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Comparative analysis of seagrass habitat structure: distinct patterns at semi-enclosed and open sites in South Sulawesi, Indonesia

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Abstract. Habitat structure in the seagrass ecosystems are crucial for coastal biodiversity and substrate stability. The purpose of this research conducted from June to December 2021 in South Sulawesi Province, Indonesia was to examine the habitat structure of seagrass beds at two sites with different levels of exposure: Puntondo (semi-enclosed bay) and Batu Kalasi (exposed). Species identification, non-metric multidimensional scaling (nMDS), Bray Curtis cluster analysis, similarity percentage (SIMPER), Particle Size Analysis (PSA), and satellite imagery were used to evaluate complexity, heterogeneity, sediment particle size, and extent. The presence of macroalgae and coral species at Batu Kalasi, likely related to substrate condition, contributed to significant differences in seagrass community composition. The nMDS and Bray Curtis cluster analyses revealed patterns of complexity, while satellite imagery revealed habitat heterogeneity. Seagrass meadow tracking showed a larger and more patchy area in Puntondo Village, measuring 164,318 m^2, while in Batu Kalasi Island, it only reached 136,901 m^2. The findings underscore the need for tailored conservation strategies for seagrass ecosystems, in particular to address the specific challenges observed at each site, emphasizing the importance of understanding and preserving diverse coastal environments.

Keywords: habitat complexity, macroalgae, maximum likelihood classification, seagrass meadows, spatial pattern.

1. Introduction

Seagrasses are angiosperms, utilizing flowers and seeds for reproduction, and thrive in marine environments, including shallow coastal waters and estuaries. Adapted to submerged salty conditions, these plants play a vital role in coastal ecosystems, supporting the ecological balance of neighboring ecosystems such as mangroves and coral reefs (Davis et al., 2009; Valdes et al., 2020). The significance of seagrass is both ecological and economic, with the value of seagrass meadows to Indonesian fisheries estimated at around US$230 million (Unsworth et al., 2010). Out of around 60 seagrass species worldwide, 16 are found in Indonesia, of which 13 are reported from the waters of the Spermonde Archipelago in South Sulawesi, forming one of the largest seagrass expanses worldwide (Nurdin et al., 2019; Short et al., 2017). Sulawesi is situated in the Wallacea Region and the Coral Triangle biodiversity hotspots (World Atlas, 2021), and this rich diversity aligns with Sulawesi's reputation for exceptional biological variety.

Despite their importance, seagrass meadows are facing serious threats from various sources, including climate change. Elevated ocean temperatures pose a multifaceted threat to seagrass ecosystems, and can result in reduced ecological services, increased vulnerability to invasive species, disrupted trophic structures, and additional loss of valuable seagrasses (McCarthy et al., 2020; Tang & Hadibarata, 2021). These effects are frequently intensified by human-induced activities, including boating, anchoring, land reclamation, coastal development and pollution, all of which have unmistakably led to the observed deterioration and loss of seagrass beds around Sulawesi (Karlina et al., 2018). Human impacts on seagrass ecosystems can have significant consequences for both the seagrass habitat itself and the biodiversity of associated organisms. When confronted with disturbances, similarly to other ecosystems, seagrass ecosystems undergo modifications, including alterations in habitat structure (Jackson-Bué et al., 2021). These modifications can involve or affect diverse processes, such as organism protection, resource regulation, and prey species sheltering, ultimately delineating habitat complexity and influencing the biodiversity and community composition of interconnected ecological communities. Therefore, habitat structural complexity becomes a key determinant of local species distribution (Downes et al., 1998), as habitat structure mediates biodiversity effects on ecosystem properties (Godbold et al., 2011).

Our understanding of habitat structure in ecosystems largely stems from the field of terrestrial landscape ecology and was first introduced by Bell et al., (1991). Nadiarti et al. (2012) adopted this concept in their study of two seagrass beds with different canopy types, although this was a preliminary study. To date, research on marine habitat structure remains limited, particularly with respect to seagrass beds. Numerous studies on habitat structure have been confined to freshwater ecosystems (Heck & Crowder, 1991; Willis et al., 2005; Santos et al., 2023) and coral reef ecosystems (e.g.; Fukunaga et al., 2020; Oakley-Cogan et al., 2020; Jackson-Bué et al., 2021; Meenapha et al., 2021; Nogueira et al., 2021). This study aims to compare the seagrass habitat structure in two areas with different environmental conditions, namely semi-enclosed (protected) waters (Puntondo site) and open (exposed) waters (Batu Kalasi site). The hypothesis of this study is that seagrass habitat structure in open waters shows a higher level of heterogeneity and complexity compared to seagrass habitat structure in semi-enclosed waters. The selection of these sites in the Spermonde Archipelago was motivated by the varying effects of wave exposure, which are known to influence habitat structure (Wernberg & Connell, 2008; Vozzo, 2020).

2. Study Area

This study was conducted in South Sulawesi Province, a province located in the southern part of Sulawesi Island, Indonesia. The study covers two locations in the coastal waters of South Sulawesi: the waters around Puntondo Village (5°35'16.93"S, 119°29'12.41"E), hereafter referred to as Puntondo, and the waters around Batu Kalasi Island (4°6'35.00"S, 119°36'18.00"E), hereafter referred to as Batu Kalasi (Fig. 1). These two locations have different characteristics; the Puntondo site a semi-enclosed bay and the Batu Kalasi is exposed to open sea. These two locations are expected to have different seagrass habitat structure characteristics.

The Puntondo site is a relatively calm bay, facilitating the deposition of sediments on the seabed, resulting in characteristically fine-grained sediment. Seagrass meadows are one of the ecosystems found in the shallow coastal waters. Seagrass distribution in the waters of Puntondo Village is uneven, forming patchy patterns. Human activities have a significant impact on the seagrass ecosystems in this location. The Puntondo Village community mostly relies on fishing as a livelihood, as evidenced by the several traditional fishing gears set up by residents in this area, and there is considerable fishing boat traffic in the surrounding waters. Seaweed is also cultivated in Puntondo waters.

Known locally as Pulau Batu Kalasi, Batu Kalasi Island is not in fact a true island, but a small (34,880 ha) sand bank covered with a mangrove ecosystem situated at approximately 4°6'35.00"S, 119°36'18.00"E. The dominant mangrove species at this location is *Rhizophora mucronata* Poir. In addition, there are dense seagrass beds around Batu Kalasi Island, especially to the northwest, north, and northeast, between the Batu Kalasi mangrove ecosystem and Labuange Hamlet in Kupa Village, Barru Regency, on the South Sulawesi mainland. Directly facing the open sea, this site is an area affected by currents and waves that influence the sediment characteristics. The Labuange Hamlet villagers exploit the wealth of marine life around Batu Kalasi Island during low tide, particularly in and around the seagrass meadows. These gleaning activities, seeking seafood such as mollusks and crustaceans, are carried out on foot, walking through the seagrass meadows to Batu Kalasi Island at low tide. The fishing boats from Labuange Hamlet also pass around Batu Kalasi Island when the tide is high enough.

3. Materials and methods

Field data collection was conducted from June to December 2021. A line transect method was used, with five line transects laid perpendicular to the shoreline at each site (Figs 2a and 2b). At Batu Kalasi, the distance between line transects was 50 m, while at Puntondo the distance between transects varied from 50 to 100 m, adjusting to the conditions in the field, as there were mangrove rehabilitation activities

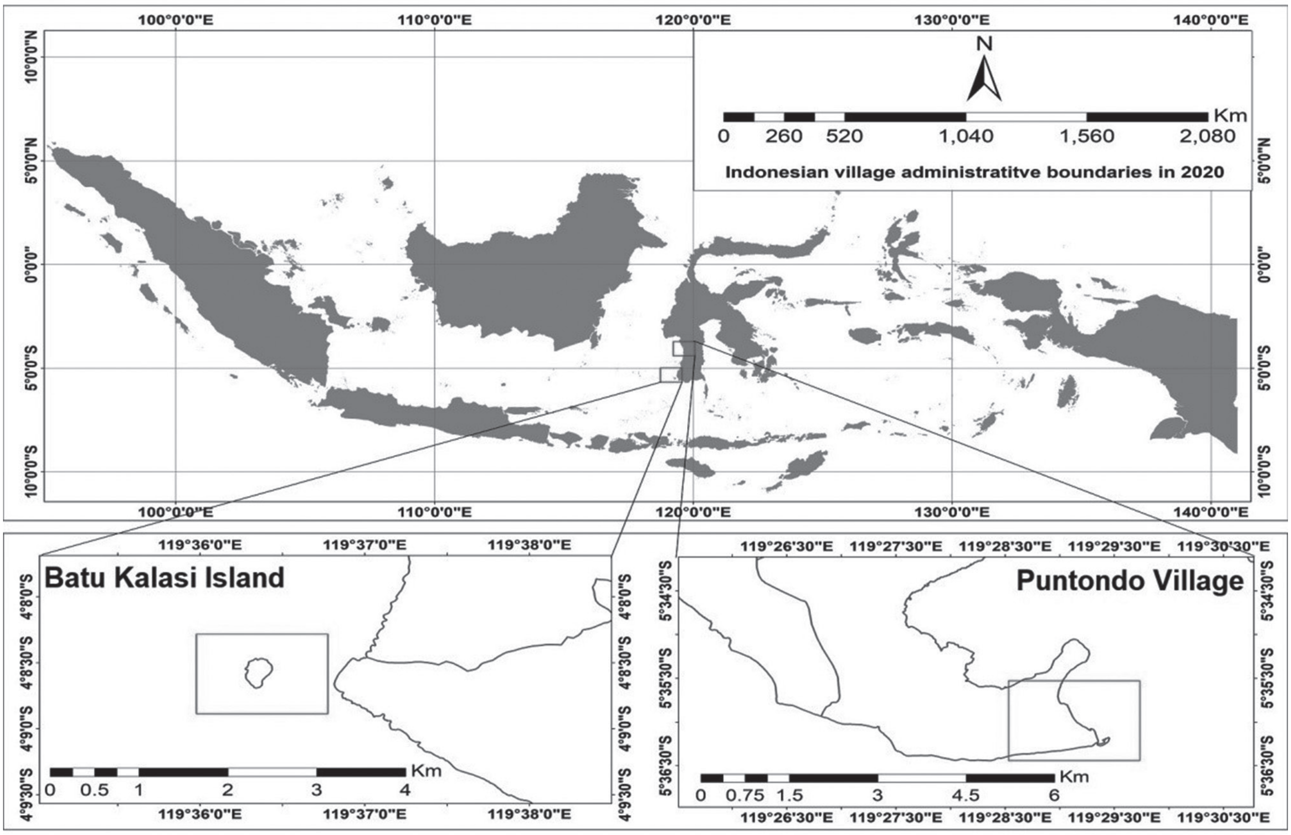


Figure 1. Study site Map

ongoing at that time. The length of each line transect was adjusted to the limits of seagrass presence, following the contour of the shoreline, following McKenzie et al. (2007). Square plots (10 x 10 m^2) were laid out along each transect line. The number of plots per transect ranged from 7 to 10, and was adjusted to the length of the line transect (Fig. 2c).

Seagrass data were collected at low tide, with a water depth of about 50 cm at Puntondo and 0 cm at Batu Kalasi. Ten quadrats (1 m^2) were randomly placed within each plot. In each quadrat, seagrass, macroalgae, and coral species were identified and percentage cover was estimated for each species. Seagrass, macroalgae and coral species were identified based on references (McKenzie et al., 2007; Martínez-Daranas et al., 2018; Richards, 2018).

Complexity in a habitat is the result of variations in the abundance of individual structural components. The term 'individual structural component' can apply to the percentage cover of each species, in line with the approach used by Hamilton and Spencer, (2007) and Nadiarti et al. (2012). Consequently, habitat complexity is influenced by the community structure, supported by diverse morphologies and variations in the abundance or percentage cover of each species shaping the habitat.

The complexity resulting from the variation in species (seagrass, macroalga, and coral) percentage cover was analyzed using non-metric Multidimensional Scaling (nMDS) and Bray Curtis cluster analysis in PRIMER 7 version 7.0.13 (Clarke & Gorley, 2015). The nMDS ordination was based on the Bray-Curtis similarity index. To minimize the effect of extremely low and high percentage covers, the data were first square root transformed to create a ranked similarity matrix. The results were then converted and plotted on a 2D scaling (nMDS) plot. The stress value calculated by the nMDS procedure indicates how well the plot reflects the dissimilarity relationships within the data, with stress values <0.2 indicating a good fit. The closer two sites are on the nMDS plot, the more similar they are in terms of the observed community composition. A Similarity of Percentage (SIMPER) analysis was also used to determine which species contributed the most to the dissimilarities in community structure shaping the seagrass habitat. Analysis of similarity (ANOSIM) was performed to evaluate the dissimilarity between the sites (Puntondo and Batu Kalasi), as represented by the R value. The R value ranges between -1 to +1, where a positive R value approaching +1 signifies a significant difference between groups, while a negative R value approaching -1 indicates high between group similarity (Clarke & Gorley, 2015). The differences in mean percentage cover of the species contributing most to dissimilarity were analyzed using two-way ANOVA in the PRISM v8 software package.

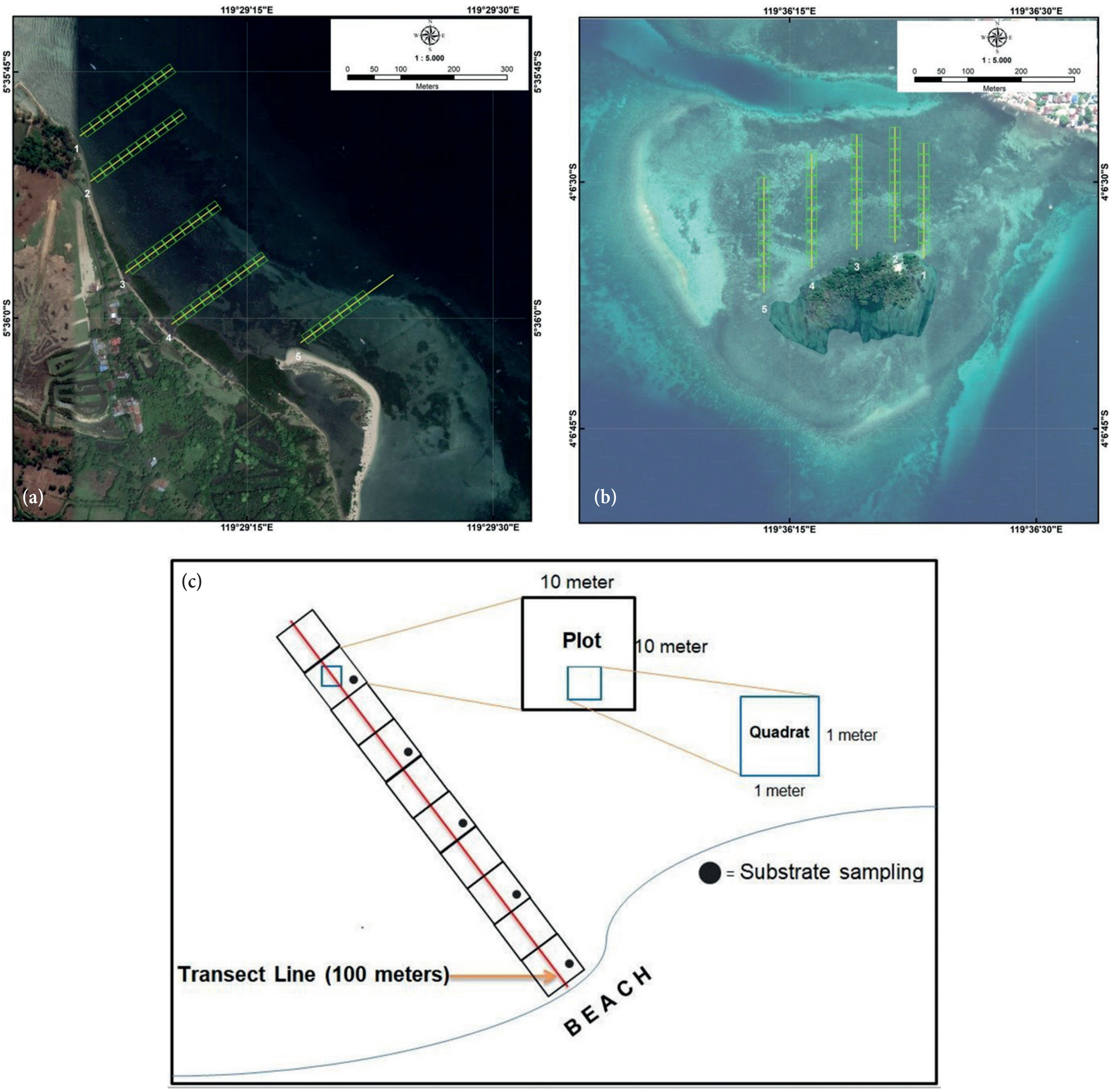


Figure 2. Layout of line transect in seagrass beds: (a) Puntondo site, (b) Batu Kalasi site, and (c) a detailed layout of plots and quadrats on each line transect

Habitat heterogeneity includes variations attributable to the relative abundance of different structural components. This is analogous with the spatial pattern (Hamilton & Spencer, 2007) of structural components (seagrass, macroalgae and coral cover). The spatial pattern was assessed using satellite imagery and the maximum likelihood classification method. Ground-truth position points, acquired through GPS field data collection, were utilized as reference points for the classification process. The classification outcomes delineated three distinct classes, representing areas characterized by dense seagrass cover, sparse seagrass cover, and macroalgal cover. Notably, the low spectral distinctiveness of coral cover rendered it indiscernible within this classification. The heterogeneity was compared descriptively based on the classified satellite images. The extent of the seagrass meadows at each site was measured by tracking the outer boundary of each meadow using a GPS (Global Positioning System) unit. The tracking results were processed in ESRI ArcGIS and Global Mapper software to determine and map the extent of the seagrass area habitat at each study site and analyzed descriptively based on the maps.

Substrate samples were collected in five of the (10 m x 10 m) plots along each line transect. These five plots served as replicates for each line transect, with a distance of 20 meters between each substrate sampling point (Fig. 2c). Substrate samples were collected using sediment corers made from iron pipes (55 mm diameter, 25 cm long). The substrate samples collected were transported to the laboratory for grain size and sediment type analyses. The sediment samples were prepared by removing any animal and plant fragments visible and then dried at 150°C for 24 hours. Grain size was classified based on the Wenworth Class. The dried sediment was sieved through a series of sieve nets (Din 4188 Pruf-Sieb) with mesh sizes of 2000, 1000, 500, 250, 130, and 63µm for 10 minutes each to obtain the grain size distribution for each sample. The difference in grain size between the two study sites was tested for significance using the independent samples t-test in PRISM v5. Particle Size Analysis (PSA) was conducted using a shade plot in PRIMER v7.

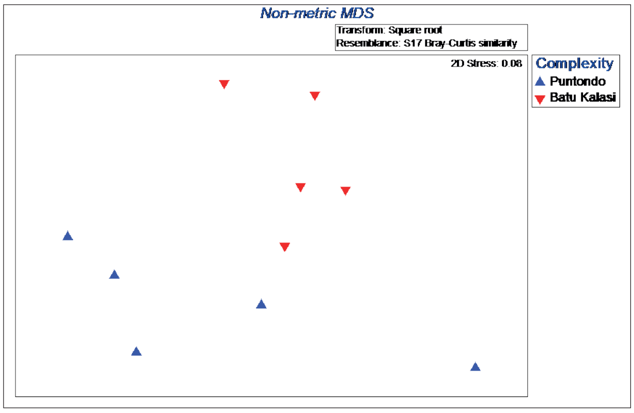


Figure 3. Two dimensional nMDS ordination plot of components shaping the complexity of seagrass habitat in Puntondo (solid red inverted triangle) and Batu Kalasi (solid blue triangle)

4. Results

4.1. Complexity of seagrass habitat

In total 14 species contributing to the seagrass habitat structure were identified in this study, each of which had different percentage cover and distribution patterns. Of these 14 species, five seagrass species were found at both study sites (Puntondo and Batu Kalasi), eight species of macroalgae were found in Batu Kalasi of which one was found in Puntondo with very low percentage cover, while the single coral species found during the study was only observed at Batu Kalasi.

The nMDS ordination of components (species percentage cover) shaping the seagrass habitat shows a clear separation between the study sites (Fig. 3). This is supported by the pairwise comparison test (one-way ANOSIM = analysis of similarity) between the two study sites based in the percentage cover of all species components shaping the seagrass habitat, which indicates that the study sites were significantly different ($R = 0.58$, $p<0.01$).

Data from Table 1 shows the cover distribution of seagrass, macroalgae and coral species found in the study site. The SIMPER analysis indicated that average dissimilarity between Puntondo Village and Batu Kalasi Island was 57.10%, with

Table 1. Percentage cover (% cover) of species shaping the seagrass habitat at the two study sites

Species	Mean % cover per transect									
	Puntondo Village					Batu Kalasi Island				
	1	2	3	4	5	1	2	3	4	5
Seagrass:										
Enhalus acoroides (L.f.) Royle	0	37	27	5	1	4	3	2	2	2
Thalassia hemprichii (Ehrenb.) Asch.	25	24	70	43	1	18	36	37	14	23
Halophila sp. Thouars	5	3	2	3	0	5	0	0	0	3
Cymodocea rotundata Asch. & Schweinf.	1	0	1	21	56	12	20	19	8	5
Halodule uninervis (Forssk.) Boiss	0	0	0	6	12	2	1	0	0	0
Macroalgae:										
Gracilaria salicornia (C. Agardh) E.Y. Dawson, 1954	–	–	–	–	–	10	18	6	8	6
Boergesenia forbesii (Harvey) Feldmann, 1938	–	–	–	–	–	5	1	3	0	0
Padina sp. Adanson, 1763, nom. cons.	–	1	–	–	–	0	3	0	5	4
Hypnea spinella (C. Agardh) Kützing, 1847	–	–	–	–	–	0	0	4	10	8
Acanthophora muscoides (L.) Bory de Saint-Vincent, 1828	–	–	–	–	–	0	0	5	8	0
Halimeda opuntia (L.) J.V. Lamouroux, 1816	–	–	–	–	–	0	0	0	0	5
Sargassum sp. C. Agardh, 1820	–	–	–	–	–	0	0	0	0	5
Caulerpa serrulata (Forsskål) J. Agardh, 1837	–	–	–	–	–	0	0	0	0	5
Coral:										
Dipsastrea veroni (Moll & Borel Best, 1984)	–	–	–	–	–	4	10	0	6	7

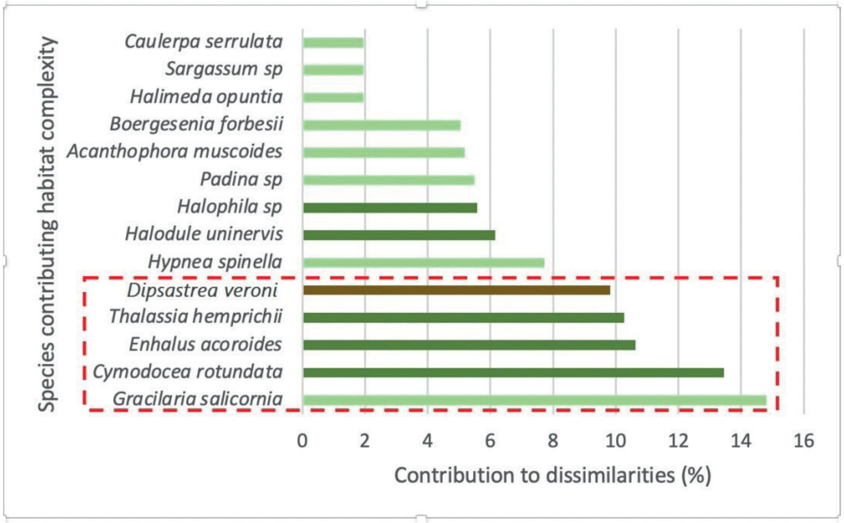


Figure 4. Contribution of species (components) to the dissimilarity in seagrass habitat complexity between the two study sites (Putondo and Batu Kalasi). Bar colors represent component type (light green for macroalgae, dark green for seagrasses, and brown for corals); Red-dash box indicate the dominant species

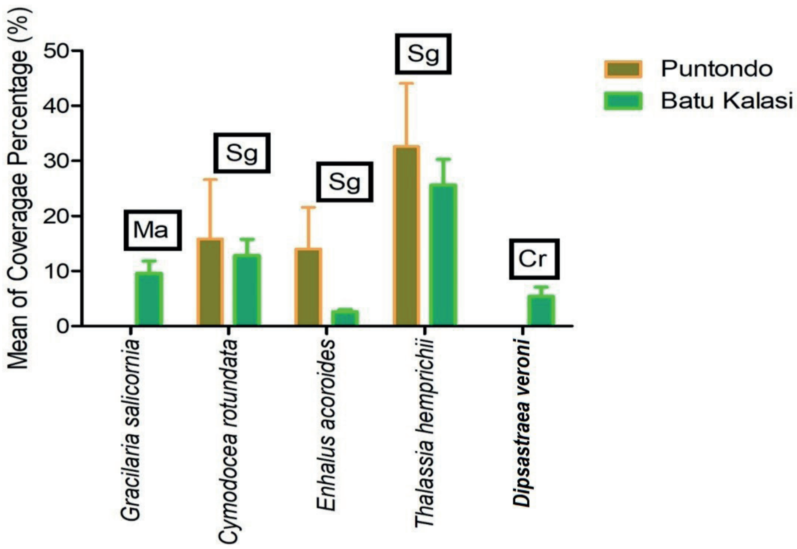


Figure 5. Mean percentage cover of major contributing species to dissimilarity in seagrass habitat community structure between the two study sites. Abbreviation in the square above the error bars indicate species component (Ma= Macroalgae, Sg= Seagrass, Cr= Coral)

varied percentage contributions from each of the 14 species components. The species contributing most to the dissimilarity (>9%) were *Gracilaria salicornia*, *Cymodocea rotundata*, *Enhalus acoroides*, *Thalassia hemprichii*, and *Dipsastrea veroni* (Fig. 4). There was a highly significant difference (P = 0.0004) between Puntondo and Batu Kalasi sites in the mean percentage covers of these five species (Fig. 5).

4.2. Heterogeneity of seagrass habitat

The analysis of satellite imagery shows that the seagrass habitat at the Puntondo Village site (Fig. 6a) is less heterogeneous compared to the Batu Kalasi Island site (Fig. 6b). The Puntondo seagrass habitat is characterized by a dominant distribution of dense (healthy) seagrass cover, particularly in areas near the mangrove ecosystem. In contrast, sparse seagrass cover is more dominant compared to dense seagrass cover at the Batu Kalasi Island site (Fig. 6b). Furthermore, macroalgal cover is only noticeable in the waters around Batu Kalasi. Although coral colonies were observed during field observations in the waters around Batu Kalasi, the coral cover was too low to enable the detection of corals from satellite imagery.

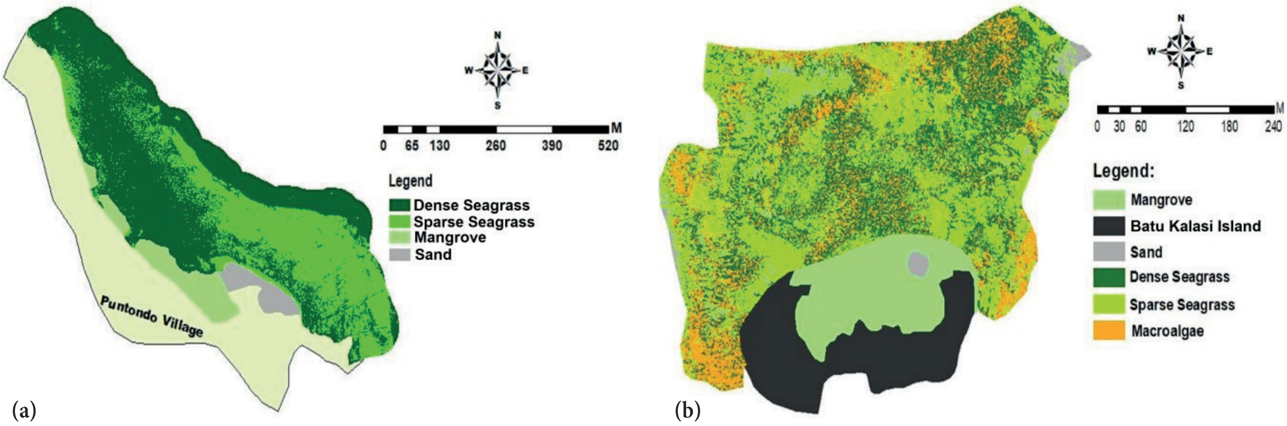


Figure 6. Heterogeneity of seagrass habitat: spatial distribution of benthic cover classes at the two study sites, (a) Puntondo Village; (b) Batu Kalasi Island

4.3. Characteristic of Substrate

The independent samples t-test showed a significant difference in substrate type between the seagrass habitat in Puntondo Village and Batu Kalasi Island ($p < 0.05$). The Particle Size Analysis (PSA) shade plots show that grain particle sizes in the seagrass habitat are generally dominated by smaller medium and fine sand particles (0.125) at the Puntondo site (Fig. 7a), while they are dominated by coarse sand (0.25-0.5) at the Batu Kalasi site (Fig. 7b).

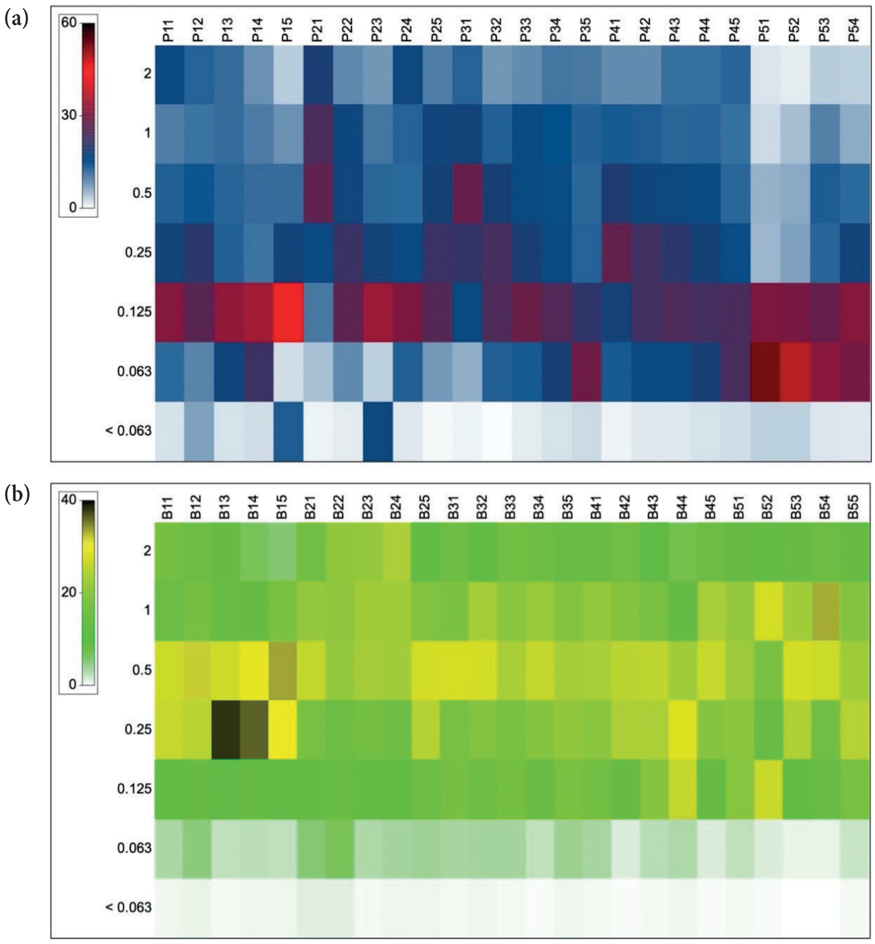


Figure 7. Shade plot of grain particle size distribution in the seagrass habitat sediment at the two study sites: (a) Puntondo Village, (b) Batu Kalasi Island

4.4. Seagrass meadow extent

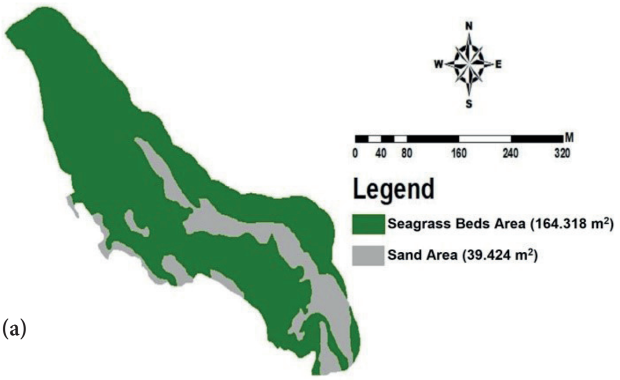
The seagrass meadow tracking showed that the extent of the seagrass meadows the Puntondo Village site (164,318 m^2) was larger than that around Batu Kalasi Island (136,901 m^2). The seagrass meadows at both research sites were unevenly distributed, forming a patchy pattern, with some areas devoid of seagrass growth. The extent of sandy areas without seagrass cover was 39,424 m^2 in the waters of Puntondo Village, and 11,518 m^2 around Batu Kalasi Island. Figure 8 illustrates the detailed extent of the seagrass meadow areas in both research locations.

5. Discussion

The seagrass habitat structure varies between Puntondo Village and Batu Kalasi Island, sites influenced by semi-enclosed and open waters, respectively. The wave exposure levels at each site likely play a crucial role in defining their respective seagrass ecosystems, as highlighted by Wernberg & Connell (2008) and by Vozzo (2020). The interplay between wave dynamics and habitat structure is a key factor influencing the composition of seagrass ecosystems. In addition to wave exposure, significant differences in sediment particle size most likely further contributed to the contrasting habitat structures observed at the Puntondo and Batu Kalasi sites (Fig. 7). Typically, the substrate in bays tends to be characterized by finer particles due to sediment settling at the bottom, a consequence of relatively calm water conditions (Tanto et al., 2016), as observed at Puntondo. In contrast, Batu Kalasi Island is situated in an area facing the open sea, experiencing relatively strong currents and waves. According to Nugroho and Basit (2014), waters with relatively strong currents and waves tend to have coarser substrates. Coarse fractions settle in open areas connected to the open sea, while fine sediments settle in waters with relatively calm conditions. This difference is visually depicted in Figure 3 and Figure 6, illustrating differences in seagrass habitat complexity and heterogeneity between the two locations.

Although Puntondo and Batu Kalasi sites shared five seagrass species, the dissimilarity in seagrass habitat complexity is primarily influenced by three species: *Cymodocea rotundata*, *Enhalus acoroides*, and *Thalassia hemprichii*. These three species had higher percentage covers in Puntondo compared to Batu Kalasi, as illustrated in Figure 5. The difference in coverage may be attributed to the finer sediment particle size at Puntondo, potentially supporting more robust seagrass growth. According to Erftemeijer and Middelburg (1993), *Enhalus acoroides* is well-adapted to growing in finer sediment, demonstrating the ability to penetrate deeper into the substrate. *Thalassia hemprichii*, while not showing a strong preference for fine or coarse sediment, tends to keep its roots or rhizomes in shallower sediment layers. While *Cymodocea rotundata*, a common species within its distribution, thrives in shallow water depths (0.15-1.17 m), on a wide range of sandy or muddy sand bottoms with varying sediment thicknesses (0.07-1.45 m) (Gaiballa & Ali, 2023). The percentage cover of *T. hemprichii* was lower at Batu Kalasi compared to Puntondo, but had a higher percentage cover than the other seagrass species present at Batu Kalasi Island (*Enhalus acoroides* and *Cymodocea rotundata*) that were also major contributors to the dissimilarity in seagrass habitat complexity. This observation suggests that *T. hemprichii* at the Batu Kalasi site may be trapping larger sediment particle sizes due to its long roots and dense hair roots, as described by Rattanachot and Prathep (2015).

Based on personal observation, the seagrass leaves in Puntondo were generally wider and longer than those of the same species at Batu Kalasi. Unfortunately, due to logistical



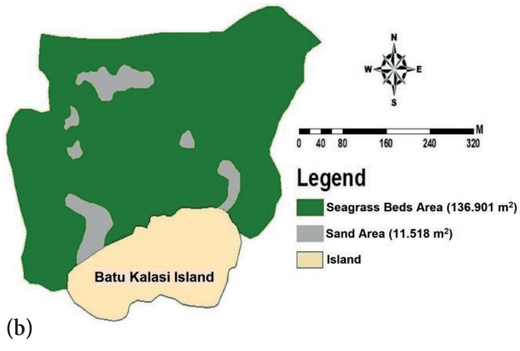


Figure 8. Map of seagrass meadow areas in the waters of (a) Puntondo Village, (b) Batu Kalasi Island

limitations, morphometric analysis was not conducted in this study. However, our personal observation aligns with morphometric studies conducted by other researchers. One of the factors influencing seagrass growth is the type of substrate. For example, Riniatsih (2016), Wangkanusa et al. (2017) and Sermatang et al. (2021) have all reported that seagrass leaves tend to be larger for plants growing in fine particle sediments compared to those growing in substrate dominated by coarse sand and gravel particles. Fine sediment substrates generally retain higher nutrient content, which is beneficial for seagrass growth. Studies such as Erftemeijer and Middelburg (1993) have shown that finer sediment particles in a substrate result in higher nutrient (nitrate and phosphate) availability. Consequently, seagrasses growing in fine or muddy sediments tend to have wider and longer leaves compared to those growing in coarse sand or mixed sand with coral rubble and shell fragments (Kiswara, 2004). The size of seagrass leaves plays a crucial role in seagrass cover. Larger seagrass leaves contribute to higher seagrass cover. This difference in seagrass leaf size may be a contributing factor to the denser seagrass observed in Puntondo compared to Batu Kalasi, as illustrated in Figure 6.

Macroalgae and corals also contribute to the dissimilarity in seagrass habitat complexity (Fig. 4). The dissimilarity arising from these groups was primarily due to the prevalence of *Gracilaria salicornia* and *Dipsastrea veroni* at Batu Kalasi, both of which were absent at Puntondo (Fig. 5). *Gracilaria salicornia* is widely distributed in the Tropical Indo-Pacific region (Coppejans et al., 2011), and its presence at Batu Kalasi is likely influenced by the environmental conditions at this site which are in line with those reported as favorable for *G. salicornia* growth, such as tidal fluctuations and coarser substrates (Erlania & Radiarta, 2015; Herlinawati et al., 2017).

The observed *Dipsastrea veroni* distribution was patchy, with a relatively low overall percentage cover ranging from 4 to 10% (Table 1). Despite this limited cover, *D. veroni* made a significant contribution to enhancing seagrass habitat complexity at Batu Kalasi (Figs 4 and 5). The colony size *of Dipsastrea* sp. in the reef flat is generally smaller compared to that in the reef crest (Loya, 1972). Given that the seagrass beds in Batu Kalasi Island are close to (and further inshore from) the reef flat, this supports the observed relatively small size of observed colonies and low percentage cover of *D. veroni* in the seagrass beds at the Batu Kalasi site. Solid sedimentary or coral rock formations typically provide a stable substrate for coral planula settlement and growth, especially for the massive life forms (Suharsono, 2008; Giyanto et al., 2017). Such stable conditions can be found at Batu Kalasi, which may explain the presence of the coral species *D. veroni* in the area, as it is a coral with a massive life form typical of *Dipsastrea* sp. (Suharsono, 2008). *D. veroni* was the sole coral species observed in the seagrass meadows at Batu Kalasi, suggesting that *D. veroni* broodstock may be available in the coral reefs adjacent to the seagrass beds at Batu Kalasi.

In Puntondo Village, where the substrate was characterized by the prevalence of fine particle sediment, the notable absence of macroalgae can be attributed to suboptimal conditions for their growth. One limitation could stem from poor oxygen circulation within the substrate, as it gets covered by silt, mud, or fine particles. As discussed by Wawu et al. (2018), this impediment can adversely affect macroalgal growth processes. Furthermore, no coral species were found at the Puntondo site, where the substrate was dominated by fine particles and medium sand sediment types. Labile substrates such as mud or fine and medium sand pose difficulties for coral planula attachment, as highlighted by Giyanto et al. (2017).

Spatial patterns of substrate cover and species (structural component) distribution at the two study locations clearly shows different patterns of seagrass habitat heterogeneity (Fig. 6). The seagrass habitat at the Batu Kalasi site was more heterogenous compared to the Puntondo site. The habitat heterogeneity at Batu Kalasi Island was associated with higher biodiversity. One likely reason is that different organisms may find suitable niches within the diverse micro-environments. In this case, the stability offered by the solid sedimentary rock formations and coarse particle size may contribute to a more robust ecosystem, allowing not only seagrasses but also other species like macroalgae and coral to thrive (Fig. 4). The ecological principle, as stated by Dronova (2017), emphasizes that heterogeneity in vegetation is vital for ecosystem complexity. This concept can be extended to the seagrass habitat in Batu Kalasi island, where the spatial distribution and different levels of seagrass, macroalgal,and coral cover contribute to enhancing habitat heterogeneity. This is analogous to the effectof diverse land cover and vegetation types on terrestrial ecosystems. This principle finds resonance in the Batu Kalasi seagrass habitat, where the varied presence of seagrass, macroalgae, and coral appears to signal a richer and more diverse marine ecosystem, likely playing a crucial role in supporting a wide array of marine life and influencing the dynamics of plant and animal diversity, as well as the flow of energy and food.

Contrary to the proposition by Gamfeldt et al. (2023) that spatial extent is positively correlated with habitat heterogeneity, enhancing biodiversity as the observed area increases, our findings indicate unexpected dynamics in this relationship. In our study, spatial patterns of seagrass coverage and distribution resulted in differential levels of habitat heterogeneity in Puntondo and Batu Kalasi (Fig. 6). Despite the larger spatial extent at Puntondo, seagrass habitat heterogeneity was lower than at Batu Kalasi Island, which displayed a more diverse range of seagrass habitats, potentially linked to the stability offered by solid sedimentary rock formations and coarse particle size, fostering the thriving coexistence of seagrasses, macroalgae, and coral species. These findings challenge the understanding that larger spatial scales inherently correlate with heightened habitat heterogeneity, highlighting the complexity of spatial scale dynamics.

Furthermore, our study aligns with the emphasis of Gallucci et al. (2020) on the critical role of habitat diversity across scales in sustaining associated fauna. The comparative analysis of Puntondo Village and Batu Kalasi Island highlights the complexity of habitat dynamics, necessitating a nuanced or fine-scale approach for effective biodiversity management. Specifically, our findings underscore the importance of considering contextual factors such as spatial extent and scale, habitat complexity, and heterogeneity in marine ecosystems. This understanding challenges preconceived notions, revealing that larger spatial extent does not always correlate with heightened habitat heterogeneity. Instead, the distinct seagrass habitats observed in Puntondo Village and Batu Kalasi Island point towards the influence of sediment characteristics and environmental conditions. The intricate dynamics indicated by this study stress the need for a comprehensive understanding of interactions between spatial scale and habitat features to ensure informed conservation strategies and sustainable ecosystem management in marine environments.

6. Conclusion

The substrate characteristics in the waters of Puntondo Village are dominated by medium and fine sand, whereas the substrate in Batu Kalasi Island is dominated by coarse sand. The seagrass habitat structure on medium sand substrates (Puntondo Village) exhibits low levels of heterogeneity and complexity, despite the larger area. In contrast, the seagrass habitat structure on coarse sand substrates (Batu Kalasi Island) shows high levels of heterogeneity and complexity, despite the smaller area. The presence of macroalgae and coral in the seagrass meadows contributes to the high levels of habitat heterogeneity and complexity.

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