RESEARCH PAPER
https://doi.org/10.1071/MF21349

MARINE & FRESHWATER RESEARCH

Spatial patterns in the cover and composition of macroalgal assemblages on fringing and nearshore coral reefs

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Handling Editor:
Jacob Johansen

ABSTRACT

Context. Although increases in macroalgal cover on coral reefs are often reported alongside declines in coral, the composition of algal assemblages and their spatial dynamics are not commonly investigated. **Aims.** To quantify changes in macroalgal assemblage composition over two spatial environmental gradients, depth and distance from shore, within a nearshore reef system in Kimbe Bay, Papua New Guinea, where coral cover has declined. **Methods.** Benthic cover was quantified at three depths (reef flat, 10 and 15 m) on the windward reef slopes of six reefs located three distances from shore (fringing reefs, and platform reefs 100–200 m and 0.7–1 km offshore). **Key results.** Macroalgal cover was highest on the reef flat, and assemblage composition varied among depths and distances from shore. Macroalgal cover was not correlated with coral cover except where macroalgal cover was greater than 20%, where a negative correlation occurred. There was no correlation between macroalgal cover and turf algal cover. All three benthic groups were negatively correlated with the combined total cover of sand and gravel. **Conclusions.** These results indicated a fine-scale spatial structure of macroalgal assemblages on coral reefs over a narrow depth range and short distance from shore and highlighted the importance of a solid substratum. **Implications.** It is likely that the ecological interactions between corals and macroalgae vary considerably over narrow spatial gradients.

Keywords: benthic community, depth distribution, macroalgal diversity, marine ecology, *Padina*, *Sargassum*, terrestrial runoff, *Turbinaria*.

Introduction

Coral reef ecosystems are faced with a host of anthropogenic threats that are on the rise, including climate change and associated thermal bleaching events (Hoegh-Guldberg 1999; Hughes *et al.* 2018; Babcock *et al.* 2021) and the severity of storms (Bender *et al.* 2010), as well as more local impacts such as terrestrial runoff (Rogers 1990; Fabricius 2005) and overharvesting (Hughes 1994; Hughes *et al.* 2007). As a consequence, there is evidence of declining coral cover and increasing cover of algae, often their primary competitors, on coral reefs around the globe (e.g. Hughes 1994; Graham *et al.* 2015; Souter *et al.* 2021). In extreme cases, coral reef ecosystems have undergone phase-shifts from coral dominant reefs to reefs dominated by macroalgae (Hughes 1994; Mumby 2009) or non-scleractinian invertebrates (Norström *et al.* 2009). These alternative stable states can be reinforced through feedback mechanisms, such as reductions in coral recruitment, that make returning to coral dominance unlikely (Mumby 2009; Dell *et al.* 2016; Johns *et al.* 2018). The switch from a coral-dominated to a macroalgal state can have adverse effects on reef ecosystems, including reductions in reef stability (Done 1992) and shelter availability (Pratchett *et al.* 2008), declines in the abundance of coral-dependent species (Jones *et al.* 2004; Munday 2004; Baker *et al.* 2008), changes in fish community structure (Bellwood *et al.* 2006, 2012) and declines in fish diversity (Jones *et al.* 2004; Chong-Seng *et al.* 2012).

The community structure of organisms on coral reefs typically varies along spatial gradients, such as depth, reef zone and distance from shore. This is due to a number of

Received: 13 December 2021
Accepted: 19 July 2022
Published: 8 August 2022

Cite this:
Webber K *et al.* (2022)
Marine and Freshwater Research, **73**(11), 1310–1322.
doi:10.1071/MF21349

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physical and biological variables that also vary along these gradients, including light intensity, water quality, wave action, and herbivory, each of which can affect macroalgal abundance and composition. Light penetration rapidly decreases with depth, with this gradient being more pronounced on high-turbidity, poor water-quality reefs (Morgan *et al.* 2020) or reefs close to mainland shores (Fabricius 2005; De'ath and Fabricius 2010). Wave energy also decreases with depth (Gourlay 1994), and because coral reefs are effective dissipators of wave energy (Ferrario *et al.* 2014), reef habitats closer to shore or behind the reef crest tend to be more protected than are their more exposed offshore counterparts. Wave energy can also interact with water quality, as sheltered conditions may exacerbate the deposition of suspended sediments and the concentration of nutrients (Wolanski *et al.* 2005; Ceccarelli *et al.* 2020). Herbivorous fish feeding activity also varies spatially in reef systems and is typically highest in shallow habitats on offshore reefs (Russ 1984; Brokovich *et al.* 2010; Cheal *et al.* 2013). The influence of each of these variables on macroalgae depends on morphological and taxonomic differences in requirements for light (Markager and Sand-Jensen 1992; Leukart and Lüning 1994; Gómez and Huovinen 2011) and water quality (McCook *et al.* 1997; Schaffelke and Klumpp 1998; Umar *et al.* 1998), as well as susceptibility to wave dislodgement (Dudgeon and Johnson 1992; Starko *et al.* 2015) and herbivory (Hay 1981*a*; Marques *et al.* 2006; Mantyka and Bellwood 2007).

Few studies have quantified patterns in the abundance and assemblage composition of macroalgae across spatial gradients on coral reefs. On the Great Barrier Reef (GBR), the brown alga *Sargassum* is most abundant on inner shelf reefs, whereas it is absent on outer shelf reefs, where macroalgae are less abundant in general and dominated by red and green algae (Done 1982; McCook 1996; McCook *et al.* 1997). Increasing dominance of red algae with increasing distance from the coast has also been observed in the Pilbara Coast, Western Australia (Olsen *et al.* 2018). In Panama, during the 1980s, the shallow feeding activity of herbivorous fishes was inferred to be responsible for the restriction of some macroalgal taxa to the sand plain below the reef slope, despite it otherwise being a suboptimal environment owing to a lack of stable substratum for holdfast attachment (Hay 1981*a*). Both depth and coastline distance were found to be important drivers of macroalgal assemblage composition in French Polynesia (Adjeroud 1997). Such spatial patterns in macroalgal composition and abundance are important to consider, because they influence the likelihood, magnitude and ecological effects of macroalgal overgrowth on degrading reef communities.

Given the high spatial variability and taxonomic specificity of macroalgal abundance, it is clear that the prevalence of macroalga–coral interactions will also be spatially variable (Brown *et al.* 2018). In addition, macroalgae may compete for space with other forms of algae, such as algal turfs (Haas *et al.* 2010; Khalil *et al.* 2017), mixed assemblages of small, filamentous and fleshy algae, and early stages of macroalgae (Scott and Russ 1987). It is important to examine the inter-relationships among macroalgal, coral and turf cover, so as to assess whether and where these organisms are interacting (Barott *et al.* 2009; Haas *et al.* 2010; O'Brien and Scheibling 2018). Macroalgae, corals and turf algae may also respond in different ways to physical gradients in turbidity and sediment deposition (Airoldi 1998; Fabricius 2005; McCook 2001); however, these relationships have not commonly been quantified.

In the past three decades, the coastal reefs of Kimbe Bay, Papua New Guinea, have experienced multiple disturbances, including coral bleaching, increasing sedimentation from terrestrial runoff and crown of thorns starfish outbreaks, which have led to declines in coral cover (Brodie and Turak 2004; Jones *et al.* 2004; Chin *et al.* 2008; Souter *et al.* 2021). Effects appear to be worse in the coastal fringing reefs where land use is high (Brodie and Turak 2004). Despite recent increases in macroalgal cover in Kimbe Bay (G. P. Jones, pers. obs.), research into the algal assemblages present has been scarce, and has largely focused on fish–algae interactions within small, shallow areas defended by territorial damselfishes (e.g. Ceccarelli *et al.* 2005; Ceccarelli 2007; Eurich *et al.* 2018). In this study, we examined spatial patterns in the cover and assemblage composition of macroalgae on inshore reefs in Kimbe Bay. Across these spatial gradients, we also examined whether macroalgal cover was related to the cover of other benthic organisms, such as corals and turf algae, or sediments (such as sand or gravel), which may limit the availability of stable substratum for attachment (Hay 1981*a*). The following specific questions were addressed: (1) how does the cover and assemblage structure of macroalgae vary by depth, reef zone and distance from shore; and (2) are the spatial patterns in macroalgal cover related to those of corals, turf algae and sand–gravel?

Materials and methods

Study site and field methods

This research was conducted in Kimbe Bay, on the northern coast of West New Britain, Papua New Guinea, during November 2019. The sheltered inner bay consists of a dense network of platform and fringing reefs. The reefs investigated in this study are situated adjacent to the Mahonia Na Dari Research Centre on the western boundary of the bay (5°26′S, 150°5′E). Of these, two reefs were selected randomly from each of three distances from shore: fringing reefs, platform reefs between 0.1–0.2 km from shore (termed 'mid') and platform reefs 0.7–1 km from shore (termed 'outer'; Fig. 1). Although the furthest distance is just ~1 km from shore, we know from a sediment-monitoring project conducted in the area that there is a substantial

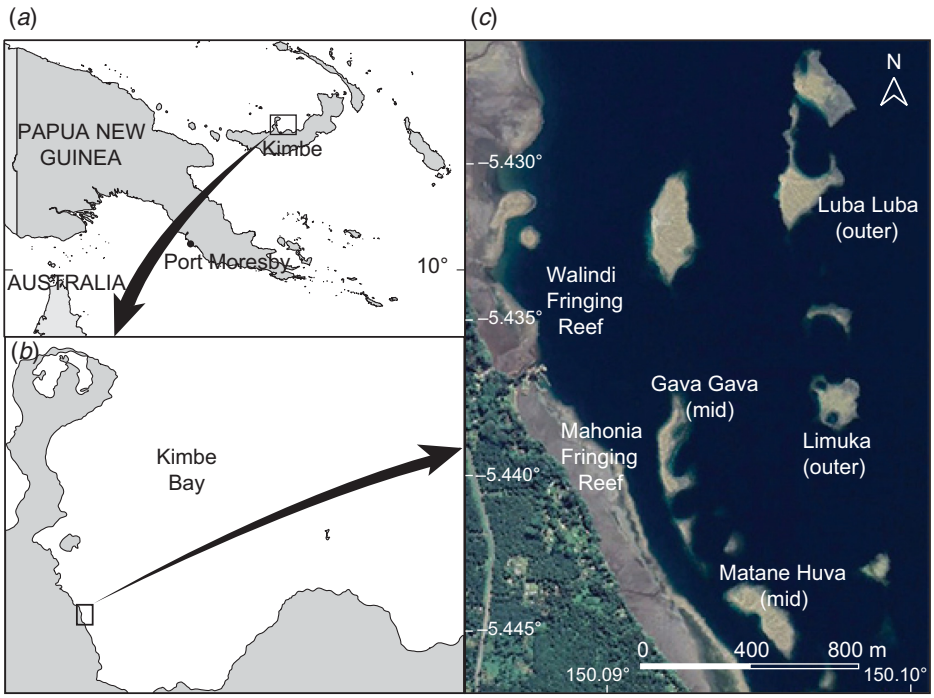

Fig. 1. Location of study sites in Kimbe Bay, West New Britain, Papua New Guinea. Coordinates of sites are as follows: Walindi Fringing Reef, 5°26′7″S, 150°5′16″E; Mahonia Fringing Reef, 5°26′22″S, 150°5′25″E; Gava Gava, 5°26′17″S, 150°5′32″E; Matane Huva, 5°26′39″S, 150°5′44″E; Luba Luba, 5°25′50″S, 150°5′49″E; Limuka, 5°26′15″S, 150°5′51″E.

reduction in suspended sediments over this distance (G. P. Jones, unpubl. data).

Macroalgae were surveyed at three depth isoclines at each reef, namely, the reef flat (~5 m behind the crest), and depths of 10 and 15 m on the windward reef slope. These depths were chosen because preliminary observations showed that macroalgae would be detected at all three depths, but would be only very seldomly encountered on shallower parts of the reef slope. At each depth, five replicate 20-m transects were surveyed, each transect being separated by at least 5 m, with the starting position of the initial transect and the direction of swimming chosen haphazardly. Ten photo-quadrats of ~1 m^2 were taken at 2-m intervals along each transect, with a 50-cm ruler placed on the benthos in the centre of each photograph for scale. In total, 900 photographs were captured using a GoPro Hero 2018 camera by using the 'wide' frame setting.

Image analysis

Photo-quadrats were analysed to determine the percentage cover of macroalgae and other benthic groups. Cover was calculated by overlaying each photograph with 25 random points and identifying the benthic organism or substratum directly beneath each point. Macroalgae were identified to the lowest taxonomic level possible. All live hard corals were pooled together, as were algal turfs (identified in photos as small filamentous and fleshy algae with no observable plant-like structure) and unconsolidated substrates (sand and gravel).

Data analysis

Mixed-effects, nested ANOVAs with three factors, namely depth, distance from shore (both fixed factors), and site nested within distance (random factor), were performed to examine spatial effects on the percentage cover of macroalgae, hard corals, algal turf and sand–gravel, by using the mean percentage cover per transect as input data. According to Quinn and Keough (2002), the following method was used to improve power because of the low sample sizes used: where *P*-values greater than 0.25 indicated that the random factor site or its interaction with depth did not differ from the residual, a 'pooled error' term was used to test the fixed factors depth and distance. This pooled error term was calculated by summing the sum of squares of the residual with the sum of squares of the random factors or interactions that did not differ from it. The same was performed for the degrees of freedom, which allowed calculation of a pooled mean square, which could be used in *F*- and *P*-value calculations (Quinn and Keough 2002). For macroalgal species that were absent from the reef flat, the reef-flat data were excluded from the ANOVA. For macroalgal species found only on the reef flat, the depth factor was dropped from the ANOVA and only reef-flat data were included. If a species was completely absent from a

particular distance from shore, data from that distance were excluded from the ANOVA. Where the assumptions of normality and homogeneity of variance were not met, square-root or log(x + 1) transformations were made. Where assumptions were still not met after transformation, ANOVAs were performed using the transformation that achieved the highest Shapiro–Wilk's test P-value, given that ANOVA is usually robust when the sampling design is balanced (Quinn and Keough 2002; Underwood 1997). The potential associations between coral cover, macroalgal cover, turf algal cover and their combined total, as well as those among these living substrata and sand–gravel cover were tested using Pearson's product–moment correlations. Data were square-root or log(x + 1) transformed if necessary. Spatial patterns in macroalgal assemblage composition were examined using non-metric multi-dimensional scaling (NMDS) using a Bray–Curtis dissimilarity matrix of the Wisconsin double-standardised percentage cover of each depth within each site for all macroalgal taxa. Overplotting was avoided by rounding the NMDS scores to two decimal places and applying random horizontal and vertical variation, with a maximum of 15% of the resolution of the rounded data. All analyses were performed using the software R (ver. 3.6.1, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/) and the 'vegan' package (ver. 2.4-1, Oksanen *et al.*, see https://CRAN.R-project.org/package=vegan, accessed 19 May 2021) was used to conduct NMDS analysis.

Ethical approval

This work was conducted in compliance with the James Cook University Animal Ethics Committee regulations (ethics approval number A2659).

Results

Cover of all macroalgae, algal turf, live coral and sand–gravel

The percentage cover of all macroalgae combined varied significantly among depth strata (Table 1), with cover on the reef flat being ~2.5 times higher, on average, than on

Table 1. Results of mixed effects, nested ANOVAs (three factors: distance, site and depth, with site nested within distance and treated as a random factor) on benthic substrata.

Benthic substratum	Distance	Site	Depth	Distance × depth	Site × depth	Residual
Total macroalgae						
d.f.	2	3	2	4	6	72
MS	25.94	4.10	33.26	7.61	5.23	1.46
F	6.33	2.81	6.36	1.45	3.59	
P	0.084	**0.045**	**0.033**	0.324	**0.004**	
Algal turf[A]						
d.f.	2	3	2	4	6	72, 81
MS	1763.76	16.24	1229.46	1178.83	59.69	128.03
F	108.58, 14.84	0.13	20.60, 10.35	19.75, 9.92	0.47	
P	**0.002, <0.001**	0.944	**0.002, <0.001**	**0.001, <0.001**	0.831	
Hard coral						
d.f.	2	3	2	4	6	72
MS	18.50	9.56	7.03	8.08	8.62	1.41
F	1.94	4.89	0.82	0.94	6.29	
P	0.288	**0.004**	0.486	0.502	**<0.001**	
Sand–gravel[A,B,C]						
d.f.	2	3	2	4	6	72, 78
MS	41.32	1.34	0.39	3.41	0.63	0.68
F	30.78	1.97	0.63, 0.58	5.04	0.92	
P	**0.010**	**0.126**	0.565, 0.561	0.034, **<0.001**	0.486	

Bold P-values indicate significance at $\alpha = 0.05$ for fixed terms, $\alpha = 0.25$ for random terms.
[A]Two values are given because random terms tested at $P > 0.25$ and were pooled with the residual as denominators for F-tests. The first value is the original, the second the result after pooling.
[B]Failed inspection for homogeneity of variance using Tukey–Anscombe and scale-location plots, cautionary results.
[C]Failed visual inspection for normality of residuals using QQ plot despite transformation, cautionary results.

the reef slope. Distance from shore did not have a significant effect on the cover of all macroalgae and there was no significant interaction between depth and distance from shore. There were significant site effects: the site with the lowest macroalgal cover was Walindi fringing reef and the site with the highest cover was Gava Gava, one of the 'mid' reefs (Fig. 2). There was a 4.5-fold difference in macroalgal cover between the reef flats of these two reefs. There was a significant interaction between site and depth (Table 1), with depth-related patterns in macroalgal cover clearly not consistent among sites. For instance, macroalgal cover was generally highest on the reef flat and declined with an increasing depth, but this was not seen at the 'outer' reef Luba Luba (Fig. 2).

The percentage cover of algal turf was generally higher than both coral and macroalgal cover. Turf cover differed significantly among distances from shore and among depths, and there was a significant interaction between distance from shore and depth, but there were no significant differences among sites and no interaction between site and depth (Table 1). The percentage cover of algal turf was highest on the 'outer' reef flats, with 62% cover, and lowest at 15 m on the fringing reefs, with 18% cover (Fig. 2). Elsewhere, turf cover was consistently high, ranging between 40 and 50% (Fig. 2).

Live coral cover did not differ significantly among depths or distances from shore, but there were significant differences among sites and a significant interaction between site and depth (Table 1). Coral cover was highly variable among sites and site-related patterns were not consistent among depths. On the reef flat, coral cover ranged from almost complete absence at the Mahonia fringing reef to 30% at the Walindi fringing reef (Fig. 2). At 10 m, whereas Gava Gava had 28% coral cover, the other sites had between 15 and 22%, and, at 15 m, the coral cover ranged from 3 to 4% at the two fringing reefs to 34% at Matane Huva. Coral cover was higher than macroalgal cover at most sites and depths, except for the reef flats of Mahonia, Gava Gava and Matane Huva, and the reef slope at 15 m at Luba Luba.

Sand–gravel cover differed significantly among distances from shore, but not among depths, and there was a significant interaction between distance from shore and depth (Table 1). The 'mid' and 'outer' reefs had similar sand–gravel cover across all depths, whereas on the fringing reefs, sand–gravel cover was greater at 15 m than it was in the shallower depths (Fig. 2). Sand–gravel cover was also higher, on average, at the fringing reefs (Table 1, Fig. 2).

Correlations among macroalgae, turf algae, coral and sand–gravel

When all data were included, there were no significant correlations between macroalgal cover and coral cover ($r = -0.04$, $P = 0.712$, d.f. = 88), turf cover and macroalgal cover ($r = 0.09$, $P = 0.394$, d.f. = 88), and turf cover and coral cover ($r = 0.07$, $P = 0.543$, d.f. = 88). The cover of macroalgae and turf algae combined was also not correlated with coral cover ($r = -0.05$, $P = 0.662$, d.f. = 88). However, on transects where macroalgae was above 20% ($n = 17$), there

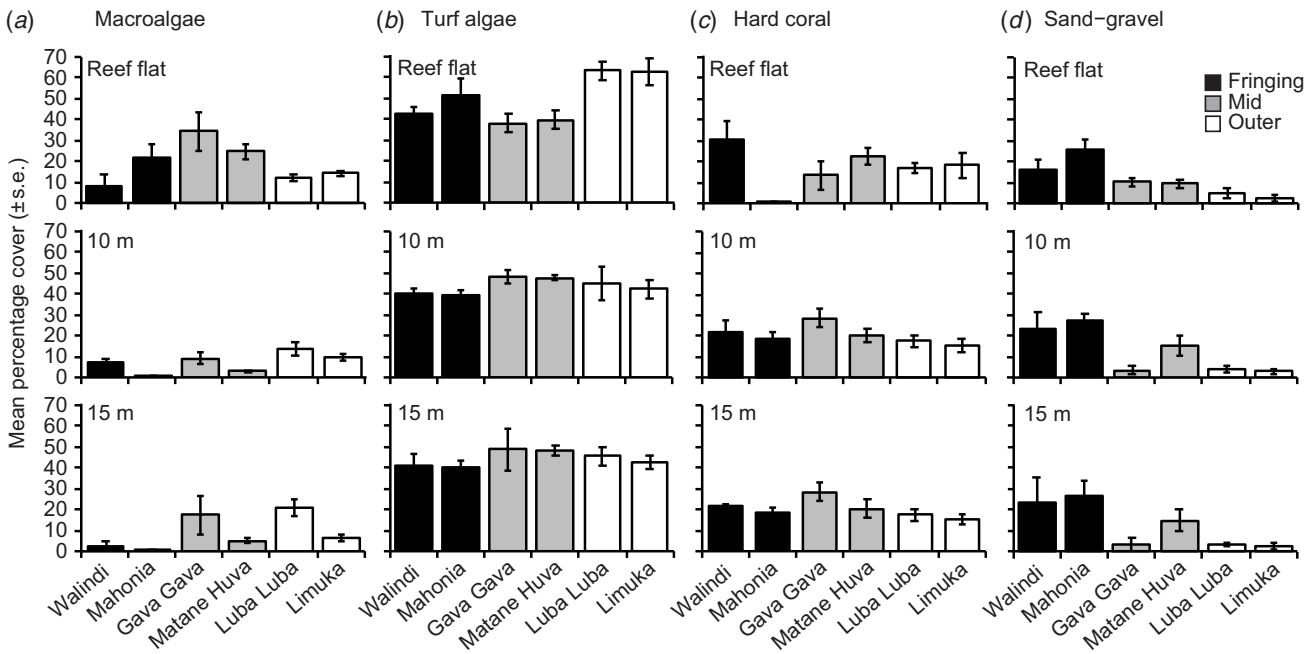

Fig. 2. Mean percentage cover (±s.e.) of (*a*) all macroalgal taxa combined, (*b*) turf algae, coral (*c*) and (*d*) sand–gravel, at each site and depth.

was a significant negative correlation between macroalgal and coral cover ($r = -0.53$, $P = 0.027$, d.f. = 15).

Macroalgal cover, coral cover and turf cover were each negatively correlated with the cover of sand–gravel (macroalgae: $r = -0.38$, $P < 0.001$, d.f. = 88, coral: $r = -0.57$, $P < 0.001$, d.f. = 88, turf: $r = -0.40$, $P < 0.001$, d.f. = 88; Fig. 3).

Species-specific patterns in macroalgal cover

Most of the of the commonly encountered macroalgal taxa were not present at one or two depths and at some distances from shore. A *Dictyota* species, a *Padina* species and a galaxaurid species (Family Galaxauraceae) were found only at 10 and 15 m (Fig. 4) and were not found on the fringing reefs. For these three species, there were no significant differences in percentage cover between 10- and 15-m depths and between 'mid' and 'outer' distances from shore, but there were significant differences among sites (Table 2). Two species of *Turbinaria* (*T. ornata* and *T. decurrens*), two species of *Sargassum* (*S. siliquosum* and *S. cristaefolium*) and one *Padina* species, which was morphologically distinct from *Padina* on the reef slope, were found only on the reef flat (Fig. 4). Two of these species, namely *T. decurrens* and *S. cristaefolium*, were not found on the fringing reefs, and one of them, *S. siliquosum*, was absent from the 'outer' reefs. Aside from these complete absences, there were no significant differences in cover among distances from shore for any macroalgal species (Table 2). There were significant differences among sites for all species except *S. siliquosum* (Table 2).

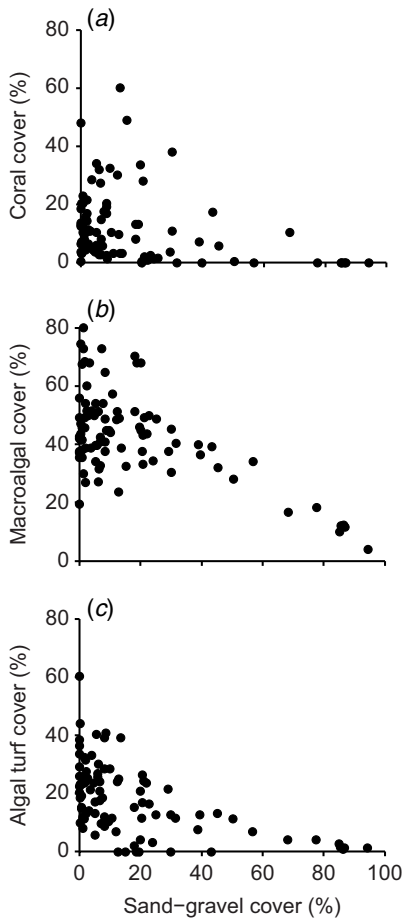

Fig. 3. Correlations between the percentage cover of (*a*) coral, (*b*) macroalgae and (*c*) algal turf, and the percentage cover of sand–gravel. Each point represents a transect ($n = 90$).

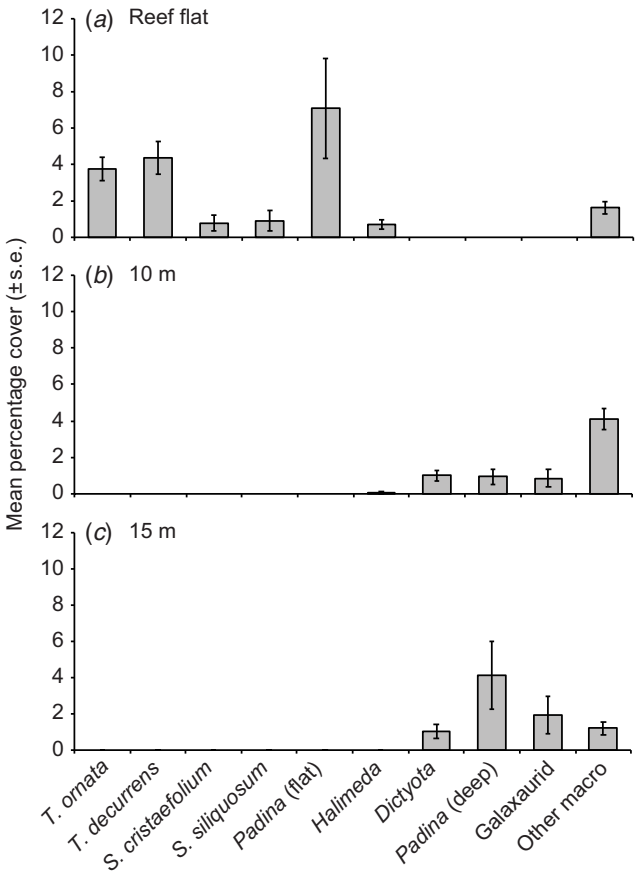

Fig. 4. Mean percentage cover (±s.e.) of macroalgal taxa at each of the three depths.

Macroalgal assemblage structure

The separation in macroalgal assemblage composition between the reef flat and the slope was strong, whereas the two reef-slope depths were comparatively similar (Fig. 5*a*). Reef-flat assemblages were loosely grouped by distance from shore, with similarities in reef-flat macroalgal assemblages between the two 'mid' reefs and between the two 'outer' reefs. However, the two fringing reef flats did not group together (Fig. 5*b*), owing to *Padina* having high cover at the Mahonia fringing reef flat, and low cover at the Walindi fringing reef flat. On the reef slope, the fringing reefs

Table 2. Results of mixed-effects, nested ANOVAs (three factors: distance, site and depth, with site nested within distance and treated as a random factor) on macroalgal taxa.

Macroalgal taxon	Distance	Site	Depth	Distance × depth	Site × depth	Residual
Padina-S[A,B,C,D]						
d.f.	1	2	1	1	2	32
MS	0.24	5.66	3.69	0.38	1.14	0.74
F	0.04	7.66	3.23	0.33	1.55	
P	0.856	**0.002**	0.214	0.622	**0.228**	
Dictyota[A,B,C,D]						
d.f.	1	2	1	1	2	32
MS	0.01	3.48	0.19	0.05	1.37	0.52
F	0.00	6.74	0.14	0.03	2.64	
P	0.957	**0.004**	0.747	0.872	**0.087**	
Galaxaurid[A,C,D]						
d.f.	1	2	1	1	2	32
MS	8.57	3.96	1.09	0.48	0.65	0.40
F	2.16	9.85	1.67	0.74	1.62	
P	0.279	<**0.000**	0.325	0.480	**0.214**	
Turbinaria decurrens[B,C]						
d.f.	1	2	NA	NA	NA	16
MS	0.09	7.43	NA	NA	NA	0.56
F	0.01	13.21	NA	NA	NA	
P	0.922	<**0.001**	NA	NA	NA	
T. ornata						
d.f.	2	3	NA	NA	NA	24
MS	17.20	33.10	NA	NA	NA	9.42
F	0.52	3.51	NA	NA	NA	
P	0.640	**0.031**	NA	NA	NA	
Padina-F[C,D]						
d.f.	2	3	NA	NA	NA	24
MS	5.14	9.41	NA	NA	NA	0.81
F	0.55	11.65	NA	NA	NA	
P	0.628	<**0.001**	NA	NA	NA	
Sargassum cristaefolium[B,C,D]						
d.f.	1	2	NA	NA	NA	16
MS	1.36	1.93	NA	NA	NA	0.24
F	0.70	7.92	NA	NA	NA	
P	0.490	**0.004**	NA	NA	NA	
S. siliquosum[C,D,E,F]						
d.f.	1	2	NA	NA	NA	16, 18
MS	0.24	0.84	NA	NA	NA	0.64, 0.66
F	0.29, 0.37	1.31	NA	NA	NA	
P	0.643, 0.551	0.298	NA	NA	NA	
Other macroalgae						
d.f.	2	3	2	4	6	72
MS	5.19	1.92	7.73	2.00	1.27	0.39

(*Continued on next page*)

Table 2. (*Continued*).

Macroalgal taxon	Distance	Site	Depth	Distance × depth	Site × depth	Residual
F	2.69	4.94	6.07	1.57	3.27	
P	0.214	**0.004**	**0.036**	0.295	**0.007**	

Padina-S, *Padina* species found only on the reef slope. *Padina*-F, *Padina* species found only on the reef flat. Bold values indicate significance at $\alpha = 0.05$ for fixed terms, $\alpha = 0.25$ for random terms. NA, not applicable, because the species was found only on the reef flat and depth was not included in analysis.
[A]Depths included in analysis were 10 m and 15 m only.
[B]Fringing reefs excluded from analysis.
[C]Failed visual inspection for normality of residuals using QQ plot, cautionary results.
[D]Failed inspection for homogeneity of variance using Tukey–Anscombe and scale-location plots, cautionary results.
[E]Offshore reefs excluded from analysis.
[F]Two values are given because random term tested at $P > 0.25$ and was pooled with the residual as a denominator for the *F*-test. The first value is the original, the second the result after pooling.

grouped together (Fig. 5), because of their macroalgal assemblages being predominantly composed of macroalgae that were not able to be identified (included in 'other macroalgae').

Discussion

Macroalgae were a prominent feature of the substratum on the inshore reefs of Kimbe Bay, with cover exceeding that of coral at some sites and depths. Overall cover of macroalgae was comparable to levels found on inshore fringing reefs of the GBR (Ceccarelli *et al.* 2020). Macroalgal cover varied among depths, being consistent with findings from other studies conducted in the Indo-Pacific (e.g. Adjeroud 1997; Fabricius 2005), with highest cover being on reef flats, reaching a maximum of 60% on some transects. Unlike studies conducted over broader spatial scales (e.g. Adjeroud 1997; Schaffelke *et al.* 2005; Olsen *et al.* 2018), overall macroalgal cover did not vary with distance from shore, although there was considerable variation among sites at this spatial scale. Macroalgal assemblage composition differed both among depths and with distance from shore, which is similar to the findings of several other studies (e.g. Done 1982; Adjeroud 1997), with a unique assemblage being dominated by *Turbinaria*, *Sargassum* and occasional large stands of *Padina* on the reef flat. Several species were completely absent from the fringing reefs and one species was absent at the furthest distance from shore. Contrary to other studies (e.g. Ceccarelli *et al.* 2020), negative correlations between macroalgal cover and coral cover, turf cover and coral cover, or macroalgal cover and turf cover were not observed when all data were included. However, macroalgal and coral cover were negatively correlated where macroalgal cover exceeded 20%, a threshold observed by Ceccarelli *et al.* (2020), above which such correlations were strong on the inshore GBR. In addition, all three benthic categories were negatively correlated with the cover of sand–gravel, suggesting, as others have (e.g. Hay 1981*a*; Brown *et al.* 2018), that the availability of consolidated substratum may be an important driver of spatial patterns of algae and other coral reef organisms attached to hard substrate.

Macroalgal depth distribution

Depth played an important role in determining spatial patterns in macroalgal cover and structuring macroalgal assemblages on inner reefs in Kimbe Bay. Depth often plays a strong role in structuring tropical benthic assemblages because of factors such as decreasing light and turbulence with increasing depth (Veron 2000; Jacobucci *et al.* 2011), as well as changes in herbivory (Costa *et al.* 2002). The reef flat, an environment of high light intensity and wave action, typically had the highest macroalgal cover, with the brown algal family Sargassaceae, particularly two species of *Turbinaria*, consistently being found there and sometimes reaching high densities.

Macroalgal species of the reef flat were typically strongly attached by holdfast, whereas the three dominant macroalgae on the reef slope were loosely attached and more delicate. Whereas the majority of macroalgae found on the reef flat were non-calcifying, calcifying taxa occurred at greater proportions on deeper transects. These included a galaxaurid and a lightly calcifying *Padina* species, both found at some platform reef sites in large, loose mats, which were completely absent on the reef flat. Benthic communities at isolated coral reefs in the Pacific, despite having much lower overall macroalgal cover than those in Kimbe Bay, have also demonstrated decreasing fleshy macroalgal cover and increasing calcified macroalgae, particularly *Halimeda*, with depth (Williams *et al.* 2013). Vulnerability to dislodgement by waves may be the shared characteristic between *Halimeda* in that study (Williams *et al.* 2013) and the *Padina* and galaxaurid species observed in this study, which explains their preference for deeper environments. In contrast, the flexible yet strongly attached nature of the species found on the reef flat (e.g. *Turbinaria* spp.) allows them to withstand moderate wave action (Stewart 2008). In addition, their exposure to waves and the high buoyancy of their blades and stipes allow transportation to and

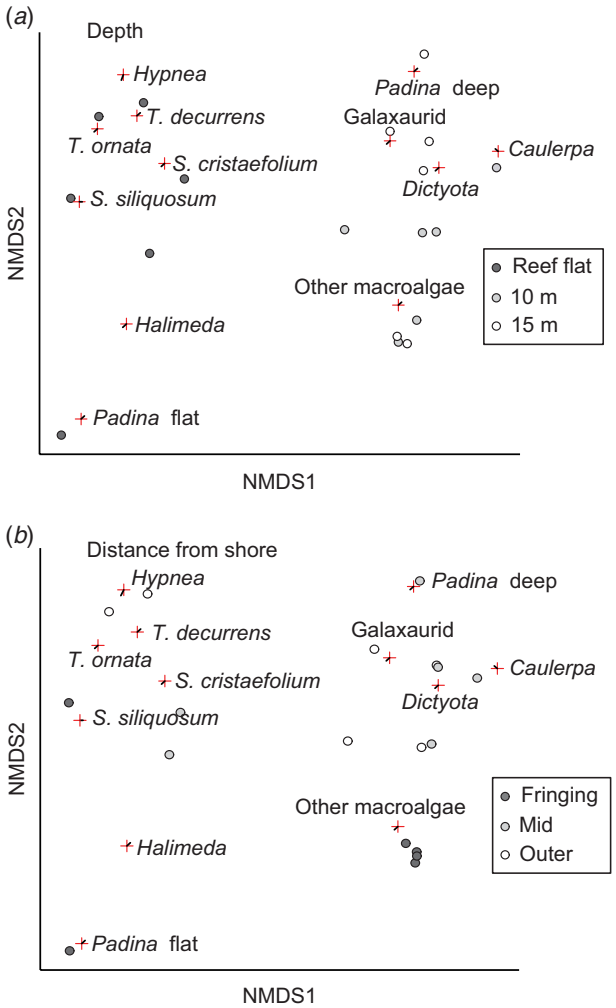

Fig. 5. Macroalgal assemblage structure of the three depths and the six sites, colour-coded by depth (*a*) and distance from shore (*b*). Points represent non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity index of Wisconsin double-standardised percentage cover, averaged within depth strata within each site ($n = 5$). Random noise added in horizontal and vertical directions at 15% of resolution when NMDS scores were rounded to two decimal places. $k = 2$, stress = 0.091.

colonisation of new shallow areas after intense wave action (Stiger and Payri 1999; Stewart 2008).

The drivers of these depth distributions require further investigation. Herbivore biomass and grazing rates often vary among different habitats and depths within coral reefs (e.g. Russ 1984; Lewis and Wainwright 1985; Fox and Bellwood 2007), and experimental studies have shown that this may have important consequences on the distribution of macroalgae (Hay 1981*a*; Lewis 1986). Some researchers have documented a peak in grazing below the first 1–2 m, where wave motion ceases to interfere with feeding by fishes, and a decline with depth (Hay 1981*b*; Vergés *et al.* 2009; Brokovich *et al.* 2010). Others have found a peak in grazing at the crest, and declines both towards the back reef and with increasing depth (Fox and Bellwood 2007), although habitat preferences for grazing differ somewhat among herbivore families (Russ 1984). Although light is potentially limiting for algal species living in deeper environments, there is likely to be some depth at which macroalgae are afforded a refuge from predation (Hay 1981*a*). This may be the reason that reef-slope macroalgal patches were present at depths of 10 m and greater but were largely absent from the shallower parts of the reef slope. Quantitative assessments of herbivory on these reefs are required, to determine whether this process has played a role in shaping the depth distributions of macroalgae.

Macroalgae and distance from shore

Overall, macroalgal cover did not vary with distance from shore. Macroalgae in other regions, such as the GBR, have been shown to increase in cover with proximity to nutrient-rich, high-turbidity coastal areas (e.g. Done 1982; Schaffelke *et al.* 2005; McClure *et al.* 2019), and also to increase in species richness (De'ath and Fabricius 2010). This is likely to be related to the large differences in scale between the present study and previous work. For example, cross-shelf gradients on the GBR occur at scales of tens to hundreds of kilometres (e.g. Schaffelke *et al.* 2005), which is multiple orders of magnitude greater than in the present study. Even so, there were assemblage-composition changes along this gradient, driven mainly by the complete absences of several macroalgal taxa on the fringing reefs. Additionally, *Sargassum siliquosum* was absent from outer reefs 0.7–1 km from shore. Macroalgae such as *Sargassum* can undergo substantial temporal changes to their biomass (Martin-Smith 1993; Fulton *et al.* 2014) and may have been detected more readily with a longer sampling period. However, as Kimbe Bay is equatorial, there is very little variation in temperature, and the major seasonal changes are in rainfall (Brodie and Turak 2004). The temporal dynamics of macroalgae have yet to be examined in this area; however, they are likely to differ, for example, from those on the nearby GBR, given the mild seasonality and non-dominance of *Sargassum* observed here.

Correlations among major substratum types

Our study found no significant overall correlation between macroalgal cover and coral cover, but the presence of such a correlation in other studies has been shown to depend on the level of macroalgae involved. For instance, Ceccarelli *et al.* (2020) found significant negative correlations between macroalgae and coral at several, but not all, sites on the GBR, and that the correlations were strongest where macroalgal cover was higher than 20%. In Kimbe Bay, in the present study, macroalgal cover was typically lower than this value (site averages ranged from 5.8 to 20.1%, overall average

was 11.5%). However, where macroalgal cover did exceed 20% cover, a negative correlation between macroalgal and coral cover was observed. Beyond certain thresholds of macroalgal cover, coral cover and herbivory, effects by macroalgae on corals such as shading, abrasion (McCook *et al.* 2001), allelopathy and inhibition of recruitment (Johns *et al.* 2018; Evensen *et al.* 2019), and on fishes such as suppression of herbivory (Dell *et al.* 2016), may reach levels where feedback loops are strong enough to prevent coral recovery and maintain macroalgal dominance (Mumby 2009). On the basis of the correlation between coral and macroalgal cover where macroalgal cover was higher than 20%, such a threshold may be exceeded in some areas of Kimbe Bay. However, further investigation into coral–algal dynamics in the Bay is required before the cause of this relationship can be identified.

As in this study, algal turfs are often a major component of reef benthic assemblages, in both tropical and temperate regions (Connell *et al.* 2014), occupying more space than does coral even on many isolated Pacific reefs with no direct human impact (Vroom *et al.* 2005, 2006). Turfs were found in almost all surveys in an examination of algal distributions across the GBR (McCook *et al.* 1997). Like other benthic organisms, algal turfs may be heavily influenced by water-quality gradients and may increase in inshore environments with higher levels of nutrients and sediments (Fabricius 2005). However, a cross-shelf comparison of epilithic algal assemblages on the GBR showed that algal tissue production may be higher at offshore *v*. inshore sites (Russ and McCook 1999). In this case, cover, rather than production, followed a similar pattern, albeit on a much smaller spatial scale; the highest cover of turf algae occurred on the reef flat of outer reef sites, and the lowest cover occurred at 15 m on the fringing reefs. This may indicate that terrestrial influences, such as sediments, are above turf tolerance thresholds (Tebbett *et al.* 2018) at the innermost sites surveyed.

The cover of turf algae was not found to be correlated with that of macroalgae in this study, and in contrast to several previous studies, turf algal cover was also not correlated with coral cover (Fabricius 2005; Teichberg *et al.* 2018). Algal and coral interactions do not always favour algae (McCook *et al.* 2001; Swierts and Vermeij 2016), even on reefs with high terrestrial influence (McCook 2001). It appears in this case that effects of algae on coral and *vice versa* are relatively weak compared with other drivers of their abundance.

The role of sediment

Limited availability of stable substrata may be responsible for some of the benthic distribution patterns observed with distance, because there were significant negative correlations between macroalgal, turf algal and coral cover and sand–gravel cover. Cover of benthic organisms was highly variable at low sand–gravel cover, but macroalgal, turf, and coral cover were always low where sand–gravel cover was at its highest. Sand–gravel cover on the fringing reef slopes was very high relative to that on the platform reefs and the macroalgal taxa that characterised the reef slopes elsewhere were absent. This was especially true at 15 m, where sand cover reached very high levels on the fringing reefs, and macroalgae, coral and turf were minimal in cover. Unlike seagrasses, which have true root systems, algae are generally unable to anchor in soft sediments (Diaz-Pulido and McCook 2008). Even the loosely attached algal mats of *Padina*, the galaxaurid and *Dictyota* found on the slopes of some platform reefs were found only on harder, more complex substrates, which may prevent them from drifting away in currents (Alfaro *et al.* 2009). Additionally, it is likely that the higher level of turbidity found on the fringing reefs (K. Webber, pers. obs.) caused light availability to decrease more rapidly with depth (Fabricius 2005; Morgan *et al.* 2020) and contributed to the declines in macroalgae, turf and coral on the fringing reef slopes. Therefore, examining these organisms at the spatial scale of the present study highlighted patterns of terrestrial influence that contrasted with those observed at larger spatial scales. Namely, limited availability of solid substrata and reduced light limited the abundance of each of these groups at the innermost reefs of this study. Turbidity and the deposition of sediments are likely to vary greatly with seasonal rainfall cycles at this location (Brodie and Turak 2004), and further investigation into the temporal dynamics of sediments and their relationship with benthic organisms may be necessary for Kimbe Bay.

Conclusions

These results highlighted that macroalgae on coral reefs can be highly spatially dynamic. This dynamism can occur on fine scales with depth, distance from shore, and with the availability of suitable substrata. Furthermore, both abundance and assemblage composition of macroalgae can change dramatically along these gradients, indicating that assessing this diverse group purely with metrics such as 'total macroalgal cover' may ignore potentially important patterns. Finally, despite higher levels of macroalgae in Kimbe Bay than in the recent past (G. P. Jones, pers. obs.), a lack of an overall correlation between macroalgal and coral cover appears to indicate that macroalgae are not directly jeopardising coral reef development at most sites within this location. However, at some sites, macroalgal cover did exceed a level where a negative correlation with coral cover became apparent. This implies that, in Kimbe Bay, adverse effects on corals by macroalgae are likely to be small in comparison to the effects of global and local

anthropogenic stressors, although macroalgae may add further stress at some, high macroalgae sites.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. This study was supported by funding allocation to G. P. Jones from the ARC Centre of Excellence for Coral Reef Studies (CE0561435), James Cook University.

Acknowledgements. We acknowledge and extend a heartfelt thank you to the traditional owners for allowing access to the Tamare-Kilu reefs in Kimbe Bay. We also thank Marta Panero and Nisha Goldsworthy for providing assistance in the field. A sincere thank you also goes to the staff at Mahonia Na Dari Research and Conservation Centre and the staff at Walindi Plantation Resort for logistical support, and especially to our boat driver, Jerry Sikatua. Thanks also go to Kai Pacey for assistance with statistical analysis, Guillermo Diaz-Pulido for assisting with macroalgal identification, and two anonymous reviewers who helped improve this paper.

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