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# Diversity and Spatial Distribution of Macroalgae in Relation to Environmental Parameters in Teluk Tamiang Waters, Indonesia

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## ABSTRACT

This study analyzed macroalgae diversity, abundance, and spatial distribution in the waters of Teluk Tamiang, Pulau Laut, South Kalimantan, and their correlation with environmental parameters. Surveys were undertaken at three shallow sites utilizing 50-m belt transects with 1 × 1m quadrats. *In situ* data included temperature, salinity, pH, dissolved oxygen, current speed, depth, water clarity (Secchi depth), dissolved nutrients (nitrate, phosphate), and substrate type. Six species were identified*: Caulerpa racemosa*, *Halimeda tuna*, *Padina australis*, *Sargassum oligocystum*, *Eucheuma cottonii*, and *Amphiroa fragilissima*. Total density was ranked S3 > S2 > S1 (178, 122, and 61 individuals, respectively), with S2 having the highest species richness. Morisita's index identified three distinct dispersion patterns: uniform at S1, mixed (uniform-random-clumped) at S2, and clumped at S3. The principal component analysis (PCA) revealed that macroalgal density was positively connected with current speed, nitrate, and phosphate; S2 was correlated with pH and temperature; and S1 was negatively correlated with depth and water clarity, indicating light constraint. Nutrient contents ($NO_3^-$ 1.1-2.1 mg $L^{-1}$; $PO_4^{3-}$ 0.84-0.99 mg $L^{-1}$) were above guideline criteria, indicating enrichment. Currents (0.15-0.22 m $s^{-1}$) presumably improved water-mass exchange and reduced fine-sediment deposition on thalli. Overall, the combination of hydrodynamics, nutrients, and light, mediated by substrate heterogeneity, appears to shape local macroalgal composition and spatial patterns. Management should focus on nutrient load reduction, maintaining water clarity and circulation, and routinely monitoring key taxa as early indicators of coastal ecosystem change.

## INTRODUCTION

Macroalgae constitute fundamental components of tropical coastal ecosystems. They function as primary producers and oxygen sources, provide essential habitats for

benthic fauna, and respond sensitively to environmental fluctuations, thereby serving as reliable indicators of water-quality dynamics **(Adarshan *et al.*, 2023; Rosic, 2023)**. Their diversity and spatial distribution are governed by interacting physical and chemical drivers, notably temperature, salinity, depth, water clarity, current velocity, pH, and concentrations of dissolved inorganic nutrients such as nitrate and phosphate **(Lane-Medeiros *et al.*, 2023; Okuhata *et al.*, 2023; Hernández *et al.*, 2024)**. Across tropical regions, variations in these parameters determine the species composition, spatial organization, and dominance patterns within macroalgal assemblages **(Potter *et al.*, 2021; Lane-Medeiros *et al.*, 2023)**. In Indonesia's Seribu Islands, for instance, water-quality attributes particularly nitrate, phosphate, and dissolved oxygen strongly influence macroalgal abundance and diversity, even under substantial anthropogenic pressure **(Handayani *et al.*, 2023)**.

Indonesia, an archipelagic nation with nearly two-thirds of its territory comprising marine waters, supports exceptionally high macroalgal diversity **(Aprilia *et al.*, 2023; Basyuni *et al.*, 2024)**. In tropical Southeast Asian waters, macroalgae hold significant ecological and economic value as contributors of carbonate to coral-reef frameworks and as sources of food, pharmaceutical compounds, and emerging bioenergy feedstocks **(Basyuni *et al.*, 2024; Diederiks *et al.*, 2025; Pessarrodona *et al.*, 2025)**. However, despite extensive studies along the coasts of Java and Sulawesi, peer-reviewed data from Kalimantan's shorelines particularly Pulau Laut, South Kalimantan remain limited. This knowledge gap constrains biodiversity conservation and evidence-based coastal management in a region experiencing rapid growth as a marine-tourism destination (**Basyuni *et al.*, 2024**).

Teluk Tamiang, located on Pulau Laut in Tanjung Selayar District, Kotabaru Regency, South Kalimantan, is a tropical embayment supporting relatively intact coral reefs but increasingly affected by settlements, aquaculture, and tourism. Earlier studies in the eastern bay identified at least sixteen macroalgal species across multiple divisions **(Rifa'i, 2016; Rifa'i *et al.*, 2016a, b; Effendi, 2020)**. More recent surveys in the western bay documented six dominant species *Caulerpa racemosa*, *Halimeda tuna*, *Padina australis*, *Sargassum oligocystum*, *Eucheuma cottonii*, and *Amphiroa fragilissima* characterized by relatively low diversity, high evenness, and low dominance. Spatial dispersion ranged from uniform to random and clumped distributions, with current velocity, nitrate, phosphate, pH, temperature, and water clarity identified as the principal correlates of macroalgal density. These physicochemical associations align with broader regional and global findings that emphasize temperature, salinity, hydrodynamic energy, and nutrient loading as key determinants of macroalgal community structure **(Lane-Medeiros *et al.*, 2023; Okuhata *et al.*, 2023; Hernández *et al.*, 2024)**.

By quantifying how hydrodynamics, nutrient availability, light penetration, and water chemistry influence macroalgal assemblages in Teluk Tamiang, this study provides

site-specific evidence to guide nutrient management, preserve water clarity and circulation, and strengthen reef–seagrass connectivity in local coastal planning. The approach highlights macroalgae as sensitive bioindicators and effective biomonitoring agents of environmental change and pollution **(AbouGabal *et al.*, 2023; Adarshan *et al.*, 2023; Diganta *et al.*, 2023)**, while situating the findings within Indonesia's ecologically rich yet increasingly pressured coastal context **(Basyuni *et al.*, 2024)**. Ultimately, this study aimed to elucidate the relationships among macroalgal diversity, spatial distribution, and key environmental parameters in Teluk Tamiang Waters, thereby contributing regionally grounded insights to the international discourse on tropical coastal ecology and supporting sustainable coastal resource management.

## MATERIALS AND METHODS

### 1. Study design and research location

Field surveys were conducted in the western sector of Teluk Tamiang Waters, Pulau Laut, Tanjung Selayar District, Kotabaru Regency, South Kalimantan, Indonesia (Fig. 1). Sampling sites were selected using a purposive (judgment) approach to represent a gradient of anthropogenic influence, ranging from harbor and settlement zones with intensive boat traffic to a relatively sheltered area used for snorkeling tourism. Three sampling stations (S1–S3) were established along the coastal transect, each representing distinct levels of exposure and human activity. Although sites were purposively chosen along a priori anthropogenic gradient, model-based controls for habitat and spatial structure indicated that anthropogenic effects persisted after adjusting for confounding. Nonetheless, inference is restricted to nearshore habitats within the observed covariate ranges. Stations were initially selected purposively to span an a priori anthropogenic gradient (harbor–settlement to low-impact tourism sites). Given the limited number of stations (S1–S3), to mitigate selection bias, we (i) randomized quadrat positions within each belt-transect, (ii) modeled species densities with hierarchical (station/sub-station) random effects and spatial smooths of coordinates, and (iii) conducted leave-one-station-out sensitivity analyses. Where auxiliary habitat data were available (substrate area and depth classes), post-stratification weights were applied to align sample composition with areal proportions. Uncertainty was quantified using nonparametric bootstrap at the quadrat level. The geographic coordinates and environmental characteristics of these stations are summarized in Table (1).

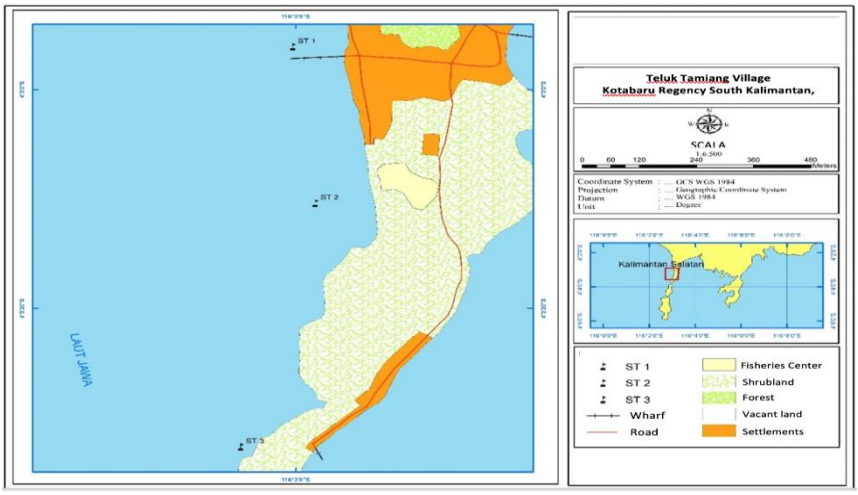
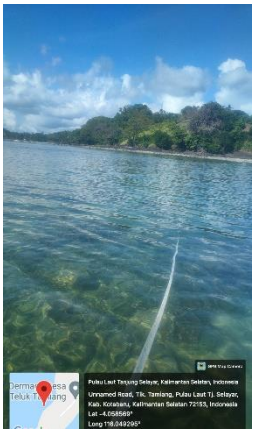



**Fig. 1.** Research location

**Table 1.** Survey stations (WGS84; decimal degrees)

| Station | Location | Description | Figure |
|---|---|---|---|
| 1 | Western shoreline of Teluk Tamiang Village, **116.05006° E; 4.049135° S** | Adjacent to a jetty, coastal settlement, and a mooring area used by artisanal fishing and tourist boats. The along-shore separation between Stations 1 and 2 is ≈ **400 m**. |  |
| 2 | Western shoreline of Teluk Tamiang Village, **116.051178° E; 4.054059° S** | Near a coastal settlement, **brackish- and marine-water aquaculture facilities,** and the main traffic lane for fishing and tourist vessels. The along-shore separation between Stations 2 and 3 is ≈ **600 m**. |  |

| | | | |
|---|---|---|---|
| 3 | Western shoreline of Teluk Tamiang Village, **116.049295° E; 4.058569° S** | Distant from settlements; one of the snorkeling sites frequently visited by tourists. The cumulative along-shore distance across Stations 1–3 is ≈ **1 km**. |  |

*Notes:* Coordinates are reported in WGS84 (decimal degrees). Distances refer to along-shore separations (not straight-line).

To address the concern that site selection based on perceived anthropogenic influence may overlook other relevant environmental gradients or confounding factors, we incorporated key environmental covariates (depth, substrate composition, Secchi transparency, and current/wave exposure) into GLMM (Generalized Linear Mixed Model)/GAM (Generalized Additive Model) with spatial controls, conducted leave-one-station-out sensitivity analyses, and assessed collinearity (VIF). This approach is intended to minimize selection bias and control for confounding, thereby yielding more reliable estimates of anthropogenic effects.

**2. Sampling design**

At each station, a 50-m belt transect was established parallel to the shoreline following the method of **Mills *et al.* (2024)**. Along each transect, 1 × 1m quadrats were positioned at 10-m intervals in an alternating left–right (zigzag) arrangement to minimize lateral bias **(Urbina-Barreto *et al.*, 2021; Kuo *et al.*, 2022)**. Each station comprised three replicate substations representing different microhabitats live coral, dead coral, sand, and coral rubble to capture within-site heterogeneity **(Smith *et al.*, 2022)**. This sampling design follows established tropical coral reef monitoring protocols for macrobenthic assemblages, including macroalgae, which employ belt and quadrat surveys within fixed areas to estimate density and benthic cover **(Urbina-Barreto *et al.*, 2021; Kuo *et al.*, 2022; Mills *et al.*, 2024)**.

**3. Macroalgal data collection and taxonomic identification**

All macroalgal thalli within each 1 × 1m quadrat were counted and identified *in situ*, and underwater photographs were taken for verification and documentation **(Roberts *et al.*, 2023; Mills *et al.*, 2024; Burgo *et al.*, 2025)**. When necessary, representative specimens were collected for laboratory identification **(Canilho Santos *et***

***al.*, 2024; Gabriel *et al.*, 2024; Min-Khant-Kyaw *et al.*, 2024)**. Species-level density (individuals $m^{-2}$) was calculated as the number of individuals per quadrat and subsequently averaged across quadrats within each station **(Burgo *et al.*, 2025)**. Collected specimens were examined under a stereomicroscope and identified using regional taxonomic references **(Kadi & Atmadja, 1988; Atmadja *et al.*, 1996; Aslan, 1998; Carpenter & Niem, 1998; Junaeidi, 2004; Jha, 2009)**. Morphological identification was based on thallus-level diagnostic traits, including overall architecture, branching pattern, holdfast structure, degree of calcification, and texture **(Cosca *et al.*, 2024; Min-Khant-Kyaw *et al.*, 2024)**. Nomenclature and synonymy were verified against AlgaeBase **(Guiry, 2024)**. Final identifications were validated at the Marine Bioecology Laboratory, where voucher specimens and photographic records were archived together with complete station- and quadrat-level metadata **(Roberts *et al.*, 2023; Canilho Santos *et al.*, 2024)**.

**4. Environmental parameters**

Physicochemical parameters were measured concurrently during the biotic surveys at each substation. Temperature (°C) was recorded using a digital thermometer; salinity (‰) with a handheld refractometer; pH with a portable pH meter; and dissolved oxygen (DO, mg $L^{-1}$) with a DO meter. Water depth (m) was determined using a graduated staff, water transparency (m) with a Secchi disk, and current velocity (m $s^{-1}$) using either a surface-drift float or a current meter **(Bowers, 2020; Pardis *et al.*, 2022; Pomeroy *et al.*, 2023; Fan *et al.*, 2024)**. We quantified depth (m), substrate composition (% rock/coral/sand/mud), water transparency (Secchi, m), current/wave exposure (ordinal index), temperature and salinity. Covariates were z-standardized. Collinearity was screened using variance inflation factors (VIF), retaining predictors with VIF < 5. The seafloor substrate was visually classified into sand, coral rubble, and live or dead coral categories **(Mills *et al.*, 2024)**. Dissolved nutrient concentrations (nitrate and phosphate) were analyzed spectrophotometrically following Standard Methods-type procedures, incorporating quality-control checks such as blanks, calibration standards, and analytical replicates **(Niu *et al.*, 2023; Mogashane *et al.*, 2025)**. For the environmental context, the measured values were descriptively compared against the Indonesian Seawater Quality Standards for marine biota and marine recreation **(State Ministry of Environment Decree No. 51/2004)**.

**5. Community quantification methods**

At each station, community structure was quantified using standard ecological metrics derived from species–abundance data: relative density (%), Shannon–Wiener diversity (H′), Pielou's evenness (J′), Simpson's dominance (D), and Morisita's index of dispersion (Id) **(Aprilia *et al.*, 2023; Hackenberger *et al.*, 2023; Hornbach *et al.*, 2023; Weckström *et al.*, 2023; Al-Qadami *et al.*, 2024; Austin *et al.*, 2024; Earp *et al.*, 2024;**

**Williams *et al.*, 2024; Barnes, 2025; Rasyid *et al.*, 2025)**. These indices collectively describe alpha diversity (H′, J′, D), the relative contribution of species to overall community composition, and small-scale spatial dispersion (Id), enabling standardized comparisons across environmental gradients **(Hornbach *et al.*, 2023; Weckström *et al.*, 2023; Earp *et al.*, 2024; Barnes, 2025)**.

### 6. Analysis of environment–community relationships

Relationships between environmental variables (temperature, salinity, pH, dissolved oxygen, depth, water clarity, current velocity, nitrate, phosphate, and substrate type) and community structure (species-level densities and aggregate diversity metrics) were examined using principal component analysis (PCA). Continuous variables were centered and standardized to unit variance (z-scores), while species density data were log(x + 1)-transformed to reduce skewness. The PCA was conducted on the correlation matrix and visualized as a biplot displaying component scores and variable loadings. Axes were interpreted based on the direction and magnitude of variable vectors, and the proportion of variance explained by each principal component was reported. This analytical workflow follows established practices in tropical benthic ecology and macroalgal community studies to identify dominant environmental gradients structuring assemblages **(Petrillo *et al.*, 2023; Vieira *et al.*, 2024; Zhang *et al.*, 2024; Buenafe *et al.*, 2025; Jamal *et al.*, 2025)**. The use of z-score normalization, log-transformation, and biplot interpretation is standard in multivariate ecological ordination, facilitating the visualization of relationships between physicochemical variables and biotic indicators **(Zhang *et al.*, 2024; Jamal *et al.*, 2025; Sørensen *et al.*, 2025)**.

## RESULTS

### 1. Macroalgal species composition

Surveys conducted at three stations in the western sector of Teluk Tamiang Waters recorded six macroalgal species representing three phyla: Chlorophyta (*Caulerpa racemosa*, *Halimeda tuna*), Phaeophyceae (*Padina australis*, *Sargassum oligocystum*), and Rhodophyta (*Eucheuma cottonii*, *Amphiroa fragilissima*) (Fig. 2).

*Caulerpa racemosa*

*Halimeda tuna*

*Eucheuma cottoni*

*Padina australis*

*Amphiroa fragillissima*

*Sargassum oligocystum*

**Fig. 2.** Macroalgal species recorded in Teluk Tamiang Waters

## 2. Distribution pattern (Morisita) and its relationship with substrate

The spatial distribution of macroalgae was evaluated using Morisita's index of dispersion (Id), which quantifies the degree of aggregation within a population. The interpretation criteria follow **Krebs (1989)**: Id = 1 indicates a random distribution, Id > 1 denotes a clumped (aggregated) distribution, and Id < 1 represents a uniform (regular) distribution. To facilitate inter-station comparisons and minimize sample-size bias, the standardized Morisita index (Ip) was also computed, as recommended in recent ecological field studies. The results of Id and Ip for each species across stations are summarized in the Table (2).

**Table 2.** Macroalgal distribution patterns

| Station | Species (with author citation) | Id | Category |
|---|---|---|---|
| 1 | *Caulerpa racemosa* **(Forsskål) J. Agardh, 1873** | 0.83 | Uniform |
| 1 | *Halimeda tuna* **(J. Ellis & Solander) J.V. Lamouroux, 1816** | 0.42 | Uniform |
| 2 | *Padina australis* **Hauck, 1887** | 0.99 | Uniform |
| 2 | *Halimeda tuna* **(J. Ellis & Solander) J.V. Lamouroux, 1816** | 0.95 | Uniform |
| 2 | *Caulerpa racemosa* **(Forsskål) J. Agardh, 1873** | 1.11 | Clumped |
| 2 | *Eucheuma cottonii* **Weber-van Bosse, 1913** | 1.43 | Clumped |
| 2 | *Sargassum oligocystum* **Montagne, 1845** | 1.43 | Clumped |
| 2 | *Amphiroa fragilissima* **(Linnaeus) J.V. Lamouroux, 1816** | 1.00 | Random |
| 3 | *Halimeda tuna* **(J. Ellis & Solander) J.V. Lamouroux, 1816** | 1.25 | Clumped |
| 3 | *Caulerpa racemosa* **(Forsskål) J. Agardh, 1873** | 1.19 | Clumped |
| 3 | *Eucheuma cottonii* **Weber-van Bosse, 1913** | 1.43 | Clumped |

Source: **Guiry and Guiry (2025)**. AlgaeBase. National University of Ireland, Galway. Retrieved October 12, 2025, from https://www.algaebase.org/

### 3. Environmental parameters and relationship to the community

Environmental measurements were conducted at three sampling stations, with the corresponding geographic coordinates and local sampling times provided in Table (3). The summarized results of the environmental parameters recorded across these stations are presented in Table (4).

**Table 3.** Station coordinates and sampling time

| Station | Longitude (°) | Latitude (°) | Time (Wita, local) |
|---|---|---|---|
| 1 | 116.051178 | −4.049135 | 07.02-10.30 |
| 2 | 116.051178 | −4.054059 | 13.45-14.45 |
| 3 | 116.049295 | −4.058569 | 16.30-19.25 |

**Table 4.** Environmental parameters measured at the study sites

| No. | Parameter | St.1 | St.2 | St.3 | Reference criterion |
|---|---|---|---|---|---|
| 1 | Temperature (°C) | 29 | 32 | 30 | 25–35 (¹) |
| 2 | Salinity (ppt) | 28 | 30 | 29 | 13–37 (²) |
| 3 | Nitrate (mg $L^{-1}$) | 1.7 | 2.1 | 1.1 | 0.008 (³) |
| 4 | Phosphate (mg $L^{-1}$) | 0.98 | 0.99 | 0.84 | 0.10–0.201 (⁴) |
| 5 | Current speed (m $s^{-1}$) | 0.15 | 0.20 | 0.22 | 0.10–0.50 (⁵) |
| 6 | Substrate | Sand, coral rubble | Fine sand, coralline | Coarse sand, rubble, rocky | Mixed sand–rubble (⁶) |

| No. | Parameter | St.1 | St.2 | St.3 | Reference criterion |
|---|---|---|---|---|---|
| 7 | Ph | 7.0 | 7.2 | 7.0 | 7–8 ([7]) |
| 8 | DO (mg $L^{-1}$) | 7.2 | 7.9 | 7.6 | > 5 ([8]) |
| 9 | Depth (m) | 1.2 | 1.0 | 1.1 | 0–5 ([9]) |
| 10 | Secchi depth (m) | 1.2 | 1.0 | 1.1 | 0.6–5 ([10]) |

*Sources for criteria:* **([1]) Farito *et al.*, 2018; ([2]) Kadi & Atmajaya, 1988; ([3],[8]) KMLH, 2004; ([4]) Putrinella, 2001; ([5]) Widyastuti, 2008; ([6]) Kadi, 2005; ([7]) Marianingsih *et al.*, 2013; ([10]) Schaduw *et al.*, 2013; ([9]) Lüning, 1990.**

## DISCUSSION

### 1. Macroalgal species composition

This taxonomic assemblage is consistent with recent findings from the Seribu Islands and other Indonesian coastal systems, where mixed sand–rubble and reef-flat substrates typically support these genera **(Handayani *et al.*, 2023; Basyuni *et al.*, 2024)**.

Shannon–Wiener diversity (H′) varied among stations, with values of 0.6 at S1 (low), 1.5 at S2 (moderate), and 0.8 at S3 (low). Pielou's evenness (J′) remained consistently high across stations (0.79–0.80), while Simpson's dominance (C) ranged from 0.16 to 0.47, indicating the absence of strong species dominance within the assemblage. Such index patterns are characteristic of tropical benthic mosaics influenced by moderate hydrodynamic energy, where environmental heterogeneity promotes coexistence and balanced community structure **(Weckström *et al.*, 2023; Earp *et al.*, 2024)**.

The macroalgal assemblage comprised stoloniferous chlorophytes (e.g., *Caulerpa racemosa*, which rapidly colonizes sand–rubble substrates through clonal spread), calcified taxa (*Halimeda tuna* and the articulated coralline *Amphiroa fragilissima*), and canopy-forming or pioneer brown algae (*Padina australis*, *Sargassum oligocystum*). This taxonomic composition typifies shallow tropical mosaics where hard substrates coincide with moderate hydrodynamic exposure **(Handayani *et al.*, 2023; Basyuni *et al.*, 2024)**. It also aligns with broader evidence that temperature, salinity, nutrient availability, and wave or current exposure jointly regulate macroalgal community structure **(Lane-Medeiros *et al.*, 2023; Okuhata *et al.*, 2023; Hernández *et al.*, 2024)**. The occurrence of calcified algae indicates that local carbonate chemistry and irradiance are sufficient to sustain biogenic calcification. This is consistent with the ecological requirements and thermal–light sensitivities of coralline algae such as *Amphiroa* **(Yang *et al.*, 2022)**, and accords with recent findings of substantial carbonate production by coralline-dominated reefs **(Diederiks *et al.*, 2025)**.

The moderate Shannon diversity (H′) observed at Station 2 reflects a relatively balanced habitat, where substrate heterogeneity and adequate water flow likely enhance niche diversity, permitting co-occurrence of Phaeophyceae (*Padina*, *Sargassum*),

Chlorophyta, and coralline taxa. In contrast, Station 1, characterized by simpler substrates, and Station 3, influenced by stronger currents and coarser sediment, exhibited lower species richness despite high evenness. The pattern at Station 3 high total abundance but reduced species number suggests a community dominated by mechanically robust or rapidly spreading taxa (*Caulerpa*, *Halimeda*) under elevated hydrodynamic energy and episodic nutrient enrichment **(Lane-Medeiros *et al.*, 2023; Handayani *et al.*, 2024; Hernández *et al.*, 2024)**.

The combination of high Pielou's evenness (J′) and low dominance (C) across stations indicates relatively equitable resource partitioning and limited competitive exclusion, a structural pattern typical of habitats with sufficient but non-extreme levels of light, flow, and nutrient availability **(Weckström *et al.*, 2023; Earp *et al.*, 2024)**. Regionally, macroalgal studies in Indonesia report higher diversity on mixed substrates under moderate currents, with declines under light limitation (e.g., turbidity or depth) or excessive disturbance; our findings are consistent with this trend **(Handayani *et al.*, 2023; Basyuni *et al.*, 2024)**.

Ecological and management implications. Functionally, the coexistence of canopy-forming browns with calcified greens and corallines can influence sediment production, habitat complexity, and coral–algal interactions. Maintaining water clarity and moderate hydrodynamic conditions while minimizing nutrient influx may therefore help preserve microhabitat diversity and prevent community shifts toward single-taxon dominance **(Lane-Medeiros *et al.*, 2023; Diederiks *et al.*, 2025)**. Because the present study represents a single-season survey, it cannot assess temporal variability or herbivory—two key modulators of tropical macroalgal dynamics. Future multi-season monitoring that integrates grazer abundance and experimental manipulations would strengthen causal inference regarding community drivers **(Okuhata *et al.*, 2023; Hernández *et al.*, 2024)**.

**2. Distribution pattern (Morisita) and its relationship with substrate**

Based on Table (2), Station 1 (S1) exhibited a uniform distribution pattern for both Chlorophyta species *Caulerpa racemosa* (Id = 0.83) and *Halimeda tuna* (Id = 0.42). This regular spacing suggests a relatively homogeneous substrate and resource availability, or possible intraspecific competition that limits aggregation. Such uniformity is consistent with large-scale evidence that wave exposure and depth gradients can regulate macroalgal dominance and spacing on shallow tropical reefs **(Fabricius *et al.*, 2023)**.

At Station 2 (S2), distribution patterns were more heterogeneous. Three species *C. racemosa*, *Sargassum oligocystum*, and *Eucheuma cottonii* showed clumped distributions, while *H. tuna* and *Padina australis* were uniformly distributed, and *Amphiroa fragilissima* appeared randomly distributed (Id ≈ 0.99 ≈ 1.0). This mosaic pattern likely reflects the microhabitat diversity at S2, characterized by a mix of sand, coral rubble, and live/dead coral, possibly with seagrass patches. Such heterogeneity

promotes localized recruitment patches and species-specific spatial arrangements patterns that have been widely documented in Indonesian reef flats **(Aprilia *et al.*, 2023; Handayani *et al.*, 2023; González *et al.*, 2024)**. The tendency of *Sargassum* to aggregate under moderate to high energy conditions further supports its role as a pioneer canopy-forming alga in disturbed or dynamic substrates **(Cosca *et al.*, 2024)**.

At Station 3 (S3), all three recorded taxa *H. tuna*, *C. racemosa*, and *E. cottonii* displayed clumped distributions, indicative of pronounced substrate patchiness (e.g., coral-rubble pockets) and spatial variability in hydrodynamic exposure. Such patchiness can enhance recruitment and persistence of modular or mechanically resilient taxa. Reef-scale modeling has shown that forereef slopes often accumulate rubble "hotspots," while studies on *Halimeda* bioherms highlight the patchy coral-rubble facies that reinforce aggregated patterns **(Leung & Mumby, 2024; Reolid *et al.*, 2024)**.

The random distribution of *A. fragilissima* at S2 (Id ≈ 1.0) corresponds with its sporadic presence in seagrass–dead-coral mosaics on disturbed coastal flats, matching observations from post-disturbance benthic-community transitions **(Handayani *et al.*, 2023; González *et al.*, 2024)**.

Overall, spatial distribution patterns derived from Morisita's index indicate a gradient from uniform at S1 to mixed (uniform–clumped–random) at S2, and clumped at S3. This progression aligns with reef-scale evidence that wave exposure, depth, and substrate heterogeneity shape macroalgal assemblages and their spatial organization **(Fabricius *et al.*, 2023; González *et al.*, 2024)**. Species-specific tendencies *S. oligocystum* and *E. cottonii* being clumped (Id > 1), *P. australis* and *H. tuna* uniform (Id < 1 or ≈ 1), and *A. fragilissima* random (Id ≈ 1)—mirror known ecological strategies and habitat preferences. These results are consistent with substrate-dependent attachment modes and hydrodynamic adaptations: Chlorophyta (e.g., *Halimeda*, *Caulerpa*) preferentially colonize sandy or rubble substrates, while Phaeophyceae (e.g., *Padina*, *Sargassum*) often act as pioneer colonizers on newly exposed hard surfaces **(Aprilia *et al.*, 2023; Handayani *et al.*, 2023; Cosca *et al.*, 2024; Reolid *et al.*, 2024)**. Similar distributional trends are widely observed along tropical inshore–offshore and wave-energy gradients, where hydrodynamic forcing and depth interplay to structure macroalgal guild composition and spatial patterning **(Fabricius *et al.*, 2023)**.

The tendency of Chlorophyta such as *Halimeda* and *Caulerpa* to inhabit sandy or coral-rubble substrates, and of Phaeophyceae such as *Padina* and *Sargassum* to act as pioneer colonizers on newly available hard surfaces, accords well with the established tropical macroalgal ecology literature and our local observations from Teluk Tamiang **(Aprilia *et al.*, 2023; Handayani *et al.*, 2023; Cosca *et al.*, 2024)**. Comparable assemblage patterns have been widely reported along inshore–offshore and wave-energy gradients across tropical reefs, where wave exposure, current velocity, and depth collectively govern the spatial organization of dominant macroalgal guilds **(Fabricius *et al.*, 2023)**.

Differences in distributional patterns among stations closely correspond to substrate composition and local hydrodynamic conditions. Sandy and coral-rubble substrates typically support mixed assemblages of Chlorophyta and Phaeophyceae **(Kadi & Wanda, 1988)**, with *Padina* and *Sargassum* frequently appearing as pioneer colonizers in moderate-energy environments **(Aprilia *et al.*, 2023; Cosca *et al.*, 2024)**. In contrast, dead-coral and rubble patches often promote clumped distributions in taxa capable of rapid clonal propagation, such as *Caulerpa,* or in large-thallus canopy formers like *Sargassum* **(González *et al.*, 2024; Leung & Mumby, 2024)**.

Consistent with **Kadi (2005)**, species occurrence and spatial configuration are determined by the match between environmental attributes (substrate type, light regime, hydrodynamic exposure) and intrinsic species traits (thallus morphology, reproductive or clonal strategy, and attachment requirements). A close match between these factors tends to produce dense, aggregated populations (Id > 1), whereas mismatch or intense intraspecific competition results in uniform (Id < 1) or random (Id ≈ 1) distributions **(Fabricius *et al.*, 2023)**. *Caulerpa racemosa* (clonal) and *Eucheuma cottonii* (a commercially important rhodophyte) commonly form dense patches (Id > 1) where hydrodynamic and substrate conditions are favorable **(Aprilia *et al.*, 2023)**. The calcified *Halimeda* demonstrates spatial duality uniform at S1 and S2, likely reflecting its need for stable irradiance and alkalinity that favor even spacing, but clumped at S3, suggesting localized attachment hotspots and micro-topographic refuges from currents and wave stress **(Reolid *et al.*, 2024)**. Meanwhile, *Amphiroa fragilissima* displays a random distribution at S2 (Id = 1.00), consistent with its sporadic occurrence on seagrass or dead-coral patches and the absence of strong nearest-neighbor interactions **(Handayani *et al.*, 2023)**.

The mosaic distribution observed at S2 coincides with the highest species richness at that station. Here, microhabitat heterogeneity increases niche diversity, facilitating the coexistence of pioneer browns (*Padina*, *Sargassum*) with clonal and calcified greens and reds (*Caulerpa, Halimeda, Amphiroa*). In contrast, S3 exhibits high abundance but reduced species richness a pattern typical of systems dominated by monospecific patches (Id > 1 across taxa) and often linked to rubble-driven patchiness following physical disturbance **(González *et al.*, 2024Leung & Mumby, 2024)**.

### 3. Environmental parameters and relationship to the community

Measured environmental parameters across the three stations temperature (29–32 °C), salinity (28–30 ppt), pH (7.0–7.2), dissolved oxygen (7.2–7.9 mg $L^{-1}$), current speed (0.15–0.22 m $s^{-1}$), water clarity (Secchi depth 1.0–1.2 m), and depth (1.0–1.2 m) all fell within the ranges considered conducive to macroalgal growth in tropical nearshore reef systems. The combination of warm, well-oxygenated, shallow water with moderate flow is widely associated with persistent macroalgal communities on carbonate flats **(Fabricius *et al.*, 2023; Handayani *et al.*, 2023)**. By contrast, elevated nitrate (1.1–2.1

mg $L^{-1}$) and phosphate (0.84–0.99 mg $L^{-1}$) concentrations exceeded guideline thresholds, suggesting nutrient enrichment that typically favors opportunistic and canopy-forming taxa **(Aprilia *et al.*, 2023; Fabricius *et al.*, 2023)**. Substrate composition varied among stations and strongly influenced assemblage structure. Station 3, characterized by coarse sand, rubble, and rocky patches, reflected a gradient known to shape benthic patchiness and attachment opportunities **(Reolid *et al.*, 2024; Leung & Mumby, 2024)**.

Station 2 exhibited the highest nitrate (2.1mg $L^{-1}$) and dissolved oxygen (7.9mg $L^{-1}$) values, coinciding with the greatest species richness (six taxa). This aligns with evidence that moderate nutrient enrichment, when coupled with sufficient oxygenation and water movement, enhances assemblage diversity supporting coexistence among *Padina*, *Sargassum*, and *Amphiroa* alongside *Caulerpa–Halimeda* complexes **(Aprilia *et al.*, 2023; Handayani *et al.*, 2023; Cosca *et al.*, 2024)**. In contrast, Station 3 recorded the lowest nitrate and phosphate (though still above thresholds) but the highest current velocity (0.22 m $s^{-1}$) and coarsest substrate, yielding the highest total abundance yet lower species richness dominated by *Caulerpa*, *Halimeda*, and *Eucheuma*. This pattern typifies environmental filtering in rubble-rich, higher-energy settings where a few tolerant taxa dominate **(Leung & Mumby, 2024; Reolid *et al.*, 2024)**. Station 1, with intermediate nutrient levels and a relatively homogeneous substrate, supported the fewest species (two *Chlorophyta*), consistent with simpler sand–rubble plains **(Fabricius *et al.*, 2023)**.

Current velocities across all stations (0.15–0.22 m $s^{-1}$) were within an "effective" range that promotes nutrient delivery and minimizes fine-sediment accumulation on thalli. The highest flow rate at Station 3 corresponded with clumped distributions (Id > 1) of *Caulerpa*, *Halimeda*, and *Eucheuma*, suggesting colonization concentrated within micro-topographic refugia **(Leung & Mumby, 2024; Reolid *et al.*, 2024)**. Despite relatively low water clarity (1.0–1.2 m Secchi depth), light penetration remained adequate for shallow macroalgae, with *Chlorophyta* dominance typical of such nearshore, turbid flats **(Fabricius *et al.*, 2023; Handayani *et al.*, 2023)**.

Substrate heterogeneity also structured community composition. Station 2's fine sand–coralline substrate offered numerous microhabitats (crevices, firm surfaces, and sediment layers) suitable for attachment and stolon/holdfast development, promoting coexistence among diverse taxa. In contrast, Station 3's coarse rubble–rock matrix favored large, clonal, or calcified species (*Caulerpa*, *Halimeda*, *Eucheuma*) requiring firm anchorage **(Aprilia *et al.*, 2023; Reolid *et al.*, 2024)**. Slightly acidic pH values (7.0–7.2), while below open-ocean norms, remained within tolerable coastal ranges; the persistence of calcified algae (*Halimeda*, *Amphiroa*) suggests localized buffering of carbonate chemistry sufficient for calcification **(González *et al.*, 2024; Reolid *et al.*, 2024)**.

Cross-station synthesis indicates distinct ecological structuring among the three stations; (1) The highest species richness at *Station 2* reflects the synergistic influence of

elevated nutrient concentrations, high dissolved oxygen, moderate current flow, and heterogeneous coralline-influenced substrates that create multiple attachment niches **(Handayani *et al.*, 2023; Cosca *et al.*, 2024)**; (2) The highest total abundance at *Station 3* corresponds with relatively stronger currents and a coarse, rubble-dominated substrate that favor dominance by *Caulerpa*, *Halimeda*, and *Eucheuma*, while limiting the establishment of *Phaeophyceae* **(Leung & Mumby, 2024; Reolid *et al.*, 2024)**, and (3) *Station 1* exhibits intermediate nutrient levels and a homogeneous substrate, resulting in a simpler *Chlorophyta*-dominated assemblage characterized by a more uniform dispersion pattern **(Fabricius *et al.*, 2023)**.

The quantitative relationship between macroalgal density and water quality parameters is summarized in Table (5) and illustrated in Fig. (3) below.

**Table 5.** Relationship between macroalgal density and water quality

| Station | Macroalgal Density (individuals) | Temperature (°C) | Salinity (ppt) | Nitrate (mg $L^{-1}$) | Phosphate (mg $L^{-1}$) | Current speed (m $s^{-1}$) | pH | DO (mg $L^{-1}$) | Depth (m) | Secchi (m) | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 61 | 29 | 28 | 1.7 | 0.98 | 0.15 | 7.0 | 7.2 | 1.2 | 1.2 | Sand, coral rubble |
| 2 | 122 | 32 | 30 | 2.1 | 0.99 | 0.20 | 7.2 | 7.9 | 1.0 | 1.0 | Fine sand, coralline |
| 3 | 178 | 30 | 29 | 1.1 | 0.84 | 0.22 | 7.0 | 7.6 | 1.1 | 1.1 | Coarse sand, rubble, rocky |

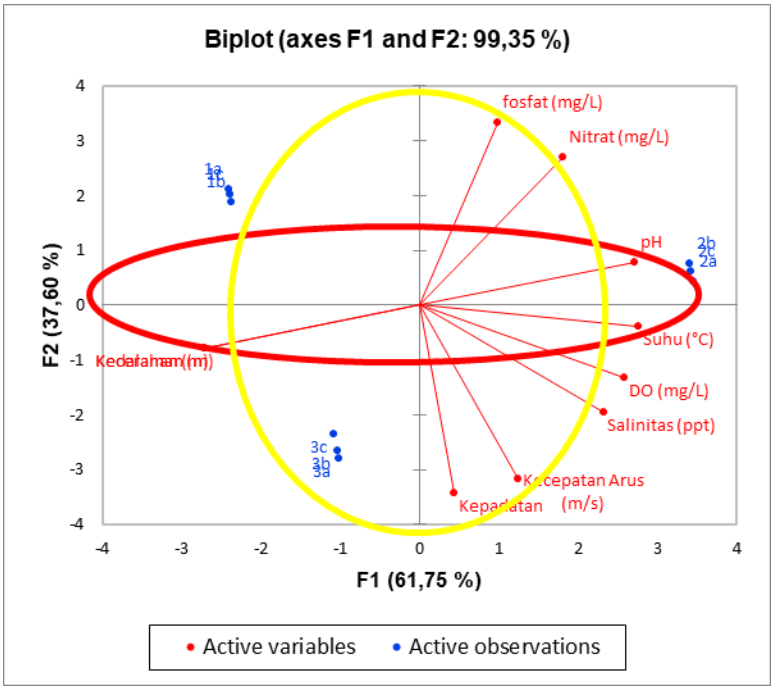



**Fig. 3.** PCA results linking macroalgal density with water-quality variables

Based on Table (5) and Fig. (3), macroalgal density ranked Station 3 > Station 2 > Station 1 (178, 122, and 61 individuals, respectively). In the PCA, *Station 3* loaded positively with density, current speed, phosphate, and nitrate; *Station 2* aligned positively with pH and temperature; whereas *Station 1* showed a negative association with depth and water clarity (Secchi depth). The environmental variables that most strongly explained variation in macroalgal density were current speed, nitrate, phosphate, pH, temperature, depth, and clarity, as indicated by vector direction and length in the biplot. These relationships mirror reef-scale findings that hydrodynamics, nutrient status, and the light–depth environment jointly shape macroalgal assemblages **(Fabricius *et al.*, 2023; González *et al.*, 2024)**.

Current speeds within the range of 0.10–0.50 m $s^{-1}$ are optimal for nutrient transport and gas exchange that support macroalgal photosynthesis. The alignment between current and density vectors in Fig. (3) suggests that sufficient water movement enhances macroalgal density, particularly at *Station 3* **(Fabricius *et al.*, 2023)**. Macroalgae depend on nitrate and phosphate as essential nutrients for growth and tissue formation; thus, the positive correlations between density and both $NO_3^-$ and $PO_4^{3-}$ indicate nutrient enrichment that, when balanced with adequate flow, oxygen, and light, promotes productivity and favors opportunistic or canopy-forming taxa **(Aprilia *et al.*, 2023; Handayani *et al.*, 2023; Cosca *et al.*, 2024)**.

The orientation of the pH and temperature vectors toward *Station 2* suggests environmental conditions conducive to enzymatic and photosynthetic efficiency, potentially explaining its higher species richness. This is consistent with trait-based evidence that warmer, well-mixed shallow waters enhance the performance of multiple macroalgal functional groups **(Fabricius *et al.*, 2023; Cosca *et al.*, 2024)**. In contrast, the negative association of *Station 1* with depth and water clarity (opposing vectors) reflects light limitation due to reduced irradiance penetration, which may constrain photosynthesis. Under such conditions, communities tend to be taxonomically simpler and dominated by tolerant Chlorophyta, a pattern widely observed on turbid nearshore flats **(Handayani *et al.*, 2023; González *et al.*, 2024)**.

Overall, the PCA findings are congruent with the Morisita dispersion results: areas with sufficient current and nutrient availability promote productive, clumped macroalgal patches, whereas deeper or more turbid sites act as environmental filters, supporting simpler and more uniform assemblages **(Fabricius *et al.*, 2023; Leung & Mumby, 2024)**.

## 4. Ecological and management implications

1. The combination of low–moderate Shannon diversity (H′), high evenness (J′), and low dominance (C) indicates a macroalgal assemblage that is relatively stable but not highly species-rich typical of tropical embayments characterized by limited substrate heterogeneity and moderate hydrodynamic energy **(González *et al.*, 2024)**.

2. Clumped dispersion in taxa such as *Sargassum* and *Eucheuma* reflects habitat patchiness and potential recruitment hotspots that are particularly sensitive to fluctuations in flow or sedimentation, especially over rubble-dominated substrates **(Leung & Mumby, 2024; Reolid *et al.*, 2024)**.
3. The PCA-derived gradients identify current velocity, light availability, and depth as the principal physical drivers, with nutrients acting as secondary amplifiers whose effects vary among taxa consistent with regional syntheses for Indonesian coastal systems **(Aprilia *et al.*, 2023; Handayani *et al.*, 2023)**.

We recommend implementing zoning measures to buffer against activities that elevate turbidity or nutrient loading, alongside routine monitoring of current velocity, water clarity, and nutrient concentrations. Recent studies emphasize that macroalgal responses to anthropogenic disturbance are taxon-specific rather than uniform; therefore, tracking key indicator taxa (e.g., *Sargassum*, *Caulerpa*, *Halimeda*, *Eucheuma*) rather than relying solely on total macroalgal cover offers more sensitive and actionable insights for adaptive coastal management **(Fabricius *et al.*, 2023; Cosca *et al.*, 2024)**.

## CONCLUSION

The macroalgal assemblage comprised six species exhibiting low–moderate diversity, high evenness, and low dominance. Spatially, Station 2 displayed the highest species richness, coinciding with elevated nutrients and dissolved oxygen, moderate flow, and heterogeneous substrates. Station 3 supported the highest total abundance but lower richness, associated with stronger currents, coarse rubble-dominated bottoms, and the dominance of *Caulerpa*, *Halimeda*, and *Eucheuma*. Station 1 exhibited the simplest community, reflecting its homogeneous substrate and moderate nutrient regime.Principal Component Analysis (PCA) indicated that macroalgal density was primarily influenced by current speed, nitrate, phosphate, pH, temperature, depth, and water clarity, underscoring the interactive role of hydrodynamics, nutrient availability, and light mediated by substrate composition—in shaping benthic assemblages. The coexistence of brown canopy/pioneer forms (*Padina*, *Sargassum*) and calcified green and red algae (*Halimeda*, *Amphiroa*) with *Chlorophyta* highlights their collective contributions to sediment production, habitat complexity, and coral–algal interactions.

To sustain community stability, management should focus on controlling nutrient inputs, maintaining water clarity and circulation, and enforcing buffer zones to minimize turbidity and eutrophication. Monitoring key functional taxa rather than aggregate macroalgal cover provides a more accurate basis for ecosystem assessment. Finally, as this study represents a single-season snapshot, it does not capture potential effects of seasonality or herbivory that influence macroalgal dynamics. Future research incorporating multi-season monitoring, grazer abundance, and experimental

manipulations would strengthen causal inference and improve predictive understanding of tropical macroalgal community responses.

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