

Interactive Effects of Sediments and Urchins on Tropical Macroalgal Forests

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Abstract

Macroalgal forests are a prominent component of tropical seascapes providing food and shelter for many species whilst subsidising secondary productivity in coastal ecosystems. Monitoring and managing macroalgae requires an understanding of key processes that alter these assemblages, especially at the local scale. Here we consider how sediment depth/cover and abundance of the macroalgal grazing urchin *Tripneustes gratilla* (Linnaeus, 1758), influence variation in community composition and physical structure of macroalgal patches within the World Heritage listed Ningaloo Reef, Western Australia.

Our study found high urchin densities in sites with lower sediment loads and that sediments, urchin abundance and seascape position combined, explained 32% of the spatial variation in macroalgal forest community composition. We also found a greater occurrence of *Sargassopsis*, *Caulerpa*, *Sirophysalis* and *Hormophysa* in the lagoon where sediment cover/depth was high. Canopy height and cover of canopy forming macroalgae was also greater where sediment loads were high and urchin abundance low. Macroalgal genera with a strong and robust thallus were found in sediment depths up to 6 cm as opposed to those with softer, fragile thalli that were found in sediments < 2 cm. Our results demonstrate that high densities of urchins and mobile sediments can have profound effects on the composition and structure of tropical macroalgal forests. Changes to macroalgal forest community composition and physical structure will have flow-on effects for ecological processes such as productivity and habitat use which can alter the ecosystem goods and services macroalgal forests provide.

Introduction

Tropical macroalgal forests comprise multiple species that form patches of habitat for a diversity of marine life (Fulton *et al.*, 2019; (Sambrook *et al.*, 2019)). Common to coastlines throughout many parts of the world, macroalgal forests can cover extensive areas of shallow-water at similar scales to coral reefs (Kobryn *et al.*, 2013; Suchley, McField and Alvarez-Filip, 2016; Gouvêa *et al.*, 2020). As primary producers, they form a major component of the productivity within tropical seascapes that underpin broader biodiversity and fuel ecosystem services and functions (Fulton *et al.*, 2019). The dynamics of community structure within macroalgal patches are complex due to a combination of large spatial and temporal-scale drivers such as currents and temperature, interacting with local drivers such as depth of water, sediment loads and herbivory within a given patch (McCook, 1996). To date, studies investigating environmental and biotic interactions of macroalgae have focused on either single species or at spatial-scales covering hundreds of kilometres, with limited relevance to the local community (Vuki and Price, 1994; Sangil *et al.*, 2018; Olsen *et al.*, 2019). It is therefore pertinent to understand how local environmental and biotic predictors, such as sediments and herbivory, influence community dynamics of macroalgal forests.

In macroalgal communities, sediment depth and cover are important environmental filters because of their influence on which species occur locally from the regional species pool (Airoldi, 2003; Götzenberger

et al., 2012). Marine sediments in the tropics are typically formed from a combination of terrestrially and marine derived material (Tebbett, Goatley and Bellwood, 2017). However, there are a few cases where sediment is produced predominately within the marine system itself, such as when rainfall is extremely low and there is a lack of major river systems (Ateweberhan, Bruggemann and Breeman, 2006; Fulton *et al.*, 2014). This is especially true on offshore tropical reefs, or reefs on arid coastlines, where sediment production is primarily derived from the scraping and grazing of herbivorous fishes upon carbonate pavement and corals (Bellwood, 1996). These fishes produce substantial volumes of sand through their excrement which is then moved across the seascape through wave action and disturbances like cyclones (Ong and Holland, 2010). These mobile sediments may bury, shade or abrade benthic primary producers, influencing benthic community dynamics within seascapes.

Interactions between macroalgae and sediments have received less attention on tropical reefs than on temperate reefs, particularly when considering how sediments influence community composition and physical structure of canopy-forming species. Species-specific studies indicate excess sedimentation can cause smothering and burial of algal recruits and algae with fragile thalli, leading to reductions in light and limitation of gas exchange, with consequences for nutrient uptake (Umar, McCook and Price, 1998; Gao *et al.*, 2019). Sediment cover is also important, particularly at the time of algal recruitment, as even a small cover of sand can inhibit attachment of macroalgal zygotes (Devinny and Volse, 1978; Gao *et al.*, 2019). Sediments can also abrade the thalli causing tissue necrosis or may remove whole individuals (Airoldi, 2003). Conversely, mild sediment deposition on the benthos may be beneficial for algae as many herbivorous fishes avoid consuming sand-laden algae (Tebbett, Bellwood and Purcell, 2018). Similarly, sedimentation reduces herbivore pressure by urchins because they tend to avoid sandy surfaces (Kriegisch *et al.*, 2019). The addition of organic particulate matter may also increase nitrogen and phosphorous availability, improving algal growth rates (Schaffelke, 1999).

How macroalgae respond to sediment will partially depend on the morphological traits of different algal orders (Littler and Littler, 1980; Clayton, 1990). Some orders have the ability to grow quickly and reproduce vegetatively if damaged by sediment; morphological and reproductive traits that make them psammophilic (sand-loving) (Daly and Mathieson, 1977). Many of the canopy forming tropical macroalgae, such as *Sargassum*, fall into the order Fucales. Species in this order have been described as 'biologically component', as they are well adapted to compete for light, long-lived and tend to have thick, robust thalli. Others orders, such as the Dictyotales, which possess a diverse range of understory genera, may be considered stress tolerant and opportunistic, as they tend to be fast growing, occur across a wide range of depths, have fairly simple construction, short lifespan and produce secondary metabolites as a deterrent to herbivory (Daly and Mathieson, 1977; Teixeira *et al.*, 2006).

Another major determinant of community dynamics of macroalgal forests is herbivory, which is often associated with fishes (Kriegisch *et al.*, 2019). However, in some systems herbivorous urchins can have a stronger effect on macroalgal communities than fish. For example, in temperate kelp forests urchins prey upon the dominant canopy-forming algae resulting in barrens with dramatically reduced ecosystem diversity (Witman and Dayton 2001). Urchins may also prevent macroalgal overgrowth on tropical reefs,

especially when fish stocks have been depleted. How herbivorous urchins and sediment presence interact to effect the composition and physical structure of tropical macroalgal forests is however, less frequently examined.

Here, we describe sediment and macroalgal associations on a tropical reef and ask whether tropical macroalgal community composition and the physical structure of canopy forming macroalgae vary predictably with benthic sediment load and herbivorous urchin abundance. Our study site is the World Heritage listed Ningaloo reef, Western Australia, where macroalgal, sediment and urchin abundance was assessed across the reef seascape to address the following questions: 1) Is variation in sediment cover and depth across the seascape a useful predictor of local-scale variation in macroalgal community composition and the physical structure of canopy forming macroalgae? and 2) How does herbivorous urchin density relate to algal morphology and life history strategy, and what influence does sediment load have on this relationship?

Materials And Methods

Study site & sampling

Ningaloo is an ideal study site for investigating natural variation in macroalgal communities as there is negligible harvesting of herbivorous fishes and a lack of broad-acre agricultural cultivation. Ningaloo has a very low human density, and the adjacent arid landscape, with no major river systems, means there is low input of terrestrially derived sediment and nutrients (Johansson, Bellwood and Depczynski, 2010; Wilson, Kendrick and Wilson, 2019). The lagoon, between the fringing coral reef and shore, is also covered by a mosaic of macroalgal and sand patches (Cassata and Collins, 2008; Fulton et al., 2019).

In the Austral summer 2019, benthic composition and fine-scale sediment measurements were undertaken south of Coral Bay, Ningaloo Reef, Western Australia ($23^{\circ}08'25.2"S\ 113^{\circ}46'12.2"E$, Fig. 1). In this region of Ningaloo, average water depth in the lagoon is 2.8 m with a range of 1–6 m. Within the lagoon the predominant underlying substrate is limestone pavement – remnants of an ancient reef – with a veneer of carbonate sediment across its surface that varies in depth/cover at relatively small scales (e.g. 100s of metres separating adjacent meadow sites (Kobryn et al., 2013)).

Data collection and design

Sediment loads, macroalgal community composition and canopy structure was described across 12 sites split into three distinct seascape positions: back reef, lagoon and nearshore (Fig. 1). Within each site there were eight haphazardly placed replicate five meter transects. Along each transect SCUBA divers recorded the benthos directly below the tape to the nearest 5 cm. Algae were recorded to genus level and sediment was classified as present when it exceeded 25 mm in depth, otherwise benthos was deemed pavement. Epiphytic algal genera were also recorded where both host and epiphyte were noted. Height of canopy forming macroalgae (*Sargassum*, *Sargassopsis*, or *Sirophysalis*) were measured every meter of the transect by manually extending the thallus and measuring thallus length. This provided $n=6$ height

measures per transect. At each meter mark, sediment depth (to the nearest mm) and holdfast density of canopy-forming genera was also measured within a 0.5 x 0.5 m quadrat ($n = 6$). Canopy forming macroalgae were separated into two life-history stages; recruit and adult. The number of stipes within a holdfast are thought to indicate age of the thallus, with new recruits having just one stipe, and adults that survive into future years adding a new major stipe each growing season (year), although this has not been investigated thoroughly (Kim *et al.*, 2018). Accordingly, recruits were classified as thalli that had only one stipe and stipe height less than 5 cm (Marks *et al.* 2018). Stipe counts per holdfast were also recorded but only within the first quadrat.

Herbivory by fishes is expected to have little effect on biomass fluctuations of macroalgae within the Ningaloo lagoon (Vergés *et al.*, 2011), however the influence of herbivorous urchins on macroalgae in the lagoon is equivocal. Hence, abundance of the grazing urchin, *Tripneustes gratilla*, was recorded within the same 0.5 x 0.5 m quadrats used to estimate macroalgal holdfast density. This urchin species has previously been recorded at Ningaloo, though in low numbers (Fromont *et al.*, 2009), and is known to have had an influence on macroalgal assemblages on reefs in other parts of the world (Valentine and Edgar, 2010). Other urchin species were also recorded, but were not included in analysis because they are drift feeders, whereas *T. gratilla* is a foraging benthic grazer, known to feed on canopy forming macroalgae (Campbell *et al.*, 1973; Hart and Chia, 1990)

To assess sediment tolerance amongst common algal genera we measured sediment depth at the base of the holdfasts of seven of the most abundant genera at four study sites (Asterix labelled sites in Fig. 1.). Sediment depth at the base of canopy forming recruits was also recorded, although recruits were not classified to genera due to difficulties in identifying canopy forming macroalgae at this life history stage in the field. At each of the four sites used to assess sediment tolerance, divers swum in a non-overlapping pattern across the patch, recording sediment depth at the base of holdfasts during a 45-minute dive. Height of canopy forming genera was also measured at the time and correlations with depth were calculated to explore if sediment depth has links to algal size. All observations were separated by at least 2 metres, with a minimum of 10 observations per genera per site. We calculated average sediment depth based on transects carried out in the larger 12-site study already mentioned by averaging across transects at each of the four sites. We also calculated the global sediment depth mean by averaging sediment depth across all four sites.

Statistical analyses

Permutational analysis of variance (PERMANOVA) was used for assessing spatial differences in sediment cover and depth, the analysis was based on Euclidean distance resemblance measures. Seascapes (back reef, lagoon and nearshore) was a fixed factor, with site a random factor nested in seascapes. 9999 permutations were used for all analyses in this study and sum of squares type III (partial) was used. The same analysis was used for assessing spatial differences in *T. gratilla*. Prior to analysis, shade plots and histograms were used to visualise and identify the best transformation to improve homogeneity of variances and reduce the skew of variables. Sediment percent cover and depth were

accordingly transformed using a $\text{Log}_{10}(x + 1)$ and both variables were normalised to account for differing units.

Spatial variation in macroalgae community composition and physical structure was analysed using permutations analysis of covariance (PERMANCOVA). Fixed and random factors in the PERMANCOVA were the same as the PERMANOVA above, and abundance estimates of the grazing urchin *T. gratilla* (Linnaeus, 1758) and sediment load were covariates. Data was “fit” using type I sum of squares type (sequential model fit). Macroalgal community composition was based on the relative abundance of genera in terms of benthic cover. Genera that were only present once across all transects were removed from analyses as they were deemed rare and likely to skew results, (e.g. *Turbinaria*). Epiphytic algae were pooled together into their own group. All community data was analysed on a fourth root transformation to down-weight the importance of abundance relative to changes in presence/absence among sample pairs. Resemblance matrices were constructed using a Bray-Curtis measure of similarity.

Canopy structure was measured as: canopy height, density of recruits/adults (no. of holdfast 0.25 m^{-2}) and stipe counts. Stipe counts were arranged into four groups based on stipe number per quadrat: 1–2, 3–4, 5–6 and > 6. These stipe groups were expressed as average numbers per transect for each site. All canopy structure data was transformed using a square root function and normalised to account for differing units. Permutational analysis of covariance (PERMANCOVA) was used with the Modified Gower base 2 measure (with a dummy variable to account for double-zeros across some sample pairs) with *T. gratilla* and sediment load as covariates. Factors were the same as previous PERMANCOVA.

Distance-based multivariate linear models (DistLM) and best-subsets model selection were used to determine which variables best explain spatial variation of macroalgae community and canopy structure. Sediment load (comprising the two elements; sediment depth and percent cover), *T. gratilla* density, and seascapes position (coded binary for each level) were the predictor variables considered in the models. Sediment was $\text{Log}_{10}(x + 1)$ transformed and macroalgae community composition was assembled into a Bray-Curtis resemblance matrix whilst canopy structure using Modified Gower (base 2) transformation. Models were compared using Akaike Information Criterion corrected for a small sample size (AICc) and best models were those within two AICc of units of the smallest AICc value. We used best subsets model selection as it considers all possible combinations of the predictors including an indicator set for sediment which included depth and cover. AICc weights were calculated for each model and the relative importance of a predictor variable was assessed by summing weights of all models in which that variable occurred (Burnham and Anderson, 2004). Multidimensional space distance-based redundancy analysis was used to visualise model results. Only variables with Pearson’s correlation > 0.3 were considered in ordination outputs. All multivariate analyses were performed in PRIMER-e (version 7.0.13) with PERMANOVA + (Anderson, Gorley and Clarke, 2008).

Results

Both percent cover and depth of sediment varied significantly across sites ($P < 0.001$, pseudo-F = 3.13, df = 9), with low sediment occurring on back reef sites MD20 and MD17, and relatively high sediment loads at MD06, a nearshore site. There was, however, no significant effect of seascape position overall ($P > 0.05$, Pseudo-F = 1.1449, df = 2) and sites with high sediment cover also tended to have deeper sediment depths ($r^2 = 0.5$, Fig. 2a). Urchin density varied significantly across sites ($P < 0.001$, pseudo-F = 4.7498, df = 9) ranging 0–17 per 0.25m^{-2} with high mean values (> 0.45 per 0.25m^{-2}) at two back reef sites and a single site in the lagoon and nearshore (Fig. 2b).

Both sediment cover/depth and density of *T. gratilla* had a significant influence on the composition of the macroalgal community, and the extent of this influence varied with seascape position (Table 1a). Sediment cover was high at lagoon sites where prominent genera were *Hormophysa*, *Sirophysalis*, *Sargassopsis* and *Caulerpa* (Fig. 3a,b and Supplementary Fig. 1 for detailed species, site, seascape-specifics). Conversely, density of *T. gratilla* was typically high on back reef sites where sediment cover was lower and *Asparagopsis* and *Laurencia* were characteristic of sites (Fig. 3). *Lobophora* and macroalgae with epiphytes were common on sites nearer to the shore which had fewer urchins and sediment depth was low. Each of the predictor variables (sediment cover, seascape position and urchin density) played a similar role in explaining spatial differences in community composition, and when combined these variables accounted for ~ 32% of the spatial variation in macroalgal community composition (Table 2a, Fig. 3c).

Canopy structure (height, density and stipe counts) varied significantly with *T. gratilla* density, sediment load and among sites (Table 1b, Supplementary Fig. 2 and Table 1). The cover of canopy forming macroalgae, canopy height and density of adult thalli were positively correlated with deeper sediments, whilst abundance of thalli with high stipe counts was associated with greater sediment cover (Fig. 3d,e). The canopy cover, height and density of adult thalli was also greater at sites where the density of *T. gratilla* was low (Fig. 3d, Supplementary Fig. 2 and Table 1). Low stipe counts were typically found at sites with more urchins and low sediment cover/depth. The best model for explaining spatial variation in canopy structure included both sediment and urchin variables ($r^2 = 0.13$, Table 2b). Summed model weights suggesting these two variables had more of an influence on canopy structure than seascape position (Fig. 3f).

Among the four survey sites that were used to investigate sediment tolerance (Asterix labelled sites in Fig. 1), the global mean sediment depth was 2.1 cm (Fig. 4). Sediment depths at the base of *Sargassum* had the greatest range whilst *Lobophora*, recruits and *Padina* were found only at sediment depths < 1.5 cm. *Sirophysalis*, *Sargassopsis*, *Hormophysa* and *Caulerpa* were surrounded by sediment depths of ~ 3 cm.

Individuals of canopy forming genera were taller in sites with greater sediment depth (*Sargassum* $P < 0.01$, *Sirophysalis* $P < 0.05$ and *Sargassopsis* $P < 0.01$, Fig. 5). However, sediment depth explained less than 10% of the variance in thallus height for all three canopy forming genera in the larger-scale study already mentioned.

Table 1

Summary of PERMANCOVA comparing macroalgal (a) community composition and (b) canopy structure in summer 2019 at 12 sites in the southern Ningaloo lagoon. Significant terms P < 0.05 are denoted with *.

(a) Macroalgal community composition			
Source	df	pseudo-F	P-value
Sediment	1	4.87	< 0.001*
<i>T. gratilla</i>	1	5.03	< 0.001*
Seascape	2	2.21	0.076
Site (seascape)	9	8.39	< 0.001*
<i>T. gratilla</i> x seascape	2	3.50	< 0.001*
Sediment x <i>T. gratilla</i>	1	0.32	0.840
Sediment x Seascape	2	2.38	0.012*
<i>T. gratilla</i> x Seascape	2	4.51	< 0.001*
Sediment x <i>T. gratilla</i> x Seascape	2	1.84	0.074
Residual	875		
Total	95		
(b) Macroalgal canopy structure			
Source	df	pseudo-F	P-value
Sediment	1	2.76	0.010*
<i>T. gratilla</i>	1	3.66	0.002*
Seascape	2	0.72	0.817
Site (Seascape)	9	4.46	< 0.001*
<i>T. gratilla</i> x Seascape	2	0.76	0.696
Sediment x Seascape	2	1.09	0.360
Sediment x <i>T. gratilla</i>	1	1.37	0.208
Sediment x <i>T. gratilla</i> x Sediment	2	0.67	0.765
Residual	875		
Total	95		

Table 2
Summary of the top models for distance-based
multivariate linear models

(a) Macroalgae community composition			
ΔAICc	AICc Weights	r²	Selections
0.00	0.81	0.32	All
4.10	0.10	0.25	Seascape x <i>T. gratilla</i>
4.76	0.08	0.26	Seascape x sediment
8.52	0.01	0.20	Seascape
12.77	0.001	0.18	Sediment x <i>T. gratilla</i>
18.28	8.67E-05	0.11	Sediment
(b) Macroalgal canopy structure			
ΔAICc	AICc Weights	r²	Selections
0.00	0.40	0.13	Sediment x <i>T. gratilla</i>
0.54	0.31	0.16	All
2.49	0.12	0.10	Seascape x <i>T. gratilla</i>
3.03	0.09	0.06	<i>T. gratilla</i>
3.26	0.08	0.07	Sediment

Discussion

Spatial variation in benthic sediment loads can have a significant influence on community composition and physical structure of tropical macroalgal communities. We found that some macroalgal genera are more abundant in areas with higher sediment loads, whilst others are typically found at sites with relatively lower loads. Moreover, our results suggest some genera are better suited to high sedimented conditions. This relationship is however inconsistent among genera within the Fucales order, implying taxonomic traits of an order are not the only factor that influences macroalgal distribution with sediments. The grazing urchin *T. gratilla* may also have a negative influence on macroalgal structure; canopy height, cover and holdfast densities being low at sites where the density of urchins is high. Collectively, these results suggest a combination of environmental conditions and grazing from herbivores can shape both community composition and canopy structure of tropical macroalgal forests.

Differences in sediment associations among macroalgal genera

Our findings suggest that genera, rather than order-specific morphological traits, are important for understanding varying levels of sediment tolerance among macroalgae at Ningaloo. *Sargassum* for example, is a genus that tends to dominate stands of macroalgal forest in many tropical and temperate coastal regions of the world (Praiboon et al., 2018; Fulton et al. 2019). Morphologically, they are extremely plastic (Cheang, Chu and Jr, 2008; Endo et al., 2013), having a flexible, strong thallus and with a range of adult growth forms, that gives them a potential advantage over other macroalgae for accessing light (Kilar, Littler and Littler, 1989; Steneck and Dethier, 1994). *Sargassum* holdfasts and stipes are also perennial, typically remaining intact when the primary fronds seasonally detach, the new thallus regrows from the original holdfast or shortened stipes. This is likely to give *Sargassum* a competitive advantage at sites with high sediment loading that accumulates at the base of holdfasts. Even without a thallus attached, stipes are raised above the sediment layer and are viable even when buried for short periods (Hymanson et al., 1990; Vuki and Price, 1994; Endo et al., 2013), whilst shorter recruits may be completely buried compromising their survival (Kawamata et al., 2012). This is likely why we saw a high number of stipes on *Sargassum* individuals at sites with high sand cover and depth and very lower numbers of recruits. Other genera such as *Hormophysa*, *Sargassopsis*, *Caulerpa* and *Sirophysalis* were however, only found in sediments > 3 cm deep, indicating they are psammophilic (sand-loving). Apart from *Caulerpa*, all of these genera grow thick, strong and robust thalli that reach heights of 0.5–1 m (Steneck and Dethier, 1994). *Caulerpa* however uses stoloniferous growth, a type of clonal architecture that requires deeper sediment to ‘anchor’ into and allows the thallus to push out from the sediment (Zubia et al., 2019). At the sediment-intolerant end of the spectrum *Lobophora* and *Padina* are small understory genera with soft corticated foliose thalli (Steneck and Dethier, 1994). We only found these genera at sites with less than 0.5 cm average sediment depth, suggesting they are easily buried at greater sediment loads. Their holdfasts are also exceptionally small compared to the psammophilic genera, and they have opportunistic traits such as being epiphytes which grow upon other species well above the sediment (Clayton, 1990; Steneck and Dethier, 1994).

We also found that canopy forming recruits and thalli with lower numbers of stipes (younger i.e. smaller individuals) were typically on areas of bare pavement or low sediment cover. Excess sediment can prevent settlement of macroalgal zygotes and those that do settle are easily smothered (Umar, McCook and Price, 1998). These effects may be greater when sediment particles are small (< 100 µm) (Gao et al., 2019), such that even thin layers of sediment within the calm lagoonal area of Coral Bay are likely to be detrimental to juvenile stages of algal development (Devinny and Volse, 1978; Schiel et al., 2006).

Interestingly, we found that the height of three canopy-formers *Sargassopsis*, *Sirophysalis* and *Sargassum* all correlated positively with sediment depth. Taller individuals tend to accumulate greater biomass, reducing water motion around the thick canopy (Stevens, Hurd and Isachsen, 2003; Pujol et al., 2019), which would allow suspended sediments to settle at holdfast bases (Shashar et al., 1996; Stimson

and Larned, 2000). However, high sediment loads around holdfasts may also be the result of environmental filtering, where some genera are better adapted to high sediment conditions (Daly and Mathieson, 1977). Deep sand may even drive individuals to keep above the sand so they can continue photosynthesising at full capacity, therefore increasing their height if sediment becomes deeper (Eriksson and Johansson, 2005).

Top-down effects of herbivorous urchins on macroalgal communities

Though the abundance of urchins was low at many of our sites, where present they had an effect on macroalgal composition and structure, suggesting top-down effects on tropical macroalgal communities are possible at Ningaloo. This is consistent with previous studies that have found urchin grazing to have significant impacts on benthic community diversity (Ling *et al.*, 2015; Kriegisch *et al.*, 2019) and that outbreaks of *T. gratilla* can cause local declines in foliose red and brown algae (Valentine and Edgar, 2010). The influence of urchins is however moderated by environmental conditions, which differed among the three seascapes positions in the Ningaloo lagoon. Relatively high densities of urchins were found at the back reef sites, which also had the lowest sediment loads. Many urchins avoid sediment-laden sites (Kawamata *et al.*, 2011; Sangil *et al.*, 2018) and our results suggest that sites where sediments are likely to accumulate may be refugia from herbivorous urchins.

Conclusions

Tropical macroalgal forests are an integral component of many seascapes, providing food, shelter and breeding grounds for a huge variety of marine life (Fulton *et al.*, 2019). Community dynamics within these forests therefore have flow on effects for the macroalgal associated fish and invertebrates (Fulton *et al.*, 2020). Here, we found a combination of environmental and biotic interactions to be influencing macroalgal community structure and composition at the local scale. There were distinct differences in macroalgal associations with sediment among genera, suggesting that sediment depth and cover could be a useful predictor of variation in macroalgae assemblage structure and composition. Interactions between sediment load, and herbivorous urchin abundance were also mediated by seascapes position.

Positioning of macroalgal patches within the seascapes clearly influences diversity and abundance of fish assemblages (van Lier *et al.*, 2018; Sievers *et al.*, 2020), although preference for specific macroalga genera (Lim *et al.*, 2016; Wenger, Lier and Fulton, 2018) or physical structures (Wilson *et al.*, 2017; Fulton *et al.*, 2020; Tang, Graba-Landry and Hoey, 2020) by some fish will also effect the composition of macroalgal associated fish assemblages. Macroalgal composition and structure is especially important for the many fish that recruit to macroalgal habitats, including taxa that are targeted by fisheries as adults and/or perform important ecologically roles (Wilson *et al.*, 2010; Evans *et al.*, 2014; Tano *et al.*, 2016). Moreover, standing biomass, productivity and phenology differ among macroalgae, the seasonal detachment of highly productive genera such as *Sargassum* resulting in transport of organic matter to other habitats, (Fulton *et al.*, 2014, 2019; Sissini *et al.*, 2017), whilst calcareous genera (e.g. *Halimeda*)

can make substantial contributions to local carbonate budgets (Rees *et al.*, 2007). Changes to the composition and physical structure of tropical macroalgal communities may therefore have important consequences for the ecological functions and services that they provide. Our findings suggest that both shifts in sediment loads and outbreaks of herbivorous urchins may alter macroalgal assemblages, although these potential drivers of change do not operate in isolation. Indeed considering interactions between sediment and urchin distributions and how this differs within the seascape is essential for understanding community dynamics of tropical macroalgae.

Declarations

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Conflict of interest/Competing interests

The authors have no conflict of interest to declare.

Availability of data and material

Raw data in this manuscript is stored in the public DRYAD database.

Code availability

Available upon request

Author's contributions

Rosalie Harris, Chris Fulton and Shaun Wilson conceived the ideas and designed methodology; all authors collected the data; Rosalie Harris and Chris Fulton analysed the data and also led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Figures

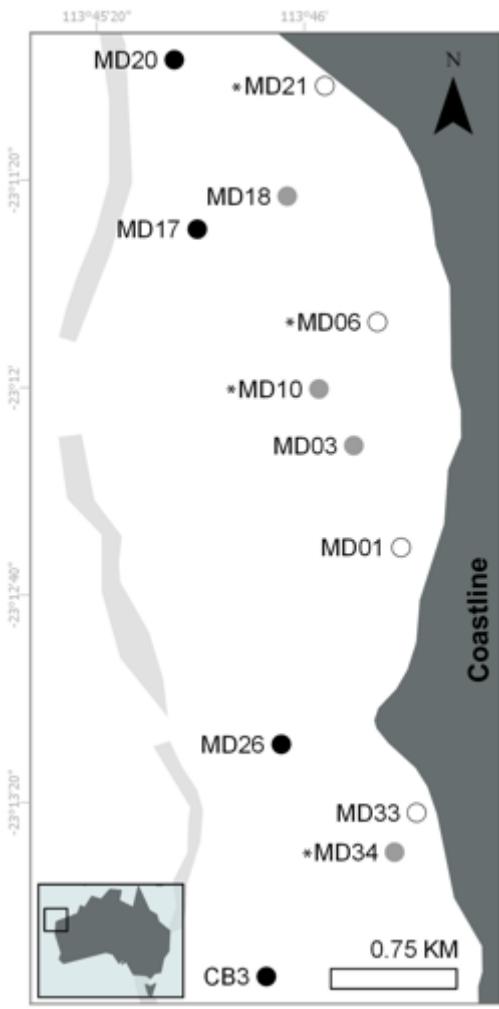


Figure 1

Location of 12 study sites within the southern region of Ningaloo Reef, Western Australia. Colour of dot indicates seascape position: back reef (black), lagoon (grey) and nearshore (white). Asterix denotes the four sites used to assess sediment tolerances among prominent macroalgae. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

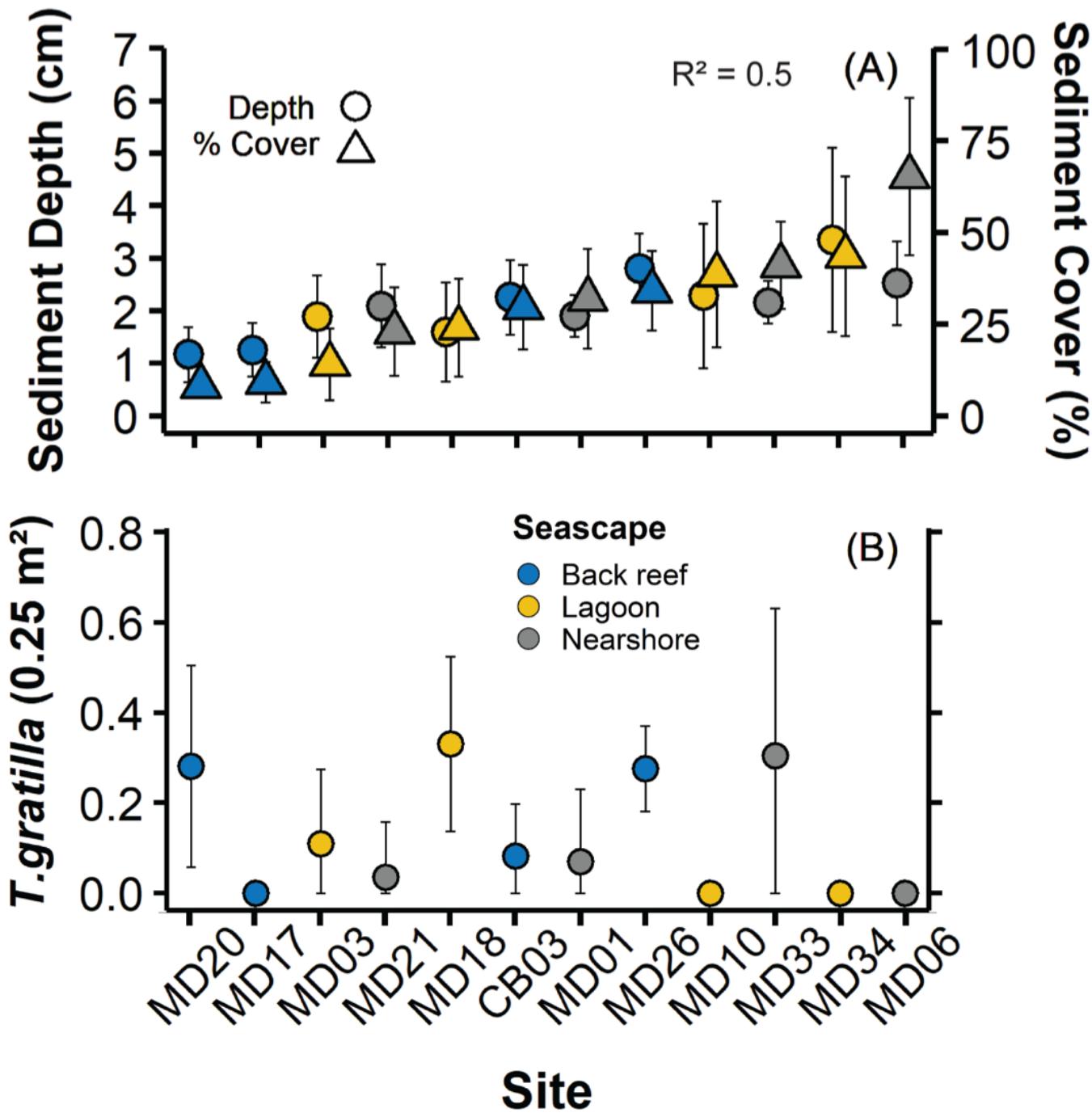
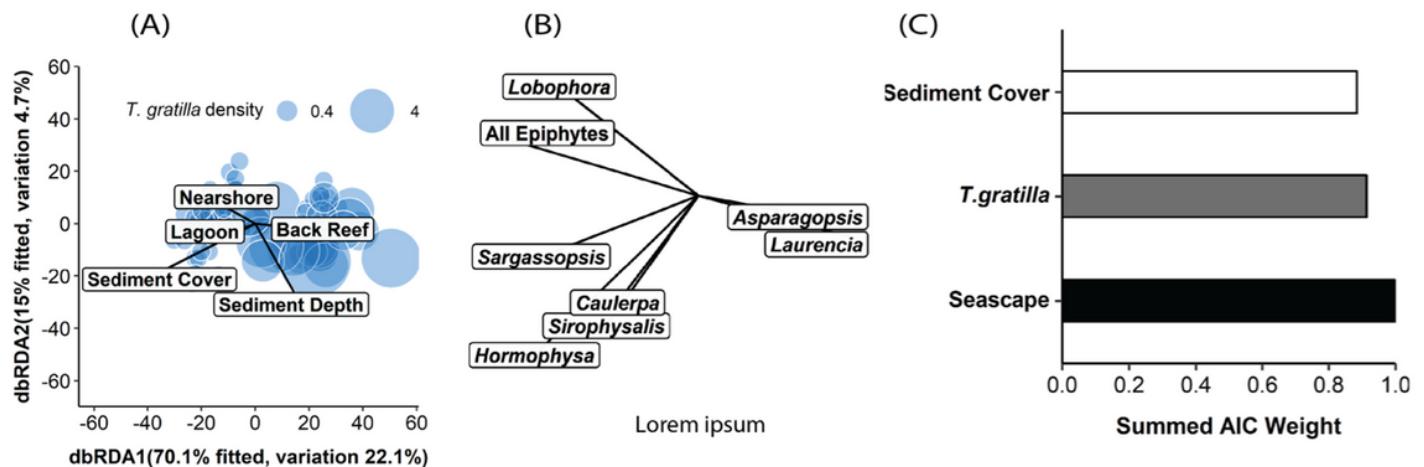


Figure 2

Gradients in sediment depth and sediment cover (A) and density of *Tripneustes gratilla* (B) across 12 sites at Ningaloo. Colour indicates seascape position: back reef (blue), lagoon (yellow) and nearshore (grey). Values are means \pm 95 % confidence interval, n = 8.

Community Composition



Canopy Structure

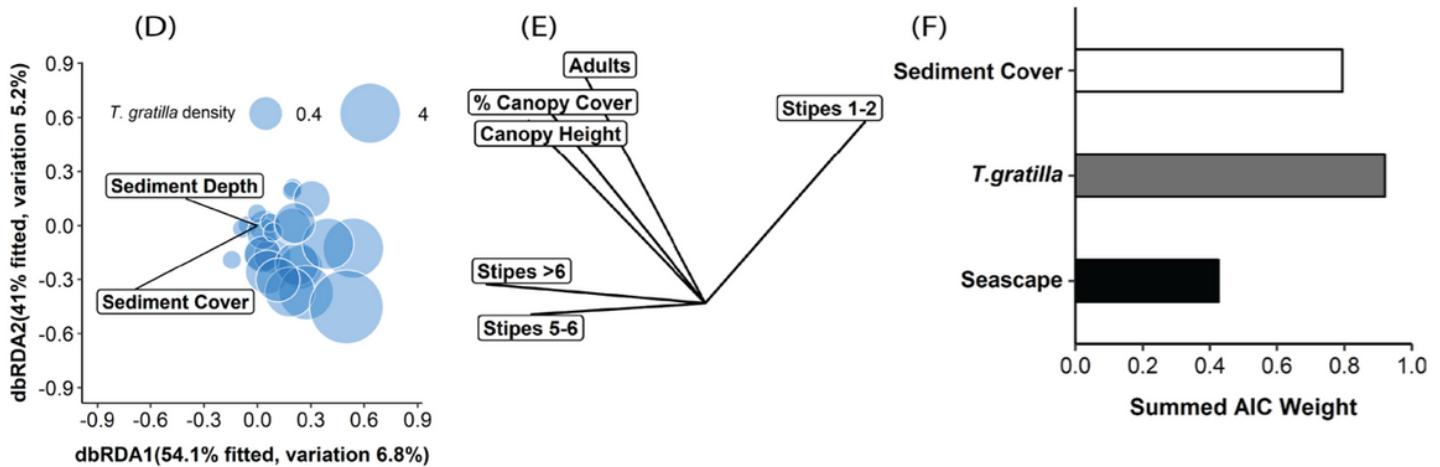


Figure 3

Composition and canopy structure of macroalgal communities at Ningaloo with respect to urchin density and best predictors from DistLM (A, D). Macroalgal genera (B) and components of the canopy structure (E) that differentiate sites are shown as vectors. Summed AIC weights provide an indication of how important each predictor from DistLM is for explaining spatial variation in community composition (C) and canopy structure (F). Bubbles represent urchin density. Only sediment cover presented in AIC weights because sediment depth and cover were tightly correlated ($r^2 = 0.5$).

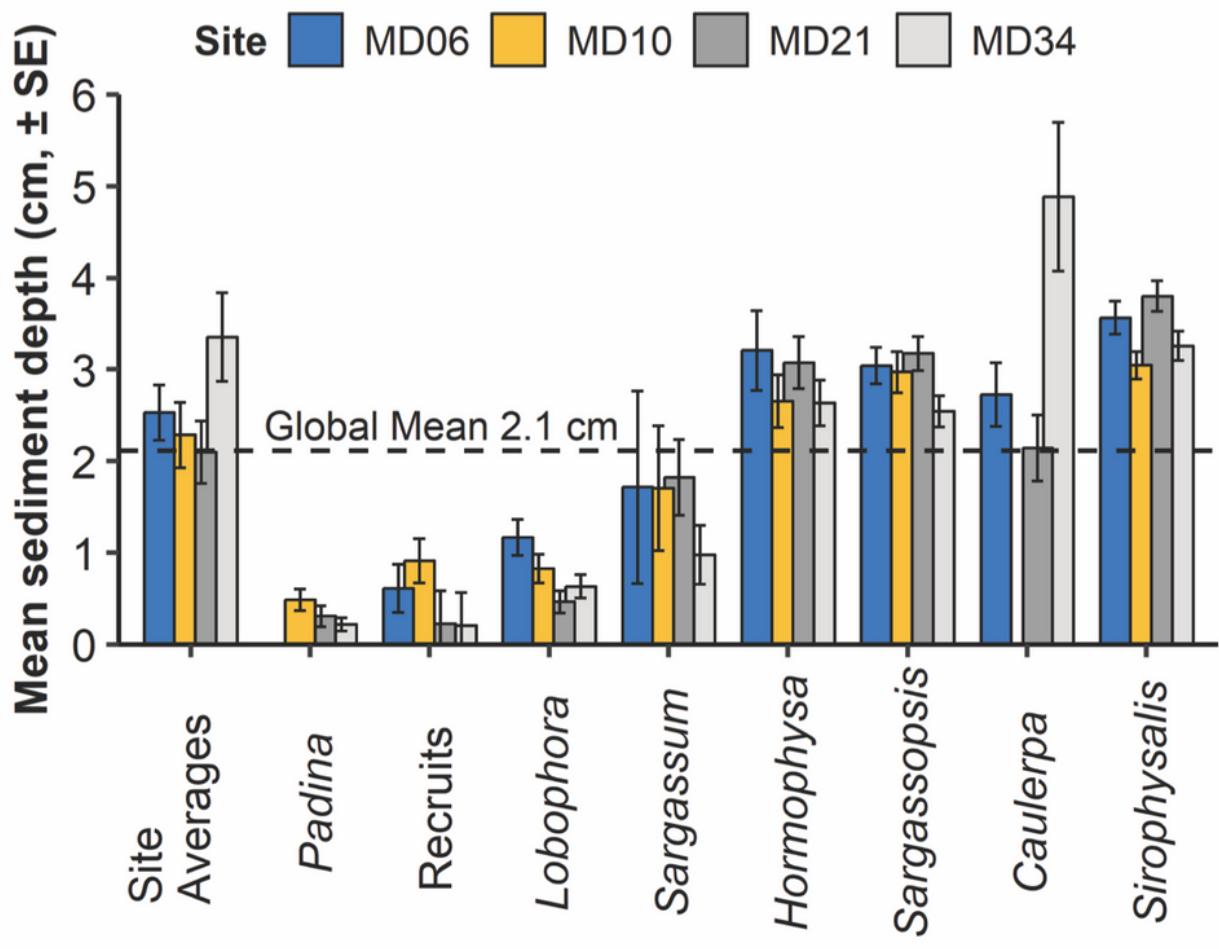


Figure 4

Sediment depth at base of holdfasts of dominant genera (including canopy-forming recruits) across four sites at Ningaloo. Total observations per site = 208 at MD06, 263 at MD10, 253 at MD21 and 281 at MD34. Minimum observations per genus per site was $n = 10$. Except for Caulerpa and Padina which were not detected at MD06 and MD10

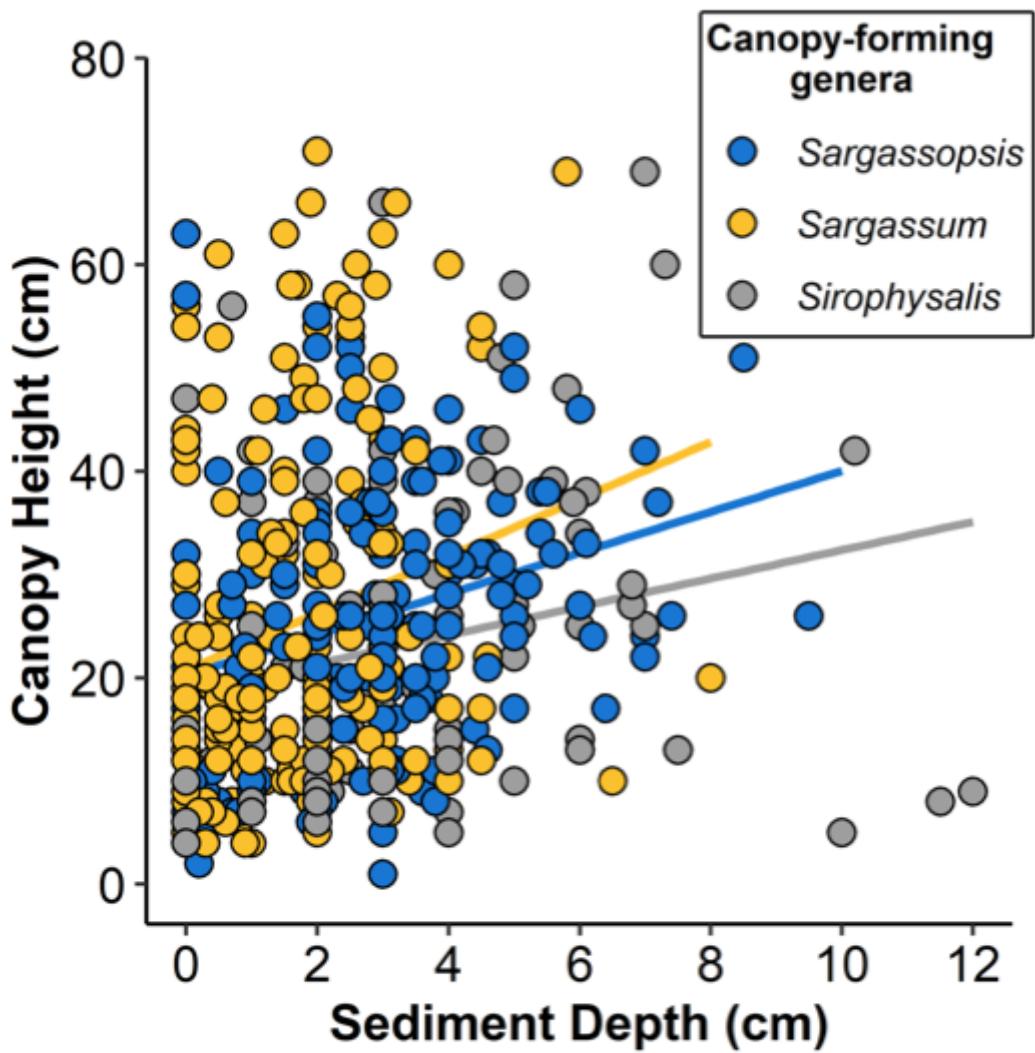


Figure 5

Height of canopy-forming species by sediment depth at the base of individual holdfasts, all samples pooled across four sites (MD06, MD10, MD21 and MD34) at Ningaloo. Sargassum: Pearson's $r = 0.23$, $df = 188$, $P < 0.01$, Sargassopsis: Pearson's $r = 0.29$, $df = 160$, $P < 0.001$, Sirophysalis: Pearson's $r = 0.24$, $df = 105$, $P < 0.05$.

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