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# Seagrass diversity profile and water quality in some coastal ecosystems in East Nusa Tenggara, Indonesia

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**Abstract.** *Sombo IT, Arisoesilaningsih E, Sartimbul A, Kurniawan N, Retnaningdyah C. 2025. Seagrass diversity profile and water quality in some coastal ecosystems in East Nusa Tenggara, Indonesia. Biodiversitas 26: 5931-5943.* Seagrass ecosystems provide critical services including carbon sequestration, coastal protection, and fisheries support, yet face accelerating degradation from anthropogenic pressures. Indonesia harbors 13 of 60 global seagrass species, with East Nusa Tenggara, Indonesia, supporting exceptional diversity within the Coral Triangle biodiversity hotspot. We analyzed seagrass community structure and water quality relationships across eight coastal locations spanning Timor, Rote, and Alor Islands to establish conservation baselines. Field sampling employed 120 quadrats (1 × 1 m$^2$) along transects at 0.5-2.0 m depths, with species identification following standard taxonomic keys. Seven physicochemical parameters were measured in situ and through laboratory analysis. Eight seagrass species were documented (92% of Indonesia's flora), with coverage ranging from 2,000 to 16,000 individuals/site. Three dominant species, *Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea rotundata*, occurred at all locations with 39% average coverage. Shannon-Wiener Diversity Index ranged from 1.5 to 2.7 (peak at Onan Ana), with 62.5% of sites maintaining moderate-to-high diversity. Critical environmental stress was widespread: nitrate exceeded standards (0.06 mg/L) at all sites by 100-717% (0.12-0.49 mg/L), temperatures surpassed optimal thresholds (> 33°C) at 50% of locations, and hypoxic conditions (DO < 5 mg/L) occurred at 25% of sites. Principal component analysis explained 69.61% of variation, revealing strong negative correlations between nutrients and diversity (orthophosphate-diversity: $r = -0.78$; nitrate-richness: $r = -0.53$). Despite environmental degradation, dominant species demonstrated remarkable resilience. Urgent conservation actions required include: implementing nutrient reduction targeting < 0.06 mg/L nitrate through watershed management, establishing thermal refugia protection at sites maintaining < 30°C, and designating high-diversity locations as genetic reserves for regional restoration programs.

**Keywords:** Alor Island, eutrophication, Rote Island, seagrass, Timor Island

## INTRODUCTION

Seagrass ecosystems, covering about 160,387 km$^2$ globally, are among the world's most valuable coastal habitats, with ecosystem services valued at US$1.9 trillion annually (McKenzie et al. 2020). These marine plants provide critical services such as sediment stabilization, coastal protection, and carbon sequestration at rates 35 times higher than tropical forests (Stankovic et al. 2021; Sogin et al. 2022). Seagrass meadows support over 1000 fish species and various marine invertebrates, acting as important nursery areas that boost fish biomass and economic value for coastal communities through fisheries and aquaculture (Nordlund et al. 2018; McHenry et al. 2021).

Despite their ecological and economic importance, seagrass ecosystems are declining globally, with a 30% cover loss over the past decade (Morris et al. 2022). This degradation results from anthropogenic pressures such as coastal development, pollution, dredging, unsustainable tourism, and climate stressors like ocean warming and acidification (Unsworth et al. 2018). These combined stressors threaten seagrass functions, reducing their role as nursery habitats and destabilizing marine ecosystems (Hastings et al. 2020; Inoue et al. 2021).

Indonesia, home to 13 of the world's 60 seagrass species, faces severe degradation rates of 2-5% annually (Unsworth et al. 2018; Nugraha et al. 2023). Satellite and field data from the LIPI Oceanography Research Center show Indonesian seagrass meadows cover 293,464 hectares (Sjafrie et al. 2018). National assessments reveal moderate ecosystem health, with an average Seagrass Ecological Quality Index (SEQI) of 0.68, though regional conditions vary from poor in Java and Sumatra to good in eastern Indonesia (Hernawan et al. 2021; Dewi et al. 2024). Dominant species *Thalassia hemprichii* (Ehrenb. ex Solms) Asch. and *Enhalus acoroides* (L.f.) Royle, acoroides cover 39% of Indonesian waters, but restoration efforts struggle with survival rates below 30% due to ongoing environmental degradation (Nadiarti et al. 2021).

East Nusa Tenggara represents an exceptional study system within the Coral Triangle biodiversity hotspot. The region supports 12 of Indonesia's 13 seagrass species (92% of national diversity) across three major islands where convergence of Indonesian Throughflow, South Equatorial Current, and Leeuwin Current creates unique oceanographic conditions (Nugraha et al. 2021; Nur et al. 2024). This biodiversity supports 5.3 million coastal residents who depend on seagrass-associated fisheries, yet declining seagrass health has caused 25% reduction in fish catches over five years, severely impacting community welfare (Hilyana et al. 2021). The region experiences intensifying pressures: coastal development increased 300% since 2000, aquaculture operations cover 50,000 hectares, and temperature anomalies exceed 2°C above historical means, creating a natural laboratory for examining multiple stressor interactions.

Current seagrass monitoring initiatives, including Indonesia's Seagrass Ecosystem Rehabilitation and Management Program since 2016, remain limited in effectiveness due to insufficient scientific understanding of environment-ecosystem relationships (Risandi et al. 2023). Previous studies in Indonesian waters provide valuable but fragmented insights: species distribution mapping (Sjafrie et al. 2024), and descriptive surveys (Pelasula et al. 2023). However, these investigations fail to provide quantitative analysis of physicochemical-biological relationships necessary for evidence-based management.

Three key knowledge gaps hinder effective conservation. First, no quantitative thresholds exist for environmental stressors specific to tropical multispecies seagrass, with existing standards based on temperate or single-species systems (Viana et al. 2020). Second, most research focuses on single stressor-response relationships, neglecting the combined, often synergistic effects of multiple stressors (Bass et al. 2024). Third, the lack of integrated physicochemical monitoring and detailed community assessments prevents the establishment of baseline conditions and management targets for Indonesia's biodiverse seagrass regions (Hernawan et al. 2021). Without these, managers cannot develop early warning systems or adaptive protocols for ecosystems nearing tipping points.

This study addresses these gaps by analyzing seagrass community structure and water quality relationships across eight coastal locations spanning Timor, Rote, and Alor islands in East Nusa Tenggara. We test three specific hypotheses: (H1) Seagrass diversity decreases along nutrient gradients with threshold responses at established eutrophication limits (0.06 mg/L nitrate); (H2) Temperature stress above 33°C significantly reduces species richness and shifts communities toward thermally tolerant species; (H3) Multiple stressor interactions (nutrients × temperature × dissolved oxygen) explain more variance in community structure than individual parameters alone.

Through integrated analysis of seven physicochemical parameters and comprehensive diversity metrics across 120 sampling plots, this research provides the first quantitative framework linking environmental conditions to seagrass community patterns in the Indo-Pacific's biodiversity center. The significance extends beyond regional assessment—by establishing dose-response relationships and environmental thresholds, results enable predictive modeling of ecosystem trajectories under climate change scenarios. This evidence-based approach directly informs adaptive management strategies, contributing to global seagrass conservation while supporting local livelihoods dependent on these critical marine ecosystems.

## MATERIALS AND METHODS

### Study area

The study was conducted on three islands in the East Nusa Tenggara Province, Indonesia (Table 1): Timor Island (Pasir Panjang Beach, Onan Ana Beach, Tablolong Beach, and Teluk gurita Beach), Rote Island (Oenggaut Beach and Oeseli Beach) and Alor Island (Mali Selatan and Mali Utara). Sampling was carried out from July to November 2023 (Figure 1).

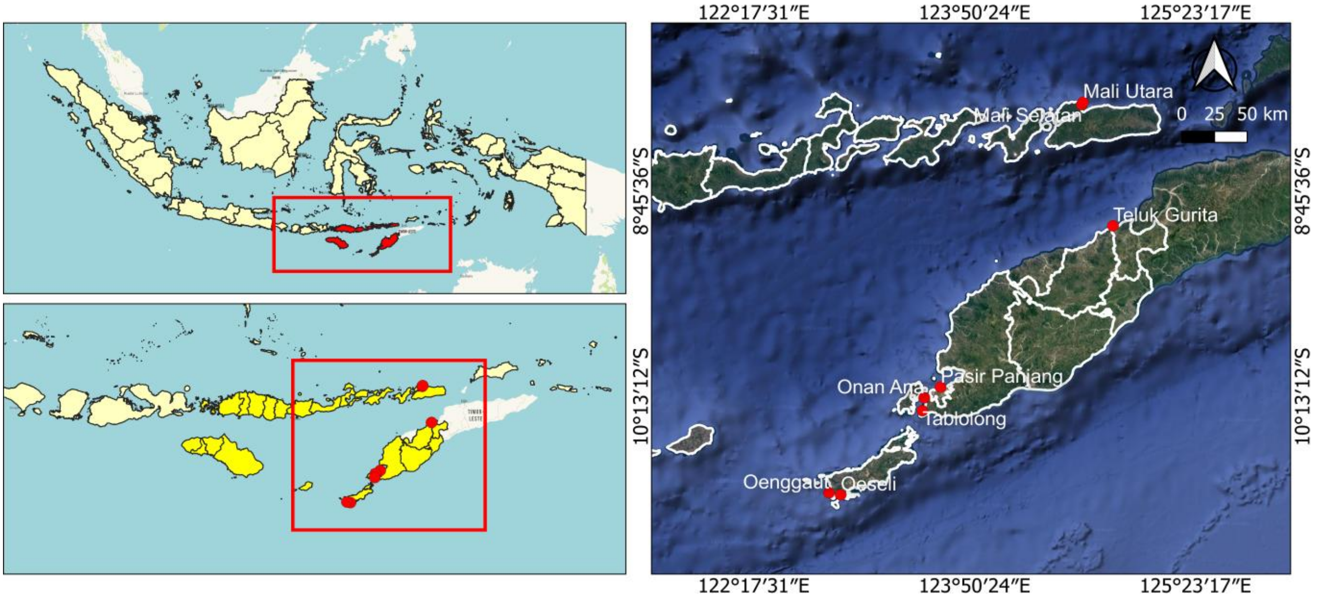


**Figure 1.** Maps of the study area in some coastal of East Nusa Tenggara, Indonesia

**Table 1.** Description of research stations in East Nusa Tenggara, Indonesia

| Island | Station (beach) | Coordinate | Description |
|---|---|---|---|
| Timor | Pasir Panjang | 10°09'02.2"S, 123°36'08.3"E | This beach is located in Kupang Bay, with the current conditions that have been built many hotels, restaurants, seaweed cultivation and high population activity. |
| | Onan Ana | 10°13'35.3"S, 123°29'19.0"E | This beach is located in Bolok Village, West Kupang District, Kupang District. Residents' activities include seaweed farming, pearl farming by PT. TOM to the east, and a Steam Power Plant (PLTU) to the west. |
| | Tablolong | 10°19'04.7"S, 123°28'28.9"E | This beach is located on the west side of Timor Island, where various activities are carried out such as seaweed cultivation, tourist attractions, a place for residents to park their boats, and residents are often seen trading oil and diesel with sea cucumber fishing boats belonging to the Bajo Tribe. |
| | Teluk Gurita | 09°00'21.7"S, 124°48'39.8"E | Teluk Gurita beach is located in the northern part of Belu District, this beach is a tourist spot, and there is a harbor, local residents also use the sea to search for fish, octopus, and another marine biota. |
| Rote | Oeseli | 10°54'46.4"S, 122°54'06.8"E | Oeseli Beach is located south of Rote Island, where there are local activities such as seaweed cultivation, sea cucumber cultivation, and the construction of an abandoned pier. |
| | Oenggaut | 10°53'57.4"S, 122°49'13.8"E | This beach is located in the west of Rote Island, where there are activities such as seaweed cultivation, tourism and surfing. |
| Alor | Mali Selatan | 08°08'37.3"S, 124°35'32.3"E | Mali Selatan Beach is a natural beach and has become a tourist beach due to the presence of dugongs and the activities of local residents such as fishermen. |
| | Mali Utara | 08°07'33.8"S, 124°36'07.7"E | On the coast of Mali Utara there is an airport, the coastal ecosystem is degraded, and there is sand mining. |

### Sampling design and procedures

The ex post facto design with nested hierarchical sampling included: (1) spatial replication across eight sites, (2) within-site replication using three transects per site (minimum distance of 50 m), (3) plot-level replication with five 1 × 1 $m^2$ quadrats per transect, and (4) measurement replication with three readings per parameter. This design resulted in 120 sampling plots (8 sites × 3 transects × 5 plots), which provided robust statistical power with adequate pseudoreplication control (English et al. 1997).

Identification of seagrass species was performed using a standard morphological approach using taxonomic keys from "A Guide to Tropical Seagrasses of the Indo-West Pacific" (Waycott et al. 2004), " Field Guide to Seagrasses of the Red Sea" (El Shaffai 2015) and “Seagrass Educator Handbook” (McKenzie 2008) In each plot, each species was identified based on morphology. Individual shoot counts were performed to estimate abundance, while percentage cover was assessed using a visual estimation technique calibrated with the point-intercept method.

The physicochemical parameters measured included temperature (degrees Celsius), turbidity (NTU), salinity (ppt), dissolved oxygen (mg/L), pH, nitrate (mg/L), and orthophosphate (mg/L). Temperature, salinity, DO, turbidity, and pH were measured in situ at each location in triplicate, while nitrate and orthophosphate were analyzed at the Tropical Ecosystem Ecology and Restoration Laboratory, Universitas Brawijaya, East Java, Indonesia.

### Data analysis

Data were analyzed using Microsoft Excel and SPSS. A one-way ANOVA was used to test differences in physicochemical parameters, followed by Tukey HSD for normal data and Games-Howell for non-normal data. Seagrass community structure was analyzed with the Important Value Index (IVI), Shannon-Wiener Diversity Index (H'), Evenness Index (E), Dominance Index (D), and Taxa Richness (S). The relationship between physicochemical parameters and biotic index was analyzed using PCA and Pearson correlation with PAST 16.0 software.

The following is the equation of the biotic index that was measured:

*Importance Value Index (Barnes and Mann 1994)*

The formula used to calculate INP is:

$$IVI = RF + RD$$

Where, IVI: Importance Value Index, RF: Relative Frequency, KR: Relative Density

*Shannon-Wiener Diversity Index (Shannon and Wiener 1949):*

$$H' = -\sum_{i=1}^{s} Pi^2 \log Pi$$

Where, H': Shannon-Wiener Diversity Index, pi: Proportion of the i-th species, ln: Natural logarithm

Pi: Σ ni / N (Calculation of the number of individuals of a species with the total number of species)

Where, H' value criteria according to Wilhm and Dorris (1968): $0 \leq H' \leq 2.302$ (low diversity), $2.302 \leq H' \leq 6.907$ (moderate diversity), $H' \geq 6.907$ (high diversity).

*Dominance Index (D)*

$$Id = N_i(N_i(t-1)) \times N(N-1)$$

Where, D: Simpson's Dominance Index value, Ni: Number of individuals of the i-th species, N: Total number of individuals found

*Uniformity Index / Evenness (E)*

$$E = \frac{H'}{Hmax}$$

Where: E: Uniformity Index, Hmax: 2 Log S, H': Shannon-Wiener Diversity Index value

## RESULTS AND DISCUSSION

### Physicochemical parameters: Environmental stress patterns in the East Nusa Tenggara seagrass ecosystem

Environmental parameters indicated critical stress thresholds exceeded at multiple sites (Table 2). Statistical analysis (One-way ANOVA: $p < 0.05$ for all parameters except salinity) identified three primary stressor categories impacting seagrass. Nutrient stress was the most pervasive, with nitrate concentrations exceeding Indonesian standards (0.06 mg/L) by 100-717% across all sites (0.12-0.49 mg/L). This eutrophication triggers ecological effects, including algal proliferation, reduced light availability, and altered nitrogen cycling through denitrification and DNRA, changing ecosystem function (Moreno-Marín et al. 2016; Liu et al. 2017; Aoki and McGlathery 2018; Jiménez-Ramos et al. 2022).

Thermal stress affected 50% of sites, with four locations exceeding optimal ranges (28-30°C): Mali Utara (35.56±0.51°C), Teluk Gurita (32.13±1.46°C), Mali Selatan (30.13±0.15°C), and Tablolong (30.1±1.13°C). Mali Utara's extreme temperature approaches critical thresholds where photosynthesis-respiration balance collapses, threatening seagrass growth, development, and survival (Collier et al. 2017; Danaraj et al. 2021; Gao et al. 2019; George et al. 2018; Hansen et al. 2022; Pedersen et al. 2016; Said et al. 2021; Walker et al. 2024).

Hypoxic stress occurred at 25% of locations, with Pasir Panjang (4.53±0.05 mg/L) and Teluk Gurita (4.73±0.11 mg/L) falling below the 5 mg/L threshold. These conditions increase sulfide damage to seagrass tissues and produce sub-lethal effects on associated fish populations, disrupting overall ecosystem functioning (Hasler-Sheetal 2023; Montesinos et al. 2016). Critically, multiple stressor convergence created synergistic impacts. Sites experiencing combined stress Mali Utara (thermal + nutrient: 35.56°C + 0.49 mg/L nitrate) and Pasir Panjang (hypoxic + nutrient: 4.53 mg/L DO + 0.36 mg/L nitrate) showed significantly reduced diversity compared to single-stressor sites (ANOVA: $F_{7,16} = 6.23$, $p < 0.001$).

Despite stress conditions, favorable parameters persisted. All locations maintained suitable turbidity (<5 NTU), ensuring optimal light penetration, which is ideal for aquatic biota (Bulmer et al. 2018; Cussioli et al. 2019). pH values (7.79-8.36) supported photosynthesis and may buffer ocean acidification impacts (Camp et al. 2016; Cyronak et al. 2018; Ricart et al. 2021). Salinity (29.03-30.60‰) was below standards (33-34‰) but still within tolerance limits, with species showing osmotic adjustment despite ionic ratio changes affecting metabolism (Garrote-Moreno et al. 2015, 2016; Jespersen et al. 2021; Kongrueang et al. 2018). These conditions were still within the adaptability limits of tropical seagrass (Shen et al. 2022; Webster et al. 2021).

These environmental patterns directly address our hypothesis that multiple stressor interactions drive community structure more strongly than individual parameters, with sites maintaining single favorable conditions supporting higher diversity than those experiencing multiple concurrent stressors.

**Table 2.** Physicochemical water quality profiles in eight ecosystems in the waters of East Nusa Tenggara, Indonesia

| **Locations** | **Chemical parameters** | | | | | **Physical parameters** | |
|---|---|---|---|---|---|---|---|
| | **Orthophosphate (mg/L)** | **Salinity (%)** | **DO (mg/L)** | **pH** | **Nitrate (mg/L)** | **Turbidity (NTU)** | **Water temp. (°C)** |
| Pasir Panjang | **0.09±0.03a** | 30.00±0.50a | 4.53±0.05a | 8.36±0.09c | **0.36±0.06a** | 0.73±0.01c | 27.96±1.00ab |
| Tablolong | **0.04±0.01a** | 30.30±0.57a | 5.60±0.98abc | 7.79±0.08a | **0.19±0.04a** | 1.00±0.21abcd | 30.1±1.13bc |
| Onan Ana | **0.06±0.03a** | 30.00±1.00a | 8.03±0.20c | 7.84±0.19a | **0.21±0.03a** | 0.62±0.01b | 27.66±1.05ab |
| Teluk Gurita | **0.06±0.02a** | 30.43±0.66a | 4.73±0.11a | 8.21±0.19bc | **0.12±0.01a** | 1.24±0.23abcd | **32.13±1,46c** |
| Mali Selatan | **0.07±0.03a** | 29.03±0.45a | 7.90±0.30c | 8.02±0.02abc | **0.14±0.01a** | 0.49±0.02a | 30.13±0.15bc |
| Mali Utara | **0.03±0.01a** | 30.60±0.36a | 5.16±0.47ab | 8.32±0.13c | **0.49±0.49a** | 0.67±0.02bc | **35.56±0.51d** |
| Oenggaut | **0.04±0.01a** | 30.40±0.52a | 6.93±0.32bc | 8.12±0.09abc | **0.26±0.22a** | 0.55±0.06abc | 26.46±1.81a |
| Oeseli | **0.04±0.00a** | 30.00±0.30a | 4.63±0.15a | 7.89±0.13ab | **0.13±0.01a** | 1.48±0.05d | 28.13±1.42ab |
| Indonesian Standard* | – | 33-34 | >5 | 7-8,5 | 0.06 | <5 | 28-30 |
| ASEAN Standard** | 0.015 | – | >4 | – | 0.06 | <5 | 25-32 |
| EPA*** | Vary <10% from natural condition | – | >5 | 6.5-8.5 | Vary <10% from natural condition | – | – |

Note: The bold values exceed the quality standard, The same notation for each parameter shows no significant difference based on the Anova test followed by Tukey HSD (Water Temperature, Salinity, DO, Turbidity, pH) and the Brown Forsythe test followed by Games Howell (Orthophosphate, Nitrate) with α 0.05. *: Seawater quality standards for Marine Biota (PP RI No. 22 of 2021) Attachment VIII, **: ASEAN Marine Water Quality Criteria for the Protection of Aquatic Life, ***: Environmental Protection Authority (EPA): Marine Water Quality Regulations to protect aquatic life, –: There is no standard

## Seagrass community structure: Response to environmental gradients

Eight seagrass species were documented across the study region, representing 92% of Indonesia's seagrass flora and confirming East Nusa Tenggara’s significance as a biodiversity hotspot (Figures 2 and 3). Community structure exhibited clear responses to the environmental stress gradients identified earlier.

Core species resilience emerged as a critical pattern, with three species (*E. acoroides, T. hemprichii, Cymodocea rotundata* Asch. & Schweinf.) maintaining 100% site occupancy despite varying stress levels. This finding parallels observations from comparable tropical systems worldwide. In the Philippines seagrass meadows, Quiros et al. (2017) documented that three core species similarly maintained consistent presence across multiple environmentally stressed sites, while sensitive species disappeared from high stress areas a pattern directly comparable to our East Nusa Tenggara observations. This functional redundancy operates through complementary ecological strategies: *E. acoroides* functions as the highest biomass producer with deep root systems accessing subsurface resources across 0-4 m depths (LaRoche et al. 2019), *T. hemprichii* demonstrates substrate versatility supporting fish spawning habitats at 0-15 m depths (Ling et al. 2018), while *C. rotundata* exhibits broad environmental tolerance to temperature, light, $CO_2$, and air exposure fluctuations (Soonthornkalump et al. 2022; Zhang et al. 2022; Rao et al. 2023).

Stress induced community filtering was evident in species distribution patterns. Sensitive species (*Halophila minor* (Zoll.) Hartog, *Syringodium isoetifolium* (Asch.) Dandy) were conspicuously absent from high-stress sites (Mali Utara, Pasir Panjang), indicating threshold responses to multiple stressor combinations. This biotic homogenization from 8 species at optimal sites to four species at high-stress locations represents a 50% reduction in functional diversity, compromising ecosystem services.

Diversity environment coupling demonstrated that community metrics directly reflected integrated stress levels. Sites with optimal conditions (Onan Ana: DO: 8.03 mg/L, temperature: 27.66°C) supported highest diversity (H': 2.7), while multiple-stress sites exhibited 40-60% lower diversity. Critically, the disconnect between abundance and diversity revealed stress-induced dominance shifts rather than ecosystem collapse. Teluk Gurita maintained maximum biomass (16,000 individuals) through single-species dominance despite moderate diversity (H' = 2.0), while Mali Selatan achieved high diversity (8 species) with lower total abundance (11,000 individuals).

These patterns confirm our hypothesis that environmental stress acts as a community filter, with functional redundancy among core species maintaining ecosystem structure while sensitive species loss indicates approaching ecological thresholds. The persistence of biomass despite diversity decline suggests systems in transition, where ecosystem functions may persist short-term through compensatory growth of tolerant species, but long-term stability remains compromised without the insurance effects of biodiversity.

## Abundance, seagrass diversity index, and seagrass uniformity at each location

A comparison of seagrass diversity index values at eight different locations measured using three methods: HSW (Shannon-Wiener), H Simpson, and H Margalef can be seen in Figure 4. Shannon-Wiener (HSW) index values less than 1.0 indicate low diversity, 1.0-3.0 moderate diversity, and >3.0 high diversity. Onan Ana location showed the highest HSW index value of around 2.7, followed by Tablolong (2.3), Mali Selatan (2.2), and Teluk Gurita (2.0), indicating a moderate level of diversity. Meanwhile, Simpson's H value (range 0-1, where values close to 1 indicate high diversity) was relatively stable across all locations with a range between 0.8 and 1.0, with the highest values found in Oeseli, Oenggaut and Mali Utara, indicating a fairly high level of diversity. For the H Margalef Index (values <2.5 are classified as low diversity), the highest values were found in Mali Selatan at around 1.8 each, while other locations ranged from 1.0 to 1.6, indicating relatively low diversity.

Locations such as Mali Utara, Oenggaut, Oeseli and Pasir Panjang showed lower HSW values of around 1.5-1.8, which are still classified as medium diversity, but these lower values are likely influenced by high human activity around the location and less than optimal air quality. Several studies have shown that locations experiencing high anthropogenic pressure consistently have lower Shannon-Wiener Diversity Index (1.2-1.7) compared to locations with minimal human disturbance (2.0-2.6), indicating the negative impact of human intervention on seagrass ecosystems. Anthropogenic activities such as domestic waste disposal, boat traffic, and tourism activities have been shown to contribute significantly to seagrass diversity through various mechanisms, including physical disturbance of habitat structure, direct damage to vegetation, and changes in air quality. Anthropogenic disturbances also cause homogenization of seagrass-associated fish communities, where more sensitive species are replaced by more disturbance-tolerant generalists, resulting in a decline in the overall functional diversity of the ecosystem.

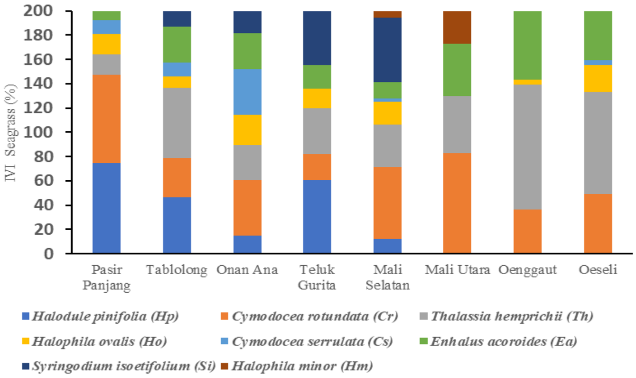


**Figure 2.** Spatial variation of seagrass dominancy in some coastal ecosystems in East Nusa Tenggara, Indonesia

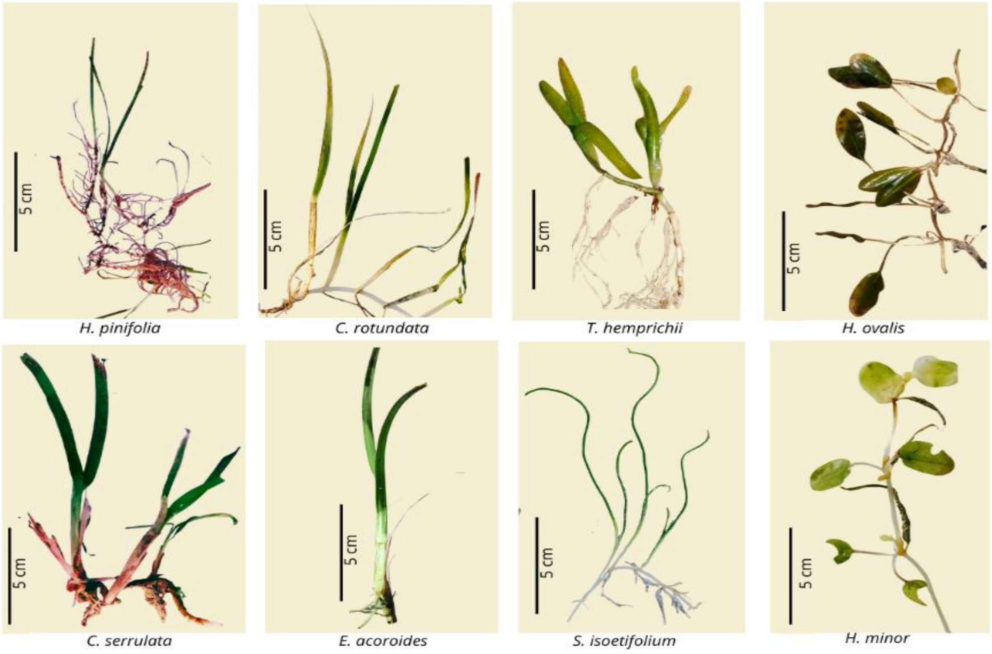


**Figure 3.** The dominant seagrass in some coastal ecosystems in East Nusa Tenggara, Indonesia

Furthermore, human activities contribute to the fragmentation of seagrass meadows, which reduces connectivity between habitats and restricts the movement of organisms, further threatening the ecological sustainability and resilience of seagrass ecosystems to additional environmental stressors such as climate change and sea-level rise (Iacarella et al. 2018; Swadling et al. 2023).

Teluk Gurita exhibits a moderate Shannon-Wiener (HSW) diversity index of approximately 2.0, with a Margalef richness index of approximately 1.2, and a relatively lower Simpson Dominance Index compared to other locations such as Onan Ana and Mali Selatan, indicating the presence of limiting factors affecting the seagrass community structure at the site. Environmental conditions such as sedimentation and anthropogenic disturbance are likely the primary causes of these lower diversity values, consistent with findings that sediment characteristics significantly influence the distribution and morphology of certain seagrass species, including rhizome formation and root growth. Possible eutrophication conditions in Teluk Gurita may suppress the release of dissolved organic carbon from seagrass roots, reducing symbiotic interactions with rhizosphere microorganisms that are essential for nutrient cycling and protection against pathogens. Monitoring of seagrass status descriptors, particularly indicator species such as *T. hemprichii*, demonstrates a strong correlation between environmental parameters and seagrass health and diversity, whereby simultaneous increases in nutrients and sedimentation can decrease species diversity, although some species may exhibit higher tolerance. Spatial patterns of diversity in biological communities often vary as a continuous function of geographic location, reflecting complex environmental gradients, while the use of multiple diversity index provides a more comprehensive perspective on community dynamics because each index emphasizes different aspects of the community (Rattanachot and Prathep 2015; Ali et al. 2018; Jiang et al. 2022a, b).

Overall, the three diversity index indicate that the majority of sample sites have moderate levels of seagrass diversity, consistent with the general pattern found in the Indo-Pacific region. The Shannon-Wiener Diversity Index at most study sites was in the moderate range (1.5-2.7), reflecting a pattern similar to the findings of a comprehensive study analyzing 446 seagrass sites in the Indo-Pacific region, where approximately 60% of sites exhibited diversity levels in the same range. Spatial variation in seagrass diversity at the study sites can be explained by the complex interactions between natural environmental factors and anthropogenic pressures. Natural factors such as substrate type, water depth, and hydrodynamic conditions play a significant role in shaping seagrass community structure, as demonstrated by differences in species composition between estuarine and open-ocean habitats. Meanwhile, anthropogenic pressures such as nutrient pollution, increased turbidity, and direct physical disturbance contribute to diversity variation among sites, with areas experiencing higher stress exhibiting relatively lower diversity index values. Broad-scale mapping and community-based monitoring have helped identify that even extreme natural events such as earthquakes and tsunamis can significantly impact seagrass diversity and abundance, demonstrating the sensitivity of these ecosystems to disturbance and the importance of conservation efforts that consider spatial variation in drivers of diversity (Bramante et al. 2018; Lin et al. 2018; Moseby et al. 2020; Trinh and Takeuchi 2020).

Seagrasses face multiple environmental pressures, and their decline is multifaceted, including increased water turbidity, destructive fishing practices, and nutrient pollution. These factors collectively reduce light availability, cause physical damage, and encourage competitive algal growth, leading to significant declines in seagrass abundance and health. Meanwhile, locations with moderate abundance, such as Pasir Panjang, Tablolong, and Onan Ana, exhibit relatively stable conditions but may still face certain environmental pressures that prevent them from reaching optimal abundance levels. Effective management and mitigation strategies are essential to address these issues and support the recovery and conservation of seagrass ecosystems (Bulmer et al. 2018; Vieira et al. 2020a; Luo et al. 2022; Liu et al. 2023).

The results of the uniformity index were 0.5-0.9, indicating that the evenness was high because the value was close to 1. This is in accordance with the Dominance Index value which shows a value close to 0, namely low dominance. This condition indicates that the seagrass community at the research. The results of the study showed variations in total abundance and Taxa Richness of seagrass across eight different locations. Teluk Gurita exhibited optimal seagrass habitat conditions, with the highest total abundance reaching approximately 16,000 individuals and a Taxa Richness of 6 species. Mali Selatan also exhibited fairly good conditions, with a total abundance of approximately 11,000 individuals and a Taxa Richness of 8 species. Pasir Panjang, Tablolong, and Onan Ana locations had relatively moderate total abundances, ranging from 8,000 to 10,000 individuals, with a Taxa Richness of 6-7 species. Mali Utara, Oengaut, and Oeseli showed lower total abundances, ranging from 2,000 to 4,000 individuals, with a Taxa Richness of 4-5 species. The high abundance and Taxa Richness in Teluk Gurita can be attributed to optimal environmental conditions for seagrass growth. High seagrass abundance (>10,000 individuals/m²) is typically found in locations with good water clarity, stable substrates, and minimal anthropogenic pressure. These conditions support the photosynthesis needs of seagrass, provide a stable environment for growth, and mitigate the negative impacts of human activities (Blake and Duffy 2016; Statton et al. 2018; Vieira et al. 2020b; Zhang et al. 2020).

In contrast, locations with lower seagrass abundance, such as Mali Utara, Oengaut, and Oeseli, have an even distribution of individuals among species, and no species exhibits extreme dominance. High evenness and low dominance can occur due to several interrelated ecological factors. Seagrass ecosystems with high evenness (E>0.7) generally reflect stable habitats that have achieved ecological equilibrium through a long successional process. This stability is supported by mechanisms such as sexual reproduction, phenotypic plasticity, biodiversity, and feedback interactions within the ecosystem. Subsequent restoration efforts have demonstrated the resilience and ability of seagrass ecosystems to maintain ecological equilibrium (Park et al. 2021; Marín-Guirao et al. 2022; Steinfurth et al. 2022; Titioatchasai et al. 2023; da Silva et al. 2024).

### Relationship between physico-chemical parameters and seagrass diversity

The results of the biplot analysis using Principal Component Analysis (PCA) showed a total variance of 69.61%, with Component 1 explaining 50.34% and Component 2 explaining 29.37% of the data variation. Based on this analysis, four distinct ecosystem groups were identified based on air quality characteristics and seagrass community structure.

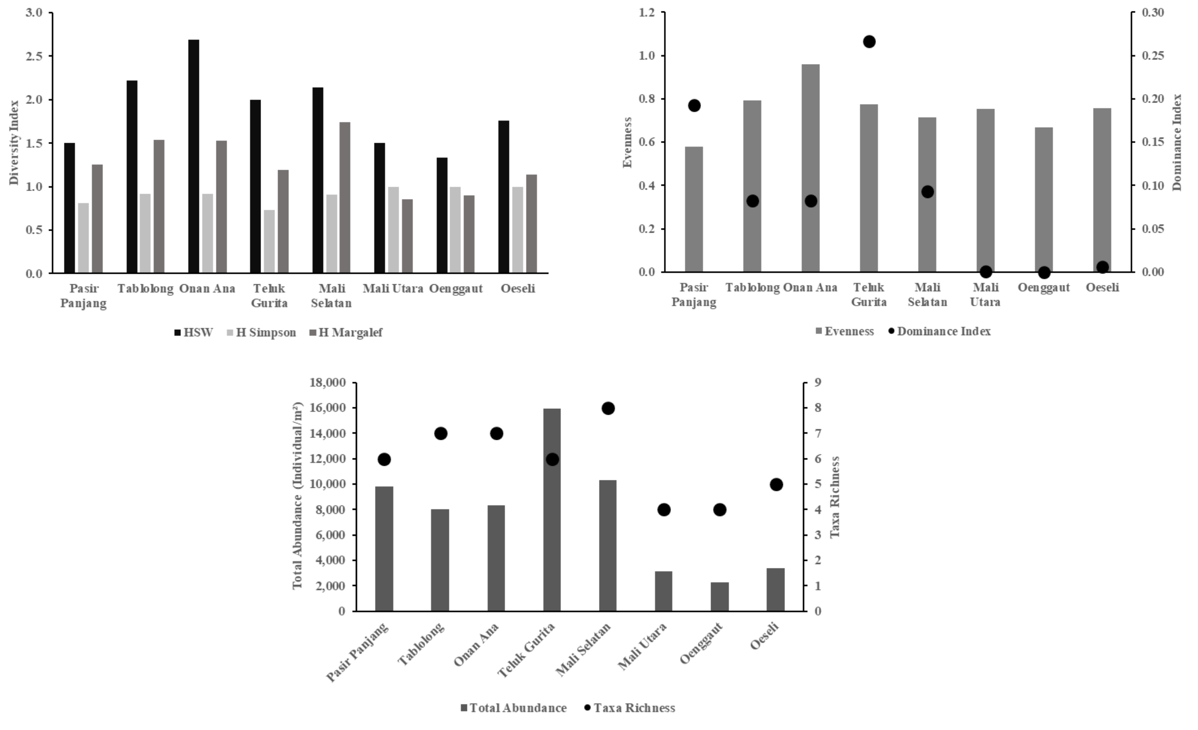


**Figure 4.** Diversity of seagrass species and abundance at each research location

Group I, consisting of Mali Selatan, Tablolong, and Onan Ana, demonstrated the best ecosystem quality, categorized by the highest Taxa Richness, H Margalef values, and Shannon-Wiener (HSW), as well as optimal Dissolved Oxygen (DO) levels. The high seagrass diversity at these locations deteriorated positively with favorable DO conditions, consistent with the findings of Xu et al. (2016) who showed that air oxygenation >6 mg/L supports optimal habitat in tropical seagrass ecosystems. A similar pattern was reported by Tuya et al. (2021) in the Canary Islands, where oxygen gradients explained 45% of the variation in seagrass community structure.

Group II, Oeseli, exhibits unique characteristics that distinguish it from the other groups, likely due to a combination of different environmental factors. Biplot analysis revealed that orthophosphate had a strong negative correlation with H Simpson's H (r = -0.78), while nitrate had a negative correlation with Taxa Richness (r = -0.53), confirming the findings of Roca et al. (2016) on the effect of nutrient thresholds on Mediterranean seagrass biodiversity. The complex interactions between these stressors were elucidated by O'Brien et al. (2018) through structural equation modeling, which showed that the synergistic effects of nutrients and temperature reduced ecosystem resilience by up to 70%.

In contrast, group III, consisting of Mali Utara and Oenggaut, exhibited different characteristics, with high pH and nitrate levels but low diversity (low Simpson's H). High nitrate levels in these locations likely contribute to eutrophication, negatively impacting seagrass diversity, consistent with a meta-analysis by Griffiths et al. (2020) that found a 35% decrease in seagrass diversity at nitrate concentrations > 0.05 mg/L. This mechanism involves the proliferation of epiphytic algae, which reduces light penetration by up to 60%, as documented by Mvungi and Pillay (2019) in a South African seagrass system.

Group IV Pasir Panjang and Teluk Gurita formed distinct clusters with the highest Dominance Index (ID) and orthophosphate levels. This indicates the dominance of certain species that are more tolerant of high phosphate levels, consistent with research by Artika et al. (2020) who reported the dominance of *E. acoroides* under high phosphate conditions in Indonesian waters. Viana et al. (2020) showed that orthophosphate levels >0.05 mg/L triggered a community shift from multispecies to monodominance within 2-3 years.

The results of the Pearson correlation analysis (Figure 6) show that Dissolved Oxygen (DO) has a moderate positive correlation with Taxa Richness (r = 0.43698) and Margalef's H (r = 0.51691), indicating that higher dissolved oxygen levels support seagrass species diversity. DO has a very weak relationship with orthophosphate (r = 0.054122) and a weak negative correlation with nitrate (r = -0.23099), indicating that dissolved oxygen is not directly affected by these nutrient parameters.

Orthophosphate showed a very strong negative correlation with H Simpson's (r = -0.77978) and a very strong positive correlation with the Dominance Index (r = 0.77978), indicating that increasing orthophosphate levels significantly reduced diversity and increased dominance of certain species. Orthophosphate also had a moderate positive correlation with Taxa Richness (r = 0.5618) and Margalef's H (r = 0.4878). Meanwhile, nitrate had a moderate to strong negative correlation with Taxa Richness (r = -0.53478) and Margalef's H (r = -0.62456), indicating that increased nitrate can reduce seagrass diversity. The relationship between nutrients and seagrass diversity is complex, with excessive nutrient levels disrupting the balance of the seagrass ecosystem (Green et al. 2015; Thomsen et al. 2020; Jiménez-Ramos et al. 2024). Analysis of the relationships between diversity index showed a consistent and complementary pattern. Taxa Richness was strongly positively correlated with H Margalef's (r = 0.95889), confirming the close relationship between species richness and the Margalef diversity index.

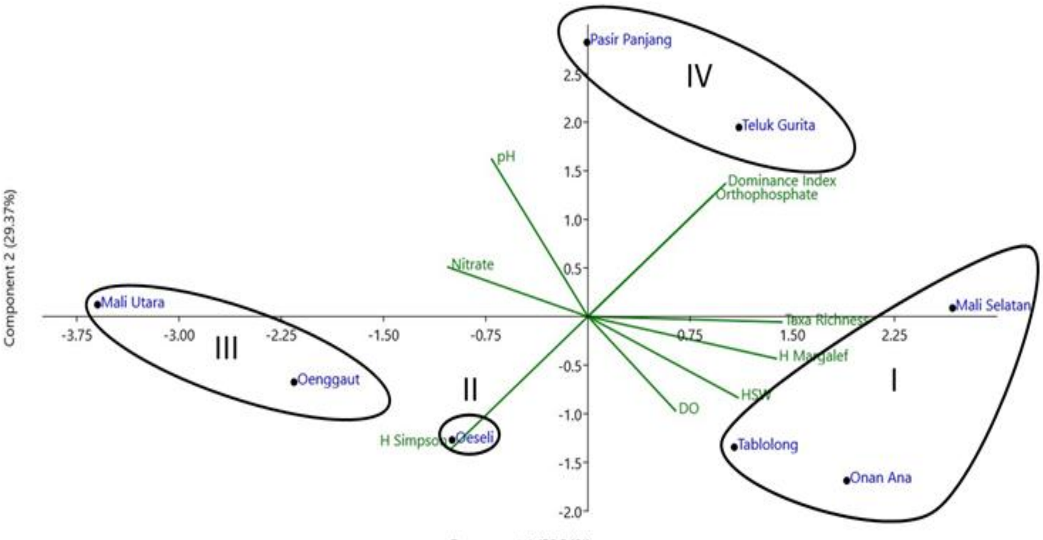
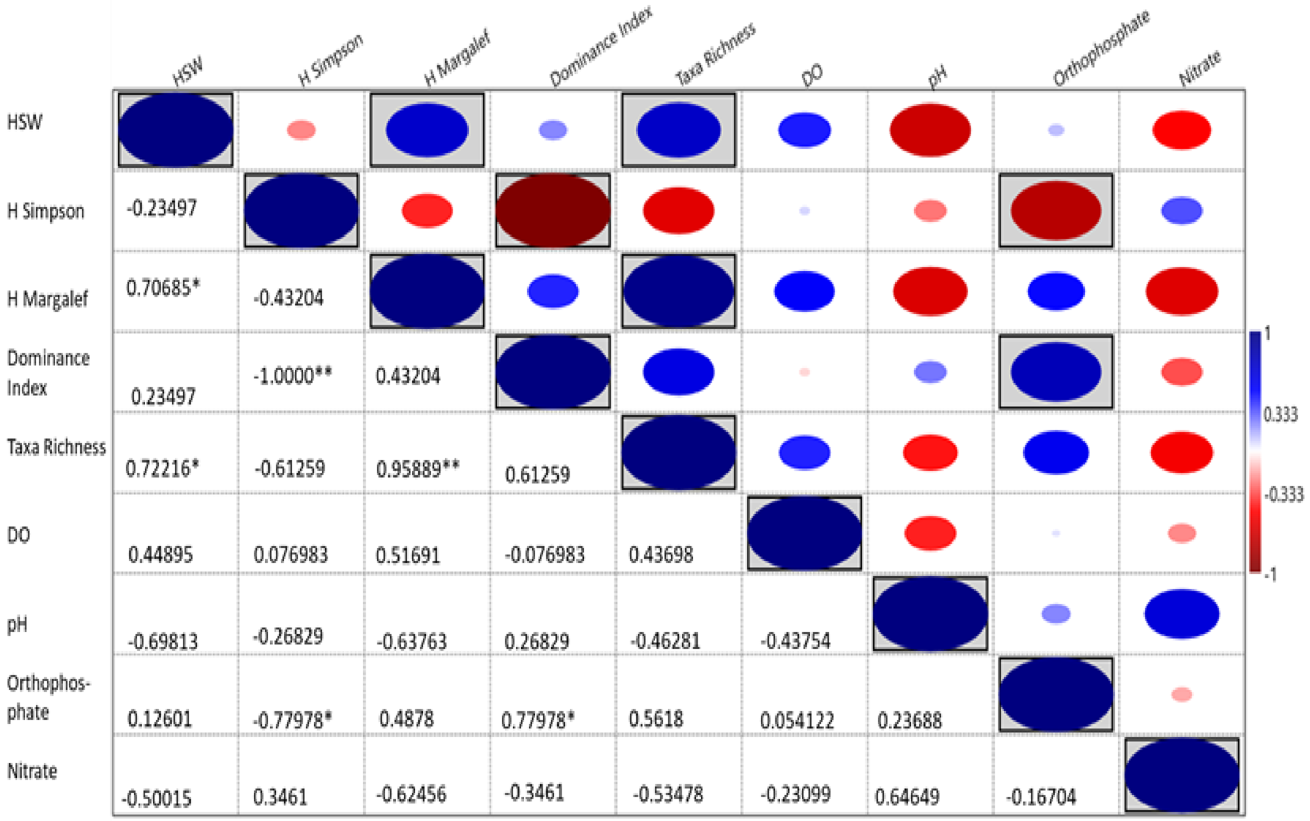


**Figure 5.** Biplot using PCA showing the grouping of seagrass ecosystems on several beaches of East Nusa Tenggara, Indonesia, based on water quality and seagrass diversity



| | HSW | H Simpson | H Margalef | Dominance Index | Taxa Richness | DO | pH | Orthophosphate | Nitrate |
|---|---|---|---|---|---|---|---|---|---|
| HSW | | | | | | | | | |
| H Simpson | -0.23497 | | | | | | | | |
| H Margalef | 0.70685* | -0.43204 | | | | | | | |
| Dominance Index | 0.23497 | -1.0000** | 0.43204 | | | | | | |
| Taxa Richness | 0.72216* | -0.61259 | 0.95889** | 0.61259 | | | | | |
| DO | 0.44895 | 0.076983 | 0.51691 | -0.076983 | 0.43698 | | | | |
| pH | -0.69813 | -0.26829 | -0.63763 | 0.26829 | -0.46281 | -0.43754 | | | |
| Orthophosphate | 0.12601 | -0.77978* | 0.4878 | 0.77978* | 0.5618 | 0.054122 | 0.23688 | | |
| Nitrate | -0.50015 | 0.3461 | -0.62456 | -0.3461 | -0.53478 | -0.23099 | 0.64649 | -0.16704 | |

**Figure 6.** Pearson correlation between several parameters (water quality: Dissolved Oxygen (DO), pH, orthophosphate, nitrate) and seagrass diversity (Taxa Richness, H Simpson, H Margalef, Shannon-Wiener (HSW) and Dominance Index) observed in the study, coastal areas in East Nusa Tenggara, Indonesia

HSW (Shannon-Wiener) also showed a strong positive correlation with Taxa Richness (r = 0.72216) and Margalef's H (r = 0.70685), demonstrating consistency among diversity index in measuring seagrass diversity. Simpson's H is perfectly negatively correlated with the Dominance Index (r = -1.00000), indicating that the two index provide conflicting information about community structure, where increasing the dominance of a particular species will decrease the Simpson's index. There is a moderate negative correlation between Simpson's H and Margalef's H (r = -0.43204), indicating that the two index measure different aspects of diversity in seagrass communities.

## Discussion

### *Mechanisms driving seagrass community patterns*

The universal nitrate exceedance (100-717% above standards) driving diversity loss in East Nusa Tenggara operates through cascading biogeochemical mechanisms well-documented globally but with tropical-specific intensification. Elevated nutrients trigger epiphytic algal proliferation that reduces light availability by 40-60%, paralleling Caribbean studies where similar nitrate levels (>0.05 mg/L) caused ecosystem phase shifts within 2-3 years (Thomsen et al. 2020). Our sites likely experience compounding sulfide stress nitrate levels suggest $H_2S$ concentrations exceeding the 100 µM toxicity threshold, consistent with Mediterranean systems showing sulfide-induced mortality at comparable nutrient loads. The novel orthophosphate and temperature interaction we documented (explaining 31% of diversity variance) reveals tropical-specific vulnerability where warming accelerates microbial decomposition, intensifying nutrient cycling and creating positive feedback loops absent in temperate systems. Temperature stress mechanisms at Mali Utara (35.56°C) approach critical thresholds where photosystem II quantum yield declines 50% and carbon balance becomes negative experimentally verified at 36-37°C for tropical species (Collier et al. 2017; George et al. 2018). Yet core species persistence suggests potential thermal adaptation through heat shock protein expression and alternative carbon concentration mechanisms, paralleling Red Sea populations surviving comparable temperatures through similar physiological modifications.

### *Resilience mechanisms and ecological vulnerability*

The remarkable persistence of three core species (*E. acoroides*, *T. hemprichii*, *C. rotundata*) across all stress gradients reveals complementary resilience strategies maintaining ecosystem function despite degradation. *Enhalus acoroides*, accessing subsurface nutrients through 1-2m rhizomes bypasses surface eutrophication (LaRoche et al. 2019), *T. hemprichii* exhibits morphological plasticity reducing metabolic demands under stress (Ling et al. 2018), while *C. rotundata* tolerates environmental fluctuations through osmotic adjustment mechanisms (Soonthornkalump et al. 2022). This functional redundancy provides insurance effects critical for ecosystem persistence. However, vulnerability indicators suggest approaching tipping points. The absence of *Halophila* species at high-stress sites signals recruitment failure these pioneer species typically colonize disturbed areas first, their absence indicating compromised recovery capacity. The 62.5% of sites maintaining moderate-high diversity despite stress suggests systems approaching but not exceeding the 40% habitat loss threshold identified globally as the point of irreversible transition. Without intervention, projected warming of 0.3°C/decade will push 75% of sites beyond thermal tolerance by 2050.

### *Global context and regional implications*

East Nusa Tenggara's intermediate diversity (H' = 1.5-2.7) between degraded Java H' = 0.8-1.5 (Solihuddin et al. 2021) and pristine Raja Ampat waters reflects the west-east Indonesian development gradient correlating with human population density (r = -0.72) and industrial activity (r = -0.68), patterns replicated across the Indo-Pacific (McKenzie et al. 2020; Sudo et al. 2021). Comparison with Philippines sites H' = 3.2-3.8 (Quiros et al. 2017) and northern Australia H' = 2.8-3.4 (York et al. 2015) reveals East Nusa Tenggara maintains 50-70% of pristine diversity despite stress a critical threshold as systems retaining >60% diversity show greater recovery potential. Our nutrient thresholds (0.06 mg/L nitrate) are notably lower than temperate systems (0.14 mg/L), indicating reduced tropical buffering capacity critical as 40% of global seagrass occurs in rapidly developing tropical regions. This heightened sensitivity, combined with multiple stressor interactions, suggests tropical systems require more stringent management targets than currently recognized in global frameworks.

### *Management implications for ecosystem services*

The quantitative thresholds identified enable targeted interventions protecting ecosystem services valued at US$34,000/hectare/year. Based on mechanistic understanding: 1. Nutrient management targeting <0.06 mg/L nitrate through constructed wetlands (80% removal efficiency) could restore diversity within 2-3 years at moderately degraded sites. The success requires addressing sources watershed management reducing agricultural runoff by 60-75% through riparian buffers proved effective in analogous systems; 2. Thermal refugia conservation at sites maintaining <30°C (Oenggaut, Onan Ana) preserves adaptive genetic diversity. These populations likely harbor heat tolerant genotypes essential for assisted migration as regional temperatures rise. Protection must include maintaining water circulation patterns preventing thermal stratification; 3. Carbon finance integration leveraging 2.5 million tons $CO_2$ sequestration capacity (139 g C/m$^2$/year × 45,000 hectares) into Indonesia's Nationally Determined Contributions could access US$50 million for conservation. Expansion of Coral Triangle Initiative recognizing seagrass connectivity corridors supporting transboundary megafauna movements provides regional framework (Grech et al. 2016).

The persistence of moderate diversity despite widespread stress indicates recovery remains possible if root causes are addressed promptly. However, the convergence of multiple stressors approaching critical thresholds demands immediate action delays risk pushing these ecosystems beyond recovery capacity, with cascading impacts on the 5.3 million people dependent on associated fisheries.

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## REFERENCES

Ali SM, He J, Goh BPL, Sin TM. 2018. Environmental correlates of *Thalassia hemprichii* status descriptors: An evaluation of tools for diagnostic monitoring. Bot Mar 61 (4): 321-335. DOI: 10.1515/bot-2017-0083.

Aoki LR, McGlathery KJ. 2018. Restoration enhances denitrification and DNRA in subsurface sediments of *Zostera marina* seagrass meadows. Mar Ecol Prog Ser 602: 87-102. DOI: 10.3354/meps12678.

Artika SR, Ambo-Rappe R, Teichberg M, Moreira-Saporiti A, Viana IG. 2020. Morphological and physiological responses of *Enhalus acoroides* seedlings under varying temperature and nutrient treatment. Front Mar Sci 7: 325. DOI: 10.3389/fmars.2020.00325.

Barnes RSK, Mann KH. 1994. Fundamentals of Aquatic Ecology. Blackwell Scientific Publication, Oxford

Bass AV, Falkenberg LJ, Thibodeau B. 2024. Seagrasses under stress: Independent negative effects of elevated temperature and light reduction at multiple levels of organization. Limnol Oceanogr 69: 1-16. DOI: 10.1002/lno.12759.

Blake RE, Duffy JE. 2016. Influence of environmental stressors and grazer immigration on ecosystem properties of an experimental eelgrass community. J Exp Mar Biol Ecol 480: 45-53. DOI: 10.1016/j.jembe.2016.03.007.

Bramante JF, Ali SM, Ziegler AD, Sin TM. 2018. Decadal biomass and area changes in a multi-species meadow in Singapore: Application of multi-resolution satellite imagery. Bot Mar 61 (3): 289-304. DOI: 10.1515/bot-2017-0064.

Bulmer RH, Townsend M, Drylie T, Lohrer AM. 2018. Elevated turbidity and the nutrient removal capacity of seagrass. Front Mar Sci 5: 462. DOI: 10.3389/fmars.2018.00462.

Camp EF, Suggett DJ, Gendron G, Jompa J, Manfrino C, Smith DJ. 2016. Mangrove and seagrass beds provide different biogeochemical services for corals threatened by climate change. Front Mar Sci 3: 52. DOI: 10.3389/fmars.2016.00052.

Collier CJ, Ow YX, Langlois L, Uthicke S, Johansson CL, O'Brien KR, Hrebien V, Adams MP. 2017. Optimum temperatures for net primary productivity of three tropical seagrass species. Front Plant Sci 8: 1446. DOI: 10.3389/fpls.2017.01446.

Cussioli MC, Bryan KR, Pilditch CA, de Lange WP, Bischof K. 2019. Light penetration in a temperate meso-tidal lagoon: Implications for seagrass growth and dredging in Tauranga Harbour, New Zealand. Ocean Coast Manag 174: 25-37. DOI: 10.1016/j.ocecoaman.2019.01.014.

Cyronak T, Andersson AJ, D'Angelo S, Bresnahan P, Davidson C, Griffin A, Kindeberg T, Pennise J, Takeshita Y, White M. 2018. Short-term spatial and temporal carbonate chemistry variability in two contrasting seagrass meadows: Implications for pH buffering capacities. Estuar Coast 41: 1282-1296. DOI: 10.1007/s12237-017-0356-5.

da Silva TD, Mullarney JC, Pilditch CA, Coco G. 2024. The interaction between vegetation patchiness and tidal flows in a shortleaf seagrass meadow. Limnol Oceanogr 69 (10): 2422-2435. DOI: 10.1002/lno.12679.

Danaraj J, Ayyappan S, Mariasingarayan Y, Packiyavathy IASV, Sweetly Dharmadhas J. 2021. Chlorophyll fluorescence, dark respiration and metabolomic analysis of *Halodule pinifolia* reveal potential heat responsive metabolites and biochemical pathways under ocean warming. Mar Environ Res 164: 105248. DOI: 10.1016/j.marenvres.2020.105248.

Dewi CSU, Wahyudi S, Widodo, Tarno H, Ciptadi G, Wiadnya DGR. 2024. Analyzing seagrass species and distribution for sustainable management of coastal areas and small islands: A case study of Java Island, Indonesia. BIO Web Conf 106 (9): 02003. DOI: 10.1051/bioconf/202410602003.

El Shaffai A. 2015. Field Guide to Seagrasses of the Red Sea. Second Edition. Gland Switzerland: IUCN and Courbevoie, Total Foundation, France.

English S, Wilkinson C, Baker V. 1997. Survey Manual for Tropical Marine Resources (2nd ed.). Australian Institute of Marine Science, Townsville.

Gao Y, Jiang Z, Du M, Fang J, Jiang W, Fang J. 2019. Photosynthetic and metabolic responses of eelgrass *Zostera marina* L. to short-term high-temperature exposure. J Ocean Limnol 37: 199-209. DOI: 10.1007/s00343-019-7319-6.

Garrote-Moreno A, Cambridge M, Sánchez-Lizaso JL. 2016. Ion concentrations in seagrass: A comparison of results from field and controlled-environment studies. Estuar Coast Shelf Sci 181: 209-217. DOI: 10.1016/j.ecss.2016.08.034.

Garrote-Moreno A, McDonald A, Sherman TD, Sánchez-Lizaso JL, Heck Jr KL, Cebrian J. 2015. Short-term impacts of salinity pulses on ionic ratios of the seagrasses *Thalassia testudinum* and *Halodule wrightii*. Aquat Bot 120: 315-321. DOI: 10.1016/j.aquabot.2014.09.011.

George R, Gullström M, Mangora MM, Mtolera MSP, Björk M. 2018. High midday temperature stress has stronger effects on biomass than on photosynthesis: A mesocosm experiment on four tropical seagrass species. Ecol Evol 8 (9): 4508-4517. DOI: 10.1002/ece3.3952.

Grech A, Wolter J, Coles R, McKenzie L, Rasheed M, Thomas C, Waycott M, Hanert E. 2016. Spatial patterns of seagrass dispersal and settlement. Divers Distrib 22 (11): 1150-1162. DOI: 10.1111/ddi.12479.

Green L, Lapointe BE, Gawlik DE. 2015. Winter nutrient pulse and seagrass epiphyte bloom: Evidence of anthropogenic enrichment or natural fluctuations in the Lower Florida Keys? Estuaries Coast 38: 1854-1871. DOI: 10.1007/s12237-015-9940-8.

Griffiths LL, Connolly RM, Brown CJ. 2020. Critical gaps in seagrass protection reveal the need to address multiple pressures and cumulative impacts. Ocean Coast Manag 183: 104946. DOI: 10.1016/j.ocecoaman.2019.104946.

Hansen AB, Pedersen AS, Kühl M, Brodersen KE. 2022. Temperature effects on leaf and epiphyte photosynthesis, bicarbonate use and diel $O_2$ budgets of the seagrass *Zostera marina* L. Front Mar Sci 9: 822485. DOI: 10.3389/fmars.2022.822485.

Hasler-Sheetal H. 2023. Detrimental impact of sulfide on the seagrass Zostera marina in dark hypoxia. PLoS One 18 (12): e0295450. DOI: 10.1371/journal.pone.0295450.

Hastings R, Cummins V, Holloway P. 2020. Assessing the impact of physical and anthropogenic environmental factors in determining the habitat suitability of seagrass ecosystems. Sustainability 12 (20): 8302. DOI: 10.3390/su12208302.

Hernawan UE, Rahmawati S, Ambo-Rappe R, Sjafrie NDM, Hadiyanto H, Yusup DS, Nugraha AH, La Nafie YA, Adi W, Prayudha B, Irawan A, Rahayu YP, Ningsih E, Riniatsih I, Supriyadi IH, McMahon K. 2021. The first nation-wide assessment identifies valuable blue carbon seagrass habitat in Indonesia is in moderate condition. Sci Total Environ 782: 146818. DOI: 10.1016/j.scitotenv.2021.146818.

Hilyana S, Gigentika S, Tezar Rafandi M, Hernawati. 2021. Assessment of grouper and snapper fisheries with EAFM approach and sustainable strategy management in Sumbawa-Indonesia. IOP Conf Ser: Earth Environ Sci 712: 012049. DOI: 10.1088/1755-1315/712/1/012049.

Iacarella JC, Adamczyk E, Bowen D, Chalifour L, Eger A, Heath W, Helms S, Hessing-Lewis M, Hunt BPV, MacInnis A, O'Connor MI, Robinson CLK, Yakimishyn J, Baum JK. 2018. Anthropogenic disturbance homogenizes seagrass fish communities. Glob Chang Biol 24 (5): 1904-1918. DOI: 10.1111/gcb.14090.

Inoue H, Mizutani A, Nanjo K, Tsutsumi K, Kohno H. 2021. Fish assemblage structure response to seagrass bed degradation due to overgrazing by the green sea turtle *Chelonia mydas* at Iriomote Island, southern Japan. Ichthyol Res 68: 111-125. DOI: 10.1007/s10228-020-00775-1.

Jespersen E, Kirk GH, Brix H, Eller F, Sorrell BK. 2021. Shade and salinity responses of two dominant coastal wetland grasses: Implications for light competition at the transition zone. Ann Bot 128: 469-480. DOI: 10.1093/aob/mcab089.

Jiang Z, Li L, Fang Y, Lin J, Liu S, Wu Y, Huang X. 2022a. Eutrophication reduced the release of dissolved organic carbon from tropical seagrass roots through exudation and decomposition. Mar Environ Res 179: 105703. DOI: 10.1016/j.marenvres.2022.105703.

Jiang Z, Liu S, Cui L, He J, Fang Y, Premarathne C, Li L, Wu Y, Huang X, Kumar M. 2022b. Sand supplementation favors tropical seagrass *Thalassia hemprichii* in eutrophic bay: Implications for seagrass restoration and management. BMC Plant Biol 22 (1): 296. DOI: 10.1186/s12870-022-03647-0.

Jiménez-Ramos R, Brun FG, Vergara JJ, Hernández I, Pérez-Lloréns JL, Egea LG. 2024. Nutrient enrichment and herbivory alter carbon balance in temperate seagrass communities. Mar Pollut Bull 206: 116784. DOI: 10.1016/j.marpolbul.2024.116784.

Jiménez-Ramos R, Villazán B, Egea LG, Cantero R, Pérez-Lloréns JL, Vergara JJ, Brun FG. 2022. Differential ecophysiological responses to inorganic nitrogen sources (ammonium versus nitrate) and light levels in the seagrass *Zostera noltei*. Mar Ecol Prog Ser 702: 57-70. DOI: 10.3354/meps14206.

Kongrueang P, Buapet P, Roongsattham P. 2018. Physiological responses of *Enhalus acoroides* to osmotic stress. Bot Mar 61 (3): 257-267. DOI: 10.1515/bot-2017-0108.

LaRoche CK, Goldstein BR, Cybulski JD, Raymundo LJ, Aoki LR, Kim K. 2019. Decade of change in *Enhalus acoroides* seagrass meadows in Guam, Mariana Islands. Mar Freshw Res 70 (2): 246-254. DOI: 10.1071/MF18062.

Lin J, Huang Y, Arbi UY, Lin H, Azkab MH, 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 Oceanol Sin 37: 82-89. DOI: 10.1007/s13131-018-1181-9.

Ling J, Lin X, Zhang Y, Zhou W, Yang Q, Lin L, Zeng S, Zhang Y, Wang C, Ahmad M, Long L, Dong J. 2018. Community composition and transcriptional activity of ammonia-oxidizing prokaryotes of seagrass *Thalassia hemprichii* in coral reef ecosystems. Front Microbiol 9: 7. DOI: 10.3389/fmicb.2018.00007.

Liu S, Luo H, Jiang Z, Ren Y, Zhang X, Wu Y, Huang X, Macreadie PI. 2023. Nutrient loading weakens seagrass blue carbon potential by stimulating seagrass detritus carbon emission. Ecol Indic 157: 111251. DOI: 10.1016/j.ecolind.2023.111251.

Liu WY, Han QY, Tang YQ, Sun XY. 2017. Review of nutrient enrichment and global warming effects on seagrasses. Chin J Ecol 36: 1087-1096. DOI: 10.13292/j.1000-4890.201704.027.

Luo H, Liu S, Ren Y, Jiang Z, Wu Y, Zhang X, Li J, Huang X. 2022. Eutrophication decreases *Halophila beccarii* plant organic carbon contribution to sequestration potential. Front Mar Sci 9: 986415. DOI: 10.3389/fmars.2022.986415.

Marín-Guirao L, Bernardeau-Esteller J, Belando MD, García-Muñoz R, Ramos-Segura A, Alcoverro T, Minguito-Frutos M, Ruiz JM. 2022. Photo-acclimatory thresholds anticipate sudden shifts in seagrass ecosystem state under reduced light conditions. Mar Environ Res 177: 105636. DOI: 10.1016/j.marenvres.2022.105636.

McHenry J, Rassweiler A, Hernan G, Uejio CK, Pau S, Dubel AK, Lester SE. 2021. Modelling the biodiversity enhancement value of seagrass beds. Divers Distrib 27 (11): 2036-2049. DOI: 10.1111/ddi.13379.

McKenzie LJ, Nordlund LM, Jones BL, Cullen-Unsworth LC, Roelfsema C, Unsworth R. 2020. The global distribution of seagrass meadows. Environ Res Lett 15: 074041. DOI: 10.1088/1748-9326/ab7d06.

McKenzie LJ. 2008. Seagrass Educator Handbook. Seagrass Watch HQ/DPI&F, Australia.

Moreno-Marín F, Vergara JJ, Pérez-Llorens JL, Pedersen MF, Brun FG. 2016. Interaction between ammonium toxicity and green tide development over seagrass meadows: A laboratory study. PLoS One 11: e0152971. DOI: 10.1371/journal.pone.0152971.

Morris LJ, Hall LM, Jacoby CA, Chamberlain RH, Hanisak MD, Miller JD, Virnstein RW. 2022. Seagrass in a changing estuary, the Indian River Lagoon, Florida, United States. Front Mar Sci 8: 789818. DOI: 10.3389/fmars.2021.789818.

Moseby KE, Daniels A, Duri V, Tropa W, Welma S, Bero A, Soapi K. 2020. Community-based monitoring detects catastrophic earthquake and tsunami impacts on seagrass beds in the Solomon Islands. Mar Pollut Bull 150: 110444. DOI: 10.1016/j.marpolbul.2019.07.032.

Mvungi EF, Pillay D. 2019. Eutrophication overrides warming as a stressor for a temperate African seagrass (*Zostera capensis*). PLoS One 14 (4): e0215129. DOI: 10.1371/journal.pone.0215129.

Nadiarti N, La Nafie YA, Priosambodo D, Umar MT, Rahim SW, Inaku DF, Musfirah NH, Paberu DA, Moore AM. 2021. Restored seagrass beds support macroalgae and sea urchin communities. IOP Conf Ser: Earth Environ Sci 860 (1): 012014. DOI: 10.1088/1755-1315/860/1/012014.

Nordlund LM, Unsworth RKF, Gullström M, Cullen-Unsworth LC. 2018. Global significance of seagrass fishery activity. Fish Fish 19 (3): 399-412. DOI: 10.1111/faf.12259.

Nugraha AH, Addini I, Halim M, Darus RF. 2023. Preliminary study on restoration of tropical seagrass ecosystem through utilization of *Enhalus acoroides* seedling in Bintan Island, Indonesia. IOP Conf Ser: Earth Environ Sci 1251: 012025. DOI: 10.1088/1755-1315/1251/1/012025.

Nugraha AH, Tasabaramo IA, Hernawan U, Rahmawati S, Putra R, Darus RF. 2021. Diversity, coverage, distribution and ecosystem services of seagrass in three small islands of northern Papua, Indonesia: Liki Island, Meossu Island and Befondi Island. Biodiversitas 22 (12): 5544-5549. DOI: 10.13057/biodiv/d221238.

Nur RM, Nurafni, Seng US, Puspita A, Djafar MNH, Paulus H, Petrus R, Polulu F. 2024. Mapping seagrass distribution and cover in Morotai Island District, North Maluku Province. Egypt J Aquat Biol Fish 28 (6): 373-398. DOI: 10.21608/ejabf.2024.392241.

O'Brien KR, Waycott M, Maxwell P, Kendrick GA, Udy JW, Ferguson AJP, Kilminster K, Scanes P, McKenzie LJ, McMahon K, Adams MP, Samper-Villarreal J, Collier C, Lyons M, Mumby PJ, Radke L, Christianen MJA, Dennison WC. 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Mar Pollut Bull 134: 166-176. DOI: 10.1016/j.marpolbul.2017.09.006.

Park HJ, Park TH, Kang HY, Lee KS, Kim YK, Kang CK. 2021. Assessment of restoration success in a transplanted seagrass bed based on isotopic niche metrics. Ecol Eng 166: 106239. DOI: 10.1016/j.ecoleng.2021.106239.

Pedersen O, Colmer TD, Borum J, Zavala-Perez A, Kendrick GA. 2016. Heat stress of two tropical seagrass species during low tides - impact on underwater net photosynthesis, dark respiration and diel in situ internal aeration. New Phytol 210 (4): 1207-1218. DOI: 10.1111/nph.13900.

Pelasula DD, Wouthuyzen S, Waileruny W, Rubamlifar A, Hukom FD, Matuankota C. 2023. The changes of coastal ecosystem in East Seram District, Maluku Province, Indonesia and its impact on the julung-julung fish (*Hemirhamphus* sp.) resources. Intl J Conserv Sci 14 (1): 285-300. DOI: 10.36868/IJCS.2023.01.18.

Quiros TEAL, Croll D, Tershy B, Fortes MD, Raimondi P. 2017. Land use is a better predictor of tropical seagrass condition than marine protection. Biol Conserv 209: 454-463. DOI: 10.1016/j.biocon.2017.03.011.

Rao R, Alcoverro T, Kongari P, Yoayela S, Arthur R, D'Souza E. 2023. Tolerance to aerial exposure influences distributional patterns in multi-species intertidal seagrass meadows. Mar Environ Res 191: 106146. DOI: 10.1016/j.marenvres.2023.106146.

Rattanachot E, Prathep A. 2015. Species specific effects of three morphologically different belowground seagrasses on sediment properties. Estuar Coast Shelf Sci 167: 427-435. DOI: 10.1016/j.ecss.2015.10.019.

Ricart AM, Ward M, Hill TM, Sanford E, Kroeker KJ, Takeshita Y, Merolla S, Shukla P, Ninokawa AT, Elsmore K, Gaylord B. 2021. Coast-wide evidence of low pH amelioration by seagrass ecosystems. Glob Chang Biol 27 (11): 2580-2591. DOI: 10.1111/gcb.15594.

Risandi J, Rifai H, Lukman KM, Sondak CFA, Hernawan UE, Quevedo JMD, Hidayat R, Ambo-Rappe R, Lanuru M, McKenzie L, Kohsaka R, Nadaoka K. 2023. Hydrodynamics across seagrass meadows and its impacts on Indonesian coastal ecosystems: A review. Front Earth Sci 11: 1034827. DOI: 10.3389/feart.2023.1034827.

Roca G, Alcoverro T, Krause-Jensen D, Balsby TJS, Katwijk MMv, Marbà N, Santos R, Arthur R, Mascaró O, Fernández-Torquemada Y, Pérez M, Duarte CM, Romero J. 2016. Response of seagrass indicators to shifts in environmental stressors: A global review and management synthesis. Ecol Indic 63: 310-323. DOI: 10.1016/j.ecolind.2015.12.007.

Said NE, McMahon K, Lavery PS. 2021. Accounting for the influence of temperature and location when predicting seagrass (*Halophila ovalis*) photosynthetic performance. Estuar Coast Shelf Sci 257: 107414. DOI: 10.1016/j.ecss.2021.107414.

Shannon CE, Weiner W. 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana.

Shen J, Wu Z, Yin L, Chen S, Cai Z, Geng X, Wang D. 2022. Physiological basis and differentially expressed genes in the salt tolerance mechanism of *Thalassia hemprichii*. Front Plant Sci 13: 975251. DOI: 10.3389/fpls.2022.975251.

Sjafrie ND, Rahmadi P, Triyono T, Kurniawan F, Supriyadi IH, Zulpikar F, Adrianto L, Rahmawati S, Hernawan UE. 2024. Monetary value of ecosystem services in unhealthy seagrass meadows in Indonesia. Ecosyst Serv 70: 101668. DOI: 10.1016/j.ecoser.2024.101668.

Sjafrie NDM, Hernawan UE, Prayudha B, Supriyadi IH, Iswari MY, Rahmat, Anggraini K, Rahmawati S, Suyarso. 2018. Indonesia's Seagrass Meadow Status 2018 [Status Padang Lamun Indonesia 2018]. Pusat Penelitian Oseanografi-Lembaga Ilmu Pengetahuan Indonesia, Jakarta. [Indonesian]

Sogin EM, Michellod D, Gruber-Vodicka HR, Bourceau P, Geier B, Meier DV, Seidel M, Ahmerkamp S, Schorn S, D'Angelo G, Procaccini G, Dubilier N, Liebeke M. 2022. Sugars dominate the seagrass rhizosphere. Nat Ecol Evol 6 (7): 866-877. DOI: 10.1038/s41559-022-01740-z.

Solihuddin T, Husrin S, Mustikasari E, Heriati A, Kepel TL, Salim HL, Risandi J, Dwiyanti D. 2021. coastal inundation and land subsidence in North Coast of West Java: A new hazard? IOP Conf Ser: Earth Environ Sci 925: 012015. DOI: 10.1088/1755-1315/925/1/012015.

Soonthornkalump S, Xiang Ow Y, Saewong C, Buapet P. 2022. Comparative study on anatomical traits and gas exchange responses due to belowground hypoxic stress and thermal stress in three tropical seagrasses. PeerJ 10: e12899. DOI: 10.7717/peerj.12899.

Stankovic M, Ambo-Rappe R, Carly F, Dangan-Galon F, Fortes MD, Hossain MS, Kiswara W, Van Luong C, Minh-Thu P, Mishra AK, Noiraksar T, Nurdin N, Panyawai J, Rattanachot E, Rozaimi M, Soe Htun U, Prathep A. 2021. Quantification of blue carbon in seagrass ecosystems of Southeast Asia and their potential for climate change mitigation. Sci Total Environ 783: 146858. DOI: 10.1016/j.scitotenv.2021.146858.

Statton J, McMahon K, Lavery P, Kendrick GA. 2018. Determining light stress responses for a tropical multi-species seagrass assemblage. Mar Pollut Bull 128: 508-518. DOI: 10.1016/j.marpolbul.2018.01.060.

Steinfurth RC, Lange T, Oncken NS, Kristensen E, Quintana CO, Flindt MR. 2022. Improved benthic fauna community parameters after large-scale seagrass (*Zostera marina*) restoration in Horsens Fjord, Denmark. Mar Ecol Prog Ser 687: 65-77. DOI: 10.3354/meps14007.

Sudo K, Quiros TEAL, Prathep A, Luong CV, Lin HJ, Bujang JS, Ooi JLS, Fortes MD, Zakaria MH, Yaakub SM, Tan YM, Huang X, Nakaoka M. 2021. Distribution, temporal change, and conservation status of tropical seagrass beds in Southeast Asia: 2000-2020. Front Mar Sci 8: 637722. DOI: 10.3389/fmars.2021.637722.

Swadling DS, West GJ, Gibson PT, Laird RJ, Glasby TM. 2023. Don't go breaking apart: Anthropogenic disturbances predict meadow fragmentation of an endangered seagrass. Aquat Conserv: Mar Freshw Ecosyst 33 (1): 56-69. DOI: 10.1002/aqc.3905.

Thomsen E, Herbeck LS, Jennerjahn TC. 2020. The end of resilience: Surpassed nitrogen thresholds in coastal waters led to severe seagrass loss after decades of exposure to aquaculture effluents. Mar Environ Res 160: 104986. DOI: 10.1016/j.marenvres.2020.104986.

Titioatchasai J, Surachat K, Rattanachot E, Tuntiprapas P, Mayakun J. 2023. Assessment of diversity of marine organisms among natural and transplanted seagrass meadows. J Mar Sci Eng 11 (10): 1928. DOI: 10.3390/jmse11101928.

Trinh XT, Takeuchi W. 2020. 30 Years National Scale Seagrass Mapping in Vietnam with Landsat and Sentinel Imagery on Google Earth Engine. In: 40th Asian Conference on Remote Sensing, ACRS 2019: Progress of Remote Sensing Technology for Smart Future.

Tuya F, Fernández-Torquemada Y, Del Pilar-Ruso Y, Espino F, Manent P, Curbelo L, Otero-Ferrer F, de la Ossa JA, Royo L, Antich L, Castejón I, Máñez-Crespo J, Mateo-Ramírez Á, Procaccini G, Marco-Méndez C, Terrados J, Tomas F. 2021. Partitioning resilience of a marine foundation species into resistance and recovery trajectories. Oecologia 196 (2): 515-527. DOI: 10.1007/s00442-021-04945-4.

Unsworth RKF, Ambo-Rappe R, Jones BL, Nafie YAL, Irawan A, Hernawan UE, Moore AM, Cullen-Unsworth LC. 2018. Indonesia's globally significant seagrass meadows are under widespread threat. Sci Total Environ 634: 279-286. DOI: 10.1016/j.scitotenv.2018.03.315.

Viana IG, Moreira-Saporiti A, Teichberg M. 2020. Species-specific trait responses of three tropical seagrasses to multiple stressors: The case of increasing temperature and nutrient enrichment. Front Plant Sci 11: 571363. DOI: 10.3389/fpls.2020.571363.

Vieira MLM, de Lima CLAD, de Souza JRB, Feitosa JLL. 2020a. Effects of beach seine fishing on the biodiversity of seagrass fish assemblages. Reg Stud Mar Sci 40: 101527. DOI: 10.1016/j.rsma.2020.101527.

Vieira R, Martin A, Engelen AH, Thomsen MS, Arenas F. 2020b. Interactive effects of co-occurring anthropogenic stressors on the seagrass, Zostera noltei. Ecol Indic 109: 105780. DOI: 10.1016/j.ecolind.2019.105780.

Walker LD, Gribben PE, Glasby TM, Marzinelli EM, Varkey DR, Dafforn KA. 2024. Above and below-ground bacterial communities shift in seagrass beds with warmer temperatures. Front Mar Sci 11: 1374946. DOI: 10.3389/fmars.2024.1374946.

Waycott M, McMahon K, Mellors J, Calladine A, Kleine D. 2004. A Guide to Tropical Seagrasses of the Indo-West Pacific. James Cook University. Townsville, Australia.

Webster CL, Kilminster KL, Sánchez Alarcón M, Bennett K, Strydom S, McNamara S, Lavery PS, McMahon KM. 2021. Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries. J Ecol 109 (9): 3260-3279. DOI: 10.1111/1365-2745.13648.

Wilhm TP, Dorris TC. 1968. Biological parameters for water quality criteria. Biol Sci 18 (6): 477-481. DOI: 10.2307/1294272.

Xu S, Zhou Y, Wang P, Wang F, Zhang X, Gu R. 2016. Salinity and temperature significantly influence seed germination, seedling establishment, and seedling growth of seagrass *Zostera marina* L. PeerJ 4: e2697. DOI: 10.7717/peerj.2697.

York PH, Carter AB, Chartrand K, Sankey T, Wells L, Rasheed MA. 2015. Dynamics of a deep-water seagrass population on the Great Barrier Reef: Annual occurrence and response to a major dredging program. Sci Rep 5: 13167. DOI: 10.1038/srep13167.

Zhang M, Zhang L, Li H, Liu J. 2022. The lack of low temperature tolerance of tropical seagrasses strongly restricts their geographical distribution. Mar Environ Res 173: 105539. DOI: 10.1016/j.marenvres.2021.105539.

Zhang X, Zhou Y, Adams MP, Wang F, Xu S, Wang P, Liu P, Liu X, Yue S. 2020. Plant morphology and seed germination responses of seagrass (*Zostera japonica*) to water depth and light availability in Ailian Bay, northern China. Mar Environ Res 162: 105082. DOI: 10.1016/j.marenvres.2020.105082.