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Influence of Coral Reef Rugosity on Fish Communities in Marine Reserves Around Lombok Island, Indonesia

Prakas Santoso · Fakhrizal Setiawan · Beginer Subhan · Dondy Arafat · Dietriech G. Bengen · Lalu M. Iqbal Sani · Austin T. Humphries · Hawis Madduppa

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Abstract Coral reef structural form is widely considered a key factor with respect to the availability of shelter and foraging spaces for fishes and invertebrates. However, anthropogenic stressors are damaging coral reefs and the structural complexity they provide for millions of marine species. It is therefore important to assess the effect of coral reef structural form on fish diversity, especially in the coral reefs within the world's hyper-diverse Coral Triangle region. This study examined the relationship between rugosity (as a proxy for complexity of form in coral reef habitat) and fish communities in three marine reserves around Lombok Island (Gili Matra, Gili Sula, and Gita Nada) in Indonesia. Data on fish (taxonomic identification, trophic guild, and abundance) and habitat rugosity were collected at six stations in each reserve using three 50 m transects at each station. Data were analysed through analysis of variance and non-metric multidimensional scaling. The results showed that species richness and abundance were strongly correlated with coral reef habitat rugosity. There was also a statistically significant relationship between three trophic guilds (corallivores, planktivores, and omnivores) and coral reef habitat rugosity. This study strongly supports the view that the fine-scale rugosity of coral reef habitat is a critical factor in maintaining abundant and diverse reef fish communities. We did not examine the mechanisms by which coral reef habitat rugosity impact fish communities, but others have found that this is likely due to increased nursery and foraging habitat availability.

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P. Santoso · F. Setiawan · B. Subhan · D. Arafat · D. G. Bengen · H. Madduppa (✉)
Department of Marine Science and Technology, Faculty of Fisheries and Marine Sciences, IPB University, Jalan Agatis No. 1, Bogor 16680, Indonesia
e-mail: hawis@apps.ipb.ac.id

P. Santoso · F. Setiawan · B. Subhan · H. Madduppa
Graduate School, Marine Science Study Program, Department of Marine Science and Technology, IPB University, Jl Agatis No 1, Bogor 16680, Indonesia

L. M. Iqbal Sani · H. Madduppa
Oceanogen Environmental Biotechnology Laboklinikum, Jl Bambu Ori III no 46 Cilendek Timur, Bogor Barat, Kota Bogor 16112, Indonesia

A. T. Humphries
Department of Fisheries, Animal and Veterinary Sciences, University of Rhode Island, 9 East Alumni Avenue, Kingston, RI 02881, USA

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Introduction

The Coral Triangle is a marine biodiversity hotspot, originally defined based on scleractinian coral diversity (Veron et al. 2009, 2011). Located in the western Pacific Ocean, the Coral Triangle includes the waters of Indonesia, Malaysia, the Philippines, Papua New Guinea, Timor Leste, and Solomon Islands. At the heart of the Coral Triangle, Indonesia is rich in coral reef habitat and associated fauna, including reef-associated fishes (Allen and Werner 2002). There have been numerous studies on coral reef ecosystems in this region (Ardiwijaya et al. 2008; Putra et al. 2018; Setiawan et al. 2013, 2016; Sahetapy et al. 2018; Carvalho et al. 2021). These include studies aiming to determine relationships within coral reef ecosystems, for example, between substrate variables and associated marine organisms, such as the connectivity between substrate topology (e.g., spaces formed) and fish assemblages (Sale and Dybdahl 1975; Luckhurst and Luckhurst 1978; Bell and Galzin 1984; García-Charton and Pérez-Ruzafa 2001; García-Charton et al. 2004; Hackradt et al. 2011; Dustan et al. 2013). The complexity in the form of corals, often described as the roughness or rugosity of coral reefs, arises due to a combination of physical and biological factors (Montaggioni 2005). The biological factors include the formation of limestone due to the skeletal growth of the coral animals (Veron 1995; Tomascik et al. 1997), while physical factors can include tsunamis, wave energy, and currents (Nakamura and Nakamori 2007). The processes involved in forming coral reef substrate result in various levels of roughness, including differences in reef surface elevation and the availability of spaces or niches in the reef habitat (Harborne et al. 2012).

The habitat complexity resulting from the availability of interstitial spaces and the diversity of substrates affect the species richness and abundance of biotic communities living in coral reefs (Darling et al. 2017; Richardson et al. 2017), with key factors including coral cover (Komyakova et al. 2013), coral species richness (Messmer et al. 2011), and coral lifeforms (Madduppa et al. 2012). The characteristics of the fish assemblages that inhabit these ecosystems are intrinsically linked to the availability of suitable substrate as habitat (Friedlander et al. 2003; Madduppa et al. 2013, 2014). Species have diverse patterns of behaviour and adaptations which determine their needs in terms of shelter and foraging opportunities (Syms and Jones 2000; Munday 2004).

Many studies have reported a positive relationship between coral cover and reef fish abundance and/or diversity (Chabanet et al. 1997; Setiawan et al. 2013, 2016). Others have shown that this is only true to a certain point or threshold where additional coral cover does not support more fishes (Gorospe et al. 2018). In addition, the extent of coral cover also plays a role in determining the abundance of specific functional groups of fishes living in reef habitats, such as herbivores (Choat et al. 2002) and corallivores (Madduppa et al. 2014). Conversely, the loss of coral cover can have a negative effect on the presence and abundance of reef fish (Yap and Gomez 1985; Jones et al. 2004; Munday 2004). The factors thought to affect the presence of reef-associated fishes include substrate roughness or rugosity, as a loss or decline in rugosity will lead to a reduction in the availability of living spaces (Kuffner et al. 2007; Dunn and Halpin 2009). A variety of niches in coral reef habitats increase the availability of protective space and reduces competition (Enochs et al. 2011). The presence of three-dimensional spaces, such as vertical and horizontal gaps, nooks and crannies, or even large crevasses or caves will encourage reef fish to settle (Chabanet et al. 1997).

Even though rugosity is an important indicator of coral reef health, it is rarely assessed in Indonesia, even when carrying out reef fish surveys. The reefs and associated fish communities around Lombok Island little scientific information available even though there are three marine protected areas (Gita Nada, Gili Sula, and Gili Matra). However, these areas are notable for the diverse forms of relief or growth and formation of coral reefs (i.e., rugosity, habitat typology, and hard coral coverage). This diversity of form may be due to a combination of natural processes (e.g., waves, currents, and earthquakes) and human activities (e.g., the use of coral mining as building materials) (Caras and Pasternak 2009), as well as the use of explosives during fishing (Nurdin and Grydehøj 2014). These factors have a considerable influence on rugosity in the three conservation areas with potential cascading impacts to fish and fisheries (Humphries et al. 2019). Natural factors with a significant impact on the rugosity also include abrasion, for example, in Gili Matra abrasion caused by waves has resulted in sediment transport affecting the coral reef habitat (Pradjoko et al. 2015). Conversely, reefs in Gili Sula and Gita Nada are mostly affected by human activities (Bachtiar 2004). This study aimed to determine the relationship between variations in the rugosity of coral reef habitat and the characteristics of the reef fish communities, including trophic guilds, in the three marine reserves around Lombok Island.

Methods

Study sites and data collection

Data were collected in July 2018. The study area comprised three marine reserves around Lombok Island, Indonesia. Gita Nada is in western Lombok, while Gili Sulat is in the eastern area and Gili Matra is in the northern area. The Gita Nada marine protected area is where destructive fishing gears including explosives were often used in the past, with additional habitat damage due to human activities associated with a large port and tourism. There are three small islands in the Gili Sulat marine protected area: Gili Sulat, Gili Lawang, and Gili Kondo. Around Gili Sulat the coral reef habitat has been damaged by anchors for pearl oyster farming, bomb fishing, and tourism activities (Bachtiar 2000; Bachtiar 2004). The Gili Matra marine protected area comprises three islands: Gili Meno, Gili Air, and Gili Trawangan. Located in the northern part of the Lombok Strait, this area is better known as a tourism destination compared to the other two reserves. Manta tow was used to select 6 representative sampling stations in each marine reserve area (Fig. 1), giving a total of 18 sampling stations. At each sampling station, data were collected from six sites with three 50-m line transects (replicates) at each site.

Rugosity assessment

Data on coral reef rugosity were collected along 50-m line transects with an estimated sweep distance of 10 m (5 m to the left and 5 m to the right of the line) using an underwater visual method following Wilson et al. (2007). The observers used SCUBA equipment. The transect lines were laid following the reef contour at a depth of approximately 6–10 m, with 5 m between transects. Each 50-m line transect was divided into five 10-m segments, with rugosity observed from 5 m on the left to 5 m on the right of the transect, giving five segments per transect (15 segments per site). Coral substrate rugosity categories were modified from Polunin and Roberts (1993) and Wilson et al. (2007), where both use a 6-point scale as a measure of reef complexity (Suppl. 1). Their scale for the visual assessment of reef rugosity is K0 = no vertical relief or relief less than 10 cm; K1 = low and sparse relief or low and sparse vertical relief less than 30 cm; K2 = low but widespread relief or vertical relief, 31 to 50 cm; K3 = moderately complex or vertical relief 71 to 100 cm, with several holes; K4 = very complex with numerous fissures and caves or vertical relief 71 to 100 cm with several holes; and K5 = exceptionally complex vertical relief with numerous caves and overhangs. Based on the similarity between the rugosity characteristics of each transect, correspondence analysis (CA) showed the number of rugosity categories could be reduced to three types (flat, low, and high) through combining categories (Fig. 2).

Reef fish assemblages

Data were collected using a visual census method (English et al. 1997) using the same 50-m line transect laid for the coral reef rugosity data collection with an estimated sweep distance of 5 m (2.5 m to the left and 2.5 m to the right of the line). The observers counted and recorded the number of fish belonging to each individual species present while swimming slowly along the transect line.

Data analysis

The reef fish were analysed and grouped by family and trophic guild (Froese and Pauly 2010; Graham and Nash 2012; Madduppa et al. 2014). The five trophic guilds (carnivores, herbivores, corallivores, omnivores, planktivores) correspond to those used in FishBase, the global database of fishes (Froese and Pauly 2017). The CA was used to evaluate the relationships between rugosity and other parameters observed along the transect lines as well as to reduce the number of rugosity categories from six to three: flat, low, and high, following Greenacre (2015). The CA was carried out using the FactoMineR package (Husson et al. 2016) implemented in R version 3.6.1 (R Core Team 2013). Analysis of variance (ANOVA) was used to evaluate the relationships between rugosity and reef fish community characteristics including differences in the abundance of fish based on trophic guild and habitat rugosity (Chambers et al. 1990).

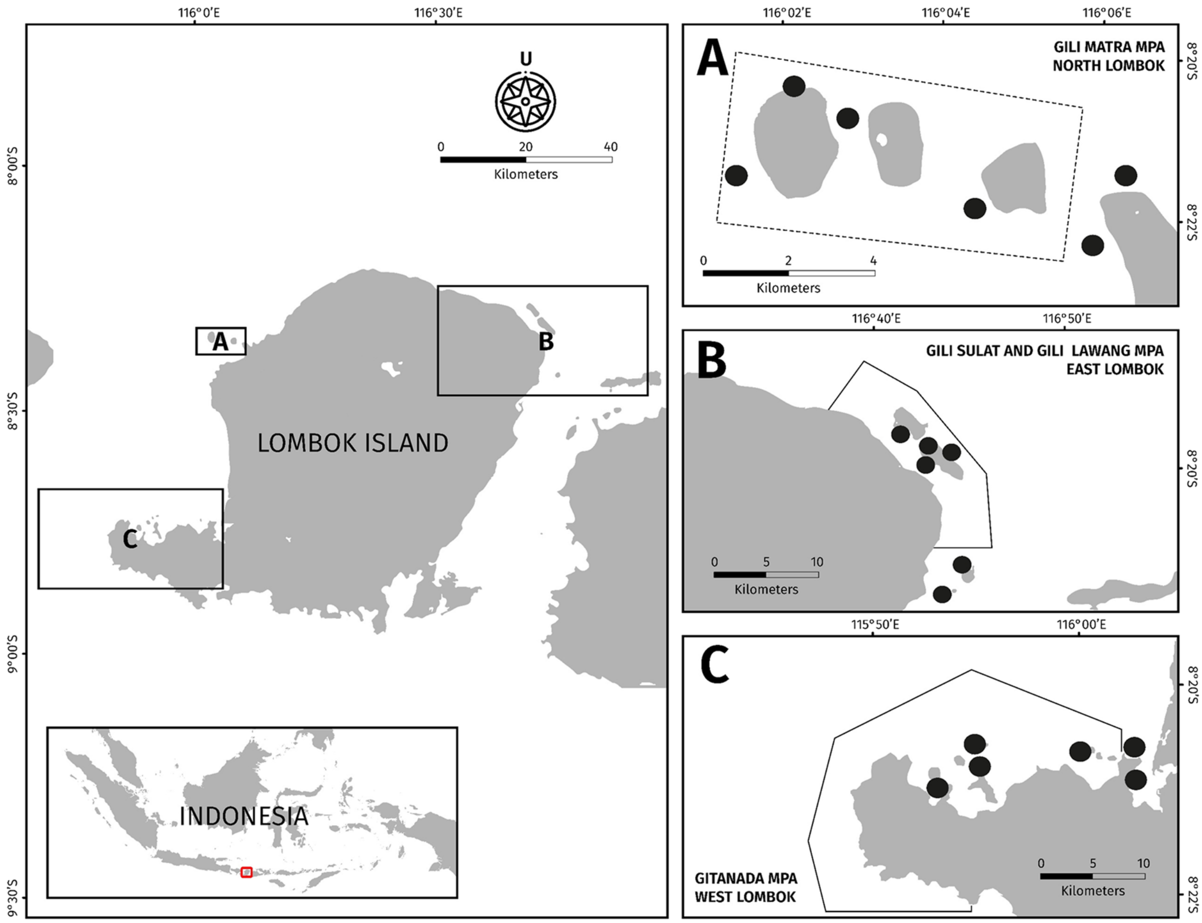

Fig. 1 Map of coral reef research stations in three marine protected areas (marine tourism reserves): (**a**) Gili Matra, (**b**) Gili Sulat Lawang, and (**c**) Gita Nada. There were 6 sampling stations in each reserve with 3 transects/station

Multivariate analysis was used to evaluate the interaction between reef fish community composition and habitat rugosity, based on the Bray–Curtis species similarity calculation implemented in the R Vegan package (Oksanen et al. 2013). The non-metric multidimensional scaling (nMDS) was applied to determine whether the fish assemblage composition differed between levels of habitat complexity (Kruskal 1964). Analysis of similarity (ANOSIM) was applied to determine the total abundance (all species) for each rugosity category using 999 permutations (Clarke 1993; Warton et al. 2012), while the similarity percentage (SIMPER) was used to determine the reef fish species making the greatest contribution to differences in the fish assemblages between the rugosity categories (Clarke 1993).

Ethics and data availability statement

Scientific observation or data collection in the Lombok Marine Reserves was conducted according to the provisions of dive protocols appropriate to that area issued by the Ministry of Marine Affairs and Fisheries of the Republic of Indonesia. The data supporting the findings of this study are publicly available (http://ipb.link/rugositylombok).

Results

Rugosity of Lombok Island coral reefs

The high rugosity or complex coral reef habitat group (K4 and K5 categories) comprised transects in Gili

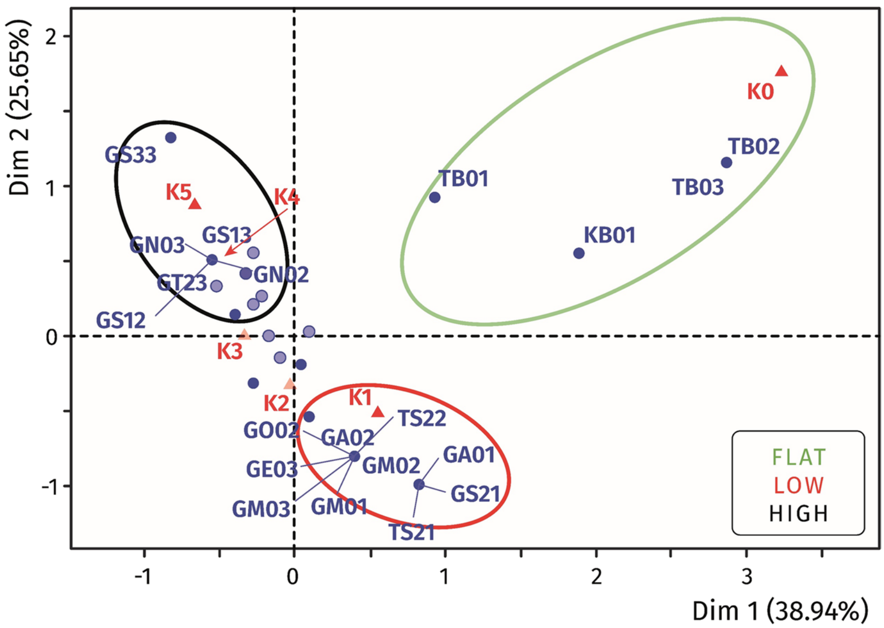

Fig. 2 Biplot of the first two axes of the correspondence analysis (CA) showing the relationship between the rugosity categories and the coral reef habitat rugosity along the transects observed at each station within the three marine reserves in Lombok

Sula (GS13), Gili Trawangan (GT23), Gili Nanggu (GN03), Gili Sula (GS12), Gili Nanggu (GN02), and Gili Nanggu (GS33). Transects in the low rugosity coral reef habitat group (category K1) were found at Tanjung Sireu (TS22), Gili Air (GA01), Gili Sula (GS21), Tanjung Sireu (TS21), Gili Meno (GM02), Gili Meno (GM01), Gili Meno (GM03), Gili Gede (GE03), Gili Golek (GO02), and Gili Air (GA02). The flat rugosity coral reef habitat group (category K0) was found at Tanjung Bunutan (TB01, TB02, TB03,) and Bunutan (KB01), as shown in Fig. 2.

Reef fish community composition and trophic guilds

In this study, 5862 reef fish were identified, representing 235 species from 35 families. Approximately 68 species were found in flat rugosity habitats, 143 species in low rugosity habitats, and 142 species in high rugosity habitats. Table 1 shows the reef fish community compositions depending on trophic guilds, family, and rugosity type (flat, low, and high). Herbivorous reef fish of the Acanthuridae family were found in high numbers in flat, low, and high rugosity environments. Labridae was the most abundant carnivore family in flat and low rugosity environments, whereas Apogonidae was the most abundant in high rugosity habitat. In this study, the corallivore guild consisted of only two families (Chaetodontidae and Labridae), with Chaetodontidae being more abundant than Labridae in all habitats, irrespective of the coral reef rugosity. Members of the Pomacentridae family were the most common omnivores across all rugosity categories. Planktivores belonging to the Pomacentridae were frequently observed in both flat and high rugosity habitats, while Labridae was the most abundant planktivore family in low rugosity habitats.

Correlation between reef fish communities and rugosity

The number of reef fish observed in each habitat varied from 33 to 825 individuals based on the rugosity type (flat, low, and high), while the species richness ranged from 5 to 65 species. Reef fish abundance and species richness were highest in complex (high rugosity) habitat, followed by the low and flat rugosity habitat (Fig. 3). Correlation between rugosity and reef fish species richness was significant ($p < 0.01$) across all rugosity types (flat, low, and high). All rugosity types and reef fish abundance were also significantly correlated ($p < 0.001$) in this study.

The fish guild most observed in all habitat types was the planktivores (18–651 fish/site) followed by omnivores (1–172 fish/site), carnivores (4–153 fish/site), herbivores (3–145 fish/site), and corallivores

Table 1 Mean reef fish community abundance (fish/250m^2) and composition (%) for three tourism reserves around Lombok Island based on trophic level and family by rugosity category (100m^2 per category)

Trophic guild	Fish family	Rugosity category					
		Flat		Low		High	
		abundance	%	abundance	%	abundance	%
Herbivores	Acanthuridae	16	3.77	312	73.58	96	22.64
	Pomacentridae	5	3.50	46	32.17	92	64.34
	Scaridae	5	5.00	77	77.00	18	18.00
	Pomacanthidae	2	2.50	34	42.50	44	55.00
	Siganidae			11	57.89	8	42.11
Carnivores	Labridae	13	6.31	134	65.05	59	28.64
	Apogonidae	8	5.52	8	5.52	129	88.97
	Balistidae	1	1.72	49	84.48	8	13.79
	Mullidae	1	1.89	50	94.34	2	3.77
	Pomacentridae			9	20.00	36	80.00
Corallivores	Chaetodontidae	9	6.92	69	53.08	52	40.00
	Labridae			1	4.76	20	95.24
Omnivores	Pomacentridae	78	6.23	599	47.81	576	45.97
	Zanclidae	4	9.09	20	45.45	20	45.45
	Pomacanthidae	1	4.76	9	42.86	11	52.38
	Monacanthidae			12	60.00	8	40.00
	Tetraodontidae	3	16.67	12	66.67	3	16.67
Planktivores	Labridae	29	1.94	719	48.16	745	49.90
	Pomacentridae	60	5.93	232	22.92	720	71.15
	Serranidae			2	1.67	118	98.33
	Caesionidae	9	9.00		0.00	91	91.00
	Apogonidae	57	80.28	7	9.86	7	9.86

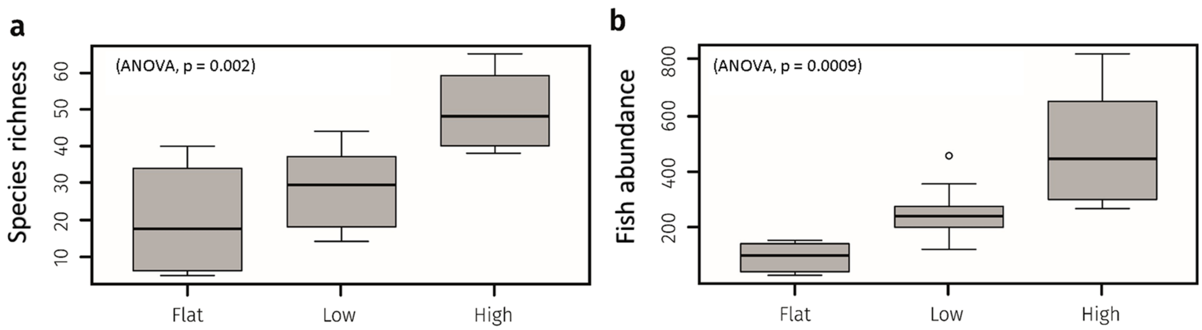

Fig. 3 Box plots showing reef fish species richness (**a**) and abundance (fish/250m^2) (**b**) of reef fish species differed significantly ($p<0.05$) between coral reefs around Lombok Island in three rugosity categories

(2–18 fish/site). The abundance of planktivores ($p=0.02$), omnivores ($p=0.02$), and corallivores ($p=0.04$) differed significantly between habitat rugosity types; conversely, the abundance of herbivores ($p=0.19$) and carnivores ($p=0.54$) did not differ significantly between the three rugosity types (Fig. 4). However, herbivores were more abundant in habitat with low rugosity than in habitat with high or flat rugosity, while carnivores were more commonly found in habitat with high rugosity compared to low or flat rugosity type habitat.

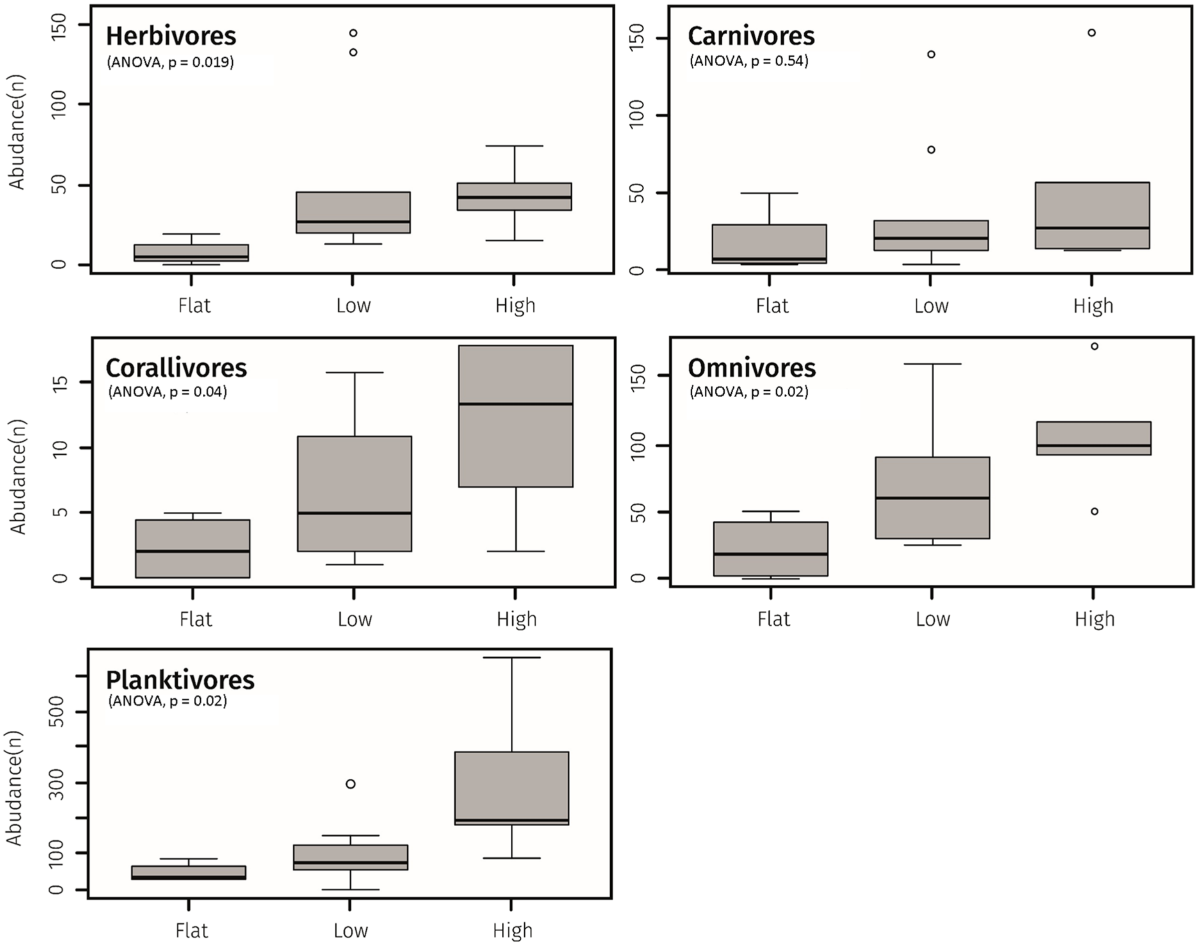

Fig. 4 Box plots showing reef fish abundance (fish/250m^2) by trophic guild on coral reefs around Lombok Island in three rugosity categories

The ANOSIM analysis revealed a significant difference in reef fish community composition among habitats belonging to the three rugosity types (Table 2). There were significant differences between reef fish communities in high and flat rugosity habitat ($p < 0.01$) as well as low and high rugosity habitat ($p = 0.012$). The difference between reef fish communities in low and flat rugosity habitat was not significant ($p = 0.057$). Figure 5 shows the grouping of reef fish communities based on rugosity type.

Species that contributed significantly to differences between fish communities in low and high rugosity habitat included *Cirrhilabrus cyanopleura*, *Chromis ternatensis*, *C. solorensis*, and *Pomacentrus brachialis* (Table 3). Coral reef fish communities in habitat with low or flat rugosity were mostly dominated by the following species: *C. solorensis*, *Pomacentrus coelestis*, *C. cyanopleura*, and *Archamia macroptera*. Meanwhile, *C. cyanopleura*, *C. ternatensis*, *P. brachialis*, and *P.*

Table 2 Pairwise ANOSIM comparing total reef fish abundance between rugosity categories

Relative abundance			
Factor	Test pairs	R	*P*
Rugosity		0.3354	0.003
	Low vs high	0.2911	0.012
	Low vs flat	0.3623	0.057
	High vs flat	0.5159	0.007

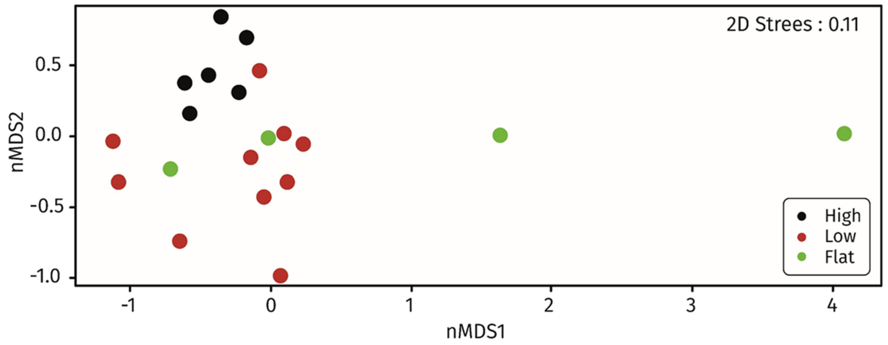

Fig. 5 nMDS plot of fish communities at sites around Lombok Island in coral reef habitat with three rugosity categories (Flat, Low, and High) based on 235 fish species

Table 3 The five reef fish species making the largest contribution to pairwise between-category differences in SIMPER analysis of fish communities on reefs with rugosity in Flat, Low, and High categories

Species	Contribution	Average abundance	
Low vs high (88.05%)	%	Low	High
Cirrhilabrus cyanopleura	12.77	11.7	120.5
Chromis ternatensis	6.59	3.1	58.5
Cirrhilabrus solorensis	6.06	43.8	0
Pomacentrus brachialis	3.39	1.9	21.7
Pomacentrus auriventris	2.78	8.3	19
Low vs Flat (91.15%)	%	Low	Flat
Cirrhilabrus solorensis	12.16	43.8	7.25
Pomacentrus coelestis	5.18	18.3	0
Cirrhilabrus cyanopleura	3.94	11.7	0
Archamia macroptera	3.61	0.0	10.25
Dascyllus carneus	3.12	6.2	7.75
High vs Flat (93.23%)	%	High	Flat
Cirrhilabrus cyanopleura	15.57	120.5	0
Chromis ternatensis	7.94	58.5	0
Pomacentrus brachialis	4.71	21.67	1.3
Pomacentrus auriventris	3.67	19	5.8
Pseudanthias squamipinnis	2.75	13	0

auriventris made variable contributions to fish communities in habitats with high and flat rugosity.

Discussion

Our study shows that habitat rugosity in coral reefs of Lombok Indonesia are a significant predictor of fish community composition and abundance; structural complexity is positivity associated with more diverse fish assemblages and supports more individuals for groups such as corallivores. Rugosity measures grouped into three distinct categories: high, low, and flat. The 235 unique species of reef fish identified during this study, however, was relatively low relative to several other areas in Central and Eastern Indonesia such as Bunaken National Park (365), northern Minahasa (267) (Setiawan et al. 2013, 2016), and Raja Ampat (1320) (Allen and Erdmann 2009). Environmental factors that contribute to coral composition and resulting habitat complexity are likely contributing to these differences in fish communities across Indonesia, but our study confirmed that even within the marine reserves of Lombok, there is a gradient of fish community assemblages driven at least in part by changes in rugosity. Wrasses and damselfishes contributed the most to between-category differences in fish assemblages among the habitat rugosity categories. Planktivores were also closely associated with high complexity reefs despite having life histories and feeding strategies less dependent on coral than other functional groups.

Habitat complexity of the reefs around Lombok was significantly and positively correlated with reef fish abundance and species richness. The results indicate that rugosity type could be used as a predictor or indicator of the abundance and species richness of reef fish communities. Similar results have been reported from several other regions including the Seychelles, Maldives, Chagos Archipelago, and Australia's Great Barrier Reef (Wilson et al. 2006; Darling et al. 2017). Generally, damage to the reef structure negatively affects the reef fish communities (Chabanet et al. 1997; Munday 2004; Harris et al. 2018), as most reef fish have specific food and shelter requirements and are highly dependent on (often specific) coral reef habitats (Angel and Ojeda 2001; Rilov et al. 2007; Darling et al. 2017). Therefore, the availability of space with diverse habitats can play a vital role in mediating predator–prey relationships and providing nursery habitat. We did not measure or tease out these mechanisms with our study, but that would be a good next step for the reefs of Indonesia in order to determine what is most important in determining how fishes use the coral reefs.

Differences in abundance patterns of fishes among reef structural complexity were evident in our study. For example, the corallivore, omnivore, and planktivore guilds were significantly greater in abundance in complex habitats. For corallivores, this is likely due to their dependence on coral for food; there are over 150 species globally that feed directly on coral tissue, either as obligate or facultative feeders (Cole et al. 2008). These species have a particularly tough time recovering from coral loss and/or low habitat complexity caused by anthropogenic stressors (Pratchett et al. 2004). The Labridae family comprises both corallivores and planktivores. Other planktivores came from families like Pomacentridae and Caesionidae. These families have been shown to respond strongly to fishing pressure in Indonesia, such that where marine reserves are located, they are highly abundant (Campbell et al. 2020). This could be one reason why our study showed high abundances of planktivores in the marine reserves of Lombok; however, within the same reserve, habitat rugosity seemed to drive local abundances. Other functional groups like herbivore and carnivore guilds showed a weak response to rugosity type; they were unaffected by differences in habitat complexity.

The abundance of the omnivore guild was positively correlated with the complexity of coral reef habitat. This trophic guild depends on the number of nooks and crannies present in the reef to be used for shelter and foraging. The majority of these fishes are small and display territorial behaviour, in addition to their high dependence on the complexity of form of their coral reef habitat (Carassou et al. 2008; Lamb and Johnson 2010). Furthermore, most small omnivores make use of this topographical rugosity only for shelter rather than for seeking food sources (Sano et al. 1984; Wilson et al. 2007). In contrast, planktivores utilize the topographical rugosity both for shelter and in connection with seeking food, often along the reef crest where water is locally upwelled and mixing occurs with plankton-rich water. A complex coral reef habitat plays a vital role in the availability of plankton as well as mediating water currents that transport them. Also, it has been shown that planktivores forage in complex structures because zooplankton tend to become trapped in such coral reef habitats (Hobson and Chess 1978; Thresher 1983; Zamon 2003) as well as taking refuge in the numerous holes and gaps to avoid predators (Turner and Mittelbach. 1990; Osuka et al. 2018).

The lack of a significant correlation between rugosity and the abundance of carnivorous or herbivorous fishes in this study points to the existence of other factors that influence their abundance, for example, the nature of their diets. Herbivores are generally benthic grazers; therefore their presence tends to be positively correlated with the distribution and abundance of algae more so than coral (Choat et al. 2002; Russ, 2003; Green and Bellwood 2009; Burkepile and Hay 2011). The herbivores observed in this study were evenly spread across all rugosity types, indicating that these habitats are similar in terms of their ability to support benthic algae. Meanwhile, one factor that tends to strongly influence the abundance of carnivores is the presence and abundance of visible prey (Turner and Mittelbach. 1990; Turner et al. 1999; Soler et al. 2015). The results from this study indicate that predators might utilize complex structures for protection, but few of these predators fall prey themselves in areas with flat rugosity, although their presence could affect the abundance and distribution of other reef fish, especially prey species through trait-mediated indirect interactions (Werner and Peacor 2003).

Reduced rugosity in degraded reefs could lead to the development of dominant species due to a decrease in species diversity (Nagelkerken et al. 2018). However, in complex ecosystems, this does not always alter the species richness of fish groups. The availability of three-dimensional space with a variety of substrates to suit different specialised needs tends to boost the diversity and abundance of reef fish communities (Garpe and Öhman 2003; Darling et al. 2017). According to this study, the availability of specific types of niches in reef structures with specific rugosity types can lead to habitat specialization, as well as impacting fish community structure and contributing to reef fish diversity. The findings in this study indicate that biomonitoring of habitat complexity or rugosity can be used as a complementary tool to estimate the abundance of reef-associated fishes should there be the need for rapid assessment and there is low local capacity for counting fish (e.g., community-based monitoring). With respect to the coral reef rehabilitation efforts around Lombok, it is important to monitor and assess habitat complexity or rugosity as an indicator of rehabilitation success, considering the empirical relationship between rugosity and reef fish community structure.

Conclusions

This study demonstrates a close relationship between the level of habitat complexity or rugosity and the reef fish community structure. This empirical relationship is most likely related to the ability of the habitat to provide foraging, shelter, and nursery space for specific fish guilds. Reef rugosity was positively correlated with reef fish abundance and species richness. In order to meet their nutritional needs, fishes belonging to several functional groups tend to settle in or explore coral reefs in search of food. It would be interesting to compare the results of this research with similar studies in other locations, particularly within Indonesia as a major Coral Triangle country, in order to further advance efforts to understand the extreme complexity of coral reef ecosystems.

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