Interactive effects of sediments and urchins on the composition and structure of tropical macroalgal assemblages

Rosalie J. Harris1 · Shaun K. Wilson2,3 · Christopher J. Fulton1

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Abstract
Macroalgal-dominated reefs 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 require 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 urchin Tripneustes gratilla 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 cover and depth and that sediments, urchin abundance, and seascape position explained 32% of the spatial variation in macroalgal community composition with 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 were also greater where sediments 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 assemblages. Changes to macroalgal 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-dominated habitats provide.

Introduction

Tropical macroalgal assemblages 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-dominated reefs can cover extensive areas of shallow-water at similar scales to coral reefs (Kobryn et al. 2013; Suchley et al. 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 composition and structure of macroalgal assemblages are also important for the many fish that recruit to macroalgal habitats, including taxa that are targeted by fisheries as adults and/or perform important ecological roles (Wilson et al. 2010; Evans et al. 2014; Tano et al. 2016).

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 tropical macroalgae have mostly 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 the community dynamics of macroalgal reefs.
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; Götznerberger et al. 2012). Marine sediments in the tropics are typically formed from a combination of terrestrial and marine-derived material (e.g., coral fragments, CCA and other biogenic carbonates) (Tebbett et al. 2017). In a few cases, 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 et al. 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; Johansson et al. 2010; Cuttler et al. 2018). These fishes produce substantial volumes of sand through their excrement which is then moved across the seascape through wave action, currents and disturbances like cyclones (Ong and Holland 2010; Cuttler et al. 2015; Pomeroy et al. 2018). The suspended particles are carried by hydrodynamic forces; particle size, shape, density, mineral and chemical composition, determine how far they will travel (Airoldi 1998; Purcell 2000). The highly dynamic nature of sediment can mean deposition can fluctuate hourly to yearly on a substrate. These mobile sediments may bury, shade or abrade benthic primary producers, influencing benthic community dynamics within seascapes (Tebbett et al. 2018).

Although algal turfs and sediments in the tropics have been well studied (Tebbett et al. 2018; Hayes et al. 2021), interactions between macroalgae and sediments have received less attention on tropical reefs than on temperate reefs (Airoldi 2003), particularly when considering how sediments influence community composition and physical structure of canopy-forming species (Singhal and Juan 2020). 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 et al. 1998; Gao et al. 2019). Sediment cover is also important, particularly at the time of algal recruitment in non-calcifying algae, as even a small cover of sand can inhibit attachment of macroalgal zygotes (Devinney 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 et al. 2018). Similarly, sedimentation reduces herbivore pressure by urchins because they tend to avoid sandy surfaces (Kriegisch et al. 2019). The addition of particulate organic matter associated with fine sediments may also increase nitrogen and phosphorous availability, improving algal growth rates in some species more than others which can have bottom-up community-scale effects (Schaffelke 1999).

How macroalgae respond to sediment will partially depend on their morphological traits (Littler and Littler 1980; Clayton 1990). Some species have the ability to grow quickly and reproduce vegetatively if damaged by sediment; morphological and reproductive traits that make them psammothropic (sand-loving) (Daly and Mathieson 1977). In the tropics, many canopy-forming macroalgae (e.g. Sargassum spp.) have been described as ‘biotically competent’, as they are well adapted to compete for light, long-lived and tend to have thick, robust thalli (Vermeij 1978). Other species, such as a number of genera in the Dictyotales (e.g. Padina, Dictyota and Dictyopteris), which possess a diverse range of understory species, may be considered stress-tolerant and opportunistic, as they tend to be fast-growing, occur across a wide range of depths, have a fairly simple construction and a short lifespan (Daly and Mathieson 1977; Clayton 1990; Teixeira et al. 2006).

Another major determinant of community dynamics of macroalgal assemblages is herbivory, which is often associated with fishes (Kriegisch et al. 2019). However, herbivorous urchins can have a stronger effect on macroalgal communities than fish and are well-known structuring agents of coral and temperate reefs associated with canopy-forming algal communities (Poore et al. 2012). 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; Ling et al. 2015). Urchins may also prevent macroalgal overgrowth on tropical reefs, especially when fish stocks have been depleted (Ogden et al. 1973; Foster 1987; Hughes 1994). Sea urchin grazing rates are, however, sensitive to sediment (Kriegisch et al. 2019; Traiger 2019), although how sea urchin and sediment presence interact to affect the composition and physical structure of tropical macroalgal assemblages is less frequently examined, with examples mostly limited to studies on the Caribbean and Kenyan reefs (Carpenter 1986; McClanahan et al. 1996).

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 cover and depth 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 cover and depth have on this relationship?

Materials and methods

Study site and 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 urban devel-
opment and industrial agriculture that can contribute to
nutrient and sediment run-off into the marine environment
(Summer et al. 2002; Cassata and Collins 2008; Kroon et al.
2014). Moreover, the Ningaloo coast is an arid landscape
with no major river systems, such that there are low to nil
fluvial inputs of terrestrially derived sediment and nutrients
(Johansson et al. 2010; Wilson et al. 2019). Benthic habi-
tats within the lagoon, between the fringing coral reef and
shore, are characterised by a mosaic of macroalgal and sand
patches (Cassata and Collins 2008; Fulton et al. 2019), mac-
roalgal patches often dominated by canopy-forming genera
such as Sargassum (Fulton et al. 2014).

In the Austral summer 2019, benthic composition and
fine-scale sediment measurements were undertaken south
of Coral Bay, Ningaloo Reef, Western Australia across a
subset of habitats: backreef to near the shore (23°08′25.2″ S
113°46′12.2″ E, Fig. 1). In this region of Ningaloo, the aver-
age 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
veen of carbonate sediment across its surface that varies
in depth/cover at relatively small scales e.g. 100 s of metres
separating adjacent meadow sites (Collins et al. 2003; Kob-
ryn et al. 2013). Macroalgal patches are distributed across
reef zones with the highest abundance found at the shallow-
est regions of the lagoon (Johansson et al. 2010, see Fig. 2
in this paper on macroalgal distribution across reef zones
and where it is highest).

Data collection and design

Sediment, macroalgal community composition, and canopy
structure were described across 12 sites split into three dis-
tinct seascape positions: back reef, lagoon, and nearshore
(Fig. 1). Seascape positions were chosen based on previous
studies that show prolific canopy-forming patches across
the Ningaloo lagoonal system (van Lier et al. 2018; Ful-
ton et al. 2019). Within each site, eight 5 m line-intercept
transects were haphazardly placed. To measure macroalgal
composition, SCUBA divers recorded the percent cover
of different benthic categories directly below the tape to
the nearest 5 cm tape marking. These benthic categories
included: macroalgae (both canopy and understory genera),
sediment, pavement, rubble, coral, and sponges. Macroalgae
were recorded to genus level using Huisman (2000), and
sediment cover 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.

To measure macroalgal structure, the height of one can-
opy-forming macroalga (Sargassum, Sargassopsis, or Siro-
physalis) was measured at every metre along the transect, by
manually extending the thallus and measuring thallus length
using a ruler (n = 6 per transect). If the meter mark did not
have macroalgae, divers chose the next nearest plant within half a meter, and if no macroalgae were within this area, height was not recorded. We measured the holdfast density of canopy-forming macroalgae which were separated into two life-history stages: recruit and adult measured within a 0.5 × 0.5 m quadrat (n = 6). The diameter and growth rings within a holdfast are thought to indicate the age of the thallus, with new recruits having just one short stipe, although this has not been investigated thoroughly across a range of species (Murase and Kito 1998; Endo et al. 2013). Accordingly, we classified recruits as thalli that had only one stipe and stipe height less than 5 cm (Yoshida et al. 2004; Marks et al. 2018). Stipe counts per holdfast were also recorded but only within the first quadrat. At every meter mark, one measurement of sediment depth (to the nearest mm using a ruler) was also recorded.

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 unresolved. Hence, the abundance of the grazing urchin, Tripneustes gratilla, was recorded within the same 0.5 × 0.5 m quadrats in the methods above. Tripneustes gratilla on the other hand is an actively foraging benthic grazer, known to feed on canopy-forming macroalgae (Campbell et al. 1973; Russo 1980; Hart and Chia 1990).

In a separate survey, we assessed sediment tolerance amongst common algal genera. Four sites which covered a range of sediment levels based on the sediment data collected in the 12-site study were used (asterisk labelled sites in Fig. 1.). We measured sediment depth at the base of the holdfasts of seven of the most abundant genera at the four study sites. 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, divers swam in a non-overlapping pattern across the patch, recording sediment depth at the base of holdfasts during a 45-min 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 m, with a minimum of 10 observations per genera per site. We calculated the global sediment depth mean by averaging sediment depth across all four sites, including data associated with sediment at the base of holdfasts. Comparison of sediment depths about macroalgal bases with global means then gave an indication of where sediment was abnormally high and low.

Statistical analyses

Permutational analysis of variance (PERMANOVA) was used for assessing spatial differences in sediment (comprising the two elements; sediment depth and percent cover grouped using the indicator function in PRIMER-e), the analysis was based on Euclidean distance resemblance measures. Seascape (back reef, lagoon and nearshore) was a fixed factor, with site a random factor nested in a seascape with 9999 permutations 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 Tripneustes gratilla. Prior to analysis, shade plots and histograms were used to visualise data. Sediment percent cover and depth were accordingly transformed using a Log10 (x + 1) to reduce the effect of extreme values and both variables were normalised to account for differing units.

Spatial variation in macroalgal 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* and sediment 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 absolute 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 quadrant: 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 *Tripneustes gratilla* and sediment as covariates. Factors were the same as previous PERMANCOVA. Multivariate dispersion was examined using PERMDISP and although there was significant dispersion (Supp. Table 2), our balanced design is likely to be robust to such heterogeneity of multivariate dispersions (Anderson and Walsh 2013).

Distance-based multivariate linear models (DistLM) and best-subsets model selection were used to determine which variables best explain spatial variation of macroalgal community and canopy structure. Sediment (comprising the two elements; sediment depth and percent cover grouped using the indicator function in PRIMER-e), *T. gratilla* density, and seascape position (coded binary for each level, i.e. dummy independent variable) were the predictor variables considered in the models. Sediment was log$_{10}$$(x+1)$ transformed and macroalgal 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 et al. 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 cover and depth 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 0.25 m$^{-2}$ with mean values surpassing (> 0.45 0.25 m$^{-2}$) at two back reef sites MD20 and MD26 and a single site in the lagoon MD18 and nearshore MD33 (Fig. 2b). There was, however, no significant effect of seascape position overall ($P > 0.05$, Pseudo-$F = 1.1449$, $df = 2$).

Interaction between sediment and urchin factors 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 Supp. Figure 1 for detailed species, site, seascape-specifics). Conversely, the 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 cover and depth and among sites (Table 1b, Supp 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 the 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, Supp. Fig. 2a).
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 suggested 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, 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, Hymophsysa* 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.

### Discussion

Spatial variation in benthic sediment cover and depth can have a significant influence on the community composition and physical structure of tropical macroalgal communities (López et al. 2017; Fong et al. 2020). Our study found that some macroalgal genera are more abundant in areas with higher sediment cover and depth, whilst others are typically found at sites with relatively lower sediment. With a high degree of sediment mobility across the lagoon, some macroalgae genera are thus subject to frequent abrasion and burial (Pomeroy et al. 2018; Cuttler et al. 2019). Our results suggest some macroalgal genera are more tolerant to elevated sedimented conditions than others and have traits that allow them to survive inundation of sediments, such as leathery thalli, tough stipes and rhizopitic growth (Steneck and Dethier 1994; Zubia et al. 2019). 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 may shape both community composition and canopy structure of tropical macroalgal dominated assemblages.

### Differences in sediment associations among macroalgal genera

Our findings suggest that genera-specific morphology is important for understanding varying levels of sediment tolerance among macroalgae at Ningaloo. *Sargassum*, for example, is a genus that tends to dominate the stands of macroalgae in many tropical and temperate coastal regions of the world (Praboon et al. 2018; Fulton et al. 2019). Morphologically, they are extremely diverse (Cheang et al. 2008; Endo et al. 2013), having flexible, strong thallus and adult growth forms that may differ under environment and disturbance conditions, which gives them a potential advantage over other macroalgae for accessing light (Kilar et al. 1989; Steneck and Dethier 1994; Engelen et al. 2005). The semi-perennial life history of *Sargassum* (perennial base and annual reproductive thalli) may also be a trait that confers higher tolerance to sediment scouring events as the thallus can persist in a “dormant” stage giving *Sargassum* a competitive advantage at sites with highly dynamic sediment loading, whilst shorter recruits may be completely buried compromising their survival (Hymanson et al. 1990; Vuki and Price 1994; Kawamata et al. 2012; Endo et al. 2013). Indeed, our study found high numbers of stipes on *Sargassum* individuals at sites with high sediment cover and depth, but very low numbers

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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

| Source                         | df | Pseudo-F | P-value |
|-------------------------------|----|----------|---------|
| (a) Macroalgal community composition |    |          |         |
| Sediment                      | 1  | 4.87     | <0.001  |
| *T. gratilla*                 | 1  | 5.03     | <0.001  |
| Seascape                      | 2  | 2.21     | 0.076   |
| Site (seascape)               | 9  | 8.39     | <0.001  |
| Sediment × *T. gratilla*      | 1  | 0.32     | 0.840   |
| Sediment × Seascape           | 2  | 2.38     | 0.012   |
| *T. gratilla* × Seascape      | 2  | 4.51     | <0.001  |
| Sediment × *T. gratilla* × Seascape | 2  | 1.84     | 0.074   |
| Residual                      | 75 |          |         |
| Total                         | 95 |          |         |
| (b) Macroalgal canopy structure |    |          |         |
| Sediment                      | 1  | 2.76     | 0.100   |
| *T. gratilla*                 | 1  | 3.66     | 0.002   |
| Seascape                      | 2  | 0.72     | 0.817   |
| Site (Seascape)               | 9  | 4.02     | <0.001  |
| *T. gratilla* × Seascape      | 2  | 0.76     | 0.696   |
| Sediment × Seascape           | 2  | 1.09     | 0.360   |
| Sediment × *T. gratilla*      | 1  | 1.37     | 0.208   |
| Sediment × *T. gratilla* × Sediment | 2  | 0.67     | 0.765   |
| Residual                      | 75 |          |         |
| Total                         | 95 |          |         |

Significant terms $P < 0.05$ are presented in bold text.
Fig. 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 highly correlated ($R^2 = 0.5$).

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

| ΔAICc | AICc weights | $r^2$ | Selections |
|-------|--------------|-------|------------|
| (a) Macroalgae community composition |
| 0.00  | 0.81         | 0.32  | All        |
| 4.10  | 0.10         | 0.25  | Seascape × T. gratilla |
| 4.76  | 0.08         | 0.26  | Seascape × sediment |
| 8.52  | 0.01         | 0.20  | Seascape |
| 12.77 | 0.001        | 0.18  | Sediment × T. gratilla |
| 18.28 | 8.67E−05     | 0.11  | Sediment |
| (b) Macroalgal canopy structure |
| 0.00  | 0.40         | 0.13  | Sediment × T. gratilla |
| 0.54  | 0.31         | 0.16  | All |
| 2.49  | 0.12         | 0.10  | Seascape × T. gratilla |
| 3.03  | 0.09         | 0.06  | T. gratilla |
| 3.26  | 0.08         | 0.07  | Sediment |

Fig. 4 Sediment depth at the 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. Values are means ± SE, minimum observations per genus per site was $n = 10$, except for Caulerpa and Padina which were not detected at MD06. Note that site average values are means ± SE, $n = 8$. 
of recruits. Other genera such as *Hormophysa*, *Sargassopsis*, *Caulerpa* and *Sirophysalis* were only found in sediments > 3 cm deep, indicating they are psammophytic (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’ 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 psammophytic genera, and also display 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. Our findings suggest canopy-forming species cannot recruit successfully in sites of high sediment abrasion, but once individuals have matured, they seem to be able to persist and withstand high sediment loads (Deviny and Volse 1978; Umar et al. 1998; Schiel et al. 2006; Gao et al. 2019).

Interestingly, we found that the height of three canopy-formers *Sargassopsis*, *Sirophysalis* and *Sargassum* all correlated positively with sediment depth, though this was a weak correlation, and experimental work is needed to untangle the effects of sediment depth with canopy height. Taller individuals tend to accumulate greater biomass, reducing water motion around the thick canopy (Stevens et al. 2003; Pujol et al. 2019), which would allow suspended sediments to settle at holdfast bases (Shashar et al. 1996; Stimson and Larned 2000). However, deeper sediments around holdfasts may also be the result of environmental filtering, where some genera are better adapted to high sediment conditions (Daly and Mathieson 1977). Increased sand depth may even drive individuals to increase height to keep above the sand so they can continue photosynthesising at full capacity (Eriksson and Johansson 2005). Variation in exposure to mobile and settled sediments can therefore have a profound influence on macroalgal assemblages. Our findings supporting experimental studies that demonstrate even short-term burial or abrasion to the thallus of less tolerant genera can have a whole community-scale response (Francoeur and Biggs 2006).

**Top-down effects of herbivorous urchins on macroalgal communities**

Though the abundance of urchins was low at many of our sites, where present in high densities, they had an effect on macroalgal composition and structure. This is consistent with previous studies that have found urchin grazing can 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 overall abundance of *T. gratilla* at Ningaloo is, however, low compared to outbreaks at other locations, and previous studies at Ningaloo have found *T. gratilla* in either low abundance or absent (Fromont et al. 2009; Johansson et al. 2010). The influence of urchins in this study is therefore limited to a few sites and was moderated by environmental conditions, which differed.

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**Fig. 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 $r=0.24$, $df=105$, $P<0.05$
among the three seascape positions in the Ningaloo lagoon. Relatively high densities of urchins were found at the back reef sites, which also had the lowest sediment depth and cover. Many urchins avoid sediment-laden sites (Hernández et al. 2008; Kawamata et al. 2011) and our results suggest that sites, where sediments are likely to accumulate, may be refugia from herbivorous urchins.

Our results also indicate that much of the spatial variation in macroalgal composition and structure within the Ningaloo lagoon does not relate to the density of urchins and sediment cover. Other potential reasons for spatial variance in macroalgal assemblages include light availability, an essential resource which may mediate inter-specific competition among macroalgae (Carpenter 1990; McCook 1996). Ningaloo’s unique geographic positioning is also important as it is situated just below the tropic of Capricorn where tropical and temperate waters merge (Gazzani and Marinova 2007), in which in addition to wave action and reef topography, can influence the supply of new urchin colonists in larval form (Lauzon-Guay and Scheibling 2007) and increase turbidity through suspending sediments potentially inhibiting photosynthetic capacity of seaweeds (Madsen et al. 2001).

Conclusions

Tropical macroalgal-dominated reefs are an integral component of many seascapes, providing food, shelter, and breeding grounds for a huge variety of marine life (Fulton et al. 2019). 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, whilst calcareous genera (e.g. Halimeda) can make substantial contributions to local carbonate budgets (Rees et al. 2007). 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 macroalgal assemblage structure and composition. Interactions between sediment and herbivorous urchin abundance were also mediated by seascape position. Our results may also be relevant to tropical reefs with similar geomorphology. Ningaloo is not unique in its seascape structure, with other reefs in all major ocean basins (and the Red Sea) having similar coral-macroalgal seascapes with grazing urchins (Mokady et al. 1996; McClanahan 1999; Berkström et al. 2012; Fulton et al. 2019; Eggertsen et al. 2019). 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 sediments 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 the community dynamics of tropical macroalgae.

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Author contributions RH, CF, and SW conceived the ideas and designed methodology; all authors collected the data; RH and CF 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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Data availability Raw data in this manuscript are stored in the public DRYAD database.

Code availability Available upon request.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

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