

Comparisons of benthic associated fauna assemblages in seagrass meadows across conservation and non-conservation areas in Bali and Lombok, Indonesia

Putu Satya Pratama Atmaja^{1*}, I Ketut Aditya Krisna Laharjana²,
A. A. Md. Ananda Putra Suardana³, Mike Van Keulen⁴

¹Department of Marine Science, Faculty of Marine and Fisheries, Udayana University
Jl. Raya Kampus UNUD, Bukit Jimbaran, Kuta Selatan, Badung, Bali 80361 Indonesia

²Department of Environmental Science, Graduate School, Udayana University
Jl. Sudirman, Kampus UNUD Sudirman, Badung, Bali 80361 Indonesia

³Research Centre for Oceanography, National Research and Innovation Agency
Jl. Pasir Putih 1, Ancol, 14430 Jakarta, Indonesia

⁴School of Environmental and Conservation Sciences, and Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University
90 South Street, Murdoch, Western Australia 6150, Australia
Email: satyapratama@unud.ac.id

Abstract

Benthic ecosystem has been widely considered as an important feature of seagrass associated fauna, and its function as a grazer and linkage between primary producers and higher trophic level is well known. Though the importance of benthic fauna in seagrass ecosystems has been indicated in many studies, its biodiversity in spatial scale has often been poorly studied. This study aimed at examining the assemblages and diversity of benthic associated fauna in conservation areas (CA) and non-conservation areas (NCA) across the seagrass meadows in Bali and Lombok. This study found that the assemblages and diversity of benthic fauna greatly varied between the meadows. A total of 430 individuals associated to benthic fauna from 24 species were identified in Bali and Lombok. Of these, Gastropods were the highest class of taxa recorded in this study, followed by Bivalvia, Echinodermata, Decapoda, and Amphipoda. Permutation multivariate analysis of variance (PERMANOVA) revealed a significantly different benthic fauna diversity between sites. Non-metric Multidimensional Scaling (nMDS) and Bray-Curtis analysis showed a clear distinction of benthic fauna assemblages between CA and NCA, both in Bali and Lombok. These results indicated that from spatial perspective, different characteristics of seagrass meadows may represent different biodiversity of associated fauna. These differences might be driven by different anthropogenic pressure and variation of substrates among the meadows which may affect the composition of the benthic fauna ecosystems. The implication of this study was to providing baseline data on guiding the appropriate approach and strategies for management and conservations of seagrass ecosystems.

Keywords: Conservation, Associated fauna, Lesser Sunda, Seagrass, Biodiversity

Introduction

Seagrass is an aquatic angiosperm which lives submerged in coastal ecosystem. This marine flowering plant is widely distributed along temperate and tropical regions, but the highest diversity is centered in tropical Indo-Pacific (Jhon et al., 2023). Along with mangrove and coral reef, the seagrass provides ecological services such as primary producers, shoreline protection, seabed stabilizer, and it could act as nursery ground for many commercially caught species (Unsworth et al., 2019; Jiang et al., 2020; Park et al., 2020). Despite their enormous ecological services, the seagrass meadows also have the potential to sequester large amounts of organic carbon in underlying sediments (Miyajima et al., 2022).

The existence of seagrass enhances biodiversity by providing a habitat for a wide range of associated fauna. Its leaves are a suitable substrate for a number of epiphytes to grow and form laminates assemblage by high species diversity microorganism (Hartati et al., 2018; Atmaja et al., 2021). The seagrass physical structure often attracts a wide variety of benthic organisms (epifauna and infauna) such as gastropods, decapods, mollusks, and some polychaeta worms (Leopardas et al., 2014; Liao et al., 2015; Ambo-rappe, 2016). These benthic organisms play a significant role in the seagrass ecosystems as they act as macro-grazers which determine the patterns of epiphyte assemblages in seagrass, especially in high anthropogenic activities, which are positively associated with high dense of epiphytes leading to the reduction of survival rates of seagrass

because of limited light (Noisette *et al.*, 2020). In addition, epifauna organisms have been accounted as a key factor in controlling epiphytes composition and assemblages on seagrass leaves by grazing them (Murphy *et al.*, 2021). Furthermore, benthic biodiversity plays a critical role in the food web, forming trophic linkage between primary producers and higher level predators, such as fish and larger vertebrates in the food chain (Ramesh and Mohanraju, 2020).

Investigation on benthic diversity is very important to facilitate deeper understanding of monitoring seagrass beds as a vital marine ecosystem. In addition, a small alteration of this primary producer's composition can indirectly impact associated fauna communities (Blake *et al.*, 2014; Cadier and Frouws, 2019; Voigt and Hovel, 2019; Brun *et al.*, 2021). A few studies have been conducted about associated epifauna diversity in seagrass beds, yet they only focused on temperate and sub tropic regions instead of the tropical ones (McDonald *et al.*, 2016; Stark *et al.*, 2018; Whippo *et al.*, 2018; Barnes, 2021). Although the most recent study on benthic macrofauna in North Sulawesi and Northern Papua, Indonesia has been carried out in multispecific seagrass beds (Lin *et al.*, 2018; Tasabaramo and Nugraha, 2023), other areas especially in Bali and Lombok have so far received only little attention.

In the case of Bali and Lombok, these islands have gained significant attention to attract tourism, which may become a threat to seagrass ecosystem and its associated fauna. This study aimed at investigating benthic communities between seagrass meadows in non-conservation areas (NCA) and conservation areas (CA). In doing so, the goal of this study was to fill the gap on the effectiveness of conservation areas in ensuring a greater diversity, especially on seagrass benthic communities. The disparity between NCA and CA can be distinguished

from the utilization, management, protection, and goals to ensure sustainability of marine biodiversity that exists in the area. Conservation Area (CA) was built to protect vulnerable species, minimize extinction risk, and enhance the productivity and diversity of marine populations (Griffiths *et al.*, 2022).

The aforementioned meadows support the existence of benthic fauna serving a vital function as the trophic link between primary producers and larger, more mobile nekton. The need for broad scale comparisons of different seagrass characteristics is the key to understanding seagrass complexity and deducing the biodiversity consequences of habitat loss. Hence, this study examined the following hypothesis: the level of benthic fauna assemblages in CA is higher and more diverse than that of in NCA, both in Bali and Lombok.

Materials and Methods

This study was conducted on two islands, Bali and Lombok. There were four sites on each island. Each two represent Non-conservation Area (NCA) and Conservation Area (CA) (Table 1., Figure 1.).

In Bali, Shindu (SND) and Samuh (SMH), located on the south of the island, were selected as NCA sites, while Labuhan Lalang (LBL) and Teluk Terima (TTR), parts of West Bali National Park (Polunin *et al.*, 1983) were selected as the CA sites (Surat Keputusan Menteri Kehutanan No 493/Kpts/II/1995). Gili Kedis (GKD) and Tanjung Kelor (TJK), located in Southwest of Lombok Island, were selected as the NCA sites. Meanwhile, located in northeast of Lombok, Gili Lawang (GLW) and Gili Sulat (GSL) were selected as CA sites (SK Bupati No. 188.45/452/KP/2004; SK Gub. nomor 523.1-972 Tahun 2016) Tentang pengesahan RPZ KKP3K NTB Tahun 20162036).

Table 1. Sites name in each island, codes, categories, and coordinates of collecting data

Site	Code	Category	Latitude	Longitude
Bali				
Samuh	SMH	NCA	8° 47'11.14"S	115° 13'47.76"E
Shindu	SND	NCA	8° 41'1.10"S	115° 15'54.04"E
Labuhan Lalang	LBL	CA	8° 9'11.65"S	114° 31'17.18"E
Teluk Terima	TTR	CA	8° 8'31.68"S	114° 32'20.77"E
Lombok				
Tanjung Kelor	TJK	NCA	8° 44'24.10"S	116° 1'32.10"E
Gili Kedis	GKD	NCA	8° 43'50.66"S	116° 1'33.47"E
Gili Lawang	GLW	CA	8° 17'39.74"S	116° 42'27.62"E
Gili Sulat	GSL	CA	8° 20'45.61"S	116° 44'25.02"E

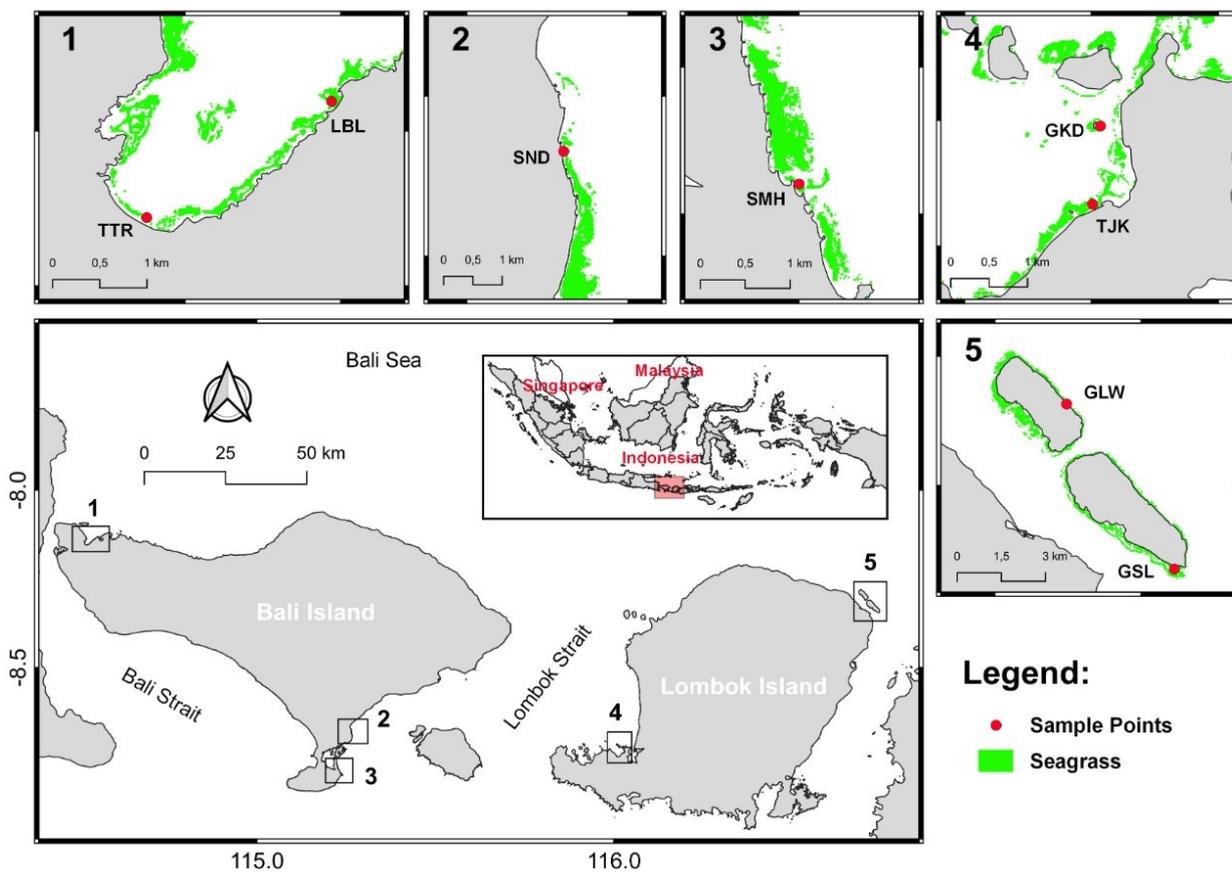


Figure 1. Plotted location of collecting data of epifauna in different seagrass meadows in Bali and Lombok: refer codes of each site from Table 1. Classification of seagrass objects using random forest method in Google Earth Engine and visualization using QGIS 3.16

All data were collected during a low tide condition to makes counting shoot density and collecting specimens possible. Based on previous studies, all of the locations consisted of heterogeneous seagrass species (Purnomo *et al.*, 2017; Atmaja *et al.*, 2021; Syukur *et al.*, 2021). Five replicates of square quadrat (1 m²) were sampled on each targeted species in every site to count seagrass percentage cover with the comparison to the picture available in each square on observation area (Figure 2.) (Mckenzie and Yoshida, 2009).

The collection of benthic fauna samples was based on previous studies which have been conducted on multispecific seagrass with a little modification (Lefcheck *et al.*, 2016; Whippo *et al.*, 2018). In each site and replicates, sampling of benthic macrofauna (> 0.5 mm in size) was done by counting any visible species found on quadrats (Wagey *et al.*, 2017). For micro benthic fauna (< 0.5 mm in size), samples were collected using PVC corer with an inner diameter 12 cm and pushed down into to a depth 20 cm (Bououarour *et al.*, 2021). All collected samples were sieved (0.5 mm mesh size).

Then, specimens were retained and preserved in a bottle containing diluted seawater with formalin. The bottle was then named according to sites and placed on cool box with ice for further analysis. In the laboratory, epifauna specimens were examined under the microscope and identified to the lowest possible taxon based on book entitled “Fauna (Epibenthic and Epifauna) associated with Seagrass Ecosystem in Palk Bay and Gulf of Mannar” by Rajan *et al.* (2017). Every identified species was counted and expressed as the density of benthic fauna (ind.m⁻²).

Data analysis

The conditions of benthic communities were described using Shannon-Wiener Index (*H'*), Evenness Index (E), and Dominancy Index (C) (Beisel *et al.*, 2003). The Shannon-Wiener Index (*H'*) was used to determined fauna diversity, as follows:

$$(H') = \sum_{i=1}^n p_i \ln p_i$$

where, *n* represents the number of species and *p_i* represents the proportion of individuals.

To identify the similarities between benthic communities among seagrasses, we used Evenness Index (E), as follows:

$$(E) = \frac{H'}{\ln S}$$

where, (H') is Shannon-Wiener Index and S is the number of taxa estimated in this study.

Meanwhile, Dominancy Index (C) was used to analyze species commonly found and dominated the communities, quantified using the following formula:

$$(C) = \sum_{i=1}^n p_i^2$$

where, n is the number of species and p_i is the proportion of individuals.

Permutational multivariate analysis of variance (PERMANOVA) has been widely used in ecology because of the sensitivity to heterogeneity and the changes in dispersions of organisms and ecological communities (Anderson and Walsh, 2013; Kelly *et al.*, 2015; Anderson, 2017) hence, PERMANOVA was used to test the difference of species richness and abundance of benthic species between the seagrass and the sites (NCA – CA). The community composition of the seagrass within the sites was analyzed using Bray–Curtis dissimilarity matrices of the epifauna abundance. Non-metric Multidimensional Scaling (nMDS) was used to visualize the distribution pattern in a two-dimensional ordination. nMDS represents the original data in a multidimensional scaling as accurately as possible using the reduction in the dimensions (Cheng, 2004). Similarity Percentage (SIMPER) of species contribution was used to investigate the species primarily accounted for observing the differences and to generate a ranking of its contribution in the benthic communities (Gibert and Escarguel, 2019). PERMANOVA, Bray–Curtis dissimilarity, nMDS, and SIMPER were conducted using PAST 4.03.

Results and Discussion

Seagrass conditions

Based on the observation, each site had different kinds of seagrass species, including their shoot density, percent coverage, and substrate characteristics (Table 2.). Also, it was observed that the density of seagrass species found in CA tended to be greater than those found in NCA, especially for the most common found species (e.g. *Enhalus acoroides*, *Cymodocea rotundata*, and *Thalassia hemprichii*), both in Bali and Lombok. These kind of seagrass

species has also found in previous study on several places in Indonesia (Kawaroe *et al.*, 2016; Hernawan *et al.*, 2021). The reason that CA has greater density of seagrass than NCA is possibly because meadows in NCA suffered more eutrophication effect that could decreased seagrass leaf production, demographic balance, growth rate, and lead to shoot mortality (Gladstone-Gallagher *et al.*, 2018; Ontoria *et al.*, 2019; Pazzaglia *et al.*, 2020). In contrary, NCA tended to have more seagrass species than those in CA, where the highest number found was in SMH (7 species). The highest percentage coverage of seagrass was found on CA in Bali (TTR and LBL), with the value of $\pm 84\%$, followed by CA in Lombok, which consisted of GSL ($\pm 69\%$) and GLW ($\pm 79\%$). The lowest mean value of percentage coverage was recorded in GKD ($\pm 35\%$), while in SMH, SND, and TJK were $\pm 62\%$, $\pm 54\%$, and $\pm 48\%$, respectively.

The meadows formed by seagrasses have characteristics that make them a suitable habitat and shelter for many species for animals, offers hiding places that protects against predation (Lin *et al.*, 2018; Cadier and Frouws, 2019; Su *et al.*, 2020). The results of this study show there were 5 groups of taxa found among the meadows, which were Gastropods, Bivalvia, Echinoderms, Decapods, and Amphipods. These groups of taxa were the most common found in the seagrass beds and were congruent with other studies' findings conducted in Akkeshi Bay, Japan (Yamada *et al.*, 2007), Virgin Islands, USA (Valdez *et al.*, 2021) Gazumbo Island, Malaysia (Vian *et al.*, 2022), Barra Grande Beach, Brazil (Cavalcante *et al.*, 2019), Philippines (Wagey *et al.*, 2017), Barrang Lompo Island, Indonesia (Ambo-rappe, 2016), and Northern of Papua, Indonesia (Tasabaramo and Nugraha, 2023).

Comparisons of benthic fauna diversity between different meadows

This study provided the first attempt in becoming a reference state of the structural community of benthic fauna among different seagrass meadows in Bali and Lombok, Indonesia. A total of 430 individuals associated benthic fauna were collected representing 24 species in seagrass meadows across Bali and Lombok (Table 3.). Of these, 5 classes of taxa were identified as follows: Bivalvia, Gastropoda, Echinodermata, Decapoda, and Amphipoda (Figure 3.). The major groups of benthic faunal, ranked by species, were Gastropods (30.93%), Bivalvia (23.25%), Echinoderms (21.62%), Decapods (13.95%), and Amphipods (10.23%).

The composition of benthic fauna assemblages was varied across the meadows in Bali and Lombok. However, on all of the taxa groups, the composition percentage of benthic fauna assemblages in CA was

higher than NCA, both in Bali and Lombok. Specifically, each of these taxa comprised of 5 species of Bivalvia, 7 species of Gastropods, 5 species of Echinoderms, 4 species of Decapods, and 3 species of Amphipods.

This study also revealed that the conservation areas (CA) were exhibited by higher and more diverse benthic fauna assemblages and composition on both islands, which supports the hypothesis in this research. As shown in Table 3, conservation area (CA) comprised of higher species richness of benthic fauna assemblages than in non-conservation area (NCA), both in Bali and Lombok.

This result was associated with the density condition of two meadows. which CA has greater density than NCA. This finding was in line with previous studies that stated higher number of shoot density is positively correlated with an increase in macrofaunal diversity (Seith and Ewers, 2018;

Lundquist *et al.*, 2018; Alsaffar *et al.*, 2020). Results of permutation multivariate analysis of variance (PERMANOVA) test revealed a clear difference between test pairs (CA and NCA) ($P < 0.01$; $P < 0.05$), each in Bali and Lombok, respectively (Table 4.). In addition, the nMDS plot (Figure 4.) and the dendrogram of Bray-Curtis (Figure 5.) showed a clear separation between prospected sites (CA and NCA, in Bali and Lombok), indicating the differentiation between benthic fauna assemblages among sites.

There are two possible reasons of the assemblages' differences found in this study. Firstly, this finding was likely driven by differences of benthic assemblages may occur due to different anthropogenic pressure between CA and NCA. Such variations in benthic fauna composition over a large scale could rise from the supposition that each habitat has its unique characteristics. All CA sites in this study, especially LBL and TTR, part of West National Bali Park, were built to ensure the sustainability

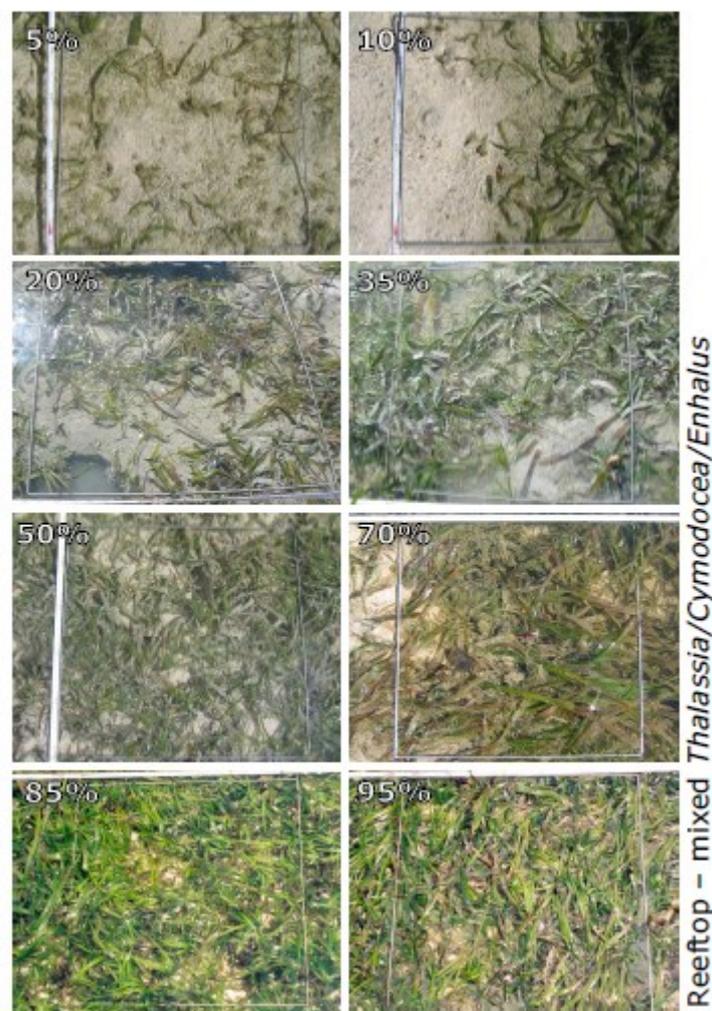


Figure 2. Percent cover standard from Seagrass – Watch to estimate percent coverage of seagrass in observation area / quadrats (Mckenzie and Yoshida, 2009).

Table 2. Condition of seagrass species found along sites of seagrass meadows in Bali and Lombok

Species	SMH	SND	LBL	TTR	TJK	GKD	GLW	GSL
EA	10,4±5,75	10,1±2,91	16,45±3,48	19,35±4,13	6,25±3,2	7,1±6,91	10,6±3,06	11,65±4,79
CR	8,3±5,87	19,5±7,61	26,35±5,35	30,2±13,41	14,9±7,26	16,2±8,3	24,15±6,5	23,95±6,99
CS	7,45±4,96	9,85±7,35	0	0	0	0	0	0
HO	5,9±4,67	3,5±4,24	5,55±4,77	0	10,55±2,9	4,95±9,17	0	0
HU	109,1±32,2	0	45,4±7,83	55,9±8,5	6±8,5	0	33,95±4,32	24,5±5,1
HP	50,65±11,74	0	13,5±5,5	0	5,75±6,1	41,95±40,3	25,2±5,5	39,35±8,39
HM	0	0	0	10,15±14,1	0	0	0	0
SI	124±82,4	0	73,4±65,3	0	0	0	0	0
TH	0	13,4±6,02	34,5±10	26,2±12,2	12,75±8,5	10,05±8,43	31,45±6,9	30,65±4,49
Av. Percent Coverage	62%	54%	84%	84%	48%	35%	69%	79%
Substrate texture	Sand	Sand	Sandy clay	Sandy clay	Sand	Sand	Sandy mud	Sandy mud

Notes: EA (*Enhalus acoroides*), CR (*Cymodoceae rotundata*), CS (*Cymodoceae serrulate*), HO (*Halophila ovalis*), HU (*Halodule uninervis*), HP (*Halodule pinifolia*), HM (*Halophila minor*), SI (*Syringodium isoetifolium*), TH (*Thalassia hemprichii*)

Table 3. Density (ind.m⁻²±SD) matrices of associated benthic fauna on seagrass meadows across Bali and Lombok

Species Name	SMH	SND	TTR	LBL	TJK	GKD	GLW	GSL
Bivalvia								
<i>Callocardia</i> sp.	1±0.7	-	7±1.1	5±0.6	2±0.8	2±0.6	7±1.09	6±0.6
<i>Limaria cumingii</i>	1±1.2	2±0.6	2±0.6	3±0.6	3±0.6	-	5±0.6	7±1.6
<i>Lioconcha castrensis</i>	2±0.7	-	2±0.8	3±0.9	-	-	4±0.6	4±0.6
<i>Modiolus</i> sp.	-	1±0.6	3±0.6	1±0.6	-	1±0.6	2±1.09	1±0
<i>Tellina</i> sp.	4±1.9	6±2.7	-	3±0.9	-	9±1.4	1±0	-
Subtotal	8	9	14	15	5	12	19	18
Gastropoda								
<i>Cerithium balteatum</i>	1±1	2±0.6	5±1.1	7±1.3	-	2±0.6	8±0.6	6±1.8
<i>Cerithium punctatum</i>	1±1.4	-	2±1.5	4±1.3	1±0.6	-	10±4.6	5±0.6
<i>Cerithium rostratum</i>	-	2±1.1	1±0.6	5±1.9	1±0.6	3±0.6	7±0.63	2±0.6
<i>Cypraea</i> sp.	1±0	2±0.6	-	1±0	1±0.6	2±0.6	-	-
<i>Littorina</i> sp.	-	1±0	2±0.6	1±0.4	-	-	3±0.63	1±0.8
<i>Sconsia</i> sp.	2±1	3±0.6	4±1.4	5±1.4	1±0	2±0.6	4±0.63	1±0.6
<i>Natica</i> sp.	-	2±0.9	4±1.9	6±1.7	-	2±1.4	5±0.63	2±0.6
Subtotal	5	12	18	29	4	11	37	17
Echinodermata								
<i>Holothuria edulis</i>	-	-	3±1.7	4±1.7	1±0	-	2±0.63	4±0.6
<i>Holothuria scabra</i>	1±1.2	-	5±1.1	3±0.6	-	1±0	-	4±0.6
<i>Diadema setosum</i>	10±2.5	9±2.8	-	-	5±0.6	7±1.4	-	-
<i>Temnopleurus</i> sp.	3±1.6	1±0.9	5±1.9	7±2.7	2±0.6	1±0	7±1.4	4±1.09
<i>Archaster typicus</i>	1±0	1±0.6	-	-	-	2±0.6	-	-
Subtotal	15	11	13	14	8	11	9	12
Decapoda								
<i>Alpheus</i> sp.	3±1	2±0.6	10±2	8±0.9	-	-	7±0.6	3±0.6
<i>Penaeus</i> sp.	1±1	-	2±0.9	4±0.6	1±1	-	2±0.6	3±0.8
<i>Callinassa</i> sp.	-	1±0	-	-	-	3±0.6	-	-
<i>Galathea</i> sp.	1±0.7	4±0.9	-	-	-	5±0	-	-
Subtotal	5	7	12	12	1	8	9	6
Amphipoda								
<i>Caprellidae</i> sp.	-	-	4±1.4	3±1.5	-	-	6±1.4	-
<i>Ampelisca</i> sp.	1±0	-	6±2	6±1.4	-	-	5±0.6	7±0.6
<i>Gammaropsis</i> sp.	-	1±0.6	-	-	2±0.6	-	-	3±0.6
Subtotal	1	1	10	9	2	0	11	10
Total	34	40	67	79	20	42	85	63

Notes: En dash indicates that the species was not detected when sampled. Site abbreviation as in Table 1.

of ecological community, including seagrass ecosystems. Thus, these areas were highly restricted, and a specific permit to access and enter is needed to keep it pristine as long as possible. This regulation was designed to protect and enhance the specific diversity of productivity of the ecosystems (Turnbull *et al.*, 2018; Griffiths *et al.*, 2022). Meanwhile, NCA sites, categorized as disturbed areas, tend to be influenced by highly anthropogenic pressure that directly impacts the seagrass ecosystems as a shelter and may lead to the decline of the abundant benthic fauna (Horinouchi, 2007). Consequently, the benthic fauna assemblages in CA were greater than those NCA among the sites in Bali and Lombok.

Secondly, their distribution and abundance may be strongly caused by different variations of substrates between sites (Table 2.). Benthic fauna generally prefers to inhabit muddy and clay substrates as a habitat (Sahidin *et al.*, 2018). Additionally, mud and clay substrates were known to have a high content of organic matter (Tranum *et al.*, 2021), and also served as the main intake for some benthic organisms that are deposit feeders such as bivalves (Sanmartí *et al.*, 2018; Gräfnings *et al.*, 2023). Based on these facts, the variation of substrates in CA, both in Bali and Lombok, may lead to significant differences in benthic fauna assemblages on those meadows.

In terms of species richness, this study also revealed diverse benthic fauna for the seagrass beds in both islands, led by gastropods, as the highest ranking of species group. This finding was in line with other studies conducted on *Amphibolis griffithii* meadows (Gartner *et al.*, 2013). Moreover, in the complex seagrass - mangrove adjacent ecosystems in Punang-Sari estuary, Sarawak (Malaysia), it was also found that gastropods had the highest documented individuals than bivalves, echinoderms, and decapods (Al-Asif *et al.*, 2020). The most dominant species was from genus *Cerithium* (e.g. *Cerithium balteatum*, *Cerithium punctatum*, and *Cerithium rostratum*). This result was in line with several studies which focused on associated fauna in seagrass beds in Malaysia (Illias *et al.*, 2021; Vian *et al.*, 2022) and Indonesia (Tasabaramo *et al.*, 2023).

Furthermore, there was evidence that due to seagrass loss, the composition and the structure of mollusks had decreased, especially for the gastropods associated with the leaf and sediment stratum (Rueda *et al.*, 2009). This indicates the gastropods and seagrass were very dependent to each other, in which the seagrass provides a suitable habitat for gastropods and the gastropods act as the grazer to clean seagrass leaves from the microalgae epiphytes attached in the leaves (Nakaoka, 2005; Nakamoto *et al.*, 2019). Thus, this could enhance the

possibility of seagrass in terms of photosynthetic activity due to light limitation caused by epiphytes' lamination and attachment (Brodersen and Kuhl, 2022; Zhang *et al.*, 2022).

Patterns and distribution of benthic faunal diversity

The Shannon-Wiener (H'), Evenness (E), and Dominancy (C) indices of benthic fauna assemblages were varied among the prospected sites (Table 5.). The Shannon-Wiener Index (H') ranged from 2.0553 to 2.5802 in all sites, which indicated high diversity and stable condition. The highest value of H' index was observed at CA Bali, while the lowest value was found at NCA Lombok. The Evenness Index ranged from 0.61203 to 0.77889 in all sites, with the lowest value at NCA Bali and the highest one at CA Lombok. This Evenness values indicate that the relative abundance was equal among the sites and was evenly distributed. Meanwhile, the Dominancy Index ranged from 0.06404 to 0.102107 in all sites, with the NCA Bali having the highest value and the CA Bali having the lowest value. The values of the Dominancy Index in this study indicate that there was no species dominating in abundance among the sites. The low stress value of nMDS ordination (0.1356) indicates that the ordination was a good representation of the underlying dissimilarity values between benthic faunal in two different seagrass meadows. The nMDS result (Figure 4.) shows that there was a clear distinction and differentiation in benthic fauna assemblages between conservation areas (CA) and non-conservation areas (NCA), both in Bali and Lombok. However, there was high similarity for conservation areas (CA) in each site, both in Bali and Lombok, gathered in one group (LBL, TTR, GLW, GSL). However, there was high similarity for conservation areas (CA) in each site, both in Bali and Lombok, gathered in one group (LBL, TTR, GLW, GSL).

Furthermore, the cluster analysis also confirmed the clear distinction of benthic fauna assemblages between the two categories of seagrass meadows in this study (Figure 5.). Bray-Curtis dendrogram cluster analysis shows there was two groups that divided the meadows (CA and NCA). The first group consisted of TJK, SND, GKD, and SMH, was categorized as NCA. Meanwhile, the second group, categorized as CA, consisted of TTR, LBL, GLW, and GSL and was characterized by having highest similarity.

According to the similarity of the percentage (SIMPER) analysis (Table 6.), valued at 56.42 % of dissimilarity between the sites, there was no species contributing more than 10% in the result analysis (Table 6.). *Diadema setosum* was the species with the highest contribution (8.966 %), followed by *Alpheus* sp. (7.476 %), *Tellina* sp. (7.136 %), *Cerithium balteatum* (6.12

%), *Ampelisca* sp. (6.074 %), and the rest with less than 6 %. According to the SIMPER analysis, *D. setosum* had the highest percentage of the contribution to dissimilarity between the sites in Bali and Lombok. *D. setosum*, a sea urchin with a black and long spine and distinct white dots on its body, is commonly found widespread along the Indo-Pacific regions and is thought to be ecologically important in shallow subtidal ecosystems. The study about associated *D. setosum* has been reported on

seagrass ecosystems in several places in Indonesia (Muzaki *et al.*, 2019; Susetya *et al.*, 2019; Moka *et al.*, 2021; Freitas *et al.*, 2022). In seagrass, *D. setosum* was reported to feeding crustaceans and foraminifera, and controlling algal coverage by acting as grazers (Ishikawa *et al.*, 2016; Luza and Malay, 2019). Thus, the *D. setosum* may play an important role as keystone species in seagrass ecosystems, especially in controlling epiphytic lamination on seagrass leaves.

Table 4. Result summary of PERMANOVA in examining benthic fauna assemblages on seagrass meadows between sites in Bali and Lombok

Factor	Test Pairs	P
Between sites	NCA Bali - CA Bali	0.0001*
	NCA Lombok - CA Lombok	0.0001*
	NCA Bali - NCA Lombok	0.0145*
	CA Bali - CA Lombok	0.0017**
	NCA Bali - CA Lombok	0.0001*
	NCA Lombok - CA Bali	0.0001*

Note: Comparisons were made using Bray-Curtis similarity matrices based on untransformed percentage cover data with the number of permutations was 9999 in all cases (*= $P < 0.01$; **= $P < 0.05$).

Table 5. Result of diversity indices consisted of Shannon-Wiener Index (H'), Evenness Index (E), and Dominancy Index (C) on benthic fauna assemblages between seagrass meadows between sites in Bali and Lombok

Sites	Shannon-Wiener (H')	Evenness (E)	Dominancy (C)
NCA Bali	2.1819	0.61203	0.102107
CA Bali	2.5802	0.74786	0.06404
NCA Lombok	2.0553	0.66669	0.095797
CA Lombok	2.5584	0.77889	0.064125

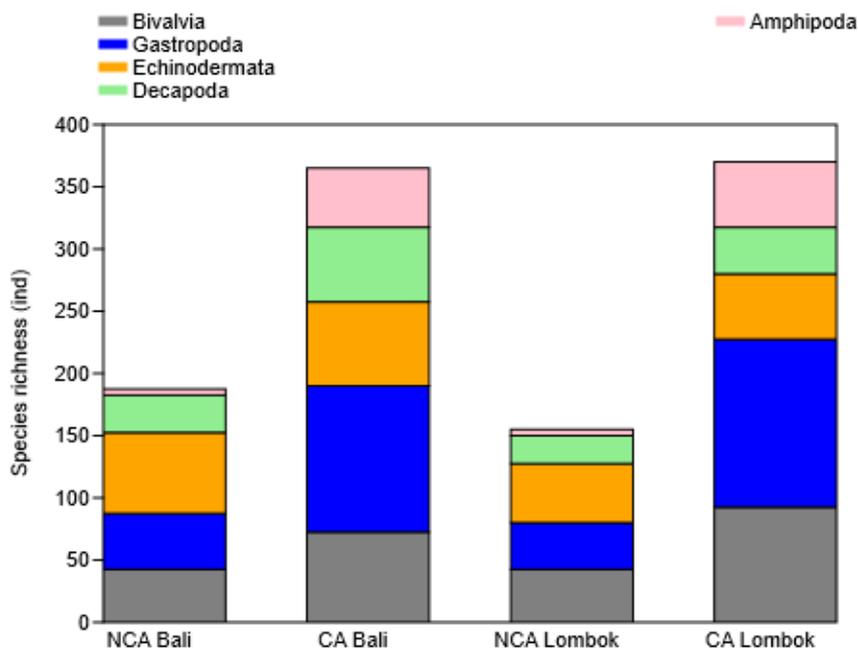


Figure 3. Species richness of benthic fauna in conservation area (CA) and non-conservation area (NCA) at Bali and Lombok

The second highest proportion of species based on the SIMPER analysis was *Alpheus* sp. These burrowing alpheid shrimps can be commonly found foraging on seagrass leaves (Palomar *et al.*, 2004). Additionally, *Alpheus* sp. plays the role of collecting seagrass leaves/litter materials and preventing the export of organic materials from seagrass meadows.

Therefore, in terms of nutrient cycling, these burrowing shrimps (*Alpheus* sp.) may tighten the pathways between seagrass and decomposition process, as this material (*i.e.*, seagrass leaf, organic litter) decomposes until they become available again for the uptake of seagrass roots (Vonk *et al.*, 2008).

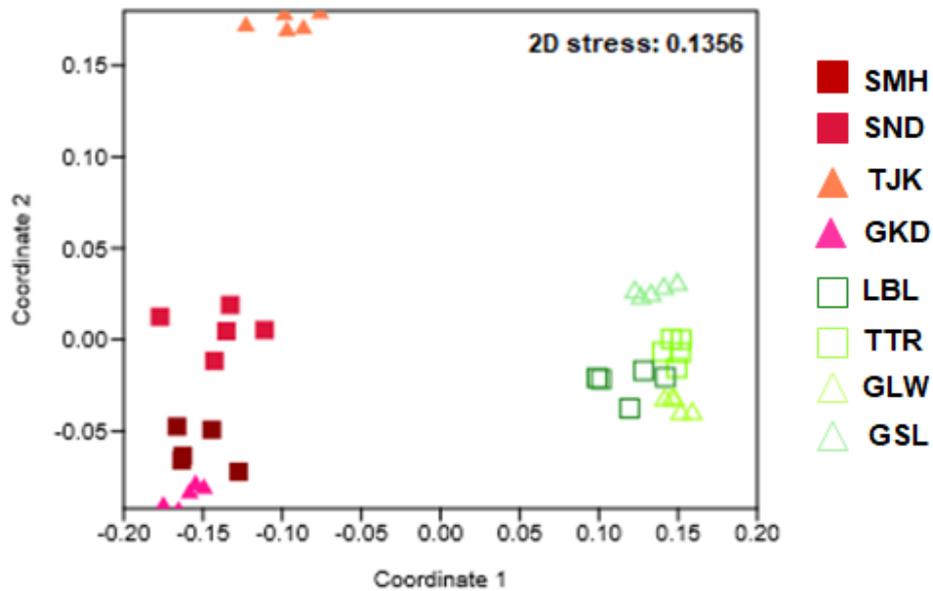


Figure 4. Two dimensional nMDS plot ordination based on benthic fauna assemblages between group of NCA (SMH, SND, TJK, GKD) and CA (LBL, TTR, GLW, GSL), both in Bali and Lombok. Ordination was based on Bray-Curtis matrices from untransformed percentage coverage data.

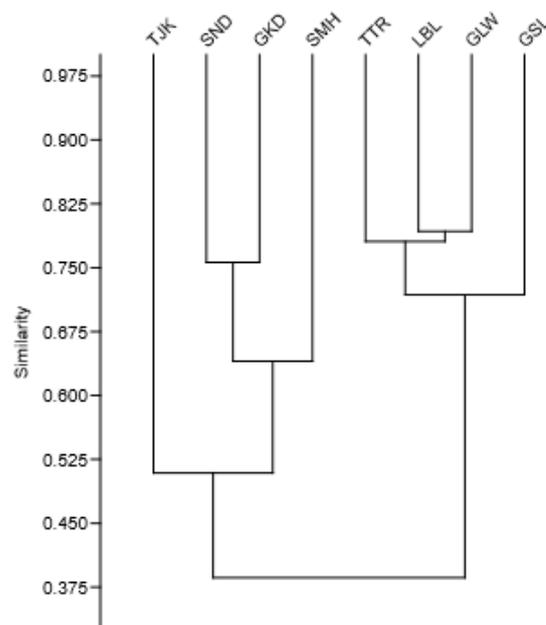


Figure 5. Dendrogram of cluster analysis in benthic fauna assemblages at each site (sites abbreviation in Table 1) based on Bray-Curtis index

Table 6. Result of similarity of percentage (SIMPER) on benthic fauna assemblages between seagrass meadows between sites in Bali and Lombok (based on average dissimilarity 56.42 % with Bray-Curtis matrices)

Taxon	Average dissimilarity	Mean Abundance	Contribution %	Cumulative %
<i>Diadema setosum</i>	5.059	19.375	8.966	8.966
<i>Alpheus</i> sp.	4.218	20.625	7.476	16.44
<i>Tellina</i> sp.	4.026	14.375	7.136	23.58
<i>Cerithium balteatum</i>	3.453	19.375	6.12	29.7
<i>Ampelisca</i> sp.	3.427	15.625	6.074	35.77
<i>Cerithium punctatum</i>	3.258	14.375	5.774	41.55
<i>Callocardia</i> sp.	3.207	18.75	5.684	47.23

Conclusion

Alteration in the composition of community or species assemblages have been and continue to be subject of intense interest, especially in the different characteristic's biodiversity spots. This study revealed that conservation area (CA) was exhibited by greater abundance of associated fauna in seagrass beds than those in non-conservation area (NCA), which was also confirm our hypothesis. Different anthropogenic pressure and characteristics of sediment could be a key point that makes a significant difference between the prospected sites. In conclusion, we addressed that the result of this study may be important in terms of seagrass management, particularly in effectiveness of conservation area to protects the biodiversity within. For further studies, we addressed the issues of climate change in seagrass ecosystems and multi decadal data of associated fauna biodiversity that must be taken in the future studies to conserve and protect our seagrass ecosystems as a whole.

Acknowledgments

The authors would like to express the utmost gratitude to the West Bali National Park (S.2044/T.16/TU/Kons/10/2019) and Lombok Province (Dinas Kelautan dan Perikanan Provinsi Lombok; Dinas Kelautan dan Perikanan Kabupaten Lombok Timur) for the permit, access, and enduring support to the researchers. The authors would also like to thank the reviewers for their invaluable comments to improve the quality of the manuscripts.

References

Al-Asif, A., Hamli, H., Kamal, A.H.M., Idris, M.H., Gerusu, G.J., Ismail, J.B. & Karim, N.U. 2020. Benthic macrofaunal assemblage in Seagrass-Mangrove complex and adjacent ecosystems of Punang-Sari Estuary, Lawas, Sarawak, Malaysia. *Biodiversitas*, 21(10): 4606–4615. <https://doi.org/10.13057/biodiv/d211019>.

Alsaffar, Z., Pearman, J.K., Curdia, J., Ellis, J., Calleja, M.L., Ruiz-Compean, P., Roth, F., Villalobos, R., Jones, B.H., Moran, X.A.G. & Carvalho, S., 2020. The role of seagrass vegetation and local environmental conditions in shaping benthic bacterial and macroinvertebrate communities in a tropical coastal lagoon. *Scientific reports*, 10(1): 13550.

Ambo-rape, R. 2016. Differences in Richness and Abundance of Species Assemblages in Tropical Seagrass Beds of Different Structural Complexity. *J. Environ. Sci. Technol.*, 9(3): 246-256. <https://doi:10.3923/jest.2016.246.256>.

Anderson, M.J. & Walsh, D.C.I. 2013. Permanova, Anosim, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing?. *Ecol. Monogr.*, 83(4): 557-574. <https://doi.org/10.1890/12-2010.1>.

Anderson, M.J. 2017. Permutational Multivariate Analysis of Variance (Permanova). *Wiley StatsRef: Statistics Reference Online*. P.1–15. <https://doi.org/10.1002/9781118445112.stat07841>.

Atmaja, P.S.P., Bengen, D.G. & Madduppa, H.H. 2021. The second skin of seagrass leaves: A comparison of microalgae epiphytic communities between two different species across two seagrass meadows in lesser sunda islands. *Tropical Life Sci. Res.*, 32(2): 97–119. <https://doi.org/10.21315/tlsr2021.32.2.7>.

Barbier, E., Hacker, S., Kennedy, C., Koch, E., Stier, A. & Silliman, B. 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.*, 81(2): 169–193. <https://doi.org/10.1890/10-1510.1>.

Barnes, R.S.K. 2021. Patterns of seagrass macrobenthic biodiversity in the warm-

- temperate Knysna estuarine bay, Western Cape: a review. *Aquatic Ecol.*, 55(2): 327-345. <https://doi.org/10.1007/s10452-021-09848-3>.
- Beisel, J.N., Usseglio-Polatera, P., Bachmann, V. & Moreteau, J.C. 2003. A comparative analysis of evenness index sensitivity. *Int. Rev. Hydrobiol.*, 88(1): 3–15. <https://doi.org/10.1002/iroh.200390004>.
- Blake, R.E., Duffy, J.E. & Richardson, J.P. 2014. Patterns of seagrass community response to local shoreline development. *Est. Coasts*, 37(6): 1549–1561. <https://doi.org/10.1007/s12237-014-9784-7>.
- Bououarour, O., Boutoumit, S., El Kamcha, R. & Bazairi, H. 2021. Latitudinal Variation into the Macrofaunal Assemblages Associated to *Zostera noltei* Seagrass along the Atlantic Coast of Morocco. *Int. J. Zool.*, 2021: p.9199654. <https://doi.org/10.1155/2021/9199654>.
- Brodersen, K.E. & Kühl, M. 2022. Effects of epiphytes on the seagrass phyllosphere. *Frontiers Mar. Sci.*, 9: p.821614. <https://doi.org/10.3389/fmars.2022.821614>.
- Brun, F.G., Cobo-Díaz, J.F., González-Ortiz, V., Varela, J.L., Pérez-Lloréns, J.L. & Vergara, J.J. 2021. Seagrass patch complexity affects macroinfaunal community structure in intertidal areas: An in situ experiment using seagrass mimics. *Diversity*, 13(11): p.572. <https://doi.org/10.3390/d13110572>.
- Cadier, C. & Frouws, A. 2019. Experimental harvest in a tropical seagrass meadow leads to shift in associated benthic communities. *Community Ecol.*, 20(2): 138–148. <https://doi.org/10.1556/168.2019.20.2.4>.
- Cavalcante, L.L., Barroso, C.X., Carneiro, P.B.D.M. & Matthews-Cascon, H. 2019. Spatiotemporal dynamics of the molluscan community associated with seagrass on the western equatorial Atlantic. *J. Mar. Biol. Assoc. U.K.*, 99(6): 1285–1294. <https://doi.org/10.1017/S0025315419000183>.
- Cheng, C.C. 2004. Statistical approaches on discriminating spatial variation of species diversity. *Bot. Bull. Acad. Sin.*, 45(4): 339–346.
- Freitas, R.D.C., Suryani, S.A.M.P. & Kawan, I.M. 2022. Community Structure of Sea Urchin (Echinoidea) in Seagrass Ecosystem at Batu Jimbar Beach Sanur Denpasar. *Sustain. Envir. Agr. Sci.*, 6(2): 119–133. <https://doi.org/10.22225/seas.6.2.4976.119-133>.
- Gartner, A., Tuya, F., Lavery, P. S. & McMahon, K. 2013. Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *J. Exp. Mar. Biol. Ecol.*, 439: 143-151. <https://doi.org/10.1016/j.jembe.2012.11.009>.
- Gibert, C. & Escarguel, G. 2019. PER-SIMPER—A new tool for inferring community assembly processes from taxon occurrences. *Global Ecol. Biogeography*, 28(3): 374–385. <https://doi.org/10.1111/geb.12859>.
- Gladstone-Gallagher, R.V., Hughes, R.W., Douglas, E.J., & Pilditch, C.A. 2018. Biomass-dependent seagrass resilience to sediment eutrophication. *J. Exp. Mar. Biol. Ecol.*, 501: 54-64.
- Gräfnings, M.L.E., Govers, L.L., Heusinkveld, J.H.T., Silliman, B.R., Smeele, Q., Valdez, S.R. & van der Heide, T. 2023. Macrozoobenthos as an indicator of habitat suitability for intertidal seagrass. *Ecol. Indic.*, 147: p.109948. <https://doi.org/10.1016/j.ecolind.2023.109948>.
- Griffiths, L., Andradi-Brown, D., Ahmadi, G., Purwanto, P., Ahmad, A., Bryan-Brown, D. & Brown, C. 2022. Linking historical fishing pressure to biodiversity outcomes to predict spatial variation in Marine Protected Area performance. *Mar. Policy*, 139: p.105024. <https://doi.org/10.1016/j.marpol.2022.105024>.
- Hartati, R., Zainuri, M., Ambariyanto, A., Trianto, A. & Mahendrajaya, R.T., 2018, March. Similarity microalgal epiphyte composition on seagrass of *Enhalus acoroides* and *Thalasia hemprichii* from different waters. In *IOP Conference Series: Earth and Environmental Science*, 139(1): p. 012011). IOP Publishing.
- Hernawan, U.E., Rahmawati, S., Ambo-Rappe, R., Sjafrie, N.D., Hadiyanto, H., Yusup, D.S., Nugraha, A.H., La Nafie, Y.A., Adi, W., Prayudha, B. & Irawan, A., 2021. The first nation-wide assessment identifies valuable blue-carbon seagrass habitat in Indonesia is in moderate condition. *Sci. Total Envir.*, 782: p.146818.
- Horinouchi, M. 2007. Distribution patterns of benthic juvenile gobies in and around seagrass habitats: effectiveness of seagrass shelter against predators. *Est. Coast. Shelf Sci.*, 72(4): 657–664. <https://doi.org/10.1016/j.ecss.2006.11.025>.
- Ilias, N., Hwai, A.T.S., Rick, F., Peng, T.C., Nilamani, N., Razalli, N.H. & Yasin, Z. 2021. Diversity of epibenthic intertidal molluscan communities on the seagrass beds of Middle Bank, Penang,

- Malaysia. *Phuket Mar. Biol. Center Res. Bull.*, 78: 39-47.
- Ishikawa, T., Maegawa, M. & Kurashima, A. 2016. Effect of sea urchin (*Diadema setosum*) density on algal composition and biomass in cage experiments. *Plankton Benthos Res.*, 11(4): 112–119. <https://doi.org/10.3800/pbr.11.112>.
- Jiang, Z., Huang, D., Fang, Y., Cui, L., Zhao, C., Liu, S., Wu, Y., Chen, Q., Ranvilage, C.I.P.M., He, J. & Huang, X. 2020. Home for marine species: seagrass leaves as vital spawning grounds and food source. *Front. Mar. Sci.*, 7: 1–9. <https://doi.org/10.3389/fmars.2020.00194>
- John, A., Raveen, B.N., Sheikh, H.I., Kamal, A.H.M., Vhedarajan, B., Pandisamy, R., Sivakumar, K., Anantharaman, P. & Appadoo, C. 2023. Seagrass of Southeast Asia: Challenges, Prospects, and Management Strategies. In: Pathak, B., Dubey, R.S. (eds) *Climate Change and Urban Environment Sustainability. Disaster Resilience and Green Growth*. Springer, Singapore. https://doi.org/10.1007/978-981-19-7618-6_15.
- Kawaroe, M., Nugraha, A.H., Juraij, J., & Tasabaramo, I.A. 2016. Seagrass biodiversity at three marine ecoregions of Indonesia: Sunda Shelf, Sulawesi Sea, and Banda Sea. *Biodiversitas*, 17(2): 585-591. <https://doi.org/10.13057/biodiv/d170228>
- Kelly, B.J., Gross, R., Bittinger, K., Sherrill-Mix, S., Lewis, J.D., Collman, R.G., Bushman, F.D. & Li, H. 2015. Power and sample-size estimation for microbiome studies using pairwise distances and Permanova. *Bioinformatics*, 31(15): 2461–2468. <https://doi.org/10.1093/bioinformatics/btv183>.
- Lefcheck, J.S., Marion, S.R., Lombana, A.V. & Orth, R.J. 2016. Faunal communities are invariant to fragmentation in experimental seagrass landscapes. *PLoS ONE*, 11(5): 1–24. <https://doi.org/10.1371/journal.pone.0156550>.
- Leopardas, V., Uy, W. & Nakaoka, M. 2014. Benthic macrofaunal assemblages in multispecies fi c seagrass meadows of the southern Philippines: Variation among vegetation dominated by different seagrass species. *J. Exp. Mar. Biol. Ecol.*, 457: 71–80. <https://doi.org/10.1016/j.jembe.2014.04.006>.
- Liao, J., Yeh, H., & Mok, H. 2015. Meiofaunal communities in a tropical seagrass bed and adjacent unvegetated sediments with note on sufficient sample size for determining local diversity indices. *Zool. Stud.*, 54(14): 1–10. <https://doi.org/10.1186/s40555-014-0101-8>.
- Lin, J., Huang, Y., Arbi, U.Y., Lin, H., Azkab, M.H., Wang, J., He, X., Mou, J., Liu, K. & Zhang, S. 2018. An ecological survey of the abundance and diversity of benthic macrofauna in Indonesian multispecific seagrass beds. *Acta Oceanologica Sinica*, 37(6): 82–89. <https://doi.org/10.1007/s13131-018-1181-9>.
- Lundquist, C.J., Jones, T.C., Parkes, S.M., & Bulmer, R.H. 2018. Changes in benthic community structure and sediment characteristics after natural recolonisation of the seagrass *Zostera muelleri*. *Sci. Rep.*, 8(1): p.13250.
- Luza, J.C. & Malay, M.C.D. 2019. Feeding preferences of the sea urchin *Diadema setosum* (Leske, 1778) in Taklong Island National Marine Reserve, Guimaras, Philippines. *PeerJ*, 7: e27733v1. <https://doi.org/10.7287/peerj.preprints.27733v1>.
- McDonald, R.B., Moody, R.M., Heck, K.L. & Cebrian, J. 2016. Fish, Macroinvertebrate and Epifaunal Communities in Shallow Coastal Lagoons with Varying Seagrass Cover of the Northern Gulf of Mexico. *Est. Coasts*, 39(3): 718–730. <https://doi.org/10.1007/s12237-015-0031-7>.
- Mckenzie, L. & Yoshida, R. 2009. Seagrass-Watch: Proceedings of a workshop for monitoring seagrass habitats in tropical Queensland. *Proc. Workshop for Monitoring Seagrass Habitats in Indonesia*. June, 46.
- Miyajima, T., Hamaguchi, M. & Hori, M. 2022. Evaluation of the baseline carbon sequestration rates of Indo-Pacific temperate and tropical seagrass meadow sediments. *Ecolog. Res.*, 37(1): 9–20. <https://doi.org/10.1111/1440-1703.12263>.
- Moka, W., Inaku, D.F., Rais, M. & Moka, W. 2021. Sea urchin identification in Kodingareng Lompo waters, Spermonde Archipelago. *IOP Conf. Ser. Earth Environ. Sci.*, 777(1): p.012015. <https://doi.org/10.1088/1755-1315/777/1/012015>.
- Murphy, C.E., Orth, R.J. & Lefcheck, J.S. 2021. Habitat Primarily Structures Seagrass Epifaunal Communities: a Regional-Scale Assessment in the Chesapeake Bay. *Est. Coasts* 44: 442–452. <https://doi.org/10.1007/s12237-020-00864-4>
- Muzaki, F.K., Setiawan, E., Insany, G.F.A., Dewi, N.K. & Subagio, I.B. 2019. Community structure of

- echinoderms in seagrass beds of pacitan beaches, East Java, Indonesia. *Biodiversitas*, 20(7): 1787–1793. <https://doi.org/10.13057/biodiv/d200701>.
- Nakamoto, K., Hayakawa, J., Kawamura, T., Ohtsuchi, N., Yamada, H., Kitagawa, T. & Watanabe, Y. 2019. Seasonal fluctuation in food sources of herbivorous gastropods in a subtropical seagrass bed estimated by stable isotope analysis. *J. Mar. Biol. Assoc. U.K.*, 99(5): 1119–1125. <https://doi.org/10.1017/S0025315418001108>.
- Nakaoka, M. 2005. Plant-animal interactions in seagrass beds: Ongoing and future challenges for understanding population and community dynamics. *Population Ecol.*, 47(3): 167–177. <https://doi.org/10.1007/s10144-005-0226-z>.
- Noisette, F., Depetris, A., Kühl, M. & Brodersen, K.E. 2020. Flow and epiphyte growth effects on the thermal, optical and chemical microenvironment in the leaf phyllosphere of seagrass (*Zostera marina*). *J. Royal Soc. Interface*, 17(171): p.20200485.
- Ontoria, Y., Gonzalez-Guedes, E., Sanmartí, N., Bernardeau-Esteller, J., Ruiz, J. M., Romero, J., & Pérez, M. 2019. Interactive effects of global warming and eutrophication on a fast-growing Mediterranean seagrass. *Mar. Environ. Res.*, 145: 27-38.
- Palomar, N.E., Juinio-Meñez, M.A. & Karplus, I. 2004. Feeding habits of the burrowing shrimp *Alpheus macellarius*. *J. Mar. Biol. Assoc. U.K.*, 84(6): 1199–1202. <https://doi.org/10.1017/S0025315404010641h>
- Park, J.M., Kwak, S.N. & Riedel, R. 2020. Crustacean decapod assemblage associated with seagrass (*Zostera marina*) beds in Southern waters of Korea. *Diversity*, 12(3): 11–13. <https://doi.org/10.3390/d12030089>.
- Pazzaglia J, Santillán-Sarmiento A, Helber SB, Ruocco M, Terlizzi A, Marín-Guirao L and Procaccini G. 2020. Does Warming Enhance the Effects of Eutrophication in the Seagrass *Posidonia oceanica*? *Front. Mar. Sci.* 7: p.564805. <https://doi.org/10.3389/fmars.2020.564805>
- Polunin, N.V.C., Halim, M.K. & Kvalvågnaes, K. 1983. Bali Barat: An Indonesian marine protected area and its resources. *Biological Conserv.*, 25(2): 171–191. [https://doi.org/10.1016/0006-3207\(83\)90059-9](https://doi.org/10.1016/0006-3207(83)90059-9).
- Purnomo, H.K., Yusniawati, Y., Putrika, A., Handayani, W. & Yasman. 2017. Keaneekaragaman spesies lamun pada beberapa ekosistem padang lamun di Kawasan Taman Nasional Bali Barat. *Pros. Sem. Nas. Masy. Biodiv. Indon.*, 3: 236–240. <https://doi.org/10.13057/psnmbi/m030213>.
- Rajan, R., Paramasivam, K., Shrinivaasu, S., Venkatraman, K., Padmanaban, P., Surendar, C., Kumar, R., & Vanishree, J. 2017. Fauna (Epibenthic and Epifauna) Associated with Sea Grass Ecosystems in Palk Bay and Gulf of Mannar. *Zoological Survey of India*. 131 pp
- Ramesh, C. & Mohanraju, R. 2020. Seagrass ecosystems of Andaman and Nicobar Islands: Status and future perspective. *Environmental and Earth Sci. Res. J.*, 7(4): 169-174. <https://doi.org/10.18280/eesrj.070407>.
- Rueda, J.L., Marina, P., Urra, J. & Salas, C. 2009. Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea). *J. Mar. Biol. Assoc. U.K.*, 89 (7): 1319–1330. <https://doi.org/10.1017/S0025315409000289>.
- Sahidin, A., Zahidah, Herawati, H., Wardiatno, Y. & Partasasmita, R. 2018. Macrozoobenthos as bioindicator of ecological status in Tanjung Pasir Coastal, Tangerang District, Banten Province, Indonesia. *Biodiversitas*, 19(3): 1123–1129. <https://doi.org/10.13057/biodiv/d190347>.
- Sanmartí, N., Solé, L., Romero, J. & Pérez, M. 2018. Seagrass-bivalve facilitative interactions: Trait-mediated effects along an environmental gradient. *Mar. Environ. Res.*, 133: 99–104. <https://doi.org/10.1016/j.marenvres.2017.12.002>.
- Seitz, R.D., & Ewers Lewis, C.J. 2018. Loss of seagrass results in changes to benthic infaunal community structure and decreased secondary production. *Bull. Mar. Sci.*, 94(4): 1273-1292. <https://doi.org/10.5343/bms.2017.1011>
- Stark, K.A., Thompson, P.L., Yakimishyn, J., Lee, L. & O'Connor, M.I. 2018. Regional connectivity, local environmental conditions, and biotic interactions jointly structure a temperate seagrass epifaunal metacommunity. *BioRxiv*, p.482406.
- Su, Z., Qiu, G., Fan, H., & Fang, C. 2020. Seagrass beds store less carbon but support more macrobenthos than mangrove forests. *Mar. Environ. Res.*, 162: p.105162. <https://doi.org/10.1016/j.marenvres.2020.105162>

- Susetya, I.E., Wahyuni, S., Fadhilah, A., Harahap, Z.A., Yusni, E. & Saridu, S.A. 2019. Community structure of echinoderms in seagrass ecosystem of Pandaratan Beach, Tapanuli Tengah Regency, North Sumatera. *IOP Conference Series: Earth and Environmental Science*, 260(1): p.012107. <https://doi.org/10.1088/1755-1315/260/1/012107>.
- Syukur, A., Hidayati, B.N., Idrus, A. & Zulkifli, L. 2021. The suitability of seagrass ecological function for the survival of the bivalvia on the East Coast of Lombok, Indonesia. *IOP Conf. Ser. Earth Environ. Sci.*, 712(1): p.012033. <https://doi.org/10.1088/1755-1315/712/1/012033>.
- Tasabaramo, I.A & Nugraha, A.H. 2023. Abundance and Biodiversity of Benthic Infauna at Seagrass Ecosystems in Three Small Islands of Northern Papua, Indonesia: Liki Island, Meossu Island, and Befondu Island. *IOP Conf. Ser. Earth Environ. Sci.*, 1148(1): p.012022. <https://doi.org/10.1088/1755-1315/1148/1/012022>.
- Trannum, H.C., Raymond, C., Næss, R., Borgersen, G., Gunnarsson, J.S. & Schaanning, M.T. 2021. Long-term response of marine benthic fauna to thin-layer capping with powdered activated carbon in the Grenland fjords, Norway. *Sci. Total Environ.*, 776(0349): p.145971. <https://doi.org/10.1016/j.scitotenv.2021.145971>.
- Turnbull, J.W., Shah Esmaeili, Y., Clark, G.F., Figueira, W.F., Johnston, E.L. & Ferrari, R. 2018. Key drivers of effectiveness in small marine protected areas. *Biodiversity Conserv.*, 27(9): 2217–2242. <https://doi.org/10.1007/s10531-018-1532-z>.
- Unsworth, R.K., Nordlund, L.M. & Cullen-Unsworth, L.C. 2019. Seagrass meadows support global fisheries production. *Conserv. Letters*, 12(1): e12566. <https://doi.org/10.1111/conl.12566>.
- Valdez, S.R., Shaver, E.C., Keller, D.A., Morton, J.P., Zhang, Y.S., Wiernicki, C., Chen, C., Martinez, C. & Silliman, B.R. 2021. A survey of benthic invertebrate communities in native and non-native seagrass beds in St. John, USVI. *Aquat. Bot.*, 175: p.103448. <https://doi.org/10.1016/j.aquabot.2021.103448>.
- Vian, L.W., Nilamani, N., Sharuddin, S.F.F., Woo, S.P., Ilias, N., Yasin, Z. & Hwai, A.T.S. 2022. Diversity and distribution of molluscs (Gastropoda and Bivalvia) in the seagrass beds at Pulau Gazumbo, Penang, Malaysia. *J. Survey in Fish. Sci.*, 9(1): 79–95. <https://doi.org/10.18331/SFS2022.9.1.7>.
- Voigt, E.P. & Hovel, K.A. 2019. Eelgrass structural complexity mediates mesograzers herbivory on epiphytic algae. *Oecologia*, 189: 199–209. <https://doi.org/10.1007/s00442-018-4312-2>.
- Vonk, J.A., Kneer, D. & Stapel, J. 2008. Shrimp burrow in tropical seagrass meadows: An important sink for litter. *Est. Coast. Shelf Sci.*, 79(1): 79–85. <https://doi.org/10.1016/j.ecss.2008.03.003>.
- Wagey, B.T., Kreckhoff, R.L. & Bucol, A.A. 2017. Comparison of abundance and diversity of benthic macroinvertebrates between disturbed and non-disturbed seagrass-algal beds in central. *AACL Bioflux*, 10 (4): 882–893.
- Whippo, R., Knight, N.S., Prentice, C., Cristiani, J., Siegle, M.R. & O'Connor, M.I. 2018. Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes. *Ecosphere*, 9(11): e02490. <https://doi.org/10.1002/ecs2.2490>.
- Yamada, K., Hori, M., Tanaka, Y., Hasegawa, N. & Nakaoka, M. 2007. Temporal and spatial macrofaunal community changes along a salinity gradient in seagrass meadows of Akkeshi-ko estuary and Akkeshi Bay, northern Japan. *Hydrobiologia*, 592(1): 345–358. <https://doi.org/10.1007/s10750-007-0767-6>.
- Zhang, Q., Kühl, M. & Brodersen, K. E. 2022. Effects of epiphytic biofilm activity on the photosynthetic activity, pH and inorganic carbon microenvironment of seagrass leaves (*Zostera marina* L.). *Frontiers Mar. Sci.*, 9: 835381. <https://doi.org/10.3389/fmars.2022.835381>.