Inshore coral reef sediment and turf dynamics unaffected by canopy-forming macroalgae

Stella E. Fulton [a,b,c,1], Tehya Hines [a,d,1], Cathie A. Page [a,b,e], Ian M. McLeod [f], James Whinney [a,d], Scott F. Heron [a,d], David G. Bourne [a,b,e], Hillary A. Smith [a,g,*]

[a] College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
[b] AIMS@JCU, Townsville, QLD 4811, Australia
[c] Fathom Pacific, Melbourne, VIC 3195, Australia
[d] Marine Geophysics Laboratory, James Cook University, Townsville, QLD 4811, Australia
[e] Australian Institute of Marine Science, Townsville, QLD 4810, Australia
[f] TropWATER, James Cook University, Townsville, QLD 4811, Australia
[g] School of Biological, Earth and Environmental Sciences, University of New South Wales, Randwick, NSW 2052, Australia

ARTICLE INFO

ABSTRACT

Nearshore coral reefs face an increasing abundance of fleshy macroalgae, an indicator of degradation and threat to ecosystem functioning. Removal of macroalgae is proposed to assist coral recovery, though the ecological and physical impacts have not been studied. Nearshore reefs are also confronted with sedimentation stress, influencing reef dynamics including algal turfs, with flow-on impacts to coral recruitment, fish diets, and trophic cascades. In this study, the interplay between macroalgal canopies, sediment deposition and algal turf environments was investigated on the nearshore Great Barrier Reef. Removal of fleshy macroalgae over two years had no significant effect on the amount or composition of sediment deposited on proxy coral (SedPods) and algal turf (TurfPods) surfaces, nor was the height of algal turfs impacted. Deposition on TurfPods was greater with high-energy currents, likely due to retention of sediment within turfs. Therefore, macroalgae removal is unlikely to exacerbate nor alleviate sediment-related stress on benthic communities.

1. Introduction

Reefs globally are subjected to increasing stress from climate change and other anthropogenic influences (Harborne et al., 2017), which has, on average, led to substantial and persistent losses of live coral cover within the last two decades (Souter et al., 2021). In addition to climatic changes, land-based sediment run-off poses an additional localized threat to reef ecosystems (Bainbridge et al., 2018; Waterhouse et al., 2017), and is a focus of reef management agencies (Eberhard et al., 2017). The interactions governing sedimentation on coral reefs are complex but are often related to terrestrial influences, local hydrodynamics, and the propensity for algal turfs to trap sediments (Tebbett et al., 2018b; Tebbett and Bellwood, 2020). Algal turfs readily trap suspended organic and inorganic sediments (when aggregated this is referred to as the epilithic algal matrix [EAM]) and the build-up of turfs and sediments can alter reef functions, including the settlement of corals (Birrell et al., 2005; Speare et al., 2019) through to trophic dynamics (Tebbett et al., 2018a, 2020a). Understanding the multiple pathways whereby sediments, algal turfs, and other reef components (e.g. corals, macroalgae) interact is of increasing importance on degraded reefs (Tebbett and Bellwood, 2019).

Inshore coral reefs of Australia's Great Barrier Reef (GBR) are exposed to waters rich in sediments and dissolved organic matter (Waterhouse et al., 2021), largely due to erosion following land clearing, nutrient-rich riverine run-off linked to agricultural development, port-associated dredging, and other coastal development activities (Bainbridge et al., 2012; De'ath and Fabricius, 2010; GBRMPA, 2019; Waterhouse et al., 2017; Williamson et al., 2019). High levels of sediments and nutrients can favour macroalgal growth over corals (Birrell et al., 2008; Sura et al., 2021), with feedback mechanisms leading to shifts in reef communities characterised by fleshy, canopy-forming macroalgae (Johns et al., 2018; Nugues and Roberts, 2003). Such

---

community shifts are generally accepted as strong indicators of coral reef degradation (Birrell et al., 2008; Diaz-Pulido and McCook, 2008; Done, 1992; Williamson et al., 2019). At some sites on the GBR, substantial declines in hard coral cover and concurrent increases of macroalgae have been reported over the last two decades (Ceccarelli et al., 2020; De'ath et al., 2012; De'ath and Fabricius, 2010; Thompson et al., 2021). However, the influence of macroalgal canopies on sedimentation regimes, particularly on inshore reefs subjected to high sediment inputs, remains to be investigated.

Macroalgae directly interact and compete for space and light, through a variety of mechanisms depending on the macroalgal taxa (Jompa and McCook, 2003), with other benthic organisms including corals and turf algae (reviewed in Birrell et al., 2008). For example, proliferation of macroalgae can reduce coral growth rates via abrasion (River and Edmunds, 2001), increase shading of corals and decrease available space for coral larval settlement and recruitment (Birrell et al., 2008), as well as affect surrounding water chemistry via allelopathic chemical release (Bonaldo and Hay, 2014). In addition to biological interactions with other reef organisms, benthic macroalgae can alter abiotic conditions by reducing turbulence, consequently trapping sediment, and enhancing deposition of sediment on the benthos (Birrell et al., 2008). Such increased sedimentation has variable flow-on effects on benthic reef taxa. For example, increased sediment deposition directly reduces coral reproduction, recruitment, survival and growth (Babcock and Smith, 2000; Bainbridge et al., 2012; Brown, 1972; Fabricius, 2005; Rogers, 1990; Weber et al., 2012). The severity of the effect varies since the capacity of corals to actively remove sediment is dependent on sediment characteristics such as particle composition and size (Weber et al., 2006). Short (<5 mm) productive algal turfs [SPATs] are major contributors to primary productivity on healthy reefs (Carpenter, 1985; Goatley et al., 2016; Hatcher, 1988; Latrille et al., 2019). Sediment deposition can reduce productivity (Tebbett and Bellwood, 2020), resulting in long (>5 mm) sediment-laden algal turfs [LSATs] (Goatley et al., 2016; Gordon et al., 2016; Purcell, 2000; Tebbett and Bellwood, 2019). LSATs are unpalatable to herbivores relative to SPATs (Goatley and Bellwood, 2013) and can further facilitate deposition of benthic sediments (Goatley et al., 2016), perpetuating a degraded algal turf environment with flow-on negative effects to other benthic organisms such as corals (e.g. pathogen proliferation causing hypoxia and infection of coral tissue) (Birrell et al., 2005; Speare et al., 2019; Tebbett et al., 2018a; Tebbett and Bellwood, 2019, 2020). Reduced sediment deposition on reef substrata could be achieved via changes to the macroalgal canopy (i.e., removal), due to the canopy's role as a physical barrier to water flow. In turn, a reduced macroalgal canopy and subsequent decrease in sediment deposition could potentially increase incident light, enhance productivity, and attract herbivores, creating conditions in favour of SPATs. Alternately, removal of the macroalgal canopy could eliminate deposition surfaces in the water column (i.e., macroalgae fronds), thereby enhancing deposition on the benthos and within the EAM.

While sedimentation is an important metric in understanding the interactions between reef community constituents, the responses of coral and other benthic reef taxa to sedimentation can further be influenced by sediment characteristics such as particle size, organic content, and duration and frequency of exposure (reviewed in Tuttle and Donahue, 2020). Fine sediment derived from agricultural runoff is recognized as one the main water quality pollutants threatening inshore areas of the GBR as it travels further offshore than larger size fractions that settle out close to shore, and aggregates with organic material making it more difficult for corals to remove relative to larger grain sizes (Bainbridge et al., 2018; Bartley et al., 2017; Fabricius and Wolanski, 2000). Furthermore, fine, organically-rich sediment particles can alter the water column both physically (reduce light attenuation) and chemically (reduce pH), and are more easily resuspended from the benthos relative to coarser, inorganic sediments (Bainbridge et al., 2018). Quantifying sediment deposition and composition in areas with

and without a macroalgal canopy will therefore provide valuable information about how sediment characteristics may be influenced by canopy-forming macroalgae.

Understanding the relationships between macroalgae and algal turfs in response to sedimentation is critical to predict the flow-on effects to other benthic reef taxa, particularly corals (both juvenile and adult life-stages). Therefore, this study investigates how removing macroalgae from degraded fringing reefs on the inshore GBR impacts sediment deposition and algal turf communities. Improved understanding of the relationships between macroalgae, algal turfs and sedimentation is not only integral to understanding inshore reefs of the Anthropocene, but necessary for developing effective management strategies to assist coral recovery on degraded inshore reefs (Bellwood et al., 2019; Tebbett et al., 2020b).

2. Methods

2.1. Study site and experimental design

This study builds upon a long-term project investigating the impacts of macroalgae removal on the fringing coral reefs of Yunbenun (Magnetic Island), on the central inshore region of Australia's Great Barrier Reef, and described previously in Smith et al. (2023, 2022). Briefly, twelve 25 m^2 (5 × 5 m) experimental plots were established in two eastward facing bays (Arthur and Florence), with six plots designated as controls (referred to herein as 'control plots') and the remaining six treatment plots periodically cleared of fleshy macroalgae (referred to herein as 'removal plots'; Supplementary Fig. 1). Within the timeline of this study, macroalgae were manually removed from removal plots in July and October 2020, and April, July, and October 2021. Removal of macroalgae was performed by SCUBA divers, where thalli were detached from the benthos by hand and placed into catch bags. Attention was paid to removal of holdfasts, though no additional tools were used to remove holdfasts. The benthic cover of control and removal plots changed over the course of the study, characterised by an increase in coral cover as described in Smith et al. (2023), though reefs in both bays were dominated by macroalgae (predominantly *Sargassum)* and corals from the encrusting genus *Montipora* and branching genus *Acropora.* Field work was completed under permit number G19/41693.1 granted by the Great Barrier Reef Marine Park Authority.

2.2. Sediment deposition and organic fraction

Net sediment deposition was measured using SedPods and TurfPods, which emulate coral and algal turf substrate, respectively (see Field et al., 2013; Latrille et al., 2019 for full descriptions). These devices are established proxies for accurate and cost-effective measurement of net sediment deposition compared to traditional methods such as sediment traps (Field et al., 2013; Latrille et al., 2019). SedPods and TurfPods allow for resuspension of material, which is not possible in sediment traps, and therefore provide a more ecologically representative estimate of what a coral or algal turf surface would experience naturally (Field et al., 2013; Latrille et al., 2019). Furthermore, sedimentation of the proxy algal turf surface may be a more relevant measure for coral recruits and juveniles on inshore reefs, whereas sedimentation of the proxy coral surface may be more relevant to coral growth and health during later life stages, and are likely more representative of encrusting and massive morphology corals (e.g. *Montipora, Porites)* than dynamic branching growth forms (e.g. *Acropora)*. SedPods were constructed using short sections (9 cm diameter, 7 cm high) of PVC pipe filled with concrete to act as a proxy coral surface. TurfPods were similarly constructed, with a layer of artificial turf 3–5 mm high ('Astroturf') affixed to the concrete to act as a proxy for algal turfs. Three 'Pods' of each type were deployed in all 24 plots over a 1- week period at each sampling timepoint, distributed haphazardly throughout each plot to account for substrate variation. Pods were affixed to the benthos using a star picket

hammered into the substrate, with a PVC ring to hold the pod in place. The baseline deployment occurred in May 2020 prior to macroalgae removal in July 2020. Further deployments occurred in August and November 2020, following removal events in July and October 2020, respectively. A final deployment occurred in February 2021 to capture summertime wet season dynamics. Pods were capped upon collection to ensure deposited sediments were retained, then sealed in plastic bags and stored at 4 °C until processed.

Sediment samples were prepared by carefully removing each pod from its bag and rinsing the collected sediment into a bucket with copious (>750 ml) reverse osmosis water to remove salts. Samples were left for >24 h to allow sediment to fully settle, after which the supernatant was siphoned off and samples topped up to approximately 500 ml with reverse osmosis water to further remove salts. Samples were then wet sieved through a 1.4 mm stainless steel mesh, retaining all material <1.4 mm. Across all samples there were negligible grain size sediment particles >1.4 mm. Each sample was brought to 900 ml with filtered fresh water, and a subsample of known volume (200 ml for SedPods, 20 ml for TurfPods) processed via vacuum filtration using a pre-weighed 42 mm glass microfibre filter (Whatman, USA) and dried at 105 °C for 24 h according to the American Public Health Association [APHA] Standard Method 2540D to yield total dry mass, with at least 10 % of all samples analyzed in triplicate (American Public Health Association, 2018). Sediment deposition rate (mg cm^{-2} d^{-1}) for both SedPods and TurfPods was calculated as follows:

$$\text{Deposition rate } (mg\ cm^{-2}\ d^{-1}) = \frac{\left[\frac{900ml \times dry\ mass\ in\ subsample\ (mg)}{subsample\ volume\ (ml)}\right] \Big/ [pod\ surface\ area\ (63.6\ cm^2)]}{number\ of\ days\ deployed\ (d)}$$

The residual filter was then combusted at 550 °C for 1 h in a Carbolite muffle furnace according to APHA Standard Method 2540E and re-weighed to yield the mass of the non-volatile solid component (American Public Health Association, 2018). The weight lost upon ignition denotes the volatile solid component in the deposited sediment, approximating the proportion of organic material in the sample.

2.3. Grain size analysis

To determine if the composition of sediments varied between control and removal plots, the distribution of grain sizes was assessed via laser diffraction in accordance with the general ISO 13320:2020(E) guidelines (International Organisation for Standardisation, 2020). The three replicate samples for each pod type in each plot were merged (see Supplementary Fig. 2) and treated with the common dispersal agent Calgon (5 % sodium hexametaphosphate solution). The merged sample was then sonicated for 10 min immediately prior to analysis to separate flocculated particles and analyzed via laser diffraction using a Malvern Mastersizer 3000 particle size analyzer with a lens range of 0.01–3500 μm (refractive index: 1.52, samples ultrasonically dispersed at 15 % power for 30 s prior to measurement) to yield grain size distribution for each sample. The average of the three measurements calculated by the Mastersizer was used for downstream analysis.

2.4. Assessment of algal turfs within experimental plots

Algal turf height was measured to quantify sediment trapping potential and productivity of the EAM. Using plastic Vernier calipers, algal turf height was recorded at 10 haphazardly selected locations within three 1 m^2 quadrats within each 25 m^2 experimental plot. This is a cost-effective, non-destructive way to quantify the EAM such that algal turf height paired with sediment deposition can serve as a predictor for benthic productivity and suitability of the substrate for coral settlement and recruitment (Ford et al., 2018; Tebbett and Bellwood, 2019). Algal turf surveys were conducted in May, July and November 2020 and February, April, and July 2021.

2.5. Physical environmental parameters

Two temperature loggers (HOBO MX2202) were installed in each bay for the duration of the study. Publicly available water temperature data for Yunbenun from loggers installed by the Australian Institute of Marine Science were also used to supplement water temperature data throughout the study period. Hydrodynamic variation in each bay was measured using a suite of current meters (Marotte HS-1; 6 in Arthur Bay, 7 in Florence Bay), deployed throughout the period November 2020 to February 2021. Additional short-term deployments were undertaken during each pod deployment (dates listed above) to enhance spatial coverage.

2.6. Statistical analysis

Following inspection of raw data, outliers due to measurement error in each of the datasets were removed prior to statistical analysis (see Supplementary Table 1). Variation in sediment deposition rate, organic content of sediment, and algal turf height was investigated using generalized linear mixed effects models (GLMMS). For sediment deposition rate and algal turf height, a gamma distribution and log link were used, and organic content was modelled using a beta distribution with logit link. Net sediment deposition rate was analyzed separately for SedPods and TurfPods because the scale of sedimentation differed by an order of magnitude between the two pod types. For each pod type, sediment deposition rate was compared between control and removal plots, across deployment dates, and between bays (Arthur and Florence). For the analysis of organic content, the proportion of organic material in the deposited sediment was compared between control and removal plots, pod types, deployments, and bays. Algal turf height was compared between control and removal plots, survey timepoints, and bays.

A suite of models was defined for both SedPod deposition and TurfPod deposition incorporating macroalgae removal treatment, bay, deployment number, and substrate type as fixed effects. For organic content, pod type was also used as a fixed effect. For algal turf height, the predictor variables (treatment, bay, and survey timepoint) were fitted as fixed effects. In all models, plot number was fitted as a random factor. For SedPod and TurfPod sediment deposition and organic content, pod number was fitted as a random factor nested within the plot to account for the dependency structure of the hierarchical blocking design. Similarly, for algal turf height, quadrat replicate was fitted as a random factor nested within the plot. SedPod and TurfPod deposition were similarly modelled against each other, and against 70th percentile current speed derived from current meters (with treatments pooled, and site as a random effect).

Model selection was informed using second-order Akaike Information Criterion (AICc), and the most parsimonious model was selected for each dataset (see Supplementary Table 1 for model details). Model fits

and assumptions were assessed via simulated residual plots, which were satisfactory in all cases. All models were fit using the glmmTMB package (Brooks et al., 2017) in the statistical and graphical software R (R Core Team, 2021). Significant differences among levels in the fixed factors as estimated by the models (estimated marginal means) were distinguished via post-hoc tests using the Tukey *p*-value adjustment method.

Grain size distribution data obtained from Mastersizer measurements were aggregated into eight grain size classes according to the Wentworth grain size intervals across the range 0.01–3500 μm (clay: <3.9 μm, fine silt: 3.9–15.6 μm, coarse silt: 15.6–63 μm, very fine sand: 63–125 μm, fine sand: 125–250, medium sand: 250–500 μm, coarse sand: 500–1000 μm, very coarse sand: 1000–2000 μm, noting that particles >1400 μm were previously removed from samples, including for the ninth category, gravel: >2000 μm) (Wentworth, 1922). Observations were examined for outliers that displayed distinctly different percent volume distributions, often with a single large peak indicative of a processing artefact and thus not reflective of the sediment sample, ascribed to measurement error. Problems like these are not uncommon when measuring particle size via laser diffraction and can lead to misrepresentation of the true particle size, which is why the results were rigorously scrutinized and inaccurate measurements rejected prior to analysis (Sabin, 2011).

Patterns in grain size distribution were visualized using a non-metric multidimensional scaling (NMDS) based on a Euclidean distance matrix of fourth-root scaled and Wisconsin double-standardized volume density data, separately for SedPods and TurfPods. Differences between control and removal plots, deployments, and bays, were assessed using a permutational multivariate analysis of variance (PERMANOVA). In the PERMANOVA, treatment, bay, and deployment were treated as fixed factors while plot number was treated as a random factor. Post-hoc pairwise tests were performed to determine where differences occurred between the factors of interest. The assumption of homogeneity of dispersion for the PERMANOVA was tested using permutational analysis of multivariate dispersions (PERMDISP). Multivariate analysis was performed using the vegan package (Oksanen et al., 2020) in the statistical and graphical software R (R Core Team, 2021).

3. Results

3.1. Removal of macroalgae

Over the five removal events from July 2020 to October 2021, 18.9 ± 1.9 (mean ± SE) kg of wet biomass per 25 m² plot were removed, with a total of 1131 kg of macroalgae removed over the study period (see Supplementary Fig. 3 for details). The biomass removed consisted predominantly of *Sargassum* spp. but included other commonly occurring macroalgae genera including *Dictyota*, *Padina*, *Colpomenia*, and *Lobophora*.

3.2. Sediment deposition

Net sediment deposition on SedPods (proxy coral surface) ranged between 0.019 and 0.75 mg cm^{-2} d^{-1} (Fig. 1). TurfPods (proxy algal turf surface) accumulated more sediment, ranging between 0.37 and 57 mg cm^{-2} d^{-1}. Overall, the removal of macroalgae had no significant effect on net sediment deposition rate on either SedPods or TurfPods. However, there was evidence for some interactions between treatment, bay, and deployment (Supplementary Table 2). Net sediment deposition on
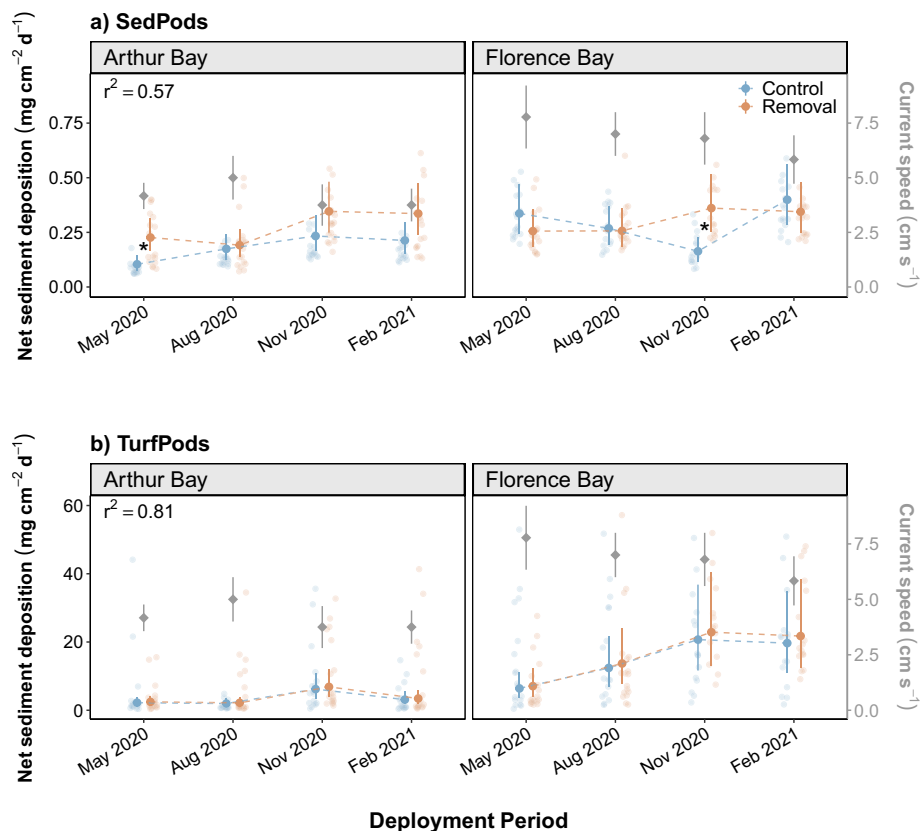

Fig. 1. Net sediment deposition rate (mg cm^{-2} d^{-1}) on **(a)** 'SedPods', a proxy hard coral surface, and **(b)** 'TurfPods', a proxy algal turf surface, for four deployment periods during 2020–2021 in two bays of Yunbenun, Australia. Coloured points are the mean predicted fits of generalized linear mixed effects models (gamma distribution with log link), with predictions for control plots shown in blue and removal plots shown in orange. Coloured vertical lines represent 95 % confidence intervals. Partialized observations (sum of fitted values and residuals) are shown as faint-coloured points. Asterisks represent statistically significant differences in net sediment deposition between control and removal plots. Grey points and vertical lines represent average current speed (cm s^{-1}) and standard error, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the SedPods in Arthur Bay was consistently lower in control plots (0.17 ± 0.02 (estimated marginal mean ± SE) mg cm^{-2} d^{-1}) relative to removal plots (0.27 ± 0.03 mg cm^{-2} d^{-1}), though this difference was only significant in May 2020 when deposition in control plots (0.10 ± 0.02 mg cm^{-2} d^{-1}) was 54 ± 11 % less than deposition in removal plots (0.23 ± 0.04 mg cm^{-2} d^{-1}; $t = -3.4$, df = 269, $p < 0.05$; Fig. 1a-left). In Florence Bay, significant differences in net sedimentation between control and removal plots was only observed during the November 2020 deployment (control plots: 0.16 ± 0.03 mg cm^{-2} d^{-1}, removal plots: 0.36 ± 0.07 mg cm^{-2} d^{-1}, $t = -3.3$, df = 269, $p < 0.05$; Fig. 1a-right). TurfPods displayed a similar pattern, with a generally lower rate of sediment deposition in control plots relative to removal plots, however this difference was not significant (Supplementary Table 2; Fig. 1b). The modelled relationship representing net sediment deposition as a function of treatment, bay, deployment, and substrate was stronger for TurfPods than SedPods, with approximately 81 % and 57 %, respectively, of the variation in net deposition rate explained by both the fixed and random effects (conditional pseudo-r^2: TurfPods = 0.81, SedPods: 0.57, Supplementary Table 2).

For both SedPods and TurfPods, there was, on average, no difference in net sediment deposition between bays. However, TurfPods had consistently greater deposition in Florence Bay than in Arthur Bay for all deployments except May 2020 (May 2020: $t = -3.2$, df = 272, $p = 0.0630$; August 2020: $t = -5.5$, November 2020: $t = -3.6$, February 2021: $t = -5.5$, df = 272, $p < 0.05$; Fig. 1b). Interestingly, for the SedPods, the May 2020 deployment was the only time when location had a significant effect on deposition ($t = -5.1$, df = 269, $p < 0.05$; Fig. 1a), with Florence Bay experiencing greater deposition than Arthur Bay. Comparison of deposition between SedPods and TurfPods revealed a weak but significantly positive relationship ($R^2 = 0.155$, $z = 3.09$, $p < 0.01$; Fig. 2a).

Low current speeds ranging from 1.0 to 17 cm s^{-1} were recorded across both bays and all deployments. Averaged across both bays, current speed was consistently low for each of the four deployments: May 2020: 6.3 ± 1.0 cm s^{-1}, August 2020: 6.0 ± 1.0 cm s^{-1}, November 2020: 5.4 ± 0.9 cm s^{-1}, February 2021: 5.0 ± 0.8 cm s^{-1}. Averaged across all deployments, current speed in Arthur Bay (4.0 ± 0.4 cm s^{-1}) was lower than in Florence Bay (7.0 ± 0.7 cm s^{-1}).

The two pod types showed contrasting responses to current speeds. During high-energy periods, represented by the 70th percentile current speed at each site, SedPods showed no significant variation in deposition with current speed ($z = 0.72$, $p = 0.48$; Fig. 2b). In contrast, deposition on TurfPods had a significant positive relationship with the 70th percentile current speed ($R^2 = 0.34$, $z = 2.68$, $p < 0.01$; Fig. 2c). Analysis of the variability in currents speeds for each site during the two (one-week) deployment periods (in November 2020 and February 2021) and for the full summer period (spanning November 2020–February 2021) indicated that the characteristics of current speeds (mean, SD) during the deployment periods were representative of those throughout the summer (Supplementary Table 3).

3.3. Organic content

Overall, the proportion of organic material in the deposited sediment in removal plots was no different to that of control plots ($t = -0.53$, df = 551, $p = 1$; Fig. 3). The sediment deposited on both SedPods and TurfPods contained between 2.5 % and 32 % organic material, with SedPods containing on average 14.0 ± 0.3 % (estimated marginal mean ± SE) organics and TurfPods 9.1 ± 0.3 % organics. There were consistently higher proportions of organic material in the SedPod sediments than the TurfPod sediments, however the statistical significance of this difference varied depending on both location and time of deployment (Fig. 3; Supplementary Table 4). Fixed and random effects explained 70 % of the variability (conditional pseudo-$r^2 = 0.70$) in organic proportion when modelled as a function of pod type, treatment, bay, and deployment (Supplementary Table 2).

Spatial variation was evident in organics, with consistently greater proportions of organic material in sediments from Arthur Bay than Florence Bay (Fig. 3; Supplementary Table 4). This difference, however, was significant for the August 2020 ($t = 5.6$, df = 551, $p < 0.05$) and February 2021 ($t = 4.2$, df = 551, $p < 0.05$) deployments only. The proportion of organic material in deposited sediment also varied temporally (Fig. 3). In particular, the proportion of organics at the end of the study (February 2021) was significantly lower than at the start of the study (May 2020) (Arthur Bay SedPods: $t = 3.6$, Arthur Bay TurfPods: $t = 4.1$, Florence Bay SedPods: $t = 5.5$, Florence Bay TurfPods: $t = 5.2$; df = 551, $p < 0.05$).

3.4. Grain size distribution

Of a total of 564 observations, 105 outliers were removed prior to analysis. Ordination plots showed no major distinction in grain size distribution between control and removal plots for both the SedPods and TurfPods (PERMANOVA: SedPods - $F_{1,73} = 1.45$, $r^2 = 0.02$, $p = 0.138$, TurfPods - $F_{1,78} = 0.29$, $r^2 = 0.00$, $p = 0.57$; Supplementary Table 5; Fig. 4). There was no difference in grain size distribution between bays
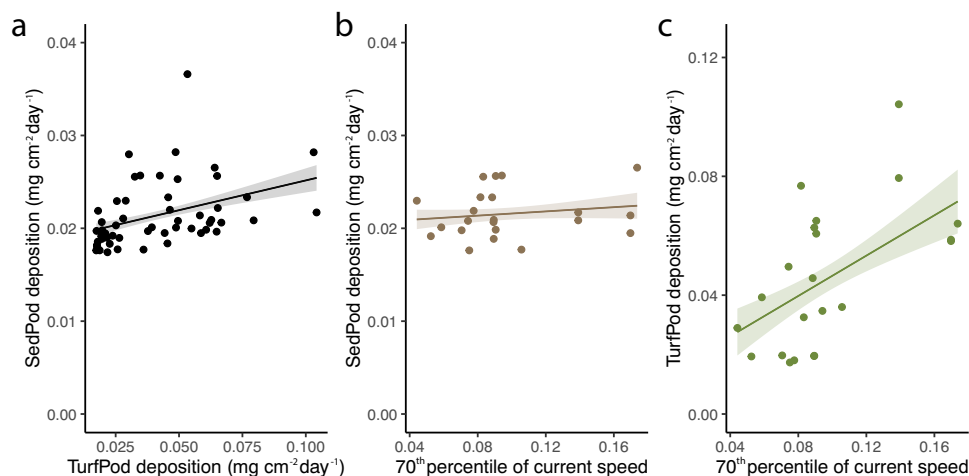

Fig. 2. Comparison of net sediment deposition rates (mg cm^{-2} d^{-1}) between **(a)** SedPods and TurfPods; and of **(b)** SedPods and **(c)** TurfPods each with the 70th percentile current speeds. Coloured lines are the mean predicted fits of generalized linear mixed effects models with shaded ribbons representing 95 % confidence intervals. Partialized observations (sum of fitted values and residuals) are shown as coloured points. Note the difference in sediment deposition scales between SedPods and TurfPods; and that current measurements were not available in proximity to all deposition observations.
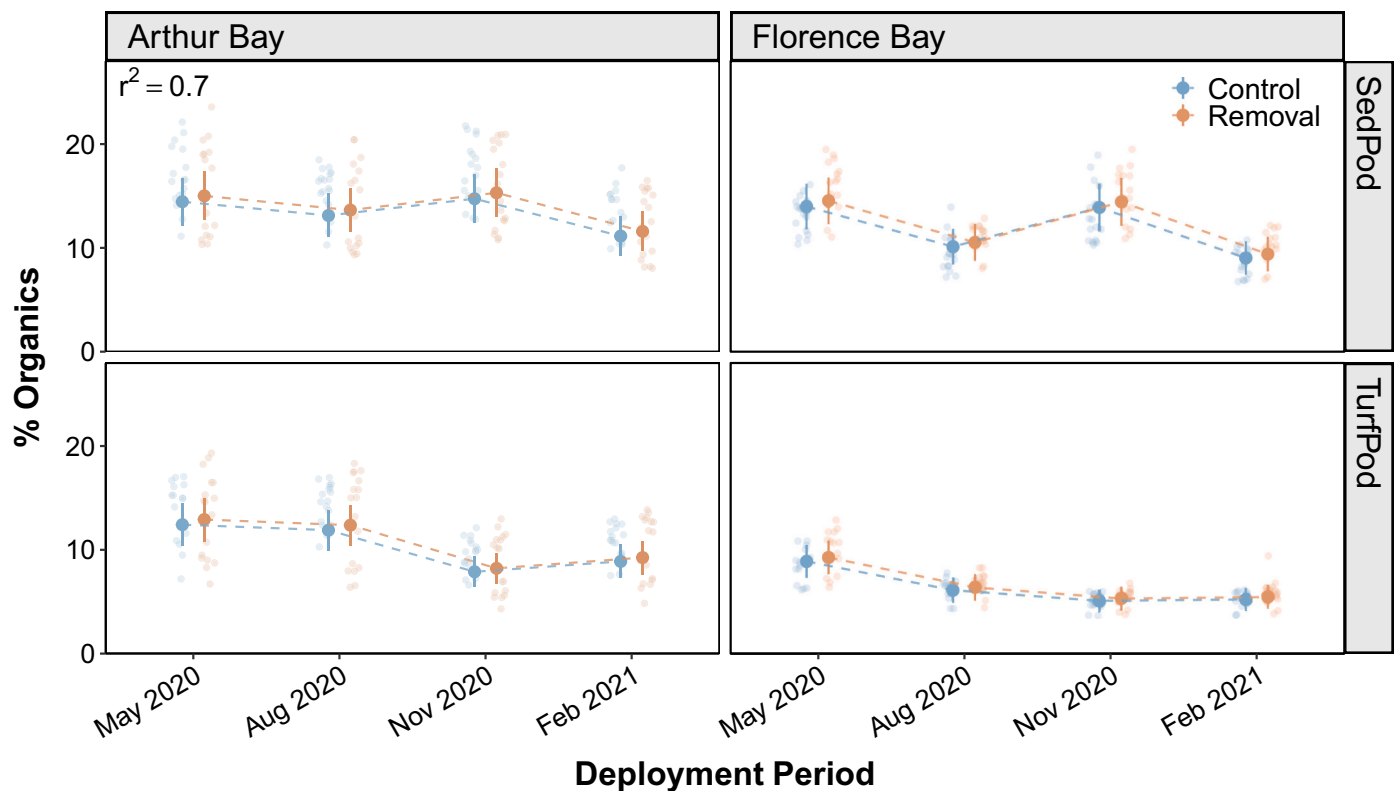
Fig. 3. Percentage of organic matter in deposited sediment samples on 'SedPods', a proxy hard coral surface, and 'TurfPods', a proxy algal turf surface, for four deployment periods during 2020–2021 in two bays of Yunbenun, Australia. Coloured points are the mean predicted fits of a generalized linear mixed effects model (beta distribution with logit link – conditional pseudo-r^2 = 0.70), with predictions for control plots shown in blue and removal plots shown in orange. Solid vertical lines represent 95 % confidence intervals. Partialized observations (sum of fitted values and residuals) are shown as faint-coloured points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for the SedPods (PERMANOVA: $F_{1,73}$ = 2.5, r^2 = 0.03, p = 0.083; Supplementary Table 5), however, a significant difference in grain size between bays was detected for the TurfPods (PERMANOVA: $F_{1,78}$ = 35, r^2 = 0.27, p < 0.05; Fig. 4; Supplementary Table 5). This may be due to significantly different dispersion in grain sizes between bays, as opposed to a true difference in grain size distribution (PERMDISP: Bay - F = 6.6, p < 0.05).

The greatest variation in grain size distribution was seen when comparing the deposition surfaces. Sediment deposited on TurfPods had a higher proportion of coarser sediments and more variable grain size distribution than sediments collected on SedPods (Fig. 5). The mean particle diameters at the 90th percentile (D90) for TurfPod sediments reflected this pattern, ranging from 118 to 433 μm, larger on average than those for SedPod sediments, which ranged from 95 to 240 μm (Supplementary Table 4). Furthermore, fine sediments (<20 μm) were more prevalent in the deposited samples from SedPods (52.0 ± 0.6 % (mean ± SE)) than the TurfPods (31.0 ± 1.1 %) (Supplementary Table 4). For both pod types, the larger grain size class (very coarse sand, >1000 μm) was present in only a few samples (Fig. 5).

3.5. Algal turf height

Algal turf height ranged from 1 to 19 mm during the study period, and the modelled relationship connecting treatment, bay, and timepoint to algal turf height was relatively weak (conditional pseudo-r^2 = 0.30; Fig. 6; Supplementary Table 2). Macroalgae removal had largely no effect on algal turf height, with the only significant difference identified in the November 2020 survey in Florence Bay, where control plot turfs (6.1 ± 0.3 mm (estimated marginal mean ± SE)) were 42 % taller than removal plot turfs (4.5 ± 0.2 mm) (t = 5.4, df = 4271, p < 0.05; Supplementary Table 2). Similarly, there was no difference in turf height

between bays. Temporal variation in turf height was the most prominent trend. Algal turfs were significantly taller at the start of the study period (May 2020, control plots: 8.5 ± 0.3 mm, removal plots: 9.1 ± 0.3 mm) relative to the end of the study (July 2021: control plots: 4.2 ± 0.1 mm, removal plots: 4.5 ± 0.2 mm) (Arthur Bay: control plots: t = 13, removal plots: t = 13; Florence Bay: control plots: t = 6.6, removal plots: t = 13; df = 4271, p < 0.05), however, there was no significant interaction between treatment and timepoint, indicating that the observed temporal trend did not differ between control and removal plots (Fig. 6; Supplementary Table 2). Temperature data showed seasonal fluctuations ranging from 21 to 31 °C throughout the study period, however, there was no distinct correlation observed between temperature and turf height (Fig. 6).

4. Discussion

Removing the macroalgal canopy, consisting predominantly of *Sargassum* spp., from inshore reefs had no significant impact on the rate of sedimentation nor the composition of deposited sediments within experimental plots. Interestingly, despite no effect of macroalgae removal on sediment dynamics, consistently less deposition was observed in control plots than in removal plots in Arthur Bay only. This indicates that removing macroalgae may allow sediments to settle out of suspension onto the benthos in low-wind and low-current conditions, rather than being accumulated on the macroalgal canopy. However, physical parameters such as wind, rain, and currents are likely to influence sediment dynamics to a greater extent and at larger spatial scales than local biological factors such as macroalgal canopies.

Hydrodynamics are the major force governing sediment deposition and resuspension, giving rise to variability in geomorphology and hydrodynamic regimes across different reefs (Purcell, 2000; Schlaefer
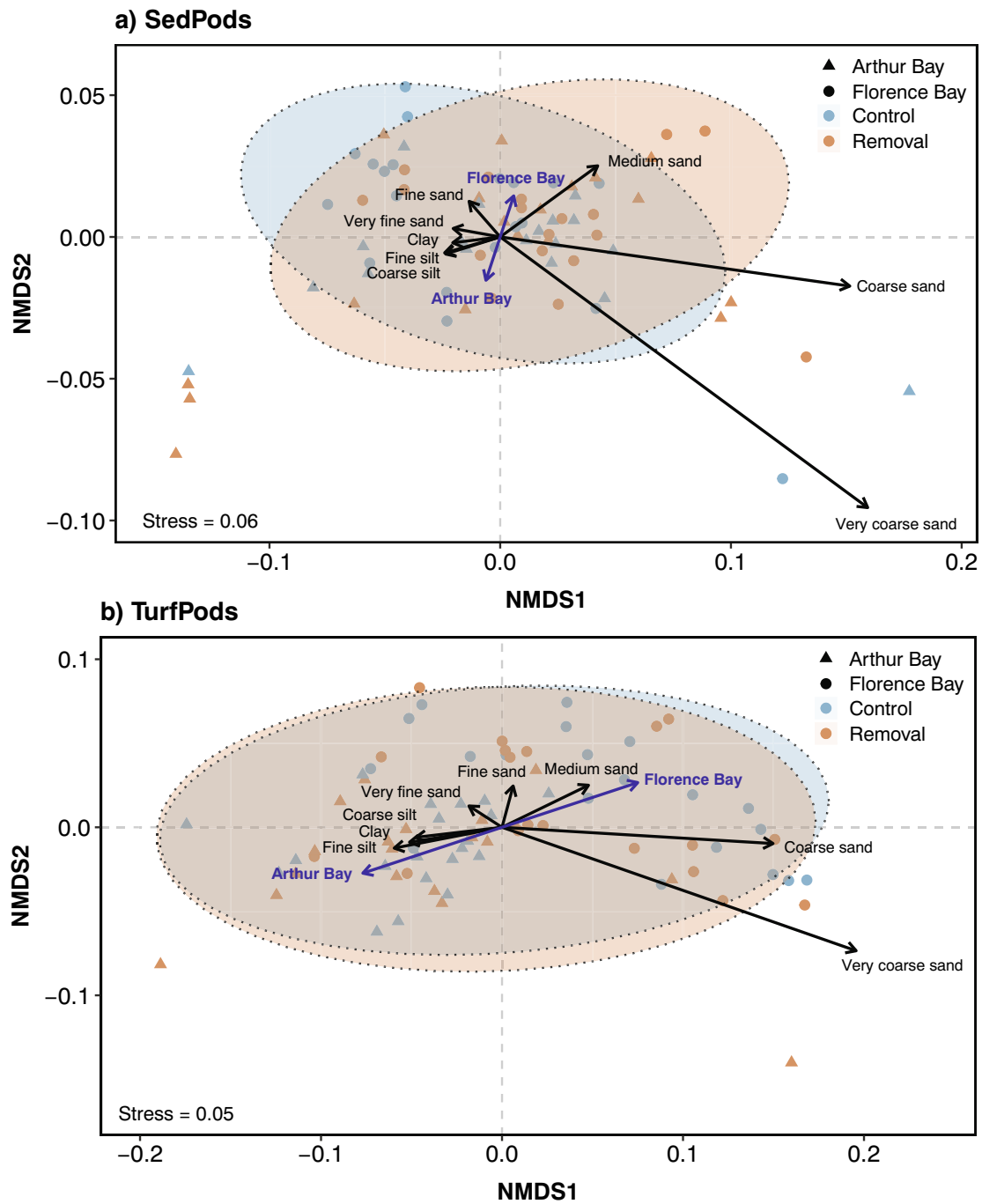
Fig. 4. Non-metric multidimensional scaling (nMDS) ordination of sampling units based on Euclidean distances of fourth-root scaled and Wisconsin double-standardized volume densities of $p = 9$ grain size classes in a total of a) $N = 74$ SedPod; and b) $N = 79$ TurfPod sampling units in two bays of Yunbenun, Australia. Symbols indicate the bay from which the sediment sample was collected (Arthur Bay shown as triangles, Florence Bay shown as circles), and colours indicate the treatment (control plots in blue, removal plots in orange). Black arrows represent loading vectors for grain size classes. Dark blue arrows represent environmental factors of interest projected onto the ordination plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2021). Both spatial and temporal variations in sediment deposition were observed in this study despite no difference between control and removal plots, which suggests that current speed and direction changing through time and space may be driving sediment deposition more so than changes in the macroalgal canopy. Canopy-forming macroalgae can influence fine-scale water dynamics (Birrell et al., 2008), though larger-scale hydrodynamic drivers (e.g. tidal currents, waves) are likely to have a greater effect on water flow and, subsequently, sediment deposition at a site (Schlaefer et al., 2021). Data collected

during this study support this with high-energy currents (given by the 70th percentile of current speeds within the deployment period) corresponding with higher sediment deposition in TurfPods (and vice versa; Fig. 2c). This likely reflects a greater amount of suspended sediment during high energy periods that is available to settle on the pods. However, in SedPods there was no relationship between deposition and the high-energy current speeds (Fig. 2b); this may indicate that the deposition was better retained in the TurfPods than in the SedPods (Schlaefer et al., 2021). This is supported by the three-fold greater range
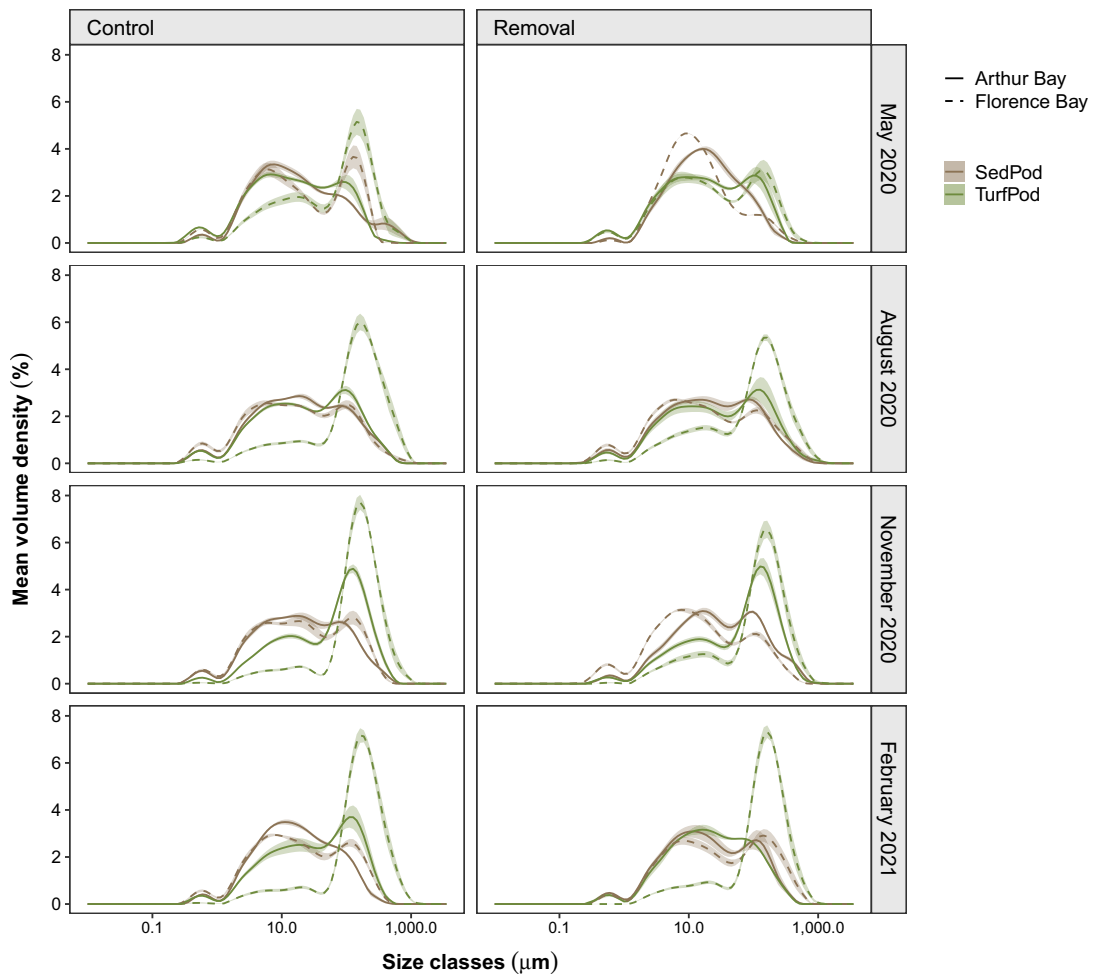
Fig. 5. Average grain size distribution represented as percent volume density (% distribution by volume) for deposited sediment samples on 'SedPods' (brown lines), a proxy hard coral surface, and 'TurfPods' (green lines), a proxy algal turf surface, for four deployment periods during 2020–2021 in two bays of Yunbenun, Australia (Arthur Bay (solid lines) and Florence Bay (dashed lines)). Coloured ribbons surrounding each line represent standard errors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
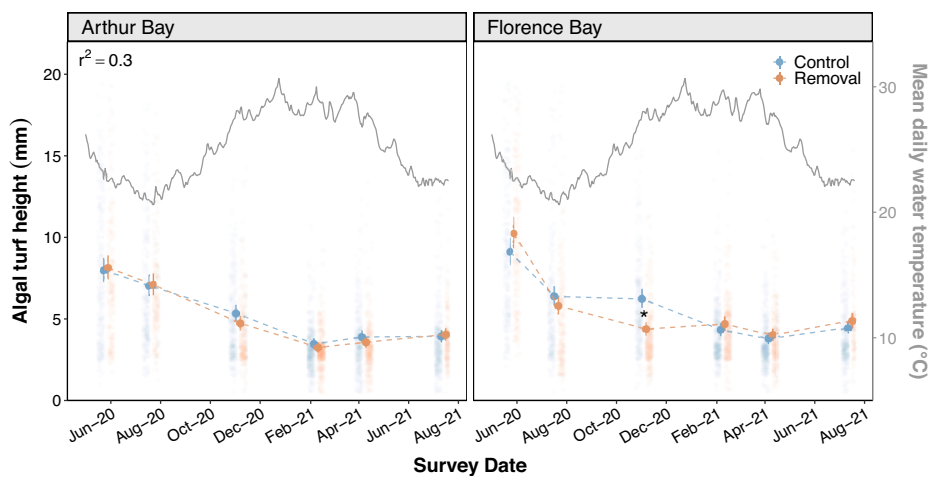

Fig. 6. Height of algal turfs in two bays of Yunbenun, Australia, across six survey timepoints throughout 2020–2021. Solid coloured points are the mean predicted fits of a generalized linear mixed effects model (gamma distribution with log link – conditional pseudo-r^2 = 0.3), with predictions for control plots shown in blue and removal plots shown in orange. Solid vertical lines represent 95 % confidence intervals. Partialized observations (sum of fitted values and residuals) are shown as faint-coloured points. Asterisks indicate statistically significant differences in algal turf height between control and removal plots. Average daily water temperature is shown as a solid grey line to provide environmental context. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of deposition values for TurfPods than for SedPods (cf. 5.7-fold in Schlaefer et al., 2021) and may explain the poor correlation between these parameters (Fig. 2a).

The temporal nature of this study has allowed consideration of the effect of varying physical conditions on sediment deposition. A previous study (Schlaefer et al., 2022) causally linked deposition with the effects of surface wave energy reaching the benthos, revealing a spatial difference between shallow reef flat areas and deeper reef slopes. Our findings complement this through exploring the suspension of sediment by currents. Focused on shallow water reef environments, the increase in availability of suspended sediment at higher current speeds translated into higher deposition on surfaces able to retain the deposited sediment (i.e., TurfPods; Whinney et al., 2017).

It is important to interpret these results in the context of the temporal and spatial scales at which this study was conducted. Coral reef sedimentation is known to vary substantially over small temporal scales due to tidal currents and wind, and their interaction (Schlaefer et al., 2021; Whinney et al., 2017). Data collection was conducted during calm weather conditions within short deployment periods (1-week), thus, under high winds and strong currents, different sediment dynamics would likely be observed. This is particularly pertinent for inshore reefs that are exposed to a relatively high proportion of fine grained, organic sediment (as observed in this study), which is more easily suspended by wind and currents (Bainbridge et al., 2018; Bartley et al., 2017; Fabricius and Wolanski, 2000). From a spatial perspective, the plots (25 m^2) used in this study may be too small to influence sediment dynamics relevant to the broader hydrodynamic patterns occurring at larger spatial scales. At a bay-wide scale, hydrodynamic patterns may be influenced to a greater extent by macroalgae removal, having flow-on effects for sedimentation and algal turfs. Furthermore, edge effects may have contributed to this lack of resolution and therefore removal from larger areas (e.g., an order of magnitude greater) may be required to avoid edge effects and enable delineation of the biological and physical parameters influencing sediment dynamics on inshore reefs.

The impact of deposited sediment on benthic organisms is influenced not only by the physical load of sedimentation but also by the amount of associated organic material and the grain size distribution (Weber et al., 2006). Organic and nutrient-related parameters of sediment are more strongly related to stress levels of benthic organisms, such as corals, than physical parameters (Weber et al., 2006). In this study, the composition of the sediments was consistent across experimental plots irrespective of fleshy macroalgae removal. Inshore coral reefs are generally at a heightened risk of exposure to organically enriched sediments derived from terrestrial runoff (Furnas, 2003; Weber et al., 2012; Wolanski et al., 2005). Organic sediment aggregates can be detrimental to corals and algal turfs, due to stimulation of microbial processes causing tissue degradation and increasing disease transmission and prevalence (Bainbridge et al., 2018; Jones et al., 2019; Studivan et al., 2022; Weber et al., 2012). Removing macroalgae at these sites on Yunbenun did not appear to expose corals to increased organic aggregates, and associated microbial stress, which could decrease algal turf productivity or contribute to coral stress or disease (Weber et al., 2012). Sediment-related stressors are therefore unlikely to be exacerbated by removal activities at the scale investigated in this study.

The grain size distribution of deposited sediment was also not influenced by macroalgae removal. Sediment grain size and propensity to aggregate with organic material can synergistically affect benthic marine organisms due to the formation of marine snow, which has been found to cause mortality to corals (Bainbridge et al., 2018; Fabricius and Wolanski, 2000). Fine grain size classes <63 μm (clay and silt) are considered more detrimental to corals than larger grain size classes (sand and gravel) because they are more difficult for corals to remove from their oral cavity (Bainbridge et al., 2018; Bainbridge et al., 2012; Jones et al., 2019; Weber et al., 2006). Moreover, finer grain sizes readily aggregate with organic material, giving rise to microbial proliferation which can result in coral tissue necrosis (Weber et al., 2012).

Accumulation of fine organic sediment aggregates in algal turfs can also elicit conditions detrimental to coral settlement and recruitment (Speare et al., 2019), reduce benthic productivity (Clausing et al., 2014; Tebbett and Bellwood, 2020), and detrimentally affect detritivore feeding behaviour (Tebbett et al., 2017). Material reaching the GBR lagoon via flood plumes is primarily constituted of terrigenous particles <20 μm, and so this finer grain size fraction is arguably the most relevant size class for inshore GBR corals (Bainbridge et al., 2018; Bartley et al., 2017). On average, between a third to a half of the sediment content analyzed in this study was <20 μm, highlighting that the reefs of Yunbenun are particularly subjected to these fine grain sizes. At the scale investigated in this study, however, macroalgae removal did not increase the risk of fine sediment accumulation and associated organic aggregation on corals and algal turfs.

Thresholds of sediment deposition as low as 1 mg cm^{-2} d^{-1} for coral larvae and 4.9 mg cm^{-2} d^{-1} for coral adults have been reported as detrimental to coral health (Tuttle and Donahue, 2020). Specific to inshore GBR corals, Fabricius et al. (2003) found coral juveniles were able to survive sedimentation up to 14 mg cm^{-2}, however, similar loads enriched with organic material resulted in increased mortality. This variability in susceptibility of corals to sedimentation depending on life stage, taxa, as well as sediment composition emphasizes the need for site-specific understanding of sedimentation thresholds to inform reef and catchment management. Interestingly, the net level of sedimentation on corals estimated in this study via the use of SedPods (0.02–0.75 mg cm^{-2} d^{-1}) was below any proposed limit for detrimental impacts to corals, however, no major acute disturbances (e.g. floods) occurred during the study period, which are the primary mechanism of sediment delivery to inshore reefs (Furnas, 2003; Schaffelke et al., 2005; Waterhouse et al., 2017). Sediment deposition thresholds have also been suggested for algal turfs, with loads higher than 10 mg cm^{-2} (sampled from natural turfs) thought to elicit declines in algal turf productivity and particulate nutritional value (Tebbett and Bellwood, 2020). Much of the sediment deposited on coral reefs is bound in algal turfs, which can reduce water flow in the boundary layer up to 15-fold relative to free-stream flow, causing sediment to settle out of suspension (Birrell et al., 2008; Carpenter and Williams, 1993). The difference in deposition between EAM colonized surfaces and surfaces not colonized by EAM (e. g., coral surfaces) was demonstrated in this study, whereby the artificial turf layer accumulated 20-fold higher levels of deposited sediment. Additionally, sedimentation on TurfPods (0.37–57 mg cm^{-2} d^{-1}) was more variable than on SedPods, and at the upper end considerably greater than the proposed 10 mg cm^{-2} threshold. Sedimentation stress may, therefore, be a more concerning factor for algal turfs and EAM productivity on Yunbenun reefs.

Turf algae is a strong indicator of benthic productivity, with a proposed SPAT height threshold of 5 mm, beyond which the EAM develops into LSATs (Goatley et al., 2016; Gordon et al., 2016; Purcell, 2000; Tebbett and Bellwood, 2019) and becomes potentially unsuitable for coral settlement and recruitment with subsequent declines in productivity (Ford et al., 2018; Tebbett and Bellwood, 2020). Algal turf height averaged approximately 5 mm in this study, which is around this critical threshold and consistent with the high but variable sediment deposition rates measured on the proxy algal turf surface. High deposition on the TurfPods occurred in surveys that recorded relatively short algal turf height (<5 mm), which is not consistent with relationships previously reported between turf height and sediment deposition (Gordon et al., 2016; Purcell, 2000; Tebbett and Bellwood, 2020). Macroalgae removal led to little change in turf height throughout this study, which suggests removal of the macroalgal canopy is unlikely to drive unwanted increases in algal turf height and associated detrimental bottom-up effects on key reef ecosystem processes such as benthic productivity, coral settlement and recruitment (Tebbett et al., 2018b; Tebbett and Bellwood, 2020). The weak statistical relationship between macroalgae removal and turf height does, however, indicate there may be a more complex suite of factors driving turf height dynamics. Other EAM

characteristics, such as algal turf cover and community composition (Arjunwadkar et al., 2022); associated microbial communities, which may influence the suitability of the EAM for coral settlement and recruitment; and benthic productivity should be investigated (Birrell et al., 2005; Cetz-Navarro et al., 2015). Furthermore, grazing patterns are known to affect algal turfs and sediment composition, thus, documenting herbivorous fish communities in conjunction with metrics quantified in this study may help to understand the relationship between macroalgae, turf algae, and sedimentation (Birrell et al., 2008; Bonaldo and Bellwood, 2011; Clausing et al., 2014; Tebbett and Bellwood, 2019).

The order of magnitude difference between deposition of sediment on the proxy coral surface and the proxy algal turf surface is consistent with previous studies utilizing these instruments (Latrille et al., 2019). These findings reflect the difference in boundary layer complexity, emphasizing the variation in sedimentation of benthic organisms occurring on coral reefs (Birrell et al., 2008; Latrille et al., 2019). Despite less net sediment deposition occurring on the SedPods, the sediment deposited contained on average approximately 50 % higher proportion of organic material and approximately 65 % higher proportion of fine grain size classes <20 μm than TurfPod sediments, consistent with previous studies (Latrille et al., 2019). The high organic proportion in SedPods is likely due to the differences between the deposition surfaces; with the propensity of the flat SedPod surface to develop a biofilm and accumulate fine organic sediment aggregates, in contrast to the artificial turf layer capable of trapping more coarse, inorganic particles. Less sediment deposition on the proxy coral surface, yet a higher organic proportion and finer grain sizes than the proxy turf surface, may indicate that the deposited sediment is disproportionate to the physical load. Furthermore, spatiotemporal variation in net sediment deposition, organic content, and grain size distribution was more pronounced for TurfPods than SedPods, suggesting sedimentation on algal turfs may be more variable through space and time than on hard corals. Measuring a range of sediment characteristics across varying temporal and spatial scales is therefore essential to accurately quantify the impact on benthic organisms.

In conclusion, results of this study provide valuable insights into the impact of macroalgae removal on sedimentation and algal turf dynamics on inshore coral reefs experiencing high sediment input. Overall, this study suggests the relationship between sedimentation, algal turfs, and macroalgae is complex on energetically dynamic Yunbenun reef communities, and likely other inshore GBR reefs. Despite the complexity of the relationships investigated in this study, it was clear that removing the macroalgal canopy on a small scale had minimal effect on sediment deposition and composition, as well as algal turfs. Thus, sediment-related stressors for corals and algal turfs are unlikely to be worsened nor alleviated following the removal of the macroalgal canopy within local-scale reef restoration programs, though larger scale removals and the resulting impacts on sedimentation dynamics require further research.

CRediT authorship contribution statement

Stella E. Fulton: Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Tehya Hines:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **Cathie A. Page:** Writing – review & editing, Supervision, Conceptualization. **Ian M. McLeod:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **James Whinney:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Scott F. Heron:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Conceptualization. **David G. Bourne:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Hillary A. Smith:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

Data availability

The data and R code that support the findings of this study are openly available in the Research Data JCU repository at https://doi.org/10.25903/54g5-fg77.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2024.117037.

References

American Public Health Association, 2018. 2540 SOLIDS (2017), in: standard methods for the examination of water and wastewater, American Public Health Association. https://doi.org/10.2105/SMWW.2882.030.

Arjunwadkar, C.V., Tebbett, S.B., Bellwood, D.R., Bourne, D.G., 2022. Algal turf structure and composition vary with particulate loads on coral reefs. Mar. Pollut. Bull. 181, 113903. https://doi.org/10.1016/j.marpolbul.2022.113903.

Babcock, R., Smith, L., 2000. Effects of sedimentation on coral settlement and survivorship. In: Proceedings 9th International Coral Reef Symposium. Bali, Indonesia, p. 5.

Bainbridge, Z.T., Wolanski, E., Álvarez-Romero, J.G., Lewis, S.E., Brodie, J.E., 2012. Fine sediment and nutrient dynamics related to particle size and floc formation in a Burdekin River flood plume, Australia. Mar. Pollut. Bull. 65, 236–248. https://doi.org/10.1016/j.marpolbul.2012.01.043.

Bainbridge, Z., Lewis, S., Bartley, R., Fabricius, K., Collier, C., Waterhouse, J., Garzon-Garcia, A., Robson, B., Burton, J., Wenger, A., Brodie, J., 2018. Fine sediment and particulate organic matter: a review and case study on ridge-to-reef transport, transformations, fates, and impacts on marine ecosystems. Mar. Pollut. Bull. 135, 1205–1220. https://doi.org/10.1016/j.marpolbul.2018.08.002.

Bartley, R., Waters, D., Turner, R., Kroon, F., Wilkinson, S., Garzon-Garcia, A., Kuhnert, P., Lewis, S., Smith, R., Bainbridge, Z., Olley, J., Brooks, A., Burton, J., Brodie, J., Waterhouse, J., 2017. Scientific Consensus Statement 2017: A Synthesis of the Science of Land-Based Water Quality Impacts on the Great Barrier Reef, Chapter 2: Sources of Sediment, Nutrients, Pesticides and Other Pollutants to the Great Barrier Reef. State of Queensland.

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., Day, J.C., Grantham, R., Grech, A., Hoey, A.S., Jones, G.P., Pandolfi, J.M., Tebbett, S.B., Techera, E., Weeks, R., Cumming, G.S., 2019. Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biol. Conserv. 236, 604–615. https://doi.org/10.1016/j.biocon.2019.05.056.

Birrell, C.L., McCook, L.J., Willis, B.L., 2005. Effects of algal turfs and sediment on coral settlement. Mar. Pollut. Bull. 51, 408–414. https://doi.org/10.1016/j.marpolbul.2004.10.022.

Birrell, C., McCook, L., Willis, B., Diaz-Pulido, G., 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. In:

Gibson, R., Atkinson, R., Gordon, J. (Eds.), Oceanography and Marine Biology, Oceanography and Marine Biology - An Annual Review. CRC Press, pp. 25–63. https://doi.org/10.1201/9781420065756.ch2.

Bonaldo, R.M., Bellwood, D.R., 2011. Spatial variation in the effects of grazing on epilithic algal turfs on the great barrier reef, Australia. Coral Reefs 30, 381–390. https://doi.org/10.1007/s00338-010-0704-4.

Bonaldo, R.M., Hay, M.E., 2014. Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. PloS One 9, e85786. https://doi.org/10.1371/journal.pone.0085786.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Brown, T., 1972. Silt Pollution - The Destruction of Magnetic Island's Coral Fringing Reefs. Australian Institute of Marine Science, Townsville.

Carpenter, R.C., 1985. Relationships between primary production and irradiance in coral reef algal communities. Limnol. Oceanogr. 30, 784–793.

Carpenter, R.C., Williams, S.L., 1993. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol. Oceanogr. 38, 687–694.

Ceccarelli, D.M., Evans, R.D., Logan, M., Mantel, P., Puotinen, M., Petus, C., Russ, G.R., Williamson, D.H., 2020. Long-term dynamics and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. Ecol. Appl. 30. https://doi.org/10.1002/eap.2008.

Cetz-Navarro, N.P., Carpizo-Ituarte, E.J., Espinoza-Avalos, J., Chee-Barragán, G., 2015. The effect of filamentous turf algal removal on the development of gametes of the coral Orbicella annularis. PloS One 10, e0117936. https://doi.org/10.1371/journal.pone.0117936.

Clausing, R.J., Annunziata, C., Baker, G., Lee, C., Bittick, S.J., Fong, P., 2014. Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. Mar. Ecol. Prog. Ser. 517, 121–129. https://doi.org/10.3354/meps11029.

De'ath, G., Fabricius, K., 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecol. Appl. 20, 840–850. https://doi.org/10.1890/08-2023.1.

De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc. Natl. Acad. Sci. 109, 17995–17999. https://doi.org/10.1073/pnas.1208909109.

Diaz-Pulido, G., McCook, L.J., 2008. State of the Reef Report Environmental Status of the Great Barrier Reef: Macroalgae (Seaweeds). Great Barrier Reef Marine Park Authority, Townsville.

Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247, 121–132.

Eberhard, R., Thorburn, P., Rolfe, J., Taylor, B., Ronan, M., Weber, T., Flint, N., Kroon, F., Brodie, J., Waterhouse, J., Silburn, M., Bartley, R., Davis, A., Wilkinson, S., Lewis, S., Star, M., Poggio, M., Windle, J., Marshall, N., Hill, R., Maclean, K., Lyons, P., Robinson, C., Adame, F., Selles, A., Griffiths, M., Gunn, J., McCosker, K., 2017. Scientific Consensus Statement 2017: A Synthesis of the Science of Land-Based Water Quality Impacts on the Great Barrier Reef, Chapter 4: Management Options and their Effectiveness. State of Queensland.

Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028.

Fabricius, K.E., Wolanski, E., 2000. Rapid smothering of coral reef organisms by muddy marine snow. Estuar. Coast. Shelf Sci. 50, 115–120.

Fabricius, K.E., Wild, C., Wolanski, E., Abele, D., 2003. Effects of transparent exopolymer particles and muddy terrigenous sediments on the survival of hard coral recruits. Estuar. Coast. Shelf Sci. 57, 613–621. https://doi.org/10.1016/S0272-7714(02)00400-6.

Field, M.E., Chezar, H., Storlazzi, C.D., 2013. SedPods: a low-cost coral proxy for measuring net sedimentation. Coral Reefs 32, 155–159. https://doi.org/10.1007/s00338-012-0953-5.

Ford, A.K., Eich, A., McAndrews, R.S., Mangubhai, S., Nugues, M.M., Bejarano, S., Moore, B.R., Rico, C., Wild, C., Ferse, S.C.A., 2018. Evaluation of coral reef management effectiveness using conventional versus resilience-based metrics. Ecol. Indic. 85, 308–317. https://doi.org/10.1016/j.ecolind.2017.10.002.

Furnas, M.J., 2003. Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef. Australian Institute of Marine Science: CRC Reef Research Centre, Townsville, Australia.

Goatley, C.H.R., Bellwood, D.R., 2013. Ecological consequences of sediment on high-energy coral reefs. PloS One 8, e77737. https://doi.org/10.1371/journal.pone.0077737.

Goatley, C.H.R., Bonaldo, R.M., Fox, R.J., Bellwood, D.R., 2016. Sediments and herbivory as sensitive indicators of coral reef degradation. E&S 21, art29. https://doi.org/10.5751/ES-08334-210129.

Gordon, S.E., Goatley, C.H.R., Bellwood, D.R., 2016. Composition and temporal stability of turf sediments on inner-shelf coral reefs. Mar. Pollut. Bull. 111, 178–183. https://doi.org/10.1016/j.marpolbul.2016.07.013.

Great Barrier Reef Marine Park Authority, 2019. Great Barrier Reef Outlook Report 2019. Great Barrier Reef Marine Park Authority, Townsville.

Harborne, A.R., Rogers, A., Bozec, Y.-M., Mumby, P.J., 2017. Multiple stressors and the functioning of coral reefs. Ann. Rev. Mar. Sci. 9, 445–468. https://doi.org/10.1146/annurev-marine-010816-060551.

Hatcher, B.G., 1988. Coral reef primary productivity: a Beggar's banquet. TREE 3, 106–111.

International Organisation for Standardisation, 2020. ISO 13320:2020(E) Particle Size Analysis–Laser Diffraction Methods. ISO, Geneva.

Johns, K.A., Emslie, M.J., Hoey, A.S., Osborne, K., Jonker, M.J., Cheal, A.J., 2018. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9, e02349. https://doi.org/10.1002/ecs2.2349.

Jompa, J., McCook, L.J., 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. Mar. Ecol. Prog. Ser. 258, 87–95. https://doi.org/10.3354/meps258087.

Jones, R., Fisher, R., Bessell-Browne, P., 2019. Sediment deposition and coral smothering. PloS One 14, e0216248. https://doi.org/10.1371/journal.pone.0216248.

Latrille, F.X., Tebbett, S.B., Bellwood, D.R., 2019. Quantifying sediment dynamics on an inshore coral reef: putting algal turfs in perspective. Mar. Pollut. Bull. 141, 404–415. https://doi.org/10.1016/j.marpolbul.2019.02.071.

Nugues, M.M., Roberts, C.M., 2003. Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs 22, 507–516. https://doi.org/10.1007/s00338-003-0338-x.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevenes, M.H.H., Szoecs, E., Wagner, H., 2020. Vegan: Community Ecology Package (R Foundation for Statistical Computing).

Purcell, S., 2000. Association of epilithic algae with sediment distribution on a windward reef in the northern great barrier reef, Australia. Bull. Mar. Sci. 66, 199–214.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

River, G.F., Edmunds, P.J., 2001. Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. J. Exp. Mar. Biol. Ecol. 261, 159–172. https://doi.org/10.1016/S0022-0981(01)00266-0.

Rogers, C.S., 1990. Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62, 185–202. https://doi.org/10.3354/meps062185.

Sabin, A., 2011. Problems in particle size: laser diffraction observations. J. GXP Compl. 15, 35+.

Schaffelke, B., Mellors, J., Duke, N.C., 2005. Water quality in the great barrier reef region: responses of mangrove, seagrass and macroalgal communities. Mar. Pollut. Bull. 51, 279–296. https://doi.org/10.1016/j.marpolbul.2004.10.025.

Schlaefer, J.A., Tebbett, S.B., Bellwood, D.R., 2021. The study of sediments on coral reefs: a hydrodynamic perspective. Mar. Pollut. Bull. 169, 112580. https://doi.org/10.1016/j.marpolbul.2021.112580.

Schlaefer, J.A., Tebbett, S.B., Bowden, C.L., Collins, W.P., Duce, S., Hemingson, C.R., Huertas, V., Mihalitsis, M., Morais, J., Morais, R.A., Siqueira, A.C., Streit, R.P., Swan, S., Valenzuela, J., Bellwood, D.R., 2022. A snapshot of sediment dynamics on an inshore coral reef. Mar. Environ. Res. 181, 105763. https://doi.org/10.1016/j.marenvres.2022.105763.

Smith, H.A., Brown, D.A., Arjunwadkar, C.V., Fulton, S.E., Whitman, T., Hermanto, B., Mastroianni, E., Mattocks, N., Smith, A.K., Harrison, P.L., Boström-Einarsson, L., McLeod, I.M., Bourne, D.G., 2022. Removal of macroalgae from degraded reefs enhances coral recruitment. Restor. Ecol. https://doi.org/10.1111/rec.13624.

Smith, H.A., Fulton, S.E., McLeod, I.M., Page, C.A., Bourne, D.G., 2023. Sea-weeding: manual removal of macroalgae facilitates rapid coral recovery. J. Appl. Ecol. 60, 2459–2471. https://doi.org/10.1111/1365-2664.14502.

Souter, D., Planes, S., Wicquart, J., Logan, M., Obura, D., Staub, F., 2021. Status of Coral Reefs of the World: 2020 - Chapter 2. Status of Coral Reefs of the World, Global Coral Reef Monitoring Network.

Speare, K.E., Duran, A., Miller, M.W., Burkepile, D.E., 2019. Sediment associated with algal turfs inhibits the settlement of two endangered coral species. Mar. Pollut. Bull. 144, 189–195. https://doi.org/10.1016/j.marpolbul.2019.04.066.

Studivan, M.S., Rossin, A.M., Rubin, E., Soderberg, N., Holstein, D.M., Enochs, I.C., 2022. Reef sediments can act as a stony coral tissue loss disease vector. Front. Mar. Sci. 8, 815698. https://doi.org/10.3389/fmars.2021.815698.

Sura, S.A., Bell, A., Kunes, K.L., Turba, R., Songer, R., Fong, P., 2021. Responses of two common coral reef macroalgae to nutrient addition, sediment addition, and mechanical damage. J. Exp. Mar. Biol. Ecol. 536, 151512. https://doi.org/10.1016/j.jembe.2021.151512.

Tebbett, S.B., Bellwood, D.R., 2019. Algal turf sediments on coral reefs: what's known and what's next. Mar. Pollut. Bull. 149, 110542. https://doi.org/10.1016/j.marpolbul.2019.110542.

Tebbett, S.B., Bellwood, D.R., 2020. Sediments ratchet-down coral reef algal turf productivity. Sci. Total Environ. 713, 136709. https://doi.org/10.1016/j.scitotenv.2020.136709.

Tebbett, S.B., Goatley, C.H.R., Bellwood, D.R., 2017. Fine sediments suppress detritivory on coral reefs. Mar. Pollut. Bull. 114, 934–940. https://doi.org/10.1016/j.marpolbul.2016.11.016.

Tebbett, S.B., Bellwood, D.R., Purcell, S.W., 2018a. Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: implications for reefs and reef fisheries. Coral Reefs 37, 929–937. https://doi.org/10.1007/s00338-018-1718-6.

Tebbett, S.B., Goatley, C.H.R., Bellwood, D.R., 2018b. Algal turf sediments across the great barrier reef: putting coastal reefs in perspective. Mar. Pollut. Bull. 137, 518–525. https://doi.org/10.1016/j.marpolbul.2018.10.056.

Tebbett, S.B., Goatley, C.H.R., Streit, R.P., Bellwood, D.R., 2020a. Algal turf sediments limit the spatial extent of function delivery on coral reefs. Sci. Total Environ. 734, 139422. https://doi.org/10.1016/j.scitotenv.2020.139422.

Tebbett, S.B., Streit, R.P., Bellwood, D.R., 2020b. A 3D perspective on sediment accumulation in algal turfs: implications of coral reef flattening. J. Ecol. 108, 70–80. https://doi.org/10.1111/1365-2745.13235.

Thompson, A., Costello, P., Davidson, J., Logan, M., Coleman, G., 2021. Marine Monitoring Program Annual Report for Inshore Coral Reef Monitoring: 2019–20. Great Barrier Reef Marine Park Authority, Townsville.

Tuttle, L.J., Donahue, M.J., 2020. Thresholds for Sediment Stress on Corals: A Systematic Review and meta-Analysis. NOAA Fisheries Pacific Islands, Hawaii.

Waterhouse, J., Schaffelke, B., Bartley, R., Eberhard, R., Brodie, J., Star, M., Thorburn, P., Rolfe, J., Ronan, M., Taylor, B., Kroon, F., 2017. Scientific Consensus Statement 2017: A Synthesis of the Science of Land-Based Water Quality Impacts on the Great Barrier Reef, Chapter 5: Overview of Key Findings, Management Implications and Knowledge Gaps. State of Queensland.

Waterhouse, J., Gruber, R., Logan, M., Petus, C., Howley, C., Lewis, S., Tracey, D., James, C., Mellors, J., Tonin, H., Skuza, M., Costello, P., Davidson, J., Gunn, K., Lefevre, C., Moran, D., Robson, B., Shanahan, M., Zagorskis, I., Shellberg, J., 2021. Marine Monitoring Program: Annual Report for Inshore Water Quality Monitoring 2019–20. Great Barrier Reef Marine Park Authority, Townsville.

Weber, M., Lott, C., Fabricius, K.E., 2006. Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. J. Exp. Mar. Biol. Ecol. 336, 18–32. https://doi.org/10.1016/j.jembe.2006.04.007.

Weber, M., de Beer, D., Lott, C., Polerecky, L., Kohls, K., Abed, R.M.M., Ferdelman, T.G., Fabricius, K.E., 2012. Mechanisms of damage to corals exposed to sedimentation. Proc. Natl. Acad. Sci. 109, E1558–E1567. https://doi.org/10.1073/pnas.1100715109.

Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 377–392. https://doi.org/10.1086/622910.

Whinney, J., Jones, R., Duckworth, A., Ridd, P., 2017. Continuous in situ monitoring of sediment deposition in shallow benthic environments. Coral Reefs 36, 521–533. https://doi.org/10.1007/s00338-016-1536-7.

Williamson, D.H., Ceccarelli, D.M., Jones, G.J., Russ, G.R., 2019. Assessing the Ecological Effects of Management Zoning on Inshore Reefs of the Great Barrier Reef Marine Park. Great Barrier Reef Marine Park Authority, Townsville.

Wolanski, E., Fabricius, K., Spagnol, S., Brinkman, R., 2005. Fine sediment budget on an inner-shelf coral-fringed island, great barrier reef of Australia. Estuar. Coast. Shelf Sci. 65, 153–158. https://doi.org/10.1016/j.ecss.2005.06.003.