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BENTHIC COMMUNITY DISTRIBUTION PATTERN IN MESOPHOTIC CORAL ECOSYSTEMS IN BALI AND LOMBOK

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Abstract

The biological communities in the shallow waters of the Lombok Strait have been reported. However, studies on the mesophotic coral reef ecosystems (MCEs) in this area remain scarce. In this study, we investigated the distribution patterns of benthic communities at two observation points, Bali and Lombok in this area taking into account depth gradients. Our results showed significant differences between Bali and Lombok with respect to dominant benthic communities (F (8,57) = 0.824, P < 0.05). In Bali, "other communities" showed predominance followed by sponges and algae. However, for Lombok, the predominant community was sponges followed by hard corals and "other communities." At both locations, the distribution patterns also showed significant depth-related differences: Bali (F (3,46) = 0.21, P<0.05) and Lombok (F(4.52) = 0.58, P<0.05). Additionally, we observed that the distribution pattern of benthic communities in the MCEs may be influenced by several factors, including depth and competition for growing space. Correlations between communities, based on depth and dominance showed conflicting results. This study also highlighted the potential of the distribution patterns of benthic communities in MCEs in Bali and Lombok to function as ecosystem buffers and raises awareness regarding the importance of protecting MCEs in conserving marine biodiversity.

Keywords: *Benthic biodiversity; Benthic ecology; Lombok strait; Coral triangle*

Introduction

Mesophotic coral reef ecosystems (MCEs), which are characterized by lower levels of light penetration and are often located at depths ranging from 30 to 50m, show changes in the distribution patterns of organisms with depth [1-6]. It has also been shown that their specific depth is determined by the environmental factors that characterize each water body [7-9]. Generally, MCEs are divided into two parts, the upper and lower parts (at depths <50m and >50m, respectively), which are typically distinguished based on the types of organisms that inhabit them or the genetic characteristics of these organisms [4, 10, 11]. For example, the upper parts of MCEs exhibit a direct interaction with shallow coral reef ecosystems, which are under considerable stress that causes extensive damage [12, 13]. Thus, it has been hypothesized that MCEs serve as protective buffers for shallow coral reef ecosystems [1, 14]. However, studies on the protective role of MCEs, particularly with respect to benthic MCE populations in Indonesia, are limited, primarily owing to their considerable depth, which limits accessibility. Advances in technology, such as the development of remotely operated vehicles (ROVs) and the possibility of modifying SCUBA components, have improved the accessibility of MCEs

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[15-19]. Studies by *S.E. Kahng et al.* [20], *E.K. Baker et al*. [1], *D. Arafat et al.* [6], *M.A. Perez-Castro et al.* [21] and *R.M. Wright et al.* [22] have shown that MCEs serve both as buffer ecosystems and unique habitats for various benthic organisms, including sponges, algae and coral reefs. Additionally, *H.T. Pinheiro et al.* [23], *R.L. Pyle and J.M. Copus* [5] and *D.A. Andradi-Brown et al.* [24] reported the presence of pelagic organisms, such as fish in MCEs. These organisms can adapt their physical structures as well as their physiological processes to ensure survival in this environment and oftentimes, this adaptation can result in genetic specialization or the emergence of endemic organisms [25-27]. According to *R.L. Pyle and J.M. Copus* [5], MCEs account for almost 80% of the total potential habitat of coral reefs worldwide. However, research on these MCEs [5, 14], particularly in the Coral Triangle region [13, 28], remains limited. Notably, there are no previous studies on MCEs in Indonesia, which is located in the Coral Triangle. Existing studies in this area have been primarily focused on shallow-water coral reef ecosystems [29-31]. Meanwhile, an accurate assessment of the geographical distribution of species in MCEs, both in terms of their regional distribution and depth, is crucial for understanding the mechanisms underlying community structure in these areas. Further, information in this regard may enhance conservation efforts and management strategies for these ecosystems.

In 2018, J.J. *Bell et al.* [18] initiated MCE research in Indonesia, initially in the Wakatobi Marine National Park. Specifically, they focused on benthic communities at depths in the range of 0–80 meters using ROV technology. Further, *D.A. Andradi-Brown et al.* [24] conducted follow-up research in the Raja Ampat MCE, observing coral reef fish communities at depths between 2 and 85m using a baited remote underwater video (BRUV) system. In Bali, *A. Chappuis et al*. [19] discovered *Pristigenys meyeri* at a depth of 96–110m. Further, based on a study on Lombok waters, *D. Arafat et al.* [6] provided insights regarding sponges at depths of 10–50m. However, no large-scale study on MCEs in the Lombok Strait has been reported so far. Thus, in-depth studies are required to bridge this knowledge gap in Indonesia, which is part of the Coral Triangle [18].

Shallow coral reef ecosystems continue to be the focus of research in the Lombok Strait [31-33], while data regarding the MCEs in this area, particularly the distribution of benthic species, including fish communities, remains limited [34, 35]. MCEs function as buffers that support life in shallow coral reef ecosystems and serve as an important habitat for benthic communities and fishes [13, 36]. Even though they are located in deep-water areas, they are still vulnerable to changes, particularly climate and anthropogenic changes [37, 38]. Thus, studying them is of great significance from a conservation perspective. In this study, we aimed to analyze the distribution of benthic communities in two observation locations, Bali and Lombok, in Indonesia, taking into account their distribution with respect to depth gradients. The results of this study may provide valuable insights regarding MCEs in one part of the Coral Triangle, through which the Indonesian Throughflow (ITF) passes and may also promote marine biodiversity conservation efforts.

Materials and methods

We conducted this study in the waters of the Lombok Strait, particularly at two locations: Amed (Bali) and Selamat (Lombok) (Fig. 1). Specifically, we performed MCE observations at five depths, i.e., 10, 20, 30, 40 and 50m and thus collected benthic diversity data. The data was collected using the Underwater Photo Transect (UPT) method, which involves SCUBA diving to each depth and using GoPro Hero 3 and Hero 7 cameras to photograph 1×1m transects 10 times.

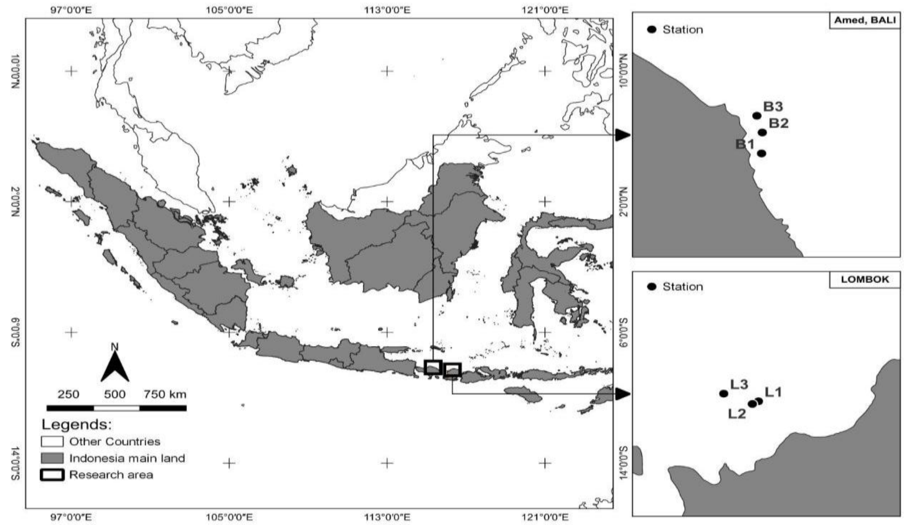

Fig. 1. Map showing the locations of observation sites. B and L represent Bali and Lombok, respectively. At each location, the observations were made at three points

The Coral Point Count method with Excel extension (CPCe) offers the possibility to use field data, such as transect photos, to obtain data on the percentage cover of life forms at each point for a given depth [33]. The life form categories used in this study included hard corals (HC), soft corals (SC), sponges and algae. We included another category, "other communities," for tubeworms, mollusks, ascidians etc.

Based on *J.J. Bell et al.* [18], we used permutational multivariate analysis of variance (PERMANOVA) to examine differences in benthic communities with respect to the depth and location of the observation site. We also employed permutation tests of multivariate dispersion (PERMDISP) to determine the homogeneity or heterogeneity of the collected observation data [34]. PERMANOVA and PERMDISP complemented each other. PERMANOVA revealed the variability in the compositional data per depth, whereas PERMDISP revealed the variability in the compositional data within each depth. The analysis of the graphic visualization of percent coverage at each depth was performed using the vegan package in R. Further, we performed non-metric multidimensional scaling (NMDS) plot analysis to visualize benthic community composition based on depth. We also conducted Pearson correlation analysis to examine the correlations between benthic communities at each observation location using two comparison factors: depth and dominant benthic community. PERMANOVA and PERMDISP were performed using the vegan package in R, NMDS plot analysis was performed using the ggplot package in R and Pearson correlation analysis was performed using the ggpubr package in R [35].

Results and discussion

Despite the influence of the Lombok Strait on Bali and Lombok, the benthic communities in the MCEs at these two locations showed significantly different distribution and dominance patterns. Specifically, PERMANOVA between Bali and Lombok showed significant differences in community composition ($F_{(8,57)} = 0.824$, $P < 0.05$). In Bali, "other communities" showed predominance (40.24 %), followed by sponges (27.53 %) and algae (21.55 %) (Fig. 2). Conversely, sponges showed predominance in Lombok (35.83%), followed by HC (21.06%) and "other communities" (18.29%), as shown in figure 3.

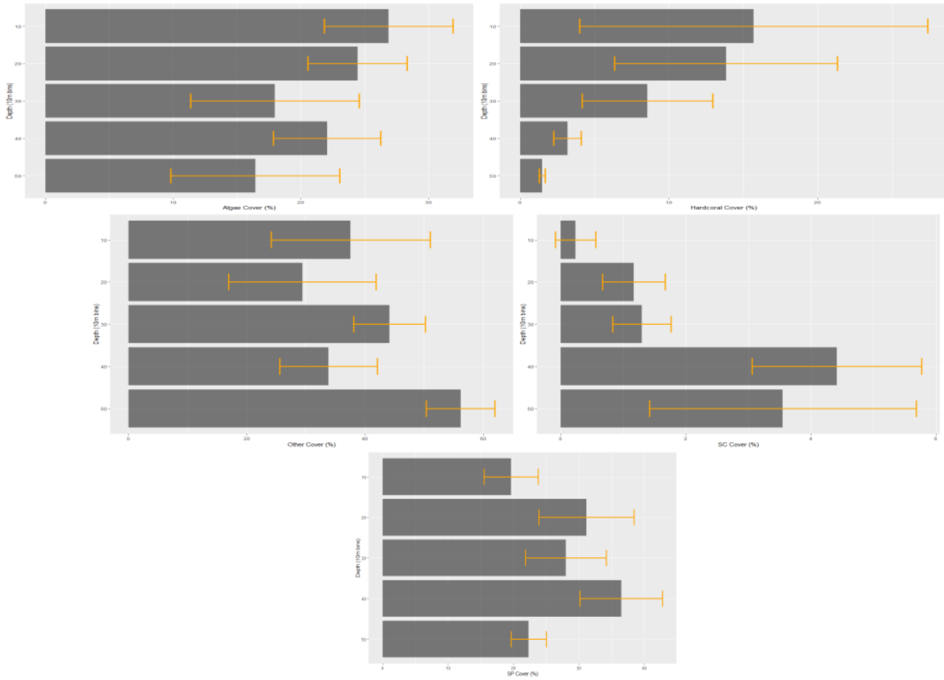

Fig. 2. Mean community abundance estimates as a function of depth at Bali.
The values presented were averaged over a depth of 10m

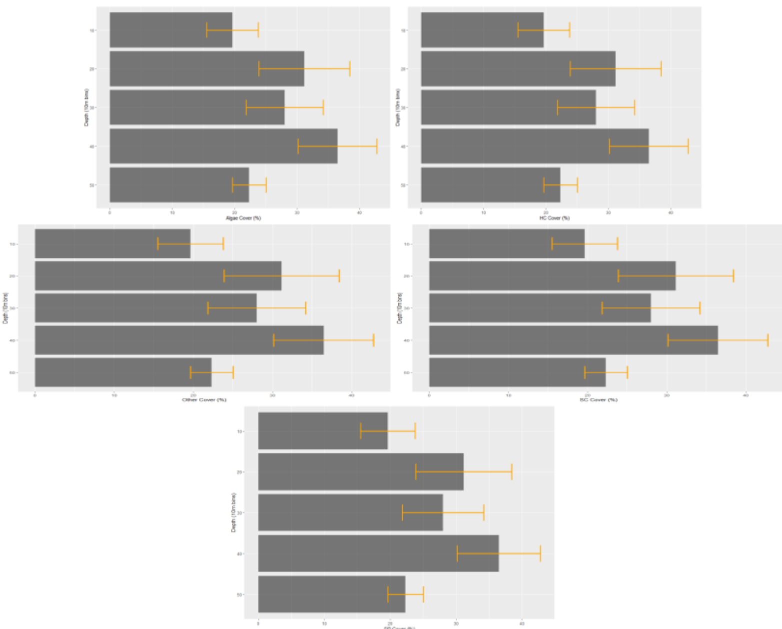

Fig. 3. Mean community abundance as a function of depth in Lombok.
The values presented were averaged over a depth of 10m

These results are similar to those reported by *M. Wakeford et al.* [37] and *V. Micaroni et al.* [9], but different from those reported by *J.J. Bell et al*. [18], indicating that the community composition at the Wakatobi Marine National Park, where *J.J. Bell et al.* [18] conducted their study, does not change significantly between observation points. NMDS also showed significant differences with respect to the location of observation sites and depth (Fig. 4A and B). The stress values for Bali and Lombok were 0.069 and 0.067, respectively, representing excellent goodness-of-fit for the 2D cross-sectional results [36]. Further, the overall test for homogeneity of distribution via PERMDISP showed no significant differences between community composition and depths in Bali (F = 0.44, p = 0.8) and Lombok (F = 0.44, p = 0.8) [34]. In other words, only the influence of location was significant (Fig. 5A and B). In Bali, “other communities” peaked at a depth of 50 m, while sponges and algae peaked at depths of 40 and 10m, respectively (Fig. 2). Further, *Crinoids* showed predominance among “other communities” (40%), followed by *Hydrozoa* (30%) and *Ascidians* (28%). In Lombok, sponges were identified as the dominant community at a depth of 50m, followed by HC at a depth of 30m and “other communities” at a depth of 10m (Fig. 3). At Lombok, Crinoids were also identified as the dominant species among “other communities” (59%), followed by *Ascidians* (30%).

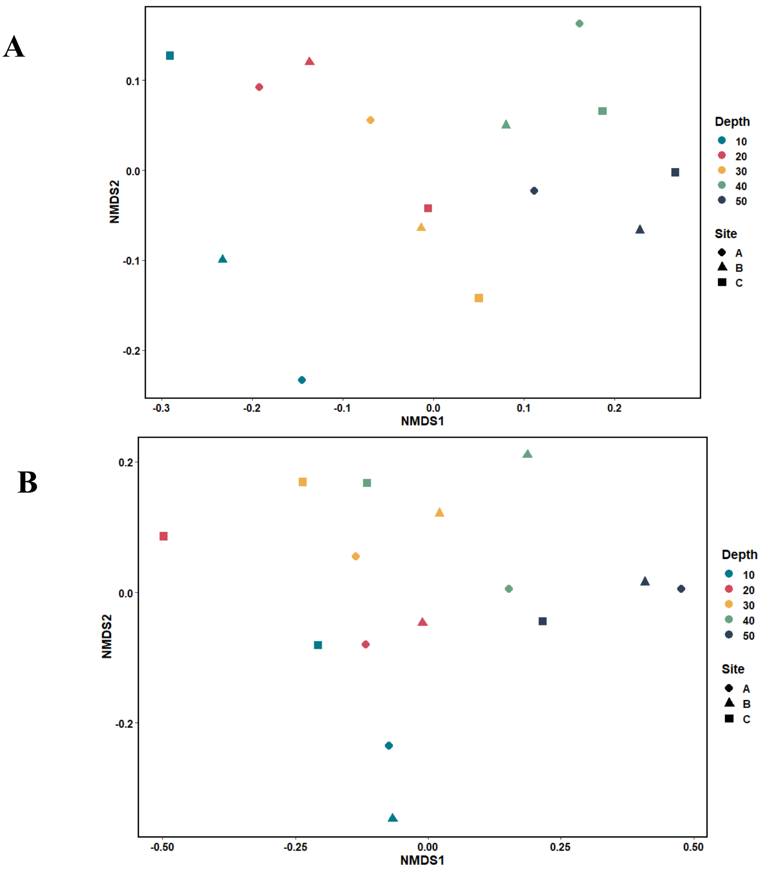

Fig. 4. Nonmetric multidimensional scaling (nMDS) of benthic communities at (A) Bali and (B) Lombok

PERMANOVA also showed depth-dependent benthic community composition differences in Bali (F(3,46) = 0.21, P<0.05) and Lombok (F(4.52) = 0.58, P<0.05). These findings support those reported by *J.J. Bell et al.* [32], *R.F. Semmler et al.* [38], *N. Englebert et al.* [39], *V. Micaroni et al.* [9] and *M.A. Pérez-Castro et al.* [21]. The composition of benthic communities is influenced by various factors, including geomorphology, temperature and water clarity [4, 40-42]. Light intensity is also an important determinant of the vertical distribution of communities in MCEs [42-44].

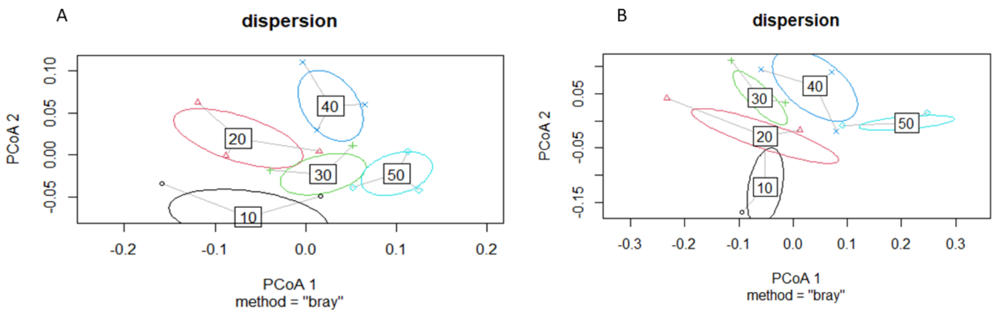

Fig. 5. PERMDISP plot showing the heterogeneity of dispersions and non-significant depth-dependent community differences in (A) Bali and (B) Lombok

MCEs in different areas differ in terms of geomorphology, implying that community geomorphology may directly affect the type of substrate as well as the function of the benthic community in terms of location and depth [41]. Geomorphological changes, which influence slope shape in benthic areas, may also cause variability in the composition of the community inhabiting a benthic area [39, 41]. The slope at each location also influences the optical effects in the water column [20, 41]. The percentage of radiation entering aquatic ecosystems, known as the optical effect, can be categorized as follows: 10% (10–20m), 1% (30–40m) and 0.1% (>60m) [21, 45]. This optical effect is a crucial factor that determines the growth of benthic communities in MCEs. According to *J.J. Baker et al.* [1], *J.H. Laverick et al.* [42] and *D. Wagner et al.* [26], the degree to which light penetrates an area affects the variability of benthic communities. Differences in water clarity level may also explain the differences in the distribution of benthic communities in MCEs [42, 46, 47]. The clarity of a body of water is also affected by its organic particle content, e.g., at high concentrations, organic particles can absorb light in the water body, hence influencing the degree of light penetration [39]. According to *M. Pichon* [48] and *M.A. Pérez-Rosales et al.* [45], if the water body is clear, the degree of light penetration at depths >40m can reach 1%. Therefore, under suitable geomorphology and water clarity conditions, surface light radiation can reach deeper water depths. Another factor that influences vertical benthic community composition is temperature. Reportedly, temperature plays a crucial role in community adaptation given that it regulates metabolic activity in organisms [11, 49, 50]. In general, temperature decreases with increasing water depth, similar to light penetration and has a direct impact on coral reef communities, which produce oxygen. As depth increases, decreasing temperatures become a limiting factor for coral reef community growth [51].

Reportedly, several of the aforementioned factors influence the complexity of benthic habitats as depth increases. It has also been shown that habitat complexity affects the abundance of associated communities. Generally, as depth increases, communities, including macroalgal and sponge communities (especially globular ones), as well as several other community groups, such as ascidians and bryozoans and several HC groups, show increases in relative abundance [9, 52-54]. However, at our two observation locations, community dominance varied with depth as well as with the location of the observation site. Benthic communities in Bali were dominated by “other communities,” which were mostly distributed at depths of 50m, followed by sponges, which were primarily distributed at depths of 40m. The benthic community distribution pattern in Bali (Fig. 6) was similar to that in Lough Hyne MCEs in Ireland [9]. Notably, macroalgae, sponges and “other communities,” such as ascidians, comprise the benthic community in Lough Hyne. For Lombok (Fig. 7), sponges were primarily distributed at a depth of 50m, while “other communities” were primarily distributed at a depth of 10m. Interestingly, HC in the benthic communities in Lombok were primarily distributed at a depth of 30m. This observation differs from that of *J.J. Bell et al.* [18], who did not observe HC in Wakatobi Marine National Park. The community distribution pattern at Lombok was similar to those of the benthic communities in the Egmont Atoll (Chago Archipelago) and the Southern Great Barrier Reef (Australia), which are both characterized by HC, sponges and macroalgae as the dominant communities [22, 43].

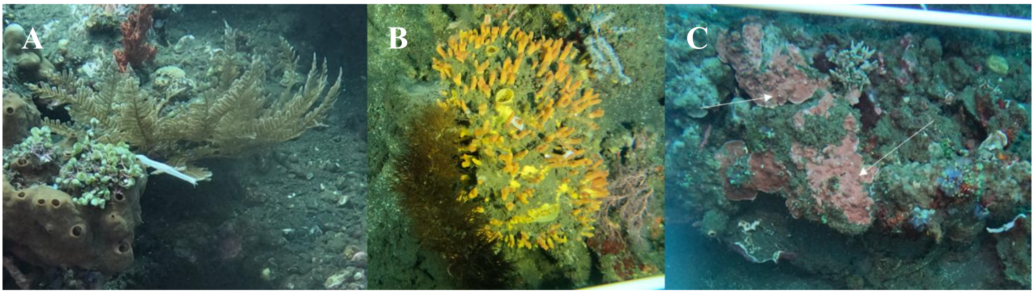

Fig. 6. Benthic communities in Bali. (A) Crinoids (other communities), (B) Sponges and (C) Encrusting red algae

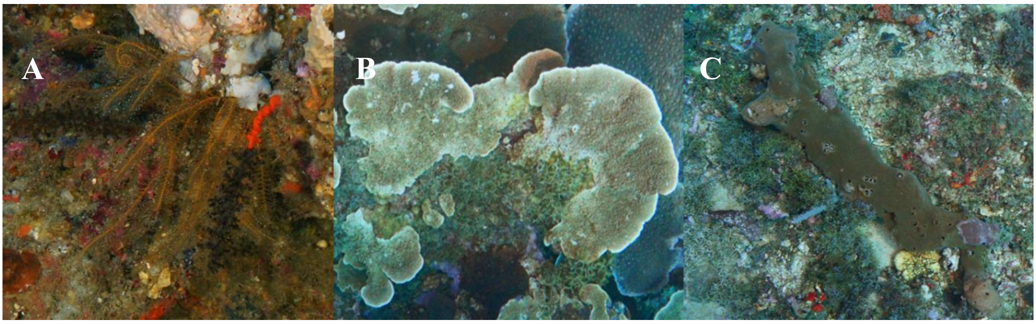

Fig. 7. Benthic communities in Lombok. (A) Crinoid (other communities), (B) Hard corals and (C) Sponges

The results of previous studies by *M.P. Lesser et al.* [41], *M. Slattery and M.P. Lesser* [55], *B. Harris et al.* [53] and *C. Diaz et al.* [43] support the hypothesis that the composition of sponges increases with increasing water depth, even up to a depth of 150m [56]. Sponges are resistant to environmental changes and high-stress levels [32]. In this study, "other communities" had high relative abundances in Bali and Lombok. Most of the constituents of "other communities" in Bali were distributed at a depth of 50m, whereas in Lombok, they were distributed at a depth of 10m. Interestingly, this study revealed that "other communities" and sponges in Bali overlapped at depths of 20 and 40m, leading to a turnover in the sponge community at deeper depths. *V. Micaroni et al.* [9] reported similar findings, highlighting the replacement of sponges by ascidian groups between 1998 and 2018. Space availability and competition are the two main factors responsible for sponge decline [41, 57]. "Other communities," such as ascidians, have the tolerance to stress levels that may affect sponges [9, 58]. Further suitable environmental conditions promote the growth of "other communities," especially ascidians [59, 60]. In Bali, the sponges were found to have pedunculated, massive and encrusting shapes, which are more susceptible to stress than globularly shaped sponges. According to *S. Fowler and D. Laffoley* [61], *J.L. Carballo and S. Naranjo* [62], *R.B. Francini-Filho et al.* [63] and *V. Micaroni et al.* [9], sponges show relatively low growth rates.

In this study, we observed a correlation between depth and benthic community composition. As shown in Table 1, row A, depth and "other communities," as well as depth and SC, showed significantly positive correlations. For the benthic community in Lombok, we observed significantly positive correlations between depth and SC and depth and sponges (Table 1, row C). These findings indicated that as depth increased, the community composition also increased. The observational results at both research locations also showed a negative correlation between depth and benthic community composition (Tables 1, rows A and C).

Specifically, in Bali, we observed significantly negative correlations between algae and depth and between HC and depth, indicating that as depth increased, the relative abundances of these communities decreased. We also conducted a correlation analysis, comparing the dominant benthic communities with other benthic communities as shown in Table 1 (rows B and D). For Bali, we observed a significant negative correlation between "other communities" and algae and between "other communities" and HC. Additionally, we observed a significant negative correlation between sponges and algae and significant positive correlations between sponges and HC and sponges and SC.

Table 1. Results of correlation analyses between dominant benthic communities and depth in Bali and Lombok MCEs

Bali			
Factor	**Community**	**Correlation**	**P-Value**
A. Depth	Algae	-0.56	0.03*
	HC	-0.71	0.003*
	Other	0.48	0.07*
	SC	0.76	0.001*
	SP	0.2	0.47
B. Other	Algae	-0.72	0.003*
	HC	-0.7	0.004*
	SC	0.07	0.8
	SP	-0.37	0.17
Lombok			
Factor	**Community**	**Correlation**	**P-Value**
C. Depth	Algae	-0.4	0.14
	HC	-0.24	0.39
	Other	-0.69	0.004*
	SC	0.79	0.0005*
	SP	0.63	0.01*
D. SP	Algae	-0.66	0.007*
	HC	-0.55	0.04*
	Lainnya	-0.48	0.07
	SC	0.54	0.04*

Notes: SP, sponges; SC, soft corals; HC, hard corals.

At a depth of 20m, sponges in Lombok overlapped with algae and algal turnover occurred at deeper depths. The negative correlation between sponges and algae, in which they opposed each other's growth, supported this observation, consistent with the findings of Cardenas et al. [64]. However, in another study, *C.A. Cardenas et al.* [65] reported contrasting results for this location, suggesting a positive relationship between sponges and macroalgal cover. Therefore, further studies are required to clarify the relationship between these two communities, considering the fact that the latitudinal gradient can also influence both their diversity and correlation [65].

We identified "other communities" and sponges as the predominant communities in Bali and Lombok, respectively. However, in Bali, algal communities replaced HC communities at a depth of 10m, whereas in Lombok, HC communities existed in the absence of algal communities. Several factors may be responsible for this observation. During their rapid growth, algae compete for space with HC, leading to a decrease in the abundance of HC. This competition not only reduces the amount of light that penetrates the water body and is used for photosynthesis but also produces chemical components that inhibit photosynthesis [66]. Thus, algae interact with coral reefs, subjecting the coral reefs to stress or killing them indirectly [67]. Additionally, factors such as decreasing water quality, increasing nutrient content, high levels of sedimentation and coral bleaching on the surface may also lead to coral reef death, accompanied by an increase in algae abundance [68]. *J. Nuryana et al.* [69] reported that 41.5% of the bleaching events observed in Tulamben occurred in 2015, confirming the dominance of algae over HC in these waters. In contrast, Bali's HC community thrives owing to the presence of numerous herbivorous fishes around the MCEs, which effectively control the algal population [70]. Further, human activities have led to a decline in water quality, which in turn causes ocean acidification. This condition has resulted in higher water CO_2 levels, which lower water pH and hence, promote algal growth [71]. The abundance of HC in Lombok indicated that the quality of the surrounding water in this area is still optimal for coral reef growth even at a depth of 30m. However, beyond this depth, at 40m, the coral reefs are being replaced by sponges.

Conclusions

The distribution patterns of the benthic communities in the MCEs in Bali and Lombok showed different compositional structures based on geographic location and depth. The Lombok Strait separates Bali from Lombok by approximately 48km. Further, the Lombok Strait, carrying the Indonesian Throughflow (ITF), passes through these two locations, resulting in water level fluctuations. Therefore, the observed differences may be due to these water level fluctuations. Our results also indicated that the benthic communities in the MCEs in these two areas are affected differently by water depth. This difference may be due to several factors, including light, substrate and competition for space. Generally, the benthic communities in Bali and Lombok were similar to those observed for other locations; however, their compositions varied depending on the specific observation location, possibly owing to current-related factors as well as substrate types. We also reported for the first time initial data regarding the distribution pattern of the benthic communities in these two areas based on observation locations and depths. Our findings indicated that the MCEs in Bali and Lombok have the potential to function as buffer ecosystems. Regardless, further studies with a focus on the structures of the different communities that populate the MCEs, as well as genetic studies to determine their connectivity, are required. These initial data may be useful for developing and supporting water management activities.

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