODS

Research site - overview of the Spermonde Islands

The Spermonde Islands lies off the southwestern coast of Sulawesi island (Indonesia) on a wide but shallow coastal shelf. Starting from the city of Makassar on the Sulawesi mainland, the shelf extends around 40 km west into the Makassar strait (Hoeksema 2012b). Around 80 small islands formed from coral sand (coral cays) are bathed by the Indonesian Throughflow (ITF) in the Makassar Strait. Due to the currents, scleractinian corals naturally grow well, forming fringing reefs and patch reefs with barrier reefs along the outer margin of the shelf.

Four zones have been delineated in the Spermonde Islands, representing an onshore-offshore gradient in both ecological conditions and anthropogenic pressures (Hoeksema 2012b). The innermost zone (Zone 1) runs parallel to the shore, and is delimited by the 20 m isobath; all potentially habitable islands in this zone are inhabited, often at very high densities. The second zone or inner mid-shelf zone (Zone 2) begins around 5 to 12.5 km from shore with a maximum depth of around 30 m. Most islands are inhabited, with many coral-covered patch reefs below the surface of the shallow waters. The third zone, around 12.5 to 30 km offshore, is the outer mid-shelf zone (Zone 3) which is influenced to some extent by offshore (oceanic) waters, with depths reaching 30 or 50 m. Corals are generally found growing on submarine shoals with no islands, or uninhabited sandy cays. The outermost reefs in the fourth (outer shelf) zone (Zone 4) form extensive but discontinuous barrier reefs around 30-40 km from land and are directly exposed to offshore conditions. Several islands along the barrier reef are inhabited, such as Langkai, Lanjukang, and the islands in the Kapoposang Marine Tourism Park (Kapoposang, Papandangan, Gondong Bali, and Suranti. Depths in this zone tend to be around 40 to 50 m, while at the outer edge of the shelf on which the Spermonde Islands is sited, the seafloor plunges steeply to depths of 100 to 200 m.

Sampling time and sites

The field survey took place in May 2019. The sampling sites comprised 12 islands, with four islands representing each of three cross-shelf zones in the Spermonde Islands (Figure 1). In Zone 2 (inner mid-shelf zone) these were: Barrang Lompo, Sanane, Polewali, and Ballang Lompo; in Zone 3 (outer mid-shelf zone): Bone Tambu, Lumu Lumu, Sarappo Lompo, and Samatellu Lompo; and in Zone 4 (outer zone): Lanjukang, Langkai, Tambakulu, Kapoposang.

Coral community data collection

This study was carried out as part of a wider research program employing Environmental DNA (eDNA) methods to evaluate the biodiversity and structure of hard coral (Scleractinia) communities in the Indonesian Wallacea region. At each site (island), three 50 m line transects were laid at a depth of around 6 to 8 m. Along each line transect, data were collected within two belt transects (each 10m x 1m = 10m^2) along the 50 m line transect (0-10 m and 30-40 m), giving a total survey area of 60m^2 per site, 240 m^2 per zone and 720 m^2 overall. Coral reef condition was evaluated based on percentage hard coral cover (%HC) using the standard established by the Indonesian Ministry of the Environment in Decree KEP - 04/MENLH/02/2001: Poor (0-24.9%); Moderate (25-49.9%); Good (50-74.9%); and Excellent (75-100%) (Kementerian Lingkungan Hidup 2001). All coral colonies within each transect were counted and identified to species level, or where this was not possible to genus level. Identification was conducted in the field and in the laboratory-based on photographs taken in the field and/or specimens. Samples of specimens that could not be identified in the field were collected, bleached and dried in the field and identified in the Coral Centre Laboratory of Hasanuddin University. The identification process was based on references (Wallace 1999; Veron 2000).

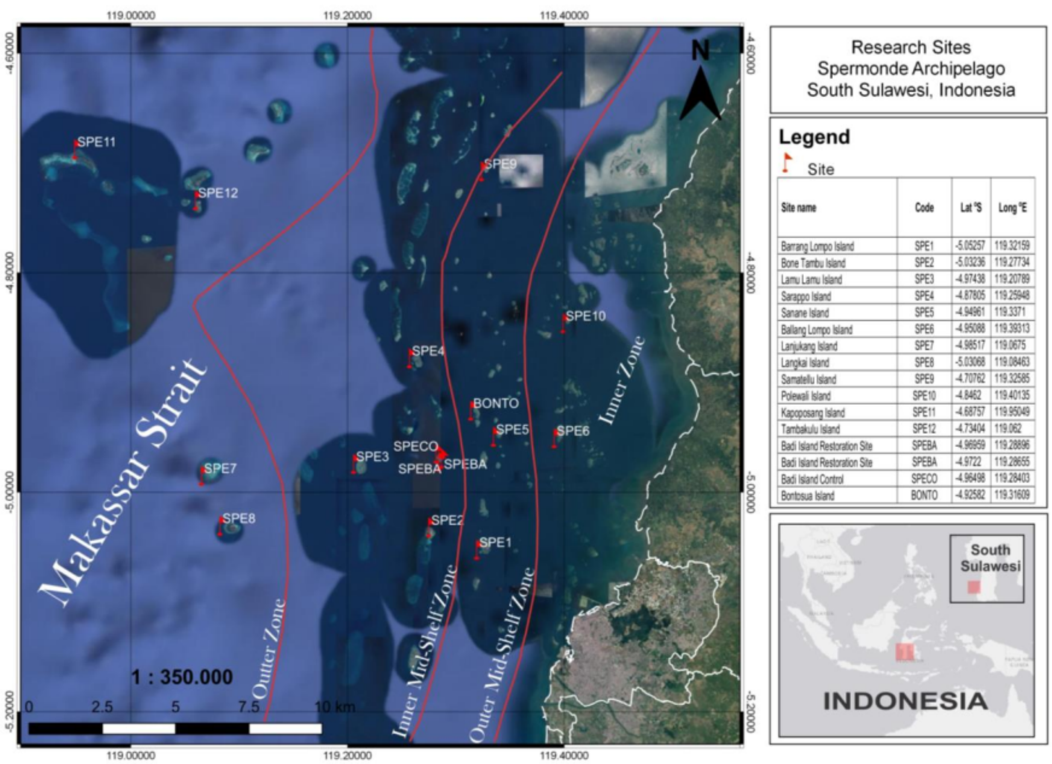

Figure 1. Cross-shelf zones and study sites in the Spermonde Islands, South Sulawesi, Indonesia

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Data analysis

Data were tabulated in Microsoft Excel 2010 and analyzed descriptively. All statistical analyses were performed, and graphics were produced in Excel 2010. Three ecological indices were calculated: the Shannon-Weiner Diversity Index (H'), the Index of Dominance (C), and Evenness Index (E), following Morris et al. (2014). The indices were evaluated as follows based on Krebs (1999): (i) Diversity Index: low diversity $H' \leq 2$; moderate diversity $2 < H' \leq 3$; and high diversity $H' > 3$; (ii) Dominance Index: low dominance $0 < C \leq 0.5$; moderate dominance $0.5 < C \leq 0.75$; and high dominance $0.75 < C \leq 1$; (iii) Evenness Index: community under pressure: $0 < E \leq 0.5$; unstable community $0.5 < E \leq 0.75$; stable community $0.75 < E \leq 1$. The statistical significance of between zone differences in the mean values of the parameters calculated was evaluated using the analysis of variance (ANOVA) routine at the 95% confidence limit (α=0.05). The correlation between coral abundance (colony count) and diversity (species count) was evaluated through a linear regression of Log_{10} transformed data.

RESULTS AND DISCUSSION

Scleractinian coral biodiversity, condition and density

From the total area of 720 m^2 studied using the belt transect method, 3079 coral colonies representing 310 species and 62 genera of scleractinian corals were recorded from the reefs around 12 islands in the Spermonde Islands (Table 1). Based on the mean % HC cover, the mean condition of the reefs in each zone and that of all sites in Zone 4 was in the moderate category, while in Zones 2 and 3 reef condition was more varied, ranging from poor to good. None of the reefs studied were in the excellent condition category.

The overall means species richness and colony abundance per site were 101 species and 575 colonies per 60 m^2, equivalent to a coral colony density of 9.6·m^{-2}. The mean coral colony count and mean species countfor each zone are shown in Figure 2.

The mean coral colony density in Zone 3, the outer mid-shelf zone, was 121 colonies per 10 m^2, considerably higher but not significantly ($p > 0.05$) different from the mean densities in Zone 2 (inner mid-shelf) and Zone 4 (outer zone), both of which averaged 87 colonies per 10 m^2 (Figure 3).

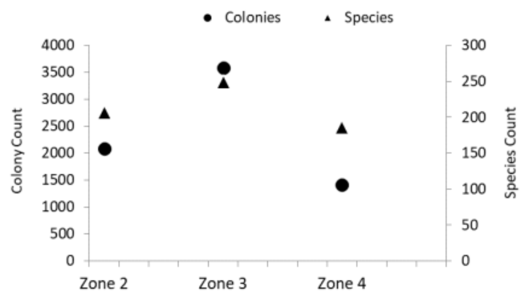

Figure 2. Coral species count and colony count by cross-shelf zone in the Spermonde Islands, South Sulawesi, Indonesia

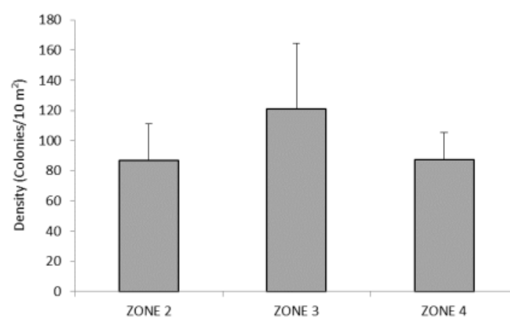

Figure 3. Coral colony density by zone in the Spermonde Islands, South Sulawesi, Indonesia (bars: mean; whiskers: standard deviation)

Table 1. Number of scleractinian coral colonies, number of species and hard coral cover (%HC) by zone (240 m^2) and island (60 m^2) in the Spermonde Islands, South Sulawesi, Indonesia (belt transect data, total area surveyed 720 m^2)

Zone	Mean HC (%)	Site (island)	Colonies	Species	Mean HC (%)
Zone 2	33.5	Sanane	705	122	50.07
		Barrang Lompo	432	109	41.25
		Ballang Lompo	570	102	17.23
		Polewali	377	88	25.56
Zone 3	32.1	Bone Tambu	347	132	8.04
		Sarappo Lompo	703	118	35.36
		Samatellu Lompo	577	111	32.84
		Lumu Lumu	1089	94	52.21
Zone 4	33.4	Lanjukang	517	103	38.08
		Kapoposang	448	96	31.26
		Langkai	457	94	26.00
		Tambakulu	679	48	38.22

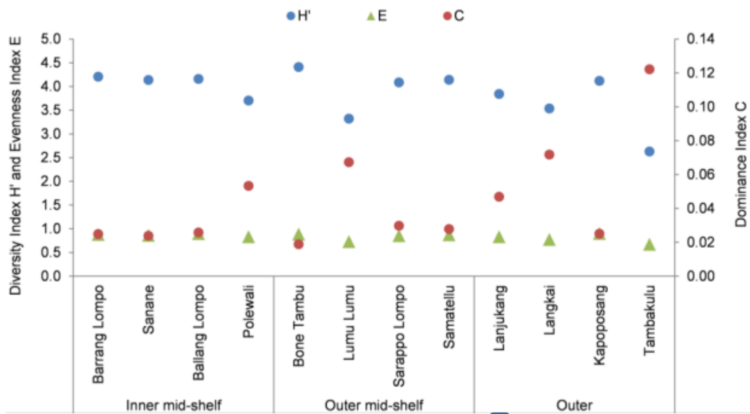

Figure 4. Ecological indices of scleractinian coral communities around 12 islands in the Spermonde Islands, South Sulawesi, Indonesia

Scleractinian coral community ecological indices

The three ecological indices calculated for the coral communities were similar for most of the 12 sites in three cross-shelf zones (Figure 4). One site (Tambakulu Island in Zone 4) differed noticeably from the overall pattern of the other 10 sites, with the lowest Diversity Index H' value and the highest value for the Dominance Index C. This site was also the only site with an E value less than 0.75, indicating an unstable community, despite having above average coral cover (38.22%).

Correlation between scleractinian coral diversity and abundance

The three genera with the highest abundance were *Fungia, Montipora* and *Porites*, accounting for nearly half (48.64%) of all colonies and 20.00% of all species recorded (Table 2). The genus *Porites* accounted for 17.93% of colonies and 5.81% of species; *Fungia* for 16.78% of colonies and 9.03% of species; and *Montipora* for 13.94% of colonies and 5.16% of species.

The linear regression of the $\log_{10}$-transformed data (Figure 5) showed a moderately strong positive correlation (R2 ≈ 0.6) between the number of species within a genus and the colony count for that genus. The R^2 value indicates that, for a given genus, around 77% of the variation in colony count can be explained by the number of congeneric species present.

Discussion

Coral biodiversity and abundance

The number of coral species identified in this study is greater than that in previous studies. For example, Moll (1983) found 262 species belonging to 69 genera, less than the current study; these figures were also presented in Best et al. (1989). However, Moll (1983) did not cover all the sites in our study, for example, Kapoposang was not included. Conversely, Moll (1983) studied islands in Zone I, at a time when environmental conditions in this zone were still relatively good. Nowadays, the degradation due to coastal development has greatly reduced both coral cover and coral diversity in Zone 1 (Heery et al. 2018), which was not included in our study.

A recent evaluation of coral reef management in Indonesia (Susanto et al. 2015) quoted the same figure, but attributed the 262 species to Kapoposang, which was not covered by Moll (1983); this could be a case of spatial confusion or due to a lack of additional species identified in that area. The Spermonde Islands has split administratively between Pangkajene Kepulauan (Pangkep) District to the north and Makassar City to the south, both within South Sulawesi Province. A survey in 2010 which was limited to reefs under the jurisdiction of Makassar City identified 191 scleractinian coral species (S. Yusuf, unpublished data 2010), while surveys in the Pangkep area in 2012 (CRITC 2012) found just 110 species. It should be noted that, while all other surveys used belt transect methods, the survey conducted by the Indonesian Institute for Science (LIPI) in 2012 used a line intercept transect (LIT) method, a factor that could account for the lower species count.

With respect to the zones, the species richness did not follow the expected pattern of inshore-offshore cross-shelf increase from Zone 2 to Zone 4. Despite the terrestrial influences apparent in Zone 2, including eutrophication due to the pollution of the rivers flowing into the sea, the lowest overall species richness was observed in Zone 4 (186 species), with the highest coral diversity in Zone 3 (249 species), followed by Zone 2 (207 species). The pattern of colony abundance was similar to that of species richness, as seen in Table 1 and Figure 2.

At a site (island) level, three of the five sites with the highest species richness were in Zone 3, with Lumu Lumu Island being the one exception. Only one site in Zone 4 (ranked 6th) had more than 100 species (Lanjukang Island), while the site with the lowest species count was Tambakulu Island in Zone 4, in the outer reaches of the Archipelago. However, it should be noted that, at each site (island), data were collected from a limited sample of the reef ecosystem. In addition to the limited total area (60m²/site), data were only collected at a single depth, 6 to 8m. It is possible that the depth at which maximum scleractinian diversity occurs may differ between sites.

Table 2. Total frequency of occurrence (number and % of colonies observed), the number and % of species within each coral genus observed in the Spermonde Islands during this research

Genus	Colonies		Species		Genus	Colonies		Species	
	n	%	n	%		n	%	n	%
Fungia	1262	17.93	18	5.81	*Pachyseris*	37	0.53	3	0.97
Montipora	1181	16.78	28	9.03	*Sandalolitha*	33	0.47	2	0.65
Porites	981	13.94	16	5.16	*Goniopora*	26	0.37	6	1.94
Acropora	319	4.53	40	12.90	*Echinophyllia*	24	0.34	4	1.29
Seriatopora	260	3.69	3	0.97	*Mycedium*	24	0.34	4	1.29
Galaxea	252	3.58	2	0.65	*Halomitra*	23	0.33	2	0.65
Echinopora	225	3.20	6	1.94	*Coscinaraea*	22	0.31	2	0.65
Goniastrea	213	3.03	10	3.23	*Coeloseris*	20	0.28	1	0.32
Pavona	178	2.53	10	3.23	*Isopora*	19	0.27	1	0.32
Cyphastrea	168	2.39	6	1.94	*Plesiastrea*	19	0.27	1	0.32
Millepora	167	2.37	3	0.97	*Leptoria*	18	0.26	1	0.32
Ctenactis	147	2.09	3	0.97	*Stylocoeniella*	17	0.24	1	0.32
Favites	131	1.86	10	3.23	*Turbinaria*	14	0.20	5	1.61
Astreopora	118	1.68	8	2.58	*Caulastrea*	13	0.18	2	0.65
Leptastrea	100	1.42	6	1.94	*Oulophyllia*	12	0.17	1	0.32
Montastrea	94	1.34	9	2.90	*Polyphillia*	12	0.17	1	0.32
Platygyra	87	1.24	7	2.26	*Herpolitha*	11	0.16	1	0.32
Favia	84	1.19	14	4.52	*Diploastrea*	10	0.14	1	0.32
Merulina	82	1.16	2	0.65	*Cycloseris*	9	0.13	3	0.97
Leptoseris	78	1.11	11	3.55	*Acanthastrea*	8	0.11	5	1.61
Pectinia	56	0.80	5	1.61	*Tubastrea*	8	0.11	2	0.65
Hydnopora	53	0.75	3	0.97	*Heliofungia*	7	0.10	1	0.32
Pocillopora	50	0.71	3	0.97	*Physogyra*	7	0.10	1	0.32
Psammocora	50	0.71	7	2.26	*Plerogyra*	5	0.07	1	0.32
Stylophora	48	0.68	2	0.65	*Australogyra*	4	0.06	1	0.32
Podabacia	41	0.58	2	0.65	*Heliopora*	4	0.06	1	0.32
Symphyllia	41	0.58	4	1.29	*Lithophyllon*	4	0.06	2	0.65
Euphyllia	39	0.55	2	0.65	*Scolymia*	4	0.06	2	0.65
Oxypora	39	0.55	3	0.97	*Tubipora*	4	0.06	1	0.32
Barabattoia	37	0.53	2	0.65	*Gardineroseris*	2	0.03	1	0.32
Lobophyllia	37	0.53	4	1.29	*Alveopora*	1	0.01	1	0.32

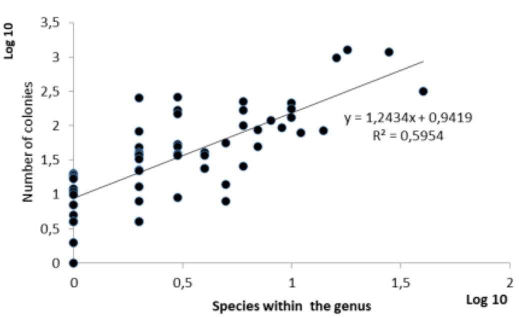

Figure 5. Log_{10} transformed linear regression relationship between species richness and total number of coral colonies for each Scleractinian coral genus recorded around 12 islands in 3 zones of the Spermonde Islands, South Sulawesi, Indonesia

At most sites, coral colony density was highest in shallow waters and decreased with increasing depth. This was especially noticeably for the genus *Acropora*, the most speciose extant coral genus (Wallace et al. 2012). Only 319 acroporid colonies were counted from all 72 transects at 6 to8 m depth. During the survey, qualitative observations showed that *Acropora* colonies were more abundant and appeared denser on the shallower areas of the reef crest and/or the reef flat. Historical data, in particular old photographs show a naturally high abundance of acroporid corals in the Spermonde Islands, and this genus was still the most abundant in 2006 (Yusuf and Jompa 2012). Therefore, it is possible that the diversity and abundance of this species were underestimated due to the survey methodology used. It is also possible that acroporid abundance was low due to direct and indirect human impacts, and that a combination of factors contributed to the relatively low abundance of the genus *Acropora* in this study. This taxon is relatively vulnerable to both mechanical damage and climate impacts, especially coral bleaching (Yusuf and Jompa 2012; Decarlo et al. 2017). Furthermore, corals of the genus *Acropora* are reputed to prefer high light intensity; their depth distribution tends to be related to and limited by light penetration (Yentsch et al. 2002), and hence water quality (Strahl et al. 2019). Coral planula settlement rates tend to be higher at higher light intensities (Yusuf et al. 2019), and juvenile *Acropora* colonies are particularly sensitive to suspended particles and sedimentation, irrespective of light intensity as well as excessively attenuated light penetration (Humanes et al. 2017; Moeller et al. 2017). Acroporid corals are also favored by *Acanthaster planci*, the corallivorous crown of thorns starfish (Wallace et al. 2012). A severe *A. planci* outbreak occurred in the Spermonde Islands in 2012-2013 (Plass-Johnson et al. 2015), resulting in high levels of coral mortality (in some cases more than 50%). Visual records from this outbreak show high levels of *A. planci* predation on *Acropora*, in particular tabulate colonies (Plass-Johnson et al. 2015).

Coral genera with very low abundance at the survey depth (6 to 8 m) were *Plerogyra, Heliopora, Australogyra, Scolymia, Tubipora, Gardineroseris* and *Alveopora*. These corals are generally considered relatively rare; they are also noted for their limited reproductive and dispersal capacity. These factors might account for the low abundance observed, although natural scarcity may have been exacerbated by mortality due to anthropogenic factors coupled with low regenerative capacity.

Scleractinian coral community characteristics and cross-shelf gradient

Overall, the values of the ecological indices are typical of relatively stable and diverse communities, with low dominance at all sites. A higher Evenness Index (E) typically indicates more diverse and balanced communities, not dominated by a few species. The one site with an E value not in the stable category was Tambakulu Island (Zone 4); however, coral cover at this site was relatively high and the Diversity Index H' was in the moderate category. The 2012 survey (CRITC 2012) reported *H'* values in the range of 1.73 to 3.06, mostly in the moderate category, and E values in the range 0.65 to0.93. Our results show generally higher *H'* values (2.63 to 4.41) and similar E values (0.675 to 0.902). As for the overall species count, one reason for this difference could be the transect methods used, i.e. LIT (Line Intercept Transect) rather than the belt transects used in this study.

In contrast to previous studies in the Spermonde Islands, we did not find a clear cross-shelf progression in any scleractinian coral community characteristic measured. The increase in density and diversity across the mid-shelf zone (from Zone 2 to Zone 3) was not statistically significant and did not continue into the outer reef area (Zone 4). The reasons for this unexpected pattern are not clear. However, in addition to water quality, which could be expected to improve across the shelf, other factors affecting coral community development and resilience include the presence of adult colonies and larval recruitment (Sawall et al. 2013). Intuitively, the outer mid-shelf (Zone 3) could receive more coral propagules, being situated between Zone 3 and Zone 4. Meanwhile, it is possible that recruitment may be less effective in the outer zone, due to stronger currents and wave action, which could reduce the settlement of coral planulae, and reduce survival of recently settled juveniles, especially on poorly consolidated substrate. As mentioned above, depth may also play a role, as in the clearer offshore reefs certain taxa might be found at a deeper depth; conversely, taxa adapted to a higher light intensity might be found above the 6-8m depth used in this study.

As mentioned above, one of the goals of this study was to provide benchmark or ground-truthing data for a survey using environmental DNA (eDNA) metabarcoding methods. In this context, it will be interesting to see whether or not the patterns observed in this study are mirrored in the metabarcoding results. In particular, whether species richness patterns between sites and zones are similar; whether relative abundances of sequences attributed to each operational taxonomic unit indicate a similar pattern of relative inter-species and inter-genus abundance; and whether there is a correlation between taxonomic diversity and abundance.

The results of our study on scleractinian coral communities in the Spermonde Islands can be considered surprising. Contrary to expectations, we did not find any significant difference between zones across an inshore-offshore gradient in scleractinian coral colony abundance, coral species richness or the ecological indices calculated. Number of colonies per genus showed a moderate but significant correlation with the number of species present within each genus. Three genera dominated the coral communities in terms of abundance: *Fungia*, *Montipora* and *Porites*. Observed coral biodiversity was high compared to historical data from this area; however the relatively low abundance of once common acroporid branching corals can be considered an indicator of direct and indirect human impacts on these reefs. We conclude that the hard coral communities in the cross-shelf zones of the Spermonde Islands can be categorized as apparently relatively stable and resilient communities characterized by mostly high diversity and low dominance indices. However, wise management at the local level will be needed to maintain the diversity and ecosystem services of these valuable ecosystems, while their ultimate fate will depend on the success of global efforts at all levels to mitigate climate change. These data provide a snapshot that can be used to compare with present and future studies on the coral communities of this region.

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