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Benthic mud content is a strong indicator of coral cover and ecosystem recovery on turbid coral reefs

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ABSTRACT

Turbid coral reefs are characterised by high turbidity and sedimentation. However, the impacts of terrestrial sediment inputs on coral communities, as well as their interactions with reef-derived carbonate sediment, remain poorly understood. Here we examine the physical properties of mixed carbonate-siliciclastic benthic sediments from six turbid reefs in southern Singapore, which exhibit coral covers ranging from 15 % to 65 %. Coral was the dominant contributor to sand and gravel sediment on reefs (mean ± SE: 57 ± 1 %), followed by molluscan grains (21 ± 1 %). Mud content ranged from 0 to 26 % between sites and there was a positive correlation ($r = 0.4$) between terrigenous mud and coral-derived sand, while coral cover significantly decreased with increasing mud. Results suggest that losses in coral cover may initially cause an increase in bioclastic carbonate sediment as the reef structure degrades. However, long-term declines in coral cover will ultimately reduce sediment supply, as live coral sources diminish on reefs. Our findings highlight the importance of mitigating high sediment loads on coral reefs, even within naturally turbid environments, to ensure continued bioclastic sand generation and ecosystem functioning. Mud content on reefs was also a strong predictor of reef recovery following major coral bleaching underscoring the need for holistic transboundary management of coral reefs as coastal urbanisation continues to intensify.

1. Introduction

Sediments play a fundamental role within coral reef ecosystems, shaping the spatial distribution of reef sedimentary habitats (Morgan and Kench, 2016; Browne et al., 2021) and contributing to the internal structure of reef frameworks (Perry et al., 2011, 2017; Kuffner and Toth, 2016). Additionally, reef-derived sediment provides an essential supply of building materials for the development and maintenance of reef islands and reef-adjacent shorelines (Perry et al., 2011; Kuffner and Toth, 2016). These coral reef sediments primarily consist of bioclastic carbonate material derived from the skeletal remains of calcifying reef organisms such as corals, molluscs, and foraminifera (Pomar et al., 2004; Pomar, 2020). In coastal or nearshore environments, reefs may also receive an influx of fine terrigenous sediment (i.e., mud) that is transported via riverine discharge and coastal runoff, which can elevate seawater turbidity and change bulk sediment composition (Fabricius, 2005; Zweifler et al., 2021). Increased turbidity, along with reduced light penetration through the water column, can also significantly constrain the depth range of coral growth and reef development (De'ath and Fabricius, 2010; Morgan et al., 2016a, 2016b, 2020), primarily due to the loss of the photosymbiotic capacity of corals under extreme low light conditions (Muscatine and Dubinsky, 1990; Anthony and Fabricius, 2000; Anthony et al., 2007). Although the ecological impacts of high turbidity on coral reef organisms have been increasingly studied (Anthony and Fabricius, 2000; Browne et al., 2012; Goh et al., 2021; Bauman et al., 2022), the effects of terrestrial sediment inputs on benthic sediments (i.e., mixed carbonate-siliciclastic environments) remains poorly documented. The paucity of data on the physical and compositional properties of sediment is concerning given the high number and spatial extent of turbid reefs within coastal areas (Zweifler et al., 2021).

Sediments play an important role in determining local environmental conditions on reefs, which in turn influence the structure of ecological assemblages (Rogers, 1990; Chou et al., 2004; Fabricius, 2005; Morgan et al., 2020). The majority of research on modern carbonate sediment dynamics has focused on atoll systems in the Indian Ocean (e.g., Maldives, Morgan and Kench, 2014, 2016; Cocos Island, Smithers, 1994; Kench, 1997; Chagos Archipelago, Perry et al., 2016,

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2020, 2023) and the central Pacific Ocean (Marshall Islands, Ford et al., 2020), or other clear-water settings (Dawson and Smithers, 2014, 2014; Harris et al., 2014; Cuttler et al., 2019; Kappelmann et al., 2024). In comparison, shelf reefs located in Southeast Asia have remained largely understudied. There is a limited understanding of the influence of allochthonous, terrestrial-derived sediment on the formation of reef detrital sediment pools (Browne et al., 2013; Van Maren et al., 2014; Morgan et al., 2020), or how turbidity-driven shifts in benthic communities may alter bioclastic sediment production. A greater understanding of the role of fine mud (<63 μm) on reefs is therefore required, as these sediments can smother coral communities (Fabricius and Wolanski, 2000; Fabricius et al., 2003; Browne et al., 2015), reduce hard benthic substrates for coral recruitment (Babcock and Davies, 1990; Ricardo et al., 2017; Tuttle and Donahue, 2022), and serve as a vector for pollutants and disease (Karickhoff et al., 1979; Fabricius, 2005; Yu et al., 2006). While turbidity is a common water quality parameter to assess terrigenous sediment inputs, it is primarily a measure of water column opaqueness that incorporates both dissolved and particulate matter (Duchrow and Everhart, 1971; Kitchener et al., 2017), and therefore does not provide information on the magnitude of net sediment deposition on reefs.

Despite the negative impacts of high turbidity and sedimentation on reefs (De'ath and Fabricius, 2010), coral communities have adapted to tolerate marginal conditions for reef growth (Burt et al., 2020), and may exhibit a greater resilience to environmental stressors compared to corals that inhabit clearer waters (Cacciapaglia and van Woesik, 2015; Johnson et al., 2017; Morgan et al., 2017). For example, palaeoecological studies indicate that Indo-Pacific reef communities have thrived under naturally high sediment conditions for millennia (Johnson et al., 2017), with evidence of coral persistence under turbid conditions in Southeast Asia dating back to the Miocene (Santodomingo et al., 2015, 2016). The addition of fine mud, and its interaction with localised carbonate framework production, is also well-documented within Holocene records (Larcombe and Woolfe, 1999; Smithers and Larcombe, 2003; Perry et al., 2012; Morgan et al., 2016b). However, contemporary datasets on reef-scale sediment dynamics in the presence of substantial terrestrial mud inputs remains limited, and even fewer studies have attempted to establish linkages with living reef biota within turbid settings. Our current bias towards understanding pre-Anthropocene turbid reef systems may therefore limit our ability to address current challenges posed by increasing sediment loads in tropical settings, particularly Southeast Asia. Additionally, as urbanisation in Southeast Asia has intensified the input of fine sediments on adjacent reefs through large-scale land reclamation and land-use changes (Chia et al., 1988; Hilton and Manning, 1995; Chou et al., 2004; Van Maren et al., 2014), turbidity and sedimentation stress in these regions is expected to increase (Neumann et al., 2015; Heery et al., 2018; Zweifler et al., 2021; Reimann et al., 2023). As water quality on contemporary reefs are driven by both natural processes and human activities, there is a need for further research specific to understanding coral reef communities under current ecological states and environmental conditions, and how these reef types may continue to generate bioclastic sediment.

Here we combine benthic sediment sampling with ecological survey data from six turbid reef sites in southern Singapore with varying coral cover to examine how turbidity-driven shifts in benthic community structure and high influxes of terrestrial mud influence the formation of mixed carbonate-siliciclastic reef sediment environments. The range of reefs offer a unique perspective on the impacts of both natural turbidity and anthropogenic influences and are used to establish primary sediment sources and their contribution to the detrital sediment pool. Given the recent rates of terrigenous sedimentation associated with rapid urbanisation and climate change, we hypothesise that sediment properties will differ between reef sites under varying degrees of terrigenous sediment inputs, with consequential effects on associated reef communities. We expect that greater sediment stress will impact habitat quality, potentially altering the diversity and relative abundance of carbonate sediment producers on reefs. Our findings highlight how turbid reef sediment dynamics may be modified by elevated terrigenous sedimentation and offers important insight into how other reef systems may adapt to future environmental changes given increasing sediment loads delivered to coastal systems globally.

2. Methods

Grain size and constituent component analyses were conducted on benthic sediment samples from four different habitat zones across six turbid reef sites in southern Singapore. The benthic sediment data was compared with reef communities at the respective reef sites to examine the role of biogenic sediment production and terrestrial inputs within mixed carbonate-siliciclastic reef systems.

2.1. *Benthic sample collection*

A total of 69 benthic sediment samples were collected from six reef platforms located within southern Singapore during November 2021 (Fig. 1). These sites were: Pulau Hantu (Hantu), Pulau Satumu (Satumu), Pulau Semakau (Semakau), Pulau Jong (Jong), Kusu Island (Kusu), and Terumbu Pempang Tengah (TPT). At each site, three replicate surface sediment samples (~50 g) were collected across the reef profile at the reef flat (1 m depth), reef crest (1–2 m depth), reef slope (3–4 m depth), and at the deep reef slope (~7 m depth). Samples were collected on SCUBA using sampling tubes, extracting the upper 2-5 cm of benthic sediment. No sample was collected from the Semakau reef flat as the site was not accessible during fieldwork.

2.2. *Grain size analysis*

Benthic sediment samples were rinsed with fresh water, oven dried at 50 °C and subsequently weighed. All samples were then wet sieved to separate fine (<63 μm) and sand fractions (>63 μm). Both fractions were dried and weighed to obtain their percentage weight relative to the total bulk sediment sample. The sand fraction was subsequently separated into standard grain size classification intervals (125 μm, 250 μm, 500 μm, 1000 μm, >2000 μm) (Wentworth, 1922). Bulk weights of the different grain size intervals were used to compute grain size statistics using GRADISTAT (Blott and Pye, 2001). However, as grain size parameters such as mean, sorting, skewness, and kurtosis are less suitable for bioclastic material (Matthews, 1991; Kench and McLean, 1997), our study focused on general grain size distribution, classification of sediments and fine fraction content.

2.3. *Sediment constituent composition*

The composition of carbonate grain components within benthic sediment were identified for all size fractions >250 μm to quantify the contribution of the main producers of carbonate sand on reefs and within habitat zones (Morgan and Kench, 2016). Grains <250 μm were not identified due to the limited identification accuracy in this size range. A minimum of 100 grains per size fraction were identified (with fewer than 100 grains typically available for the >2 mm fraction), resulting in an average of 350 grains identified per sample. Grains were identified using a binocular microscope (Leica S6D). Unidentifiable grains were labelled 'bioclasts' and not included in the count. Identified components encompassed scleractinian corals, *Heliopora coerulea*, molluscan grains, crustaceans, siliciclastic material, sponges, calcareous algae, Bryozoa, cryptofauna (Foraminifera, Serpulidae), and other minor sediment constituents, including echinoderms, fish bones and teeth, microplastic.

2.4. *Ecological survey*

Ecological surveys were conducted alongside the collection of

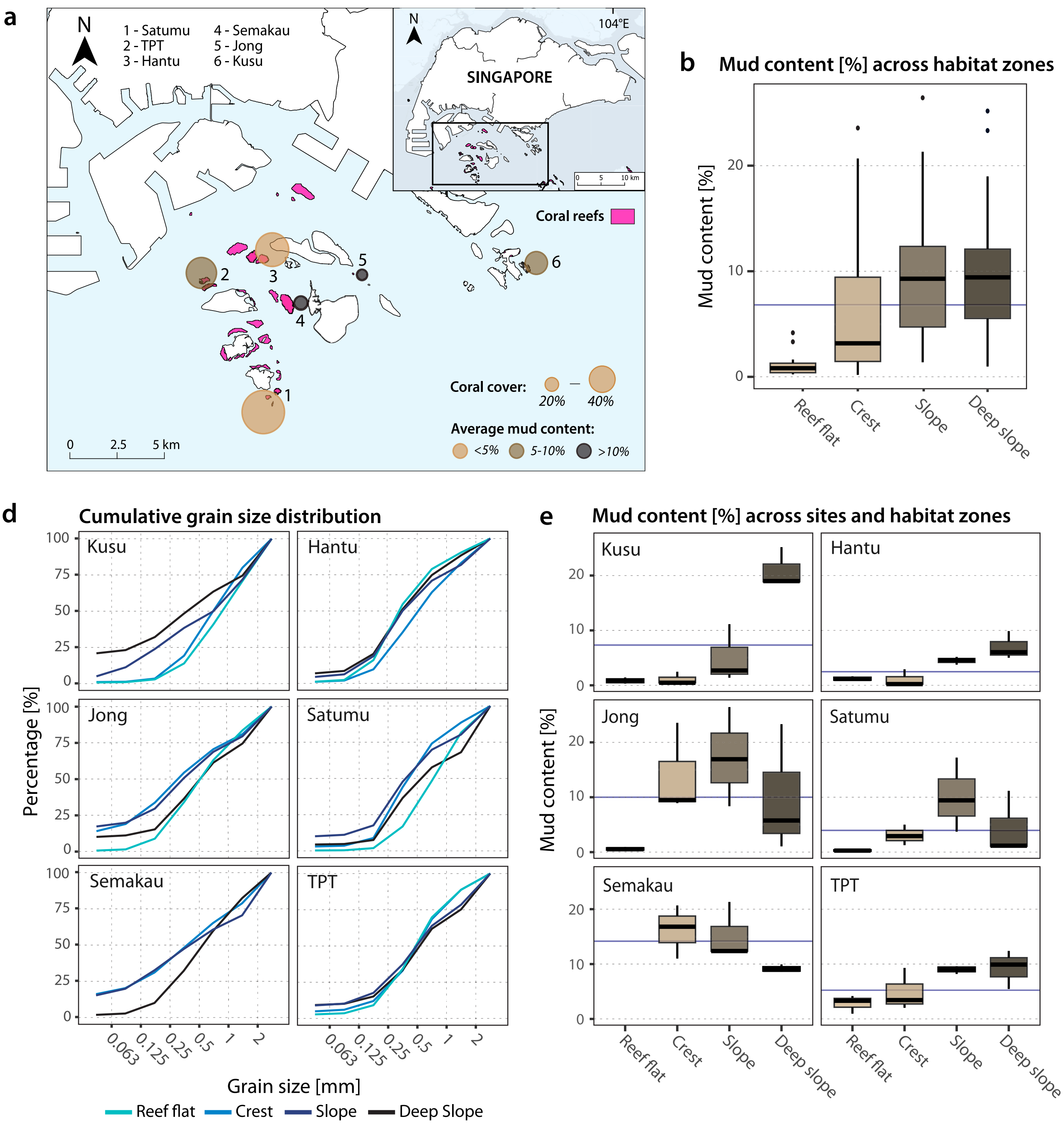


Fig. 1. Sediment characteristics across reef sites. (a) Location map of reef sites showing the percent of coral cover (shown as circle size) and average mud content; (b) mud content (%) across habitat zones for all reef sites; (c) cumulative grain size distribution curves (shades of blue indicate habitat zones); (d) mud content (%) across both reef sites and habitat zones. Horizontal blue lines in (b) and (d) denote average mud content (%) at the respective site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

benthic sediment samples. At each site, photoquadrats (0.25 m^2; n = 323) were collected every 5 m along six 30 m transects on the reef, with the exception of Jong where only five transects were recorded. Transects were conducted across the reef crest and slope, in a depth range of 2-7 m. The images were imported into CPCe (Coral Point Count with Excel extensions) to quantify benthic cover and composition. For each image, 20 random points were overlaid and manually classified according to the underlying major benthic component (e.g., coral, algae, sand). Corals were identified to genus and growth form and the percentage cover for each benthic category was calculated to determine the composition and relative abundance of reef communities.

Coral cover data from 2011 and 2017 were extracted from two existing studies (Bauman et al., 2015 and Januchowski-Hartley et al., 2020, respectively). Both studies applied established surveying methods (line-intercept transect and point intercept transect; see respective studies for detailed methodology). Coral cover data from these two preexisting studies was collected at the same sites and habitats.

2.5. Statistical analysis

ANOVA and PERMANOVA were used to assess the effects of reef site and habitat zone on the following response variables: proportions of grain size fractions (gravel, sand, mud), sediment constituents, benthic cover, and diversity of sediment constituents. Two-way ANOVAs were conducted to investigate potential interaction effects between site and habitat zone, determining whether the influence of habitat zone on sediment composition varied across different sites. A two-way ANOVA was applied to the coral cover data to examine the effects of site and year on coral cover.

ANOVAs were performed using the *car package* when the assumptions of normality and homogeneity were satisfied or when the data could be transformed to meet these assumptions. Normality of the data distribution within residuals was assessed using the Shapiro-Wilk test, and the homogeneity of variances was evaluated with Levene's test. In cases where the residuals remained non-normally distributed after transformation but exhibited homogeneous variances, ANOVA was still used, as it tolerates some degree of non-normality when variances are equal. However, ANOVA was not applied in instances of both non-normality and heterogeneity of variances. Instead, PERMANOVA (*R stats package*) was used, as it does not assume the normality of data.

To identify distinct sediment depositional environments on the reef sites, and to highlight reef sites that exhibit a similar sedimentary composition, a cluster analysis was performed on the constituent composition data (*R stats package*). A Similarity Percentage Analysis (SIMPER) was conducted using the vegan package (Oksanen et al., 2022) to evaluate the contributions of different variables (i.e., sediment constituents) to dissimilarities between sites. Pearson correlations were conducted to detect correlations between sediment constituent data and grain size composition, as well as to determine correlations within benthic community composition data. All percentages are given in mean ± SE. The Shannon-Wiener diversity index was calculated to assess the diversity of sediment composition across sites and habitat zones. Calculations were performed in R using the diversity() function from the *vegan package*.

3. Results

3.1. Variations in grain size distribution and mud content

Gravel content (>2 mm) was relatively low across all sites (19 ± 1 %). Gravel content varied significantly between the habitat zones, with gravel content at the reef slope being significantly higher than at the reef crest (2-way ANOVA; $F_{3,46} = 3.9$, $p = 0.02$). Gravel content between sites was only significantly different between Kusu and Hantu (2-way ANOVA; $F_{5,46} = 3.9$, $p = 0.005$), with Kusu having the highest gravel (26 ± 2 %) and Hantu the lowest (14 ± 2 %). The interaction of site and habitat zone had a significant impact on gravel content (2-way ANOVA; $F_{14,46} = 2.5$, $p = 0.01$), however, no distinct patterns could be observed. Sand (63 μm to 2 mm) was the dominant grain type (71 ± 2 %) and the average content differed significantly between site (2-way ANOVA; $F_{5,46} = 8.0$, $p = 1.7 \times 10^{-5}$), habitat (2-way ANOVA; $F_{3,46} = 13.9$, $p = 1.4 \times 10^{-6}$) and the interaction of site and habitat zone (2-way ANOVA; $F_{14,46} = 3.1$, $p = 0.002$). Sand was significantly higher at the reef flat (81 ± 2 %) when compared to the slope (64 ± 2 %) and deep slope (67 ± 3 %). Hantu had the highest sand content (81 ± 2 %) among the sites. In comparison, Semakau (62 ± 5 %), Jong (67 ± 4 %), and Kusu (65 ± 3 %) had significantly lower sand. Satumu (75 ± 3 %) and TPT (75 ± 3 %) also had higher sand than Semakau. Sand content showed a strong negative correlation with mud ($r = -0.7$), as well as gravel ($r = -0.8$).

Across all 96 samples, average mud content was relatively low (7 ± 1 %), ranging from 0 % (Satumu) to 26 % (Kusu) of the total bulk sediment. However, benthic sediments showed significant variations in mud across different sites (Fig. 1b), between reef habitats, and when both site and habitat was tested (Fig. 1e). Mud content at the reef flat was significantly lower than at the slope and deep slope (2-way ANOVA; $F_{3,46} = 10.4$, $p = 2.4 \times 10^{-5}$), and mud at the reef flat did not differ significantly between site (site-habitat interaction; 2-way ANOVA; $F_{14,46} = 3.2$, $p = 0.001$) (Fig. 1b). However, mud content between the other habitat zones (i.e., crest, slope, deep slope) differed significantly between site (2-way ANOVA; $F_{5,46} = 5.2$, $p = 0.0007$). Jong and Semakau exhibited significantly higher average mud loads than all other sites (10 ± 3 % and 14 ± 2 %, respectively; mean ± SE; Fig. 1e).

Total bulk sediment at Jong and Semakau were finer overall due to the greater addition of mud (*gravelly muddy sand*) and are referred to as high-mud sites in the following. The lowest mean mud content was recorded at Satumu and Hantu (4 ± 2 % and 3 ± 1 %, respectively), and these reefs are subsequently classified as low-mud sites. TPT and Kusu had a notably higher mean mud content than those in the low-mud category (7 ± 3 % and 6 ± 1 %, respectively), but values were significantly lower than Jong and Semakau. TPT and Kusu are therefore classified as moderate-mud sites.

3.2. Contributions of sand-sized sediment constituents

Benthic reef sediments were comprised of scleractinian corals, *Heliopora* grains, molluscan fragments and crustacean fragments, siliciclastic material (e.g., quartz), sponge (spicules, acanthoxea), calcareous algae, Bryozoa, Foraminifera, serpulid tubes, and other minor sediment constituents, including echinoderm spines, fish bones and teeth, and microplastics. Scleractinian corals were the primary sediment contributor across all six reef sites, contributing an average relative contribution of 57 ± 1 % ($n = 69$) to the total sediment pool (Fig. 2a). We observed a moderate positive correlation ($r = 0.4$) between coral grains and mud content where higher relative abundance of coral sand coincided with increased mud loads on reefs. Molluscan grains were the second most prevalent sediment component across all sites (21 ± 1 %), with the remaining bioclastic constituents each contributing <5 % on average to the bulk sediment.

The constituent composition of reef sediments varied significantly between sites (PERMANOVA; pseudo-$F_{5,63} = 24.9$, pseudo-p = 0.001), but not habitat zones, and could be grouped into four distinct clusters (Fig. S1, Supplementary material). A simple ANOVA was applied to investigate the variance of specific components (i.e., scleractinian grains) across sites. A two-way ANOVA was not performed, as the PERMANOVA results had already indicated no significant differences in sediment composition between habitat zones. High mud sites (Jong and Semakau) contained the highest average scleractinian content (65 ± 1 %), followed by the moderate-mud sites (TPT and Kusu; 64 ± 1 %). In contrast, scleractinian sediment content was significantly lower (44 ± 2 %) at low-mud sites (Satumu and Hantu; ANOVA; $F_{2,68} = 56.33$, $p = 5.3 \times 10^{-15}$). There was no significant variation in the relative contribution of scleractinian grains between different habitat zones (ANOVA; $F_{3,68} = 2.3$, $p = 0.09$). Molluscan grains were most abundant at low-mud sites (24 ± 1 %), followed by moderate- and high-mud sites (both 20 ± 1 %). Siliciclastic sand was most prevalent at low-mud sites (Satumu: 26 ± 5 %; Hantu: 14 ± 1 %), with only a minor contribution elsewhere. Grains were identified as granite rock fragments that originate locally from exposed bedrock observed at Satumu (Fig. S2, Supplementary material).

Low-mud and moderate-mud reefs exhibited a significantly greater diversity of sediment components compared to high-mud reefs (ANOVA; $F_{2,66} = 6.8$, $p = 0.002$). SIMPER analysis identified scleractinian corals, molluscs, siliciclastic sand, and *Heliopora* grains as the main drivers of differences between sites, with these constituents contributing to >75 % of the total cumulative difference. As *Heliopora* grains were a major contributor to sediments at Kusu, they were categorised as "coral sand" during analyses, as they produce a hard calcareous skeleton similar to Scleractinian corals. Sponges, calcareous algae, calcified cryptofauna, and other sediment constituents displayed a relatively uniform

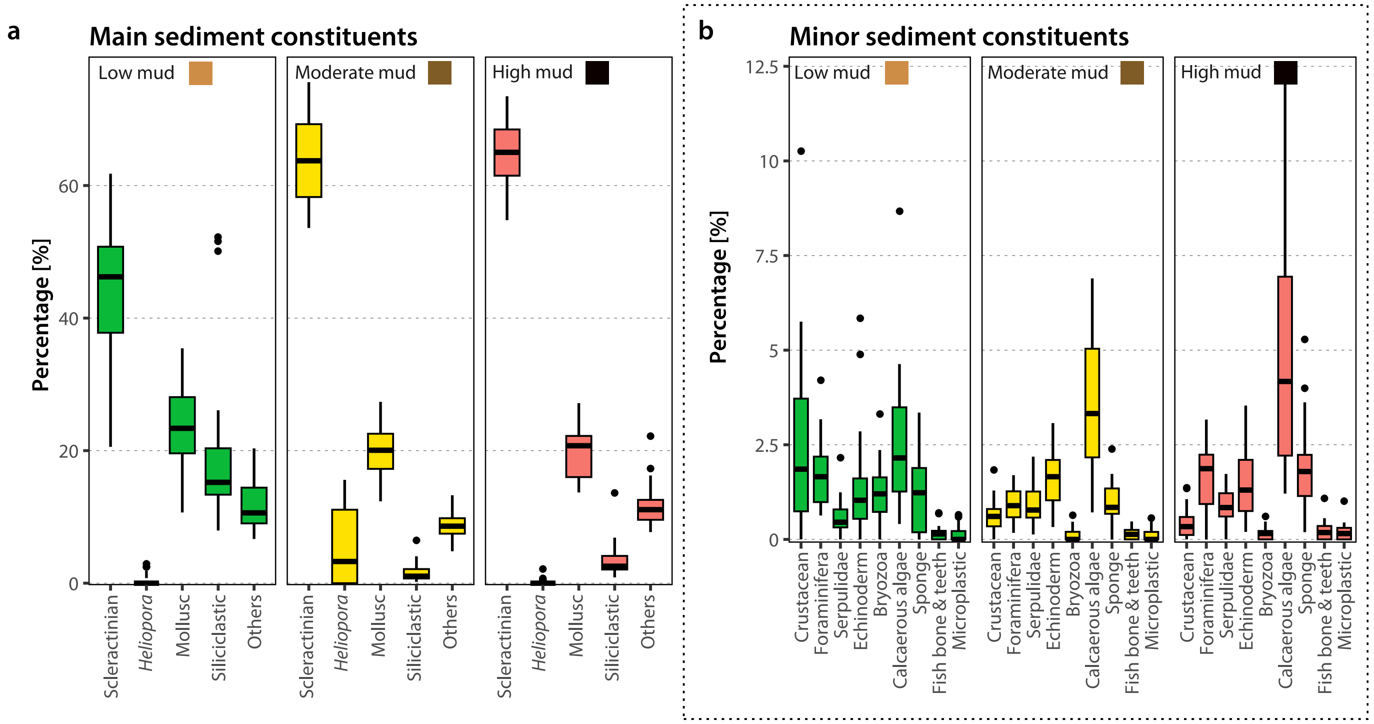


Fig. 2. Sediment composition (%) across six turbid reef sites in southern Singapore showing: (a) major sediment constituents, and (b) other minor sediment constituents. Reef sites are classified by the relative contribution of mud to total bulk sediment (low-mud <5 %, Satumu and Hantu; moderate-mud 5–10 %, Kusu and TPT; high-mud sites >10 %, Semakau and Jong).

distribution across reef sites (Fig. 2b), with minor variability observed.

3.3. Changes in coral cover and benthic community composition

The ecological surveys documented coral cover, macroalgae cover (including turf algae), dead coral cover, calcareous algae cover, soft coral cover, sponge cover, and sediment cover. A PERMANOVA confirmed significant differences in benthic community composition across sites (PERMANOVA; pseudo-$F_{5,34} = 3.2$, pseudo-$p = 0.001$). Coral cover ranged from 14 ± 4 % to 65 ± 2 % between reef sites, with a mean coral cover of 38 ± 3 % (Fig. 3). Coral cover was highest at low-mud sites and decreased significantly at high-mud and moderate-mud sites (low-mud: 58 ± 4 %; moderate-mud: 39 ± 4 %; high-mud: 17 ± 2 %; ANOVA: $F_{2,32} = 31.76$, $p = 2.51 \times 10^{-8}$; Fig. 4). There were no consistent patterns observed in coral growth forms between sites (Fig. S3, Supplementary material). Coral cover and macroalgae cover showed a negative correlation ($r = -0.6$), as well as coral cover and sediment cover ($r = -0.6$), indicating a shift from coral-dominated towards macroalgae-dominated systems. This shift occurred at high-mud sites, with macroalgae cover being significantly higher compared to low and moderate-mud sites (ANOVA: $F_{2,32} = 7.9$, $p = 0.002$). Calcareous algae (CCA, *Halimeda*) increased at high-mud sites but remained low overall. There was no observed dominance of other benthic taxa at high-mud sites (Fig. 3).

Coral cover reported in our study was compared to survey data collected in 2011 (Bauman et al., 2015) and 2016 (Januchowski-Hartley et al., 2020) (Fig. 5). Long-term trends at our sites show that while average coral cover on reefs decreased significantly following a major bleaching event in 2016 (2011: 43 ± 2.; 2017: 25 ± 2 %; 2-way ANOVA: $F_{2,98} = 24.1$, $p = 3 \times 10^{-9}$), reefs have since recovered to pre-bleaching levels at all sites except the high-mud sites of Jong and Semakau (year-site interaction; 2-way ANOVA: $F_{4,98} = 4.5$, $p = 0.002$). Coral cover in 2021 showed no significant difference when compared to 2016 data prior to the bleaching event. However, reefs at Semakau and Jong exhibited little to no recovery after the 2016 bleaching event, with coral

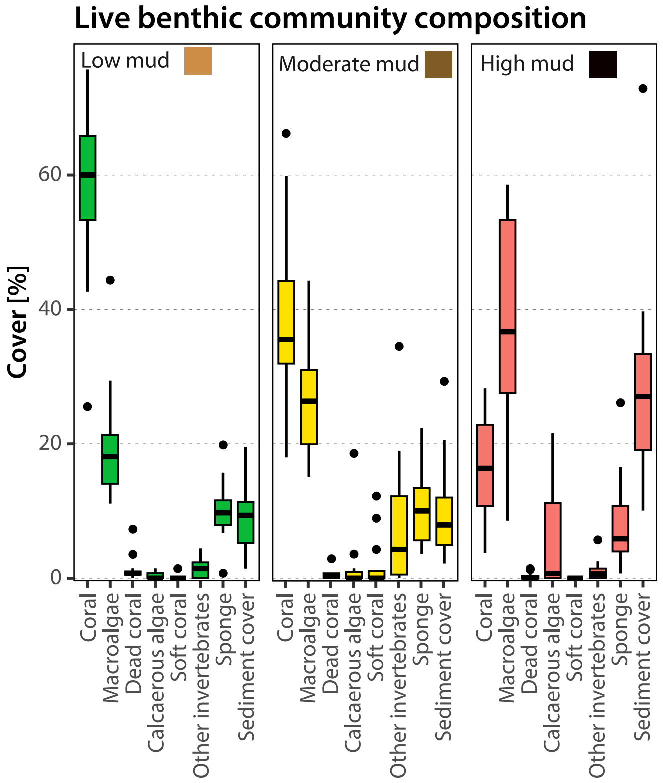


Fig. 3. Benthic cover (%) of six turbid reefs in southern Singapore. Reef sites are classified by the relative contribution of mud to total bulk sediment (low-mud <5 %, Satumu and Hantu; moderate-mud 5–10 %, Kusu and TPT; high-mud sites >10 %, Semakau and Jong).

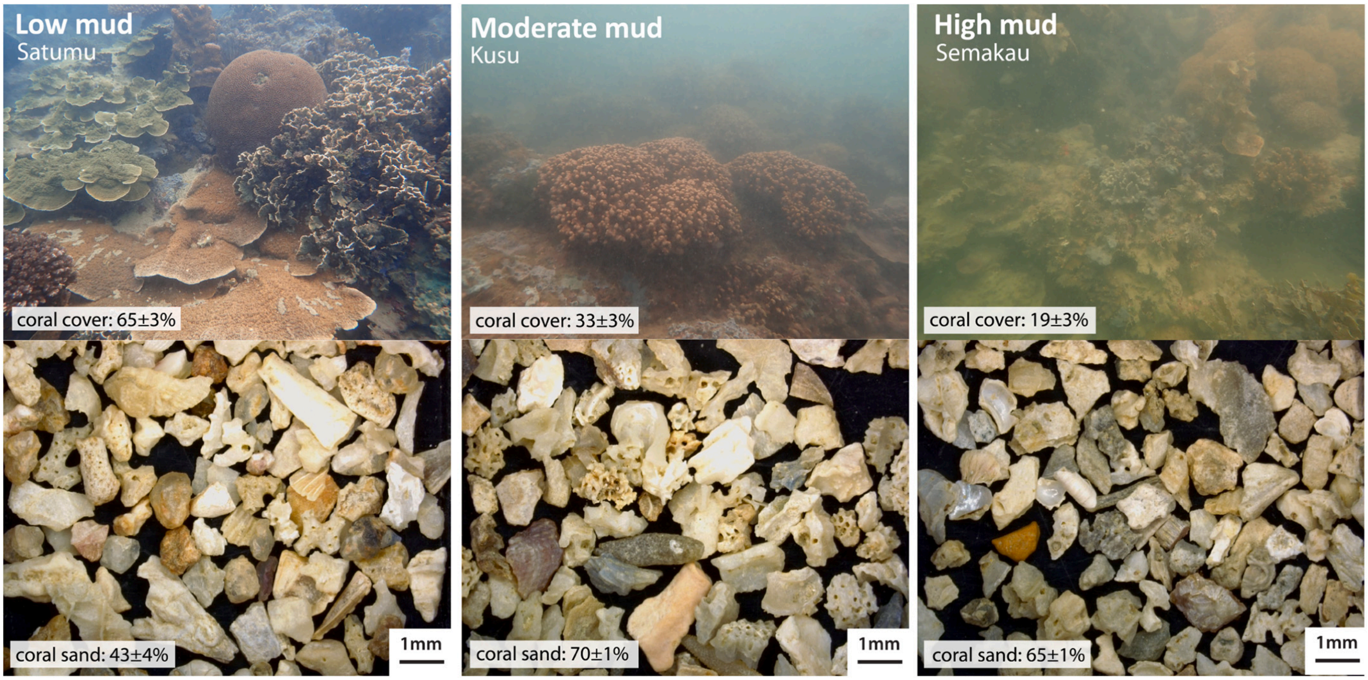


Fig. 4. Photographs of typical coral communities at low-, moderate- and high-mud sites, with corresponding photomicrographs of benthic sediment grains collected from the crest zone.

cover at both sites remaining below 20 % in 2021 (Fig. 5).

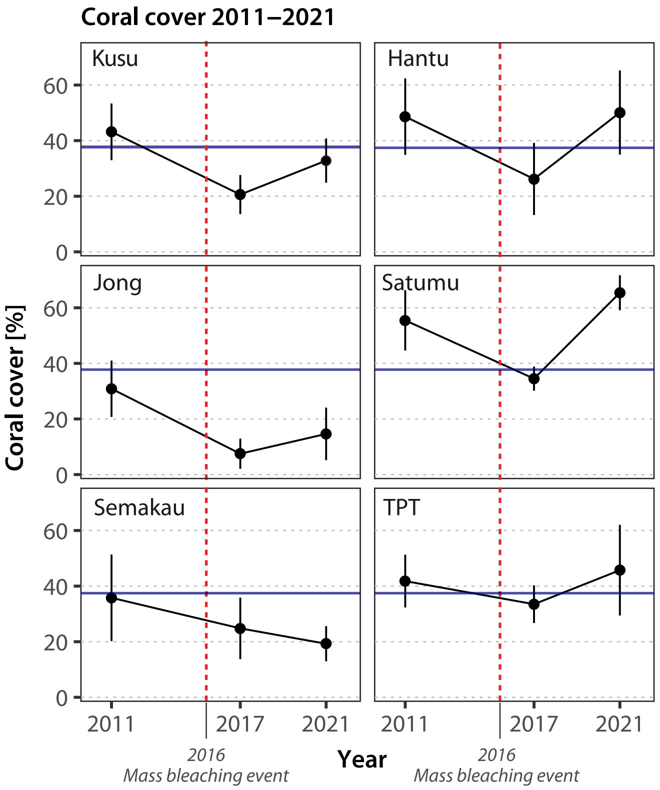


Fig. 5. Coral cover at six turbid reef sites in southern Singapore for 2011 (Bauman et al., 2015), 2017 (Januchowski-Hartley et al., 2020) and 2021 (our study). The dashed red line indicates the 2016 mass bleaching event and the blue line denotes the average 2021 coral cover across all reefs. Error bars show standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. *Mud deposition and retention in the sediment pool*

External terrigenous sediment inputs exert a major control on coral reefs, influencing various aspects of coral health (Karickhoff et al., 1979; Babcock and Davies, 1990; Fabricius and Wolanski, 2000; Fabricius, 2005; Browne et al., 2015) and driving reef zonation patterns (De'ath and Fabricius, 2010; Lai et al., 2015; Guest et al., 2016; Bauman et al., 2022). Yet, the relative contribution and impact of fine mud deposited in the sediment pool has rarely been quantified, even for turbid settings that are characterised by high turbidity and sediment loads. In this study, we examine the magnitude and spatial distribution of terrigenous mud within the detrital sediment pool of six turbid reefs under varying levels of mud loads (low, moderate, high). We assess the influence of these differing environmental states on benthic reef communities and the composition of bioclastic sediment. Our findings reveal significant variability in mud content across adjacent reefs and among habitat zones, even over small spatial scales, and highlight benthic sediment mud content as a potentially important indicator of coral cover and recovery potential following coral bleaching. We address a growing, yet understudied issue on coral reefs by examining the negative effects of land-derived mud deposition (Rogers, 1990; Fabricius, 2005; Erftemeijer et al., 2012) on aspects of biological carbonate productivity and sediment generation. By focusing on mud content within benthic sediment, we provide new insights into the sediment dynamics of mixed carbonate-siliciclastic reef systems, which are widespread globally but often overlooked.

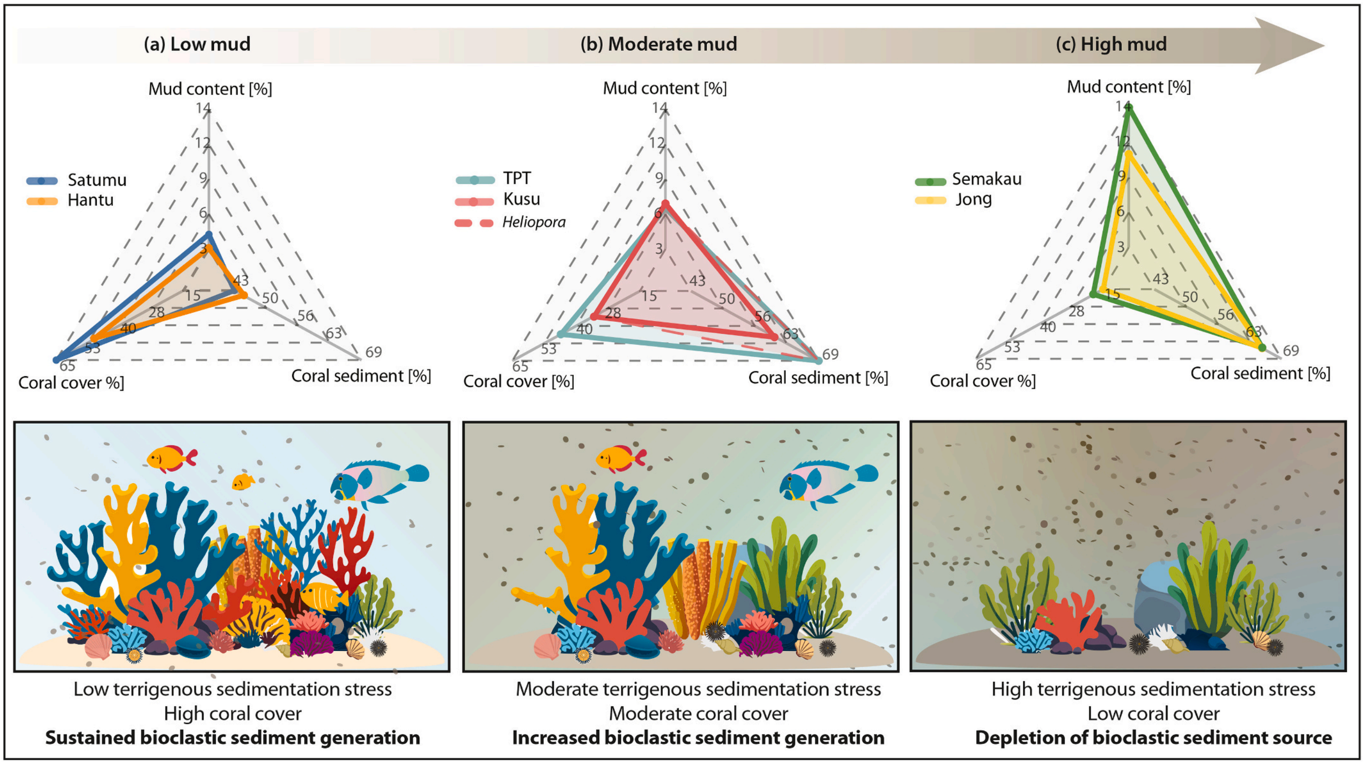
Our study quantifies the net addition of terrestrial mud to reefs, accounting for the multiple factors that contribute to sediment deposition and resuspension. As a result, mud content can provide more robust, long-term information than traditional water quality monitoring methods (e.g., sediment traps, turbidity) which typically measure gross sediment deposition or suspended sediment within the water column, and may overestimate reef sedimentation (Storlazzi et al., 2011; Morgan et al., 2020). Our results show that despite high seawater turbidity, the mud content within the sediment pool remained surprisingly low across the less impacted sites, with an average mud content of 4 ± 1 % at low-mud sites and 7 ± 1 % at moderate-mud sites (Fig. 1). Even at the sites experiencing chronic sedimentation stress, average mud content remained at 12 ± 2 % (Fig. 1). This can be attributed to the spatial variability of mud distribution across habitat zones caused by small-scale changes in physical processes, where mud primarily accumulates at the reef slope, and the reef flat and crest remain relatively mud-free due to the constant removal by currents (Fig. 1). These findings align with results that have previously been discussed by Wolanski et al. (2005) and Schlaefer et al. (2022).

4.2. *Impact of mud deposition on bioclastic sediment composition*

While the negative effects of sedimentation stress on coral cover are well established (Karickhoff et al., 1979; Babcock and Davies, 1990; Fabricius and Wolanski, 2000; Fabricius, 2005; Browne et al., 2015), our study provides new insights into the relationship between mud deposition and biogenic sediment generation on reefs. Our analysis revealed that even in high turbidity environments with substantial terrigenous inputs, coral sand remained the dominant sediment type. This highlights the significant role of local reef calcifiers in contributing to the sediment pool. Despite the prevalence of coral sand, bioclastic sediment composition varied significantly across sites, with notable differences in the contributions of coral, siliciclastic sand, calcareous algae, and crustaceans. While coral sand and calcareous algae varied with mud load, siliciclastic sand contributions were attributed to local bedrock erosion, highlighting the influence of site-specific factors on sediment composition despite the relative proximity of sites. The clear differences in sediment composition and benthic community composition across sites allowed a categorisation of reef sites into low, moderate, and high mud reefs (Fig. 6).

Low-mud sites showed a significantly higher diversity of bioclastic sediment components compared to moderate and high-mud reefs (Shannon-Wiener: low-mud: 1.21 ± 0.03; moderate-mud: 1.11 ± 0.04; high-mud: 1.05 ± 0.03). The decline or absence of minor sediment constituents may reflect changes in reef structure and habitat availability under chronic sediment stress. Specifically, high mud deposition appears to reduce sediment diversity by increasing coral sand while diminishing those of minor sediment constituents (Fig. 2). Previous studies have shown that smaller benthic organisms are generally vulnerable to mud sedimentation and are more easily smothered, which could explain the reduced abundance of minor sediment constituents (e.g., barnacles) at sites with high mud levels (Fabricius and Wolanski, 2000). Comparisons of bioclastic sediment composition and ecological survey data revealed that sediment diversity patterns generally reflect living benthic community composition (Gischler, 2006), but certain components were over- or underrepresented in sediment samples. This discrepancy may be attributed to differences in component durability (Ford and Kench, 2012), organism size, or infaunal lifestyles of benthic organisms, such as molluscs, which are often missed in benthic surveys (<1 %), but contribute significantly to the sediment pool (21 ± 1 %).

Additionally, we observed an inverse relationship between coral sand and live coral cover. This inverse relationship may result from coral die-offs driven by chronic long-term sedimentation stress and acute disturbance events, such as bleaching, coupled with the preferential preservation of coral grains (Ford and Kench, 2012; Morgan and Kench, 2016). Although dating of coral grains was not conducted, sediments from high-mud sites, as well as those at TPT (moderate-mud), exhibited weathering and a greyish colour, suggesting these grains had undergone exposure to physical and chemical diagenetic alterations. We propose that reef framework deterioration leads to periodic pulses of coral sand production (coral sand: low-mud: 44 ± 2 %; moderate-mud: 64 ± 1 %; high-mud: 65 ± 1 %). However, chronic sedimentation stress may ultimately lead to significant coral cover loss that would deplete the primary sediment source (Fig. 6). This would drastically reduce or discontinue carbonate sediment generation at these sites (Perry and



Low terrigenous sedimentation stress
High coral cover
Sustained bioclastic sediment generation

Moderate terrigenous sedimentation stress
Moderate coral cover
Increased bioclastic sediment generation

High terrigenous sedimentation stress
Low coral cover
Depletion of bioclastic sediment source

Fig. 6. Radar charts of bio-sedimentary characteristics of reef sites and a schematic diagram showing the progression of sediment stress at: (a) low-mud sites, (b) moderate-mud sites, and (c) high-mud sites.

Alvarez-Filip, 2019), leading to a fundamental shift in sediment composition, substrate type and habitat availability.

Although terrigenous mud contributes to the total sediment budget on reefs, substantial mud deposition would be needed to offset the loss of coral sand production. Our results show a strong negative correlation between sand-sized sediment and increasing mud loads ($r = -0.7$), suggesting a shift towards mud-dominated substrates. This transition towards fine mud would reduce habitat complexity and availability, inhibit recruitment of coral larvae, and alter benthic community composition. Unlike mud, coral sand is highly resistant to transport and physical degradation and plays a vital role in reef framework formation, infilling, and stabilization (Ford and Kench, 2012). Consequently, the integration and composition of reef-derived sediment is essential for maintaining reef bioconstruction.

4.3. *Implications of high mud loads for reef recovery potential and ecosystem stability*

Our results suggest good agreement between bulk sediment analysis and ecological data, with coral cover decreasing significantly under moderate and high-mud conditions (coral cover: low: 58 ± 4 %; moderate: 39 ± 4 %; high: 17 ± 2 %; Figs. 3a & 6). Mud-induced degradation of reefs, characterised by declines in coral cover, has been attributed to several key factors: (1) the deposition of fine mud causing physiological stress on corals (Erftemeijer et al., 2012; Tuttle and Donahue, 2022). For example, corals exposed to severe sedimentation stress produce mucus at over three times their usual daily energy expenditure (Riegl and Branch, 1995); (2) coral larvae require hard substrates to effectively settle and attach, making muddy, soft substrates unsuitable for coral recruitment (Babcock and Davies, 1990; Ricardo et al., 2017; Tuttle and Donahue, 2022); (3) high mud accumulation can smother corals, leading to hypoxia and increased mortality rates (Fabricius and Wolanski, 2000; Fabricius et al., 2003; Browne et al., 2015); and (4) mud has a high capacity to carry pollutants, potentially disrupting coral physiology and immune responses (Karickhoff et al., 1979; Fabricius, 2005; Yu et al., 2006; Browne et al., 2015; Chen et al., 2016). These factors significantly inhibit the ability of corals to thrive under high mud conditions and decrease the potential of reef recovery after a disturbance event.

Therefore, we suggest that, while a thermally induced mass bleaching event in 2016 caused substantial coral cover loss (Fig. 5), extensive mud deposition on reefs may have hindered recovery potential at high-mud sites (Fig. 5, Semakau and Jong). Long-term increases in fine sediment benthic cover have been reported over recent decades as local and regional drivers of sedimentation have also increased (<2 % in 1986/1987 to 25 % in 2010; Guest et al., 2016). Despite these challenges posed by high sedimentation, certain shallow coral reefs have maintained coral cover over recent decades (Fig. 5). Our results suggest that this resilience mainly applies to shallow or low-mud reef sites, where corals can sustain recovery after disturbances. In contrast, deeper habitats, or high-mud sites limit recovery potential, likely due to the rapid light attenuation and chronic sedimentation on benthic surfaces (Morgan et al., 2016a, 2020). This distinction highlights the importance of terrigenous sediment in modulating reef recovery and suggests mud content poses an additional limitation to coral cover. Persistent mud accumulation may therefore exacerbate coral decline and limit recovery potential, as seen at high mud locations of our study (Fig. 5). Our findings underscore the significant role that mud deposition plays in limiting recovery after disturbance events, highlighting the importance of considering a wider range of stressors impacting reef ecosystems.

Previous studies have shown that Singapore's coral reefs are heavily impacted by external terrigenous sediment inputs (60–80 % terrigenous mud; Van Maren et al., 2014; Morgan et al., 2020). The Singapore Strait, a largely embayed region, receives significant quantities of sediment from nearby river systems that discharge into its coastal waters (Hilton and Manning, 1995; Lai et al., 2015; Tan et al., 2016). This geographical setting, coupled with a humid tropical climate (e.g., intense rainfall and weathering) drives substantial sediment runoff from surrounding land (Hilton et al., 2008; Valentin et al., 2008; Clift, 2020). Monsoonal circulation plays a critical role in the transportation and distribution of suspended fine sediments. The northeast monsoon (December to February) generates strong eastward currents, while the southwest monsoon (June to September) results in a slower westward dispersal due to weaker flow conditions (Hasan et al., 2016; Xu and Chua, 2017; Clift, 2020; Clift et al., 2022). In addition, mixed diurnal and semi-diurnal tidal, as well as local wind patterns, in the Singapore Strait drive strong current flows on reefs which may amplify diurnal currents in response to the land–sea breeze, increasing the resuspension of fine sediment (Puah et al., 2024).

Anthropogenic activities have further increased the rate of sediment discharge into Singapore's coastal waters. Land reclamation, regional land-use change, seafloor dredging, and ship wake effects elevated local turbidity and intensify sedimentation on reefs (Chia et al., 1988; Hilton and Manning, 1995; Chou et al., 2004; Van Maren et al., 2014). Long-term increases in fine sediment benthic cover have been reported over recent decades as local and regional drivers of sedimentation have also increased (<2 % in 1986/1987 to 25 % in 2010; Guest et al., 2016). Given the increasing sediment loads from urbanisation and climate change, our findings have significant implications for coastal management and conservation strategies worldwide. High-mud sites that we report here will likely become more prevalent globally, with potential negative consequences for coral reefs. However, turbid reef sites that experience low to moderate mud loads may continue to support reef framework construction and substantial coral cover, as seen at Satumu, which has retained ecological stability over the past decade (Fig. 5; Bauman et al., 2015; Guest et al., 2016; Januchowski-Hartley et al., 2020). Importantly, Hantu has shown the second-highest coral cover continuously since 2011 (2011: 49 ± 6 %; 2017: 26 ± 5 %; 2021: 50 ± 6 %) and is characterised by high turbidity levels compared to other reef sites (Morgan et al., 2020). This supports our finding that water column turbidity is not likely the sole factor limiting coral growth, and that low mud deposition may be a more ecologically relevant indicator of sustained coral cover and recovery.

Maintaining low to moderate rates of mud deposition is essential for the continued generation of habitat forming and landform-building bioclastic sediments, as well as for sustaining long-term ecosystem stability. As climatic conditions in Southeast Asia increase terrestrial runoff and elevate turbidity on reefs due to intense rainfall and weathering (Valentin et al., 2008; Clift, 2020), or extreme weather events (Knutson et al., 2010; Emanuel, 2021; IPCC, 2023), the prevalence of turbid reefs is expected to expand (Zweifler et al., 2021). In this context, the current trajectory of Singapore's coral reefs serves as an example of how reefs globally may respond to increased inputs of terrestrial-derived mud. Regional declines in coral cover, reduced supply of bioclastic sediment, and reef framework deterioration associated with high mud loads could negatively impact shoreline maintenance. As populations in Southeast Asia's coastal regions are rapidly growing, they increasingly depend on sustained sediment supply to mitigate the impacts of sea-level rise (Nicholls and Cazenave, 2010; Woodroffe and Murray-Wallace, 2012; Nicholls et al., 2021). Effective management strategies, such as reducing terrestrial runoff and monitoring of local water quality within reef ecosystems, will be critical for enhancing resilience on these coral reefs.

5. Conclusion

This study underscores the impact of mud deposition on coral reef ecosystems in highly turbid reef systems. Our findings reveal that increased mud loads are linked to a significant reduction in coral cover, shifts in sediment composition, and a decrease in sediment constituent diversity. We highlight that while coral reefs in naturally turbid environments can sustain significant coral cover and maintain a diverse sediment pool, reefs subjected to chronic sedimentation stress exhibit diminished coral cover, reduced sediment diversity, and decreases in sand sized sediment. A shift towards mud-dominated habitats reduces overall habitat complexity and availability, limiting ecological niches and impairing the recruitment of coral larvae. Over time, these changes may result in a depletion of bioclastic sand production, further exacerbating reef degradation. Despite some resilience in low to moderate mud sites, our results suggest that elevated mud deposition plays a decisive role in diminishing reef recovery after disturbance events. These findings reinforce the idea that while high turbidity alone may not limit coral growth, the persistent deposition of fine sediments is a key driver of reef degradation. As urbanisation and climate change increase terrestrial runoff, the need for effective coastal management strategies becomes critical. Reducing terrestrial inputs and implementing continuous water quality monitoring are essential to support the long-term stability of reef ecosystems, especially in rapidly urbanising regions like Southeast Asia. To build on these findings, future research is needed to assess and mitigate the impact of terrigenous mud deposition on reefs. Comparative studies are also needed across different turbid reef systems to understand the variability in sediment sources and physical properties to refine management approaches aimed at sustaining reef ecosystems and their vital contributions to coastal protection and sediment supply.

CRediT authorship contribution statement

Marlena Joppien: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kyle Morgan:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Conceptualization.

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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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.117596.

Data availability

Data and metadata are available in the DR-NTU data repository at https://doi.org/10.21979/N9/HNPL6N upon publication.

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