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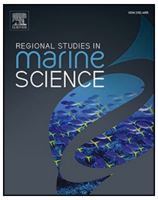

Sediment, substrate, and structure: Factors shaping algal turf dynamics in urban Indonesian reefs

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ABSTRACT

Algal turfs significantly influence coral reef ecosystems by impacting benthic community structure and overall reef health through sediment trapping and accumulation, which are vital for nutrient retention and sediment stabilization. This study examines the spatial dynamics of algal turf height and sediment thickness across eight sites in the Spermonde Archipelago, South Sulawesi, Indonesia, covering an inshore-offshore gradient (1–62 km) from reefs near urbanized Makassar city to remote reefs. Measurements of algal turf height and sediment thickness on hard substrates and coral rubble at two depths revealed a clear inshore-offshore pattern. Reefs closer to the mainland had taller algal turfs and thicker sediment layers, transitioning from long sediment-laden algal turfs (LSATs) inshore to short productive algal turfs (SPATs) offshore. Algal turfs were taller on coral rubble but had thicker sediment on hard substrates. The study showed that algal turf height had strong positive associations with both organic and inorganic sediment loads, sediment thickness, and substrate type, but was negatively associated with relative organic loads. Algal turf height was negatively correlated with reef rugosity, indicating taller algal turfs are found where reef complexity is lower, which characterized reefs closer to the mainland. These results highlight a dual role of algal turfs: increasing total sediment trapping (absolute loads) but favouring inorganic sediment deposition more than organic sediment deposition as height increases. Herbivorous fish biomass did not significantly correlate with algal turf height, suggesting that bottom-up factors, rather than top-down control, may play a more critical role in this area. These findings highlight the intricate interactions between anthropogenic influences, environmental stressors, and reef ecosystem dynamics in the Spermonde Archipelago.

1. Introduction

Algal turfs play a crucial role in the dynamics of coral reef ecosystems (Swierts and Vermeij, 2016) and are often associated with changes in substrate composition, particularly a decline in live coral cover (O'Brien and Scheibling, 2018). They consist of a multi-species community of small filamentous algae under 2 cm in height (Littler and Littler, 2013), which may also include filamentous benthic cyanobacteria and microalgae that grow on hard substrates in coral reef ecosystems (Adey and Goertemiller, 1987; Connell et al., 2014). The widespread distribution of algal turfs is primarily due to their rapid growth on available substrates (Littler and Littler, 2013). As a result, they can compete for space with other benthic organisms and dominate coral reef benthic communities (Arias-González et al., 2017), hindering the settlement and survival of coral larvae and thus compromising the resilience of coral-dominated reefs (Arnold et al., 2010; Birrell et al., 2005). Algal turf coverage on many coral reefs worldwide can reach 60–70 %, particularly in areas experiencing high disturbance or degradation (Harris, 2015; Smith et al., 2016), and may even reach 90 % in regions directly influenced by mainland activities (Teichberg et al., 2018).

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The increase in algal turf cover on coral reefs is commonly linked to anthropogenic activities that degrade reef health (Tebbett and Bellwood, 2019). The majority of the world's coral reefs are locally threatened by various human activities, including overfishing, destructive fishing practices, coastal development, and river runoff (Burke et al., 2012; Chollett et al., 2017). Additionally, frequent and prolonged rises in sea temperatures have caused widespread coral bleaching and mortality in many regions (Eakin et al., 2019; Hughes et al., 2018; Hughes et al., 2018). Collectively, these stressors contribute to reef degradation, which in turn promotes a global increase in algal turf (Tebbett et al., 2023). Algal turfs often colonize dead corals following disturbances that affect coral reefs (Diaz-Pulido and McCook, 2002; Houk et al., 2010), leading to their classification as antagonistic competitors for space with corals (McCook, 2001). However, the interactions between algal turfs and corals are complex, ranging from negative to neutral, or even positive (Harris, 2015). The impact of algal turfs on corals is not universally detrimental and often depends on the specific context (e.g., Jompa and McCook, 2003; O'Brien and Scheibling, 2018). In some cases, coral-algal turf interactions may occur as a consequence of coral mortality due to other factors (Vermeij et al., 2010). The nature of these interactions can also be influenced by local sediment regimes and ability of algal turfs to trap sediment. Sedimentation gradients and trapped sediments in algal turfs can shape coral-algal turf interactions and increase coral damage (Gowan et al., 2014; Liao et al., 2019).

In coral reef ecosystems, algal turfs serve multiple ecological functions. As primary producers, they provide food for herbivores, including herbivorous fishes (Bellwood et al., 2018). Additionally, algal turfs play a critical role in trapping and stabilizing sediments suspended in the water column (Tebbett et al., 2020). These sediments may include inorganic particles such as sand, silt, and clay with diameters less than 2 mm (Goatley and Bellwood, 2013), organic particles (Bainbridge et al., 2018), or a combination of both (Clausing et al., 2014). Sediment-laden algal turfs significantly influence the grazing patterns of herbivorous fishes and affect coral recruitment (Tebbett and Bellwood, 2019). The sediment trapped by algal turfs can originate from various sources, including terrestrial runoff and river input (Bainbridge et al., 2018), coastal development, nearshore dredging, and coastal reclamation activities (Fisher et al., 2018).

Herbivorous fish play a crucial role in controlling algal turf growth on coral reefs through grazing, which helps maintain reef health and prevents shifts from coral to algae dominance (Done, 1992; Hughes, 1994). Different groups of herbivorous fishes contribute uniquely to this balance. Detritivores, such as the surgeonfish *Ctenochaetus striatus*, consume detritus from substrates or algal turfs (Purcell and Bellwood, 1993), playing a vital role in recycling organic matter (Wilson et al., 2003). Croppers, including some surgeonfish and rabbitfish, trim the upper parts of algal turfs, which helps inhibit algae overgrowth and supports coral recruitment and survival (Tebbett et al., 2022). Scrapers and excavators, primarily parrotfish, use their beak-like jaws to remove algae and detritus (Bonaldo and Bellwood, 2009; Green and Bellwood, 2009). Scrapers take frequent, light bites that control algae without damaging the substrate, thereby maintaining ecosystem balance (Bellwood and Choat, 1990; Bonaldo and Bellwood, 2009). In contrast, excavators take stronger bites that remove substrate material, contributing to bioerosion and creating space for new coral recruits, which influences reef structure and habitat complexity (Bellwood and Choat, 1990; Bonaldo and Bellwood, 2009).

The Spermonde Archipelago, located off the coast of Makassar city in South Sulawesi Province, Indonesia, serves as a case study of coral reef ecosystems under significant anthropogenic pressure (Reuter et al., 2021). Since the 1950s, Makassar, the provincial capital, has undergone rapid urbanization, leading to increased stress on coastal ecosystems, particularly coral reefs. The benthic community composition of coral reefs in Spermonde shows strong spatial structuring (Cleary et al., 2005; Polónia et al., 2015; Teichberg et al., 2018), which potentially influences the dynamics of algal turfs and their associated sediments, thereby affecting ecological processes such as coral recruitment and fish grazing. Despite the crucial ecological role of algal turfs in coral reef ecosystems, there is currently limited information on their distribution and sediment-trapping characteristics in the Spermonde Archipelago and Indonesia in general. Most existing data come from studies in Australia (e.g., Arjunwadkar et al., 2022; Latrille et al., 2019; Tebbett et al., 2024), where fishing impacts, management regimes, and species diversity differ considerably from those in Indonesia. This study aims to investigate the spatial dynamics of algal turf height and sediment thickness within algal turfs across the Spermonde Archipelago, focusing on how factors such as substrate type, depth, structural complexity, herbivorous fish biomass, and proximity to mainland are associated with these dynamics. Additionally, it seeks to explore the relationship between algal turf height and sediment thickness, examining how these interactions may contribute to coral reef resilience or vulnerability to degradation.

2. Methods

2.1. Study area

This study was conducted from August to September 2021 at eight sites in the Spermonde Archipelago, selected along an inshore-offshore gradient based on their distance from the mainland. The sites, measured perpendicular to the mainland, included Lae-Lae (1LL, 1 km), Samalona (2SA, 7 km), Barrang Lompo (3BL, 17 km), Bonetambung (4BO, 22 km), Badi (5BA, 23 km), Lumu-lumu (6LU, 31 km), Karang Kassi (7KS, 39 km), and Kapoposang (8KP, 62 km). Sampling was generally conducted on the northwestern side of each island, where well-developed coral reef areas are less directly influenced by mainland activities (Plass-Johnson et al., 2015; Teichberg et al., 2018). An exception was made for Kapoposang (8KP), where sampling took place in the northeast because this area has the highest reef growth rate, and the northwest features a steep drop-off not comparable to the other sampling sites. Due to its distance from the mainland, 8KP is not exposed to mainland effluents (Plass-Johnson et al., 2018).

2.2. Sampling

We measured algal turf height and sediment thickness as proxies for algal turf growth and sediment accumulation within algal turfs, respectively. Measurements were taken at shallow (3–5 m) and deeper (8–10 m) depths at all sites, except for 1LL, which only had shallow reefs. At each site and depth, three 50-meter line transects were laid parallel to the shore. Six quadrats (20 cm × 20 cm) were placed along each transect at 5–10 m intervals, with three on hard substrates, such as dead corals and rocks, and three on coral rubble. Rubble fields mostly consisted of loose pieces, with varying degrees of consolidation, for example, by sponges and crustose coralline algae (CCA). Within each quadrat, algal turf height and sediment thickness were carefully measured together using a caliper to the nearest micrometer at five random spots, providing 30 paired measurements per transect. All measurements were consistently performed by a single observer (GS).

Algal turf sediment loads (g/100 cm^2) and their composition (inorganic/organic) were assessed by suctioning sediments from a 10 × 10 cm section of the quadrat using four to eight 200-mL syringes, ensuring that the algae remained intact. The sampling was conducted consistently by the same person (GS), maintaining uniform syringe suction across all sites. Although a formal calibration experiment was not conducted, the number of syringes used was adjusted to ensure complete sediment removal within the sampled area, until no further removable sediment was present. Sediments, potentially including detritus trapped within the algal turfs, were collected exclusively from shallow depths on quadrats with hard substrates. In the lab, the sediment was rinsed 3–4 times with distilled water to remove salt content, allowing a settling period after each rinse (Gordon et al., 2016; Tebbett et al., 2018). The sediment was then dried at 105°C to eliminate moisture. After drying, it was sieved using a 2 mm sieve to retain only particles smaller than 2 mm (sand, silt, and clay) (Tebbett et al., 2018) before measuring the total loads. The weights were recorded using a digital scale (OHAUS Pioneer PA214C). Organic and inorganic fractions were separated by combusting the total load at 650°C for four hours (Zhang and Wang, 2014). The weight loss represented the organic matter, while the residue was considered the inorganic fraction.

Reef rugosity and fish biomass were measured along three 50-meter transects at both shallow and deeper depths, using the same transects as for algal turf height and sediment thickness measurements. Rugosity was assessed using the chain intercept method (Hill and Wilkinson, 2004), where a 20-meter chain followed the reef contour along the transect tape. A rugosity index was calculated based on the ratio of the chain's horizontal coverage to its full length, with higher values indicating greater structural complexity. Fish biomass was estimated through underwater visual censuses (UVCs) along 5×50 m transects, with three replicates per site (Hill and Wilkinson, 2004). A trained observer consistently recorded detritivore, cropper, scraper, and excavator fishes ≥ 5 cm in length within 2.5 m on either side of the tape. Fish total length was estimated to the nearest cm. To account for the considerable diversity of herbivorous species observed during the surveys (43 species), we adopted the functional group classification framework provided by the datamermaid database (www.datamermaid.org, accessed July 2023). This classification is based on a comprehensive species list sourced from FishBase (Froese and Pauly, 2010). Fish biomass was estimated based on length-weight relationships (Kulbicki et al., 2005) using conversion parameters from FishBase (Froese and Pauly, 2010).

2.3. Data analysis

A three-way analysis of variance (ANOVA) was conducted to assess whether algal turf height and sediment thickness significantly differed across sampling sites, depths, and substrate types, with each dependent variable analyzed separately. The dataset used for this analysis included data from sites 2SA to 8KP to ensure a balanced design, as deep data from site 1LL was unavailable. Data were averaged at the transect/replicate level and square-root transformed to address skewed distributions. When significant differences were detected, Tukey's Honestly Significant Difference (HSD) tests were used for post-hoc pairwise comparisons. Model assumptions were checked using diagnostic tests, including Levene's test for homoscedasticity, the Shapiro-Wilk test for normality, and QQ plots for residuals.

We employed gamma generalized linear models (Gamma GLMs) with a log link to investigate the relationships between key ecological variables, considering the non-negative and positively skewed nature of our response variables. Six separate statistical analyses were performed, each focusing on different dependent and independent variables: (1) organic sediment loads ~ algal turf height, (2) inorganic sediment loads ~ algal turf height, (3) relative contribution of organic loads ~ algal turf height, (4) sediment thickness ~ algal turf height + substrate type, (5) algal turf height ~ detritivore biomass + cropper biomass + scraper biomass + excavator biomass + reef rugosity, and (6) algal turf height ~ total herbivorous biomass + reef rugosity. These analyses were conducted separately due to methodological differences, to avoid multicollinearity issues that could arise from including all variables in a single model, and to increase statistical power. The first, second, and third models used only shallow data on hard substrates, as sediment load data were not available for deeper depths and on coral rubble. In the third model, the relative contribution of organic sediment loads was calculated by dividing the organic sediment loads by the total sediment loads (sum of organic and inorganic sediment loads) and converting the result into a percentage. Due to insignificant effects of depth in the ANOVA, the fourth, fifth and sixth models used data from both depths and all eight sites. Prior to analysis, multicollinearity was assessed for each model using Spearman's rank correlation. As no variables exhibited high collinearity (i.e., Spearman's rank correlation > 0.8), all variables were retained for analysis.

In the first model, a small constant (0.001) was added to the six zero values (7 % of the total data at transect level) of sediment thickness to enable the application of the Gamma GLM. Logarithmic transformations were applied to the predictor variables where appropriate: algal turf height in all models except the fifth model, due to initial residual diagnostics revealing heteroscedasticity in the original data; and the biomass of croppers, detritivores, excavators, and scrapers in the fifth analysis, to handle zeros and stabilize variance. All models were subjected to diagnostic checks, including residual plots, scale-location plots, and Cook's distance metrics, to identify potential violations of model assumptions and detect outliers. The statistical significance of predictors was evaluated using robust standard errors via heteroskedasticity-consistent covariance matrix estimations. Effect sizes were visualized by overlaying model predictions on back-transformed observed data points. All statistical analyses were performed with R Studio using base packages (version 4.3.0, R Core Team, 2023).

3. Result

3.1. Algal turf height and sediment thickness

Our study revealed distinct spatial variation in algal turf height and sediment thickness across the Spermonde Archipelago (Fig. 2). From a total of 1350 paired observations, algal turf heights ranged from 0.08 to 2.00 cm, with an average height of 0.52 ± 0.05 cm (mean ± SE). Sediment thicknesses ranged from 0.00 to 1.35 cm, with an average thickness of 0.12 ± 0.03 cm. Notably, sediment was absent (i.e., 0.00 cm) in 26.8 % of paired observations, particularly at sites located further offshore (6LU, 7KS, and 8KP). The tallest algal turfs and thickest sediment layers were observed at the inshore site 1LL, with a gradual decrease toward offshore reefs. Across all sites, algal turfs consistently grew taller than the accumulated sediment (Fig. 2), with the algal turf height-to-sediment thickness ratio increasing offshore. At 1LL, algal turfs were on average 2.9 times taller than the sediment thickness, whereas at 8KP, this ratio increased to 37.8. The results indicate a spatial shift from long sediment-laden algal turfs (LSATs) in inshore reefs to short productive algal turfs (SPATs) in offshore reefs. Variations in algal turf height and sediment thickness were observed across substrate types and depths. Algal turfs were taller on coral rubble (0.57 ± 0.04 cm) compared to hard substrates (0.47 ± 0.08 cm). In contrast, sediment thickness was greater on hard substrates (0.15 ± 0.04 cm) than on coral rubble (0.11 ± 0.03 cm). Slightly taller algal turfs and thicker sediments were observed in shallow waters (0.51 ± 0.06 cm and 0.13 ± 0.03 cm, respectively) compared to deeper waters (0.48 ± 0.03 cm and 0.11 ± 0.02 cm, respectively). However, the difference in algal height across depths was not statistically significant (see below).

The three-way ANOVA results revealed significant differences in algal turf height across substrate types ($F = 50.82$, $p < 0.001$) and sites ($F = 6.89$, $p < 0.001$). Post-hoc analysis showed that algal turfs were significantly taller on coral rubble than on hard substrates and were taller in inshore reefs (2SA, 3BL) compared to further offshore (6LU, 7KS, and 8KP). Although depth alone did not show a significant effect, there was a significant interaction between depth and substrate type ($F = 4.08$, $p = 0.048$). Additionally, a highly significant interaction between substrate type and site was observed ($F = 7.35$, $p < 0.001$). However, the three-way interaction among depth, substrate type, and site was not significant.

For sediment thickness, significant effects were observed for depth ($F = 4.51$, $p = 0.038$), substrate type ($F = 9.92$, $p = 0.003$), and site ($F = 37.82$, $p < 0.001$). Sediment thickness was greater in shallow reefs and varied significantly between substrate types, with more sediment retained on hard substrates than on coral rubble. Similar to algal turf height, sediment thickness was significantly greater in reefs closer to the

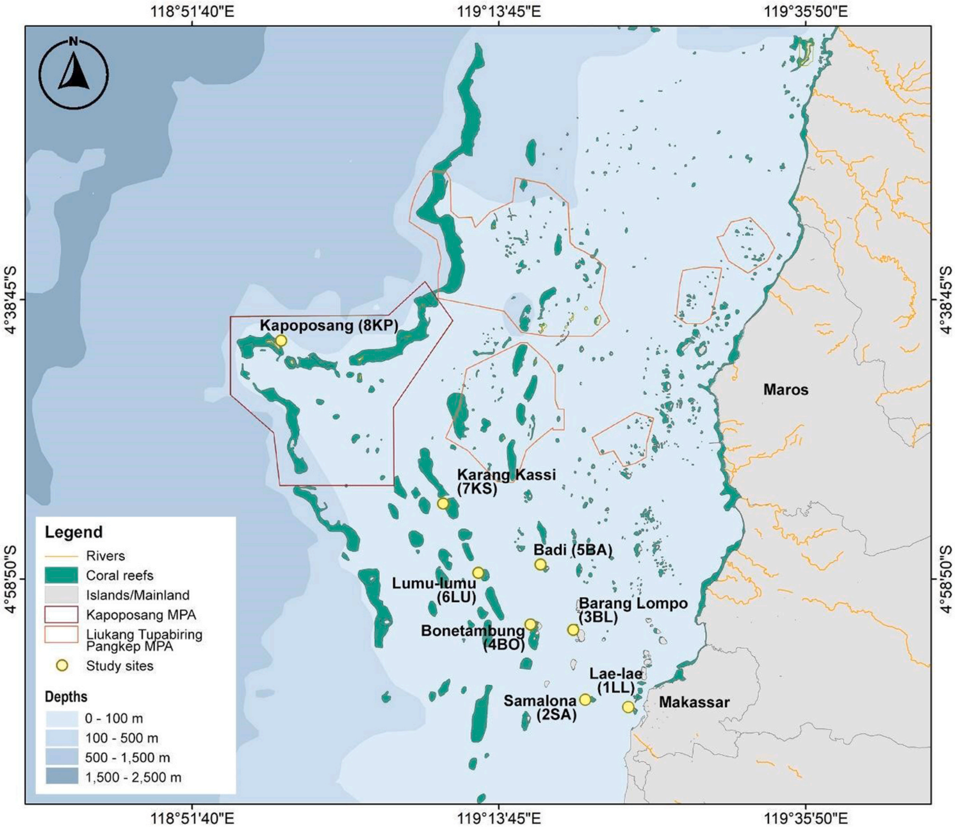

Fig. 1. Eight study sites across the Spermonde Archipelago, South Sulawesi, Indonesia (Estradivari et al., 2025).

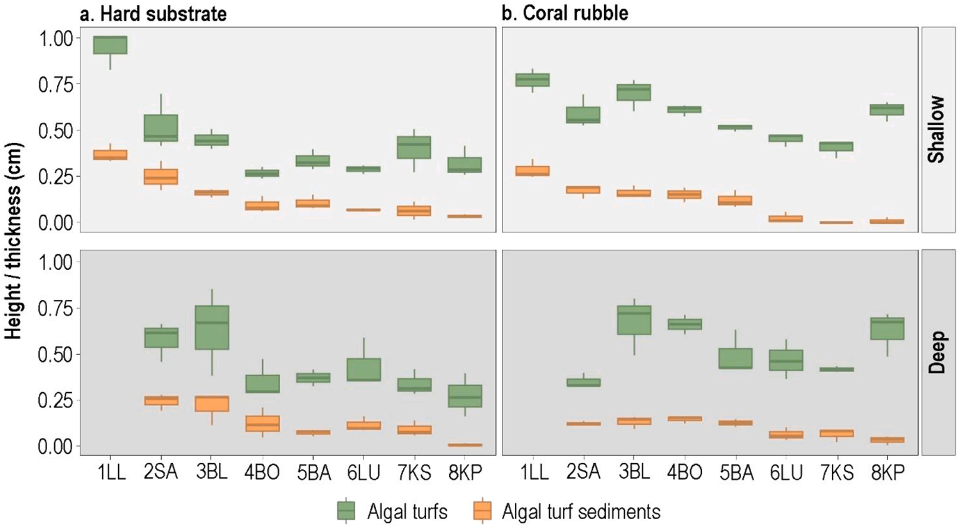

Fig. 2. Box plots showing algal turf height (green) and sediment thickness (orange) across eight sites, arranged by distance from the urban center Makassar (1LL, 1 km from the mainland, to 8KP, 62 km). Data are presented for shallow (3–5 m, light gray background) and deeper (8–10 m, dark gray background) depths and categorized by substrate type: (a) hard substrate (e.g., dead coral, rocks) and (b) coral rubble. Note that no observations were conducted at the deeper depth for site 1LL.

mainland (2SA) compared to reefs further offshore (6LU, 7KS, and 8KP). Significant interactions were observed between depth and site ($F = 3.29$, $p = 0.008$), substrate type and site ($F = 4.89$, $p < 0.001$), and a three-way interaction among depth, substrate type, and site ($F = 2.71$, $p = 0.022$).

3.2. Herbivorous fish biomass, reef structural complexity, and algal turf sediment loads

A total of 4731 herbivorous fishes were observed across 45 transects at eight sites and two depths, representing 43 species from four families: scarine Labridae (parrotfishes; 19 species), Pomacentridae (14 species), Siganidae (5 species), and Acanthuridae (5 species). These species were categorized into functional groups: detritivores (2 species), croppers (23 species), scrapers (14 species), and excavators (4 species). The average biomass across the Spermonde Archipelago was recorded as follows: detritivores at 25.9 ± 6.5 kg/ha, croppers at 87.6 ± 19.2 kg/ha, scrapers at 84.9 ± 18.3 kg/ha, and excavators at 111.0 ± 20.2 kg/ha. Spatial trends in fish biomass from 1LL to 8KP revealed distinct ecological patterns (Fig. 3a-d). Croppers and scrapers showed the highest variability and biomass, with notable peaks at 4BO, 5BA and 8KP (Fig. 3b, c). Excavators also exhibited variability (Fig. 3d), with 1LL and 6LU having the lowest excavator biomass. Detritivores maintained relatively consistent low biomass across all sites (Fig. 3a).

Reef rugosity, a measure of structural complexity in reef ecosystems, varied across the Spermonde Archipelago, with an average index of 0.326 ± 0.043. The data revealed a distinct spatial trend, with rugosity generally low at 1LL and 2SA and higher at 3BL to 8KP (Fig. 3e). The highest complexity was observed at 7KS (0.435), while the lowest was found at 1LL (0.125). Organic sediment loads across the Spermonde Archipelago averaged 0.097 ± 0.046 g/100 cm^2, ranging from 0.007 g/100 cm^2 at 8KP to 0.410 g/100 cm^2 at 1LL. Inorganic sediment loads averaged 0.772 ± 0.441 g/100 cm^2, with values ranging from 0.053 g/100 cm^2 at 8KP to 3.732 g/100 cm^2 at 1LL. Both organic and inorganic sediment loads showed a pronounced decrease from 1LL to 8KP (Fig. 3f, g); high values indicate higher sedimentation rates, higher retention rates, or both at 1LL. In contrast, the relative contribution of organic loads to total sediment loads (i.e., organic and inorganic loads) showed an increasing trend from inshore to offshore reefs (Fig. 3h), ranging from 8.3 % (2SA) to 32.2 % (6LU), with an average of 20.1 ± 2.7 % across the Spermonde Archipelago.

3.3. *Factors associated with algal turf height*

The Gamma GLM results presented in Table 1 reveal several factors significantly related to algal turf height. Algal turf height was significantly correlated to organic sediment loads ($p < 0.001$) and inorganic sediment loads ($p < 0.001$), suggesting that taller algal turfs trap and accumulate more sediments overall, both organic and inorganic sediment loads (Fig. 4a, b). In contrast, we noted a significant decreasing trend ($p = 0.036$) in the relative contribution of organic sediment loads with taller algal turfs (Fig. 4c), due to inorganic sediment loads increasing faster (coefficient estimate of inorganic loads = 7.46, Table 1, Fig. 4b) than organic sediment loads (coefficient estimate of organic loads = 3.57, Table 1, Fig. 4a) as algal turf height increased.

The fourth model indicated that both algal turf height ($p < 0.001$) and substrate type ($p < 0.001$) were significant predictors and correlated positively with sediment thickness. Specifically, for every unit increase in algal turf height, sediment thickness increased by a factor of approximately 88 ($e^{4.48} \approx 88.1$, $p < 0.001$). Sediment thickness on hard substrate was 1.65 times ($e^{0.49} \approx 1.65$) or approximately 65 % greater than the sediment thickness on coral rubble (Table 1, Fig. 4d). Hard substrates were associated with greater sediment thickness compared to coral rubble ($p < 0.001$, Fig. 4d). The fifth and sixth model revealed that reef rugosity was significantly negatively correlated to algal turf height (Estimate = −0.69, $p = 0.007$), indicating that as reef structural complexity increases, algal turf height tends to decrease (Fig. 4e). Interestingly, the biomass of different functional groups of fish (detritivores, croppers, scrapers, and excavators, Table 1, fifth model) and total nominally herbivorous fish biomass (Table 1, sixth model) did not show significant relationships with algal turf height.

4. Discussion

The spatial variation in algal turf height and sediment thickness across the Spermonde Archipelago highlights the complex interplay between anthropogenic factors, environmental stressors, and reef ecosystem dynamics. A distinct inshore-offshore gradient in algal turf

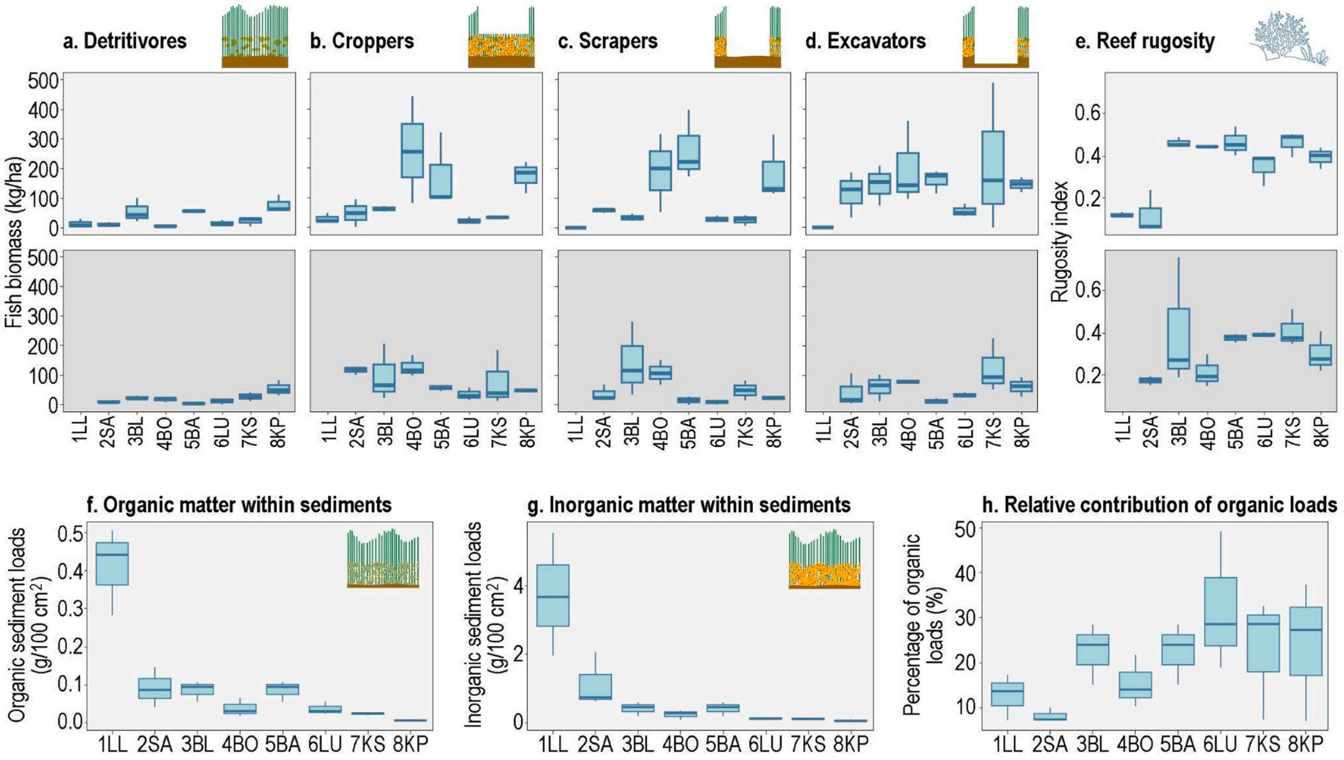

Fig. 3. Fish biomass of (a) detritivores, (b) croppers, (c) scrapers, and (d) excavators, (e) reef rugosity index, (f) organic, and (g) inorganic sediment loads within algal turfs, and (h) relative contribution of organic loads to total sediment loads across eight sites arranged by distance from the mainland (from 1LL at 1 km to 8KP at 62 km). Data are presented for shallow (light gray background) and deeper (dark gray background) depths, with the exception of site 1LL, where no observations were made at the deeper depth. Organic and inorganic sediment loads and the relative contribution of organic loads were measured only at shallow depths. Illustrations at the top of panels (a) to (d) represent the grazing impacts of different fish functional groups on algal turf and sediment dynamics.

Table 1
Environmental factors associated with algal turf heights. Significant variables (p-value <0.05) are in bold.

Coefficients	Estimate	Standard error	t-value	p-value
1. Organic sediment loads ~ algal turf height				
Intercept	-4.33	0.28	-15.24	**< 0.001**
Algal turf height	3.57	0.57	6.19	**< 0.001**
2. Inorganic sediment loads ~ algal turf height				
Intercept	-3.65	0.39	-9.26	**< 0.001**
Algal turf height	7.46	1.03	7.24	**< 0.001**
3. Relative contribution of organic loads ~ algal turf height				
Intercept	3.57	0.29	12.5	**< 0.001**
Algal turf height	-1.67	0.75	-2.24	**0.036**
4. Sediment thickness ~ algal turf height * substrate type				
Intercept	−4.26	0.27	−16.02	**< 0.001**
Algal turf height	4.48	0.57	7.83	**< 0.001**
Substrate type - hard substrate	0.49	0.13	3.74	**< 0.001**
5. Algal turf height ~ detritivore biomass + cropper biomass + scraper biomass + excavator biomass + reef rugosity				
Intercept	−0.40	0.16	−2.54	**0.015**
Detritivore biomass	0.04	0.03	1.35	0.185
Cropper biomass	0.01	0.04	0.35	0.732
Scraper biomass	−0.02	0.03	−0.75	0.458
Excavator biomass	−0.04	0.03	−1.54	0.131
Reef rugosity	−0.69	0.24	−2.82	**0.007**
6. Algal turf height ~ total herbivorous fish biomass + reef rugosity				
Intercept	−0.40	0.09	−4.66	**< 0.001**
Herbivorous fish biomass	< −0.01	< 0.01	−0.32	0.749
Reef rugosity	−0.86	0.26	−3.34	**0.002**

height and sediment thickness was observed, with taller algal turfs and thicker sediment layers consistently found in inshore reefs, gradually decreasing towards offshore reefs. This pattern likely reflects a natural gradient similar to that on the Great Barrier Reef (Tebbett et al., 2017b; Tebbett et al., 2025), with the impact of urban-associated stressors on coral reef health, such as elevated sedimentation, nutrient enrichment, and pollutant loads driven by coastal development, land reclamation, dredging activities, and riverine inputs along the coastlines of Makassar and nearby cities (Langkoke et al., 2022; Mosriula et al., 2018; Polónia et al., 2015), likely exacerbating the levels of sediments on inshore reefs.

Algal turf height in the Spermonde Archipelago is linked to multiple factors, including substrate type, site, sediment thickness, organic and inorganic sediment loads, relative contribution of organic sediment loads, and reef rugosity. Our findings highlight a positive relationship between algal turf height and both organic and inorganic sediment loads as well as sediment thickness, suggesting that sediment dynamics play a critical role in algal turf growth. This aligns with previous studies showing positive links between turf height and amount of trapped sediment (Gordon et al., 2016; Purcell, 2000), which may be bi-directional (Tebbett and Bellwood, 2019). Longer turfs may be more efficient at retaining sediments (Latrille et al., 2019). Conversely, sediment can provide nutrients and stabilize the substrate, thereby facilitating algal turf proliferation (Fabricius, 2005; Goatley and Bellwood, 2012). Additionally, substantial inorganic sediment loads may indicate higher sedimentation rates, which can benefit algae growth by providing physical support and shielding algal turfs from herbivory (Clausing et al., 2014; Rasher et al., 2012). Organic sediments, consisting of detritus and nutrient-rich materials, can further contribute to algal turf growth by supplying additional nutrients (Purcell and Bellwood, 2001; Wilson et al., 2003). Nevertheless, the positive effect of sediment on algal turf growth will cease at a certain point, as excessive sediment can result in negative impacts on algal turfs by causing anoxic conditions that can kill turfs (Clausing et al., 2014).

Interestingly, while taller algal turfs are effective at trapping greater total sediment loads, including both organic and inorganic material, our results indicate that the relative contribution of organic sediments decreases with increasing algal turf height. This is due to the higher rate of inorganic sediment accumulation compared to organic matter, as taller turfs may trap inorganic particles more efficiently and tend to be more stable (Bainbridge et al., 2018). The denser and more complex structures of taller algal turfs create hydrodynamic conditions that preferentially capture heavier and denser inorganic particles, such as carbonate or silicate sediments (Latrille et al., 2019; Tebbett and Bellwood, 2019; Arjunwadkar et al., 2022). Conversely, lighter organic particles may be less efficiently retained under these conditions (Bainbridge et al., 2018), although the increasing accumulation of sediments also contributes to the organic sediment load. However, this ultimately leads to a relative decline in the proportion of organic sediments (Tebbett et al., 2020). This trend aligns with the inshore-offshore patterns observed in urban-influenced Spermonde reefs, where taller algal turfs are found in inshore reefs with high turbidity and sedimentation caused by terrestrial runoff. These areas also exhibit the lowest relative contribution of organic loads. In contrast, offshore reefs with lower turbidity and sedimentation rates support shorter algal turfs, reduced sediment loads, and a higher relative contribution of organic loads. Such differences underscore the profound influence of sedimentation and turbidity on reef ecosystems, with taller turfs in urban reefs not only adapting to but thriving in high-sediment environments while significantly altering sediment trapping dynamics.

The gradient in algal turf height, sediment thickness, organic and inorganic sediment loads, and relative contribution of organic loads from inshore to offshore reefs reflects a transition from long sediment-laden algal turfs (LSATs) to short productive algal turfs (SPATs), indicating a shift in reef condition and functioning. LSATs, typically associated with degraded reef environments, are driven by high sedimentation and nutrient inputs, which promote the growth of long algal turfs that effectively trap sediments (Goatley and Bellwood, 2012; Tebbett and Bellwood, 2019). High sediment loads can reduce the palatability of algae for herbivorous fish, thereby weakening grazing pressure and allowing algae to proliferate unchecked, often smothering corals (Bellwood et al., 2004; Goatley and Bellwood, 2012; Tebbett et al., 2017a). In contrast, SPATs, characteristic of healthier reef systems, are maintained by lower sedimentation levels and higher rates of herbivory. These shorter, more productive algal turfs are less harmful to coral ecosystems and contribute to a more balanced reef ecology (Burkepile and Hay, 2010; Connell et al., 2014; Tebbett and Bellwood, 2019). The presence of this ecological process is further supported by observations of Estradivari et al. (2025) who reported limited or absent fish grazing in inshore reefs dominated by LSATs and high levels of fish grazing in offshore reefs where SPATs are prevalent. Together, these

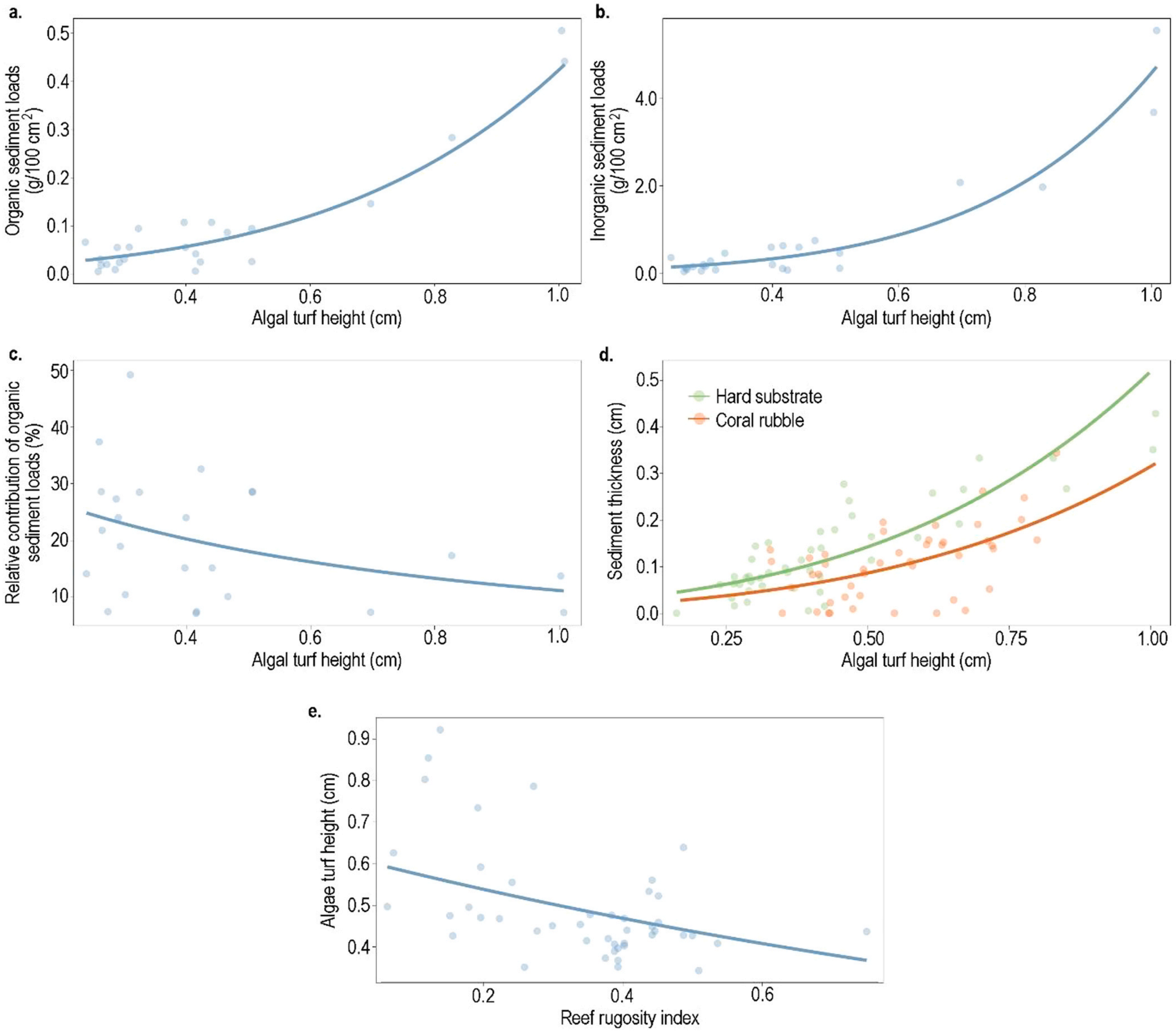

Fig. 4. Significant relationships between algal turf height and reef parameters. (a) Organic, (b) inorganic sediment loads, and (c) relative contribution of organic sediment loads versus algal turf height. (d) Sediment thickness as a function of algal turf height, differentiated by substrate type (hard substrate and coral rubble). (e) Algal turf height in relation to reef rugosity. Points represent observed data. The fitted curves illustrate significant positive or negative exponential relationships between algal turf height and each reef parameter. All relationships were modelled using Gamma GLMs with a log link function.

findings indicate that while longer algal turfs can retain more sediments, the relationship is bi-directional, with higher sedimentation rates promoting longer turfs through negative effects on herbivory, creating a self-reinforcing positive feedback loop between algal turfs and sediments that locks the ecosystem in a degraded state (Nyström et al., 2012). The results suggest that inshore reefs in the Spermonde Archipelago may be more vulnerable to degradation due to higher sediment accumulation and LSATs dominance. In contrast, offshore reefs may exhibit greater resilience due to the prevalence of SPATs. In addition, these offshore reefs are likely exposed to greater hydrodynamic energy, which naturally restricts sediment accumulation.

The role of substrate type in shaping benthic community structure is also evident in our study, as algal turfs were generally taller on coral rubble compared to hard substrates and on less rugose surfaces. This finding suggests that coral rubble and less complex substrates may provide more favorable conditions for algae growth. The irregular and fragmented nature of coral rubble increases surface area and creates varied angles, enhancing light exposure and nutrient availability (Kenyon et al., 2023; Wolfe et al., 2021). Coral rubble may offer less competition for space with other benthic organisms, such as encrusting coralline algae or sessile invertebrates, giving algal turfs a competitive advantage (Kenyon et al., 2023). Interestingly, we observed higher sediment thickness in turf of the same length on hard substrates compared to coral rubble. This could be due to differences in substrate stability and sediment-trapping efficiency. Algal turfs on hard substrates, being more stable and consolidated, tend to retain sediments more effectively, especially in areas with flat surfaces and limited water movement. In contrast, algal turfs on coral rubble, being more dynamic and easily shifted by water currents, appear to have a reduced capacity to retain and accumulate sediment (Kenyon et al., 2023). Additionally, the instability of coral rubble may expose algal turfs to less sediment accumulation, preventing smothering and allowing for more substantial growth. These contrasting patterns of algal turf height and sediment thickness between substrate types have important implications for coral reef ecology and resilience. Taller algal turfs on coral rubble may stabilize the rubble while potentially inhibiting coral recruitment (Birrell et al., 2005; Roth et al., 2018). Conversely, higher sediment thickness on hard substrates could negatively impact coral settlement and survival, particularly in areas with high terrestrial sediment input (Ricardo et al., 2017).

Our findings did not detect a relationship between algal turf height and herbivorous fish biomass, both at the functional level and for total nominally herbivorous species, which may be attributed to the unique environmental conditions of the Spermonde Archipelago. Poor water quality and high sedimentation in inshore reefs, combined with destructive fishing practices in the middle to offshore reefs, likely contribute to patchy grazing patterns (Estradivari et al., 2025). Destructive fishing methods, such as blast fishing, have been shown to degrade reef habitats, reduce fish populations, and alter ecosystem balance (Fox et al., 2003; Hampton-Smith et al., 2021; Mcmanus et al., 1997; Pet-Soede and Erdmann, 1998), disrupting the top-down control mechanism that typically regulates algal turf growth. Furthermore, high sedimentation rates, particularly in inshore areas, may shift algal turf species composition and reduce the palatability of algal turfs, making it more difficult for herbivorous fish to graze effectively (Bellwood and Fulton, 2008; Goatley and Bellwood, 2013; Tebbett et al., 2017a; Clausing et al., 2014). Given that this study focuses on observational correlations rather than manipulative experiments, the absence of a significant relationship between herbivore biomass and algal turf height should not be interpreted as evidence of a lack of ecological function. Instead, it underscores the need to account for additional environmental and anthropogenic factors that influence urban reef ecosystems.

Reef rugosity, rather than herbivorous fish biomass, emerged as a key predictor of algal turf height, suggesting that bottom-up factors, rather than top-down control, may play a more critical role in this area. More structurally complex reefs were associated with shorter algal turfs, likely due to the ability of rugosity to modify the light environment and enhance turbulent water flow, which reduces the accumulation of sediments and nutrients that promote algal growth (Graham and Nash, 2013). Additionally, structurally complex reefs enhance herbivorous fish grazing efficiency by providing shelter and feeding opportunities, maximizing the removal of algal biomass and preventing macroalgal overgrowth (Robinson et al., 2020; Williams and Polunin, 2001). Conversely, low-complexity reefs promote algal turf proliferation, with sediments accumulating to levels that even high herbivorous fish biomass cannot counteract, hampering coral reef recovery (Tebbett et al., 2020; Duran et al., 2024).

These findings have significant implications for the Spermonde coral reef systems, especially under urban pressures. The positive feedback between algal turf height and sediment thickness poses serious challenges for reef health and resilience, especially in inshore reefs. Reef rugosity remains a strong predictor of algal turf height due to its direct impact on both physical conditions (e.g., water flow and sediment removal) and habitat availability for reef fishes. This study underscores the importance of reducing sediment runoff to coral reef ecosystems and preserving reef structural complexity to maintain ecological balance in the Spermonde Archipelago, particularly in systems where traditional trophic controls may be compromised. Management strategies should focus on protecting and enhancing reef structural complexity, mitigating sedimentation and other urban-derived stressors, and developing targeted approaches to manage algal turf growth that consider both biotic and abiotic factors.

CRediT authorship contribution statement

Gunawan Syafruddin: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **Estradivari:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Andi M.A. Pratama:** Writing – review & editing, Investigation, Data curation. **Inayah Yasir:** Writing – review & editing, Supervision. **Sebastian C.A. Ferse:** Writing – review & editing, Supervision, Conceptualization. **Rohani Ambo-Rappe:** Writing – review & editing, Supervision, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data Availability

Data will be made available on request.

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