

The influence of micro-topography and external bioerosion on coral-reef-building organisms: recruitment, community composition and carbonate production over time

Jennie Mallela¹ 

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Abstract The continued health and function of tropical coral reefs is highly dependent on the ability of reef-building organisms to build large, complex, three-dimensional structures that continue to accrete and evolve over time. The recent deterioration of reef health globally, including loss of coral cover, has resulted in significant declines in architectural complexity at a large, reef-landscape scale. Interestingly, the fine-scale role of micro-structure in initiating and facilitating future reef development and calcium carbonate production has largely been overlooked. In this study, experimental substrates with and without micro-ridges were deployed in the lagoon at One Tree Island for 34 months. This study assessed how the presence or absence of micro-ridges promoted recruitment by key reef-building sclerobionts (corals and encrusters) and their subsequent development at micro (mm) and macro (cm) scales. Experimental plates were examined after 11 and 34 months to assess whether long-term successional and calcification processes on different micro-topographies led to convergent or divergent communities over time. Sclerobionts were most prevalent in micro-grooves when they were available. Interestingly, in shallow lagoon reef sites characterised by shoals of small parrotfish and low urchin abundance, flat substrates were also successfully recruited

to. Mean rates of carbonate production were 374 ± 154 (SD) $\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ within the lagoon. Substrates with micro-ridges were characterised by significantly greater rates of carbonate production than smooth substrates. The orientation of the substrate and period of immersion also significantly impacted rates of carbonate production, with CaCO_3 on cryptic tiles increasing by 28% between 11 and 34 months. In contrast, rates on exposed tiles declined by 35% over the same time. In conclusion, even at sites characterised by small-sized parrotfish and low urchin density, micro-topography is an important settlement niche clearly favouring sclerobiont early life-history processes and subsequent carbonate production.

Keywords Topographic complexity · Recruitment · Coral · Encruster · Experimental substrates · Bioerosion

Introduction

A tropical coral reef is a highly complex structure constantly being reshaped on a daily basis by biophysical processes such as herbivory (Steneck 1983) and local environmental conditions (both physical and chemical; Scoffin 1992; Eyre et al. 2014). Indeed, it is this dynamic interplay of processes that results in its complex, three-dimensional topography and enables reefs to be among the most biologically diverse and productive ecosystems on the planet (Alvarez-Filip et al. 2011; Graham and Nash 2013). At the reef-landscape scale, increasing topographic complexity is considered to be a good indicator of reef health (Alvarez-Filip et al. 2009, 2015; Richardson et al. 2017). At the macro scale (> 1 cm), recent research simulating the role of dead corymbose coral branches, and the spaces in between, highlights how critical topographic refuges are

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✉ Jennie Mallela
j.a.mallela93@members.leeds.ac.uk

¹ Research School of Biology and Research School of Earth Sciences, Australian National University, Canberra, ACT 0200, Australia

for decreasing grazing pressure on recently recruited scleractinian corals and for enriching biodiversity (Brandl et al. 2014; Brandl and Bellwood 2016; Doropoulos et al. 2016). However, there is little similar information on critical secondary reef-building organisms (encrusters) and rates of carbonate production. Natural, in situ data from reef sites characterised by limited grazer activity is also lacking, while the contribution that micro scale (< 1 cm) habitat complexity makes to reef development has also received limited attention. This study focuses on these data gaps.

Much of the reef is composed of small, cryptic spaces (Ginsburg 1983); these habitats are typically overlooked by in situ, visual surveys (Goatley and Bellwood 2011; Yadav et al. 2016). Cryptic habitats such as micro-cavities account for up to two-thirds of available space on a reef (Jackson et al. 1971; de Goeij and Van Duyl 2007). Micro-ridges and micro-grooves are formed daily by various bioeroding organisms such as parrotfish, urchins and chitons (Scoffin 1992). These bioeroding processes and subsequent regrowth by ‘tougher’ calcareous tissue are thought to strengthen the structural integrity of key reef-building crusts such as crustose coralline algae (Steneck 1983). The resulting crevices also provide refuge from predators for sclerobiont recruits, protection in high-energy environments, and enhance spat survival (Martindale 1992; Brandl and Bellwood 2016). Currently, there is still relatively little known about the importance of micro-structure at micro (mm) and macro (cm) scales for sclerobiont recruitment and drivers of growth, community composition and carbonate production.

This study aimed to experimentally test whether: (1) micro-structural complexity influenced community composition and long-term successional patterns; (2) reef-building organisms (corals and encrusting sclerobionts) preferentially recruited to micro-crevices; and (3) carbonate production (calcification, $\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) occurred more rapidly on micro-structurally complex substrates over short- (11 months) and longer-term (3 yr) time frames. For the purposes of this research, Taylor’s (1990) definition of recruitment is used: calcareous organisms (encrusters and corals) that are sessile as adults and are dependent on their free-swimming larval stages for colonisation of reef substrate. Those individuals that settle successfully and survive immediate post-settlement mortality are defined as recruits.

Methods

Study site

This study was conducted in the shallow lagoon system at One Tree Island, located in the Capricorn Bunker Group at

the southern extreme of the Great Barrier Reef, Australia (23°29′40″S, 152°4′20″E). One Tree Island is a lagoon platform reef (area 14 km²) with an emergent reef crest and three separate lagoons that are connected at high tide. The lagoon system is extensive, enclosed by the emergent rim of the reef crest and characterised by numerous patch reefs, locally called ‘microatolls’. This study was conducted within the main (first) lagoon which is totally enclosed (area 10 km²) by the reef crest. At low tide, the water depth ranges from 2 to 7 m. Water ponds at low tide within the lagoon and the continuous reef crest protects the lagoon from exposed fore-reef wave conditions for up to 5 h either side of slack tide (Koop et al. 2001). Sea water temperature varies seasonally throughout the year. Temperature loggers attached to the experimental frames recorded an annual mean temperature of 24.6 °C, a winter low of 18.4 °C in August and an annual high of 31.37 °C in January (temperature data recorded May 2012–April 2013). The residence time of the water in the lagoon is 0.5–5.4 d (Hatcher and Frith 1985). For further details of the experimental site at One Tree Island, see Mallela et al. (2017).

Experimental design

Settlement plates were deployed to assess how micro-habitat complexity influences reef growth and community development. The surfaces of custom-made, unglazed, ceramic settlement plates were characterised by two contrasting surface topographies: smooth or ridged (Electronic supplementary material, ESM, Fig. S1). All settlement plates were square (13.2 cm × 13.2 cm). Ridged plates had a series of parallel ridges and grooves running across the entire width of each tile. Each indentation was 1.1 mm from the bottom of the groove to the top of the ridge, with 1.3 mm spacing between adjacent ridges or grooves. The depth and width of grooves were based on estimates of bite scars of juvenile bioeroding parrotfish (Fox 2006; Steneck 1983). In this study, ‘micro scale’ refers to fine-scale features (e.g. ridges and grooves) < 1 cm in diameter and ‘macro scale’ refers to larger areas (e.g. entire settlement plates) ≥ 1 cm in diameter.

Settlement plates were positioned randomly within the microatoll system at One Tree Island. All plates were positioned horizontally, reflecting the natural underlying topography (angle of the substrate) on which they were positioned (between 0° and 10° slope). Plates were positioned in overlaid pairs, one on top of the other, so that each pair had an exposed (upwards-facing, well-lit) side and a cryptic (downwards-facing, shaded) side with the two middle planes flush (planes touching). As the mechanical stability of the underlying reef substrate can influence post-settlement survival of coral recruits (Yadav et al. 2016), all experimental substrates were securely anchored to the reef.

Settlement plates were attached to PVC frames through pre-drilled holes using cable ties. Plates were positioned 2–5 cm off the bottom of the microatoll enabling organisms to recruit to both the exposed and cryptic surfaces of the plates. This resulted in four habitat types: smooth-exposed, smooth-cryptic, ridged-exposed and ridged-cryptic. On the Great Barrier Reef, mass coral spawning occurs in November (Harrison et al. 1984). Settlement plates were deployed in May 2012 to allow for biofilm development prior to the mass spawning and lifted 4–6 months after the mass spawning in November to assess recruitment success and development after spawning. Plates were collected after two periods of deployment: 11 months (61 plates lifted in April 2013) to assess early community development; the remaining plates were lifted after 34 months (123 plates, lifted March 2015) to assess longer-term epibenthic community development, in particular, reef-building organisms (encrusting sclerobionts) and rates of reef growth.

Community composition

To assess how substrate topography and habitat influenced initial recruitment and colonisation and to see whether this changed over time, plates were analysed for community composition after 11 months and 34 months. The community composition (percentage cover) of each settlement plate was analysed by superimposing a 100-point grid over each tile. Benthic cover was identified under each point to taxon or order (e.g. coralline algae, scleractinian coral, cheilostome bryozoan, solitary bryozoan, calcareous worm, sponge, turf algae). Areas of uncolonised substrate were also noted, and unidentified organisms were noted as other—calcareous (organisms with a calcareous structure) or other—soft (fleshy organisms). A small subset of this community data (smooth plates immersed for 34 months) was reported in a methods validation study (Mallela et al. 2017).

Coral recruitment

Successful recruitment by scleractinian corals, and subsequent primary carbonate production, is critical for ongoing reef development and habitat growth (Stearn et al. 1977). Coral recruitment across treatments was assessed to better understand early- and mid-life-history processes and substrate choices. Using a compound microscope, the entire surface area of each tile was checked for coral recruits. The total number recruiting to each plate per habitat type after 11 months was counted (year 1 plates analysed: 15 ridged-cryptic plates, 13 smooth-cryptic, 16 ridged-exposed, 17 smooth-exposed). The underlying substrate that scleractinian corals recruited to was noted (e.g. bare tile, coralline

algae, cheilostome bryozoan). Additionally, for ridged plates, it was noted if recent coral recruits (≤ 1 mm diameter) had preferentially settled in a groove or on a ridge. Care was taken to note the difference between solitary bryozoans (e.g. *Lichenopora* sp.) and coral recruits, which may be easily mistaken in the early post-settlement stages.

Micro scale topography: ridges and grooves

Ridged plates lifted after 11 months were used to examine potential differences in coral and encruster recruitment at the micro scale (ridges vs grooves). A compound microscope was used to conduct visual transects along the width of each tile following either the top of a ridge or the bottom of a groove. Any recently recruited organism (solitary scleractinian organisms ≤ 1 mm width) touching the transect was included in the total count. All ridges and grooves were randomly selected from the lifted plates; none of the analysed belt transects were immediately adjacent to or touching each other. In total, 57 grooves and 57 ridges were analysed.

Carbonate production

Carbonate production rates were evaluated across the four habitats and after the two deployment periods. Carbonate production rates ($\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) were estimated from plates removed from the reef after 11 months ($n = 37$) and 34 months ($n = 147$) using standard methods adapted from Mallela (2007, 2013). Plates were soaked in fresh water for 24 h, rinsed to remove any loose material (e.g. sediment) and oven dried at 35 °C to constant weight. Soft, non-calcareous organisms were removed using a soft brush or forceps, taking care not to dislodge calcareous, encrusting organisms (sclerobionts). Settlement plates were weighed (m_1) and then immersed in domestic white vinegar for 3 d to remove all encrusting organisms. Plates were then rinsed in fresh water and air-dried to a constant weight (m_2). Control tests were run on manually cleared settlement plates; no weight loss from the tile material was observed on controls. Annual sclerobiont carbonate production rates were calculated as:

Carbonate production rate

$$= \left[(m_1 - m_2) / \text{number of months deployed} \right] \times 12.$$

Parrotfish and urchin communities

Parrotfish and urchins were observed using visual scuba census between 0900 and 1130 h to characterise the external bioeroder community at the study location. In

2015, nine transects were randomly conducted at the study site. Transects were 30 m long, and organisms were observed 2.5 m on either side of the transect line. Fish were observed up to 5 m above the substratum (i.e. a $30 \times 5 \times 5$ m belt transect) (Mallela et al. 2007). Transects were positioned randomly across reef areas. Parrotfish species, abundance and length estimates were noted for species capable of external bioerosion: bicolor parrotfish, *Cetoscarus bicolor*; Bleekers parrotfish, *Chlorurus bleekeri*; bumphead parrotfish, *Bolbometopon muricatum*; bullethead parrotfish, *C. spilurus* (formerly *C. sordidus*); Japanese parrotfish, *C. japonensis*; steephead parrotfish, *C. microrhinos*; and surf parrotfish, *Scarus rivulatus*. All other species were classified as ‘other parrotfish’, *Scarus* spp. Fish were grouped into total length classes in 5-cm bins (< 5, 6–10, 11–15, 16–21, etc.). Observer effort was standardised by swimming transects at a constant rate (4 m min^{-1}). Urchins were identified to species and their maximum diameter measured with callipers.

Statistical analysis

Community composition data (% cover) were analysed using multivariate statistical software packages, PRIMER 6 with the PERMANOVA package (Clarke and Gorley 2006; Anderson et al. 2008). PRIMER was used to compare the community composition of epibenthic assemblages colonising the treatments—smooth-exposed, smooth-cryptic, ridged-exposed and ridged-cryptic—over the two time periods (11 and 34 months). Non-metric multidimensional scaling (MDS) ordinations of PERMANOVA distance from centroid matrices (Anderson et al. 2008) were used to represent calcareous community assemblages (percentage cover). Data were standardised and square-root-transformed with resemblances based on Bray–Curtis similarity. In MDS plots, lower stress values indicate more reliable results. For example, stress values > 0.3 indicate that points are almost arbitrarily positioned; stress 0.1–0.2 gives a potentially useful 2-D picture but should be interpreted with caution, and stress values of < 0.05 (as in Fig. 1) indicate clear ordinations with a minimal likelihood of misinterpretation (Clarke and Gorley 2006).

One-way analyses of similarities (ANOSIM) tests were used to assess differences in community composition over time. ANOSIM R values were used to indicate the degree of overlap in encruster assemblages among sites and habitats. R values are given on a scale of 0–1; the closer the R value is to 0, the greater the degree of overlap between assemblages. When ANOSIM indicated a significant difference between substrate types ($R > 0.1$), similarity percentages analyses (SIMPER), using one-way analysis on Bray–Curtis similarities for substrate groups using a 90%

dissimilarity threshold, were used to indicate which benthic groups were responsible for these observed differences.

The abundance and substrate preferences of coral recruits and other sclerobionts were further explored using IBM SPSS 22 statistical software (www.spss.com). Where appropriate, normality of distribution and homogeneity of variance were tested using Kolmogorov–Smirnov and Levene’s tests, respectively. For normally distributed data, t tests were used to test for differences in coral recruitment between treatments. For non-normal data, the Mann–Whitney U test was used to compare successful recruitment to different topographic micro-features (ridges vs grooves).

Carbonate production data were analysed using generalised linear models (GLM; type III sum of squares, Wald Chi-square, covariance matrix, main effects build term, three-way interaction, 95% confidence interval level) and Bonferroni post hoc tests in SPSS 22. The results were considered significant where $p \leq 0.05$. The GLM was used to assess differences between immersion time (11 months and 34 months), reported here as years when plates were collected: 2013 and 2015, respectively ($df = 1$), and to determine whether significant differences occurred according to substrate architecture (micro-ridged or smooth substrate, $df = 1$) or orientation (cryptic or exposed, $df = 1$). Conservative Bonferroni post hoc tests were done to examine the source(s) of any significant differences. Post hoc results ($df = 7$) were considered significant where $p \leq 0.05$.

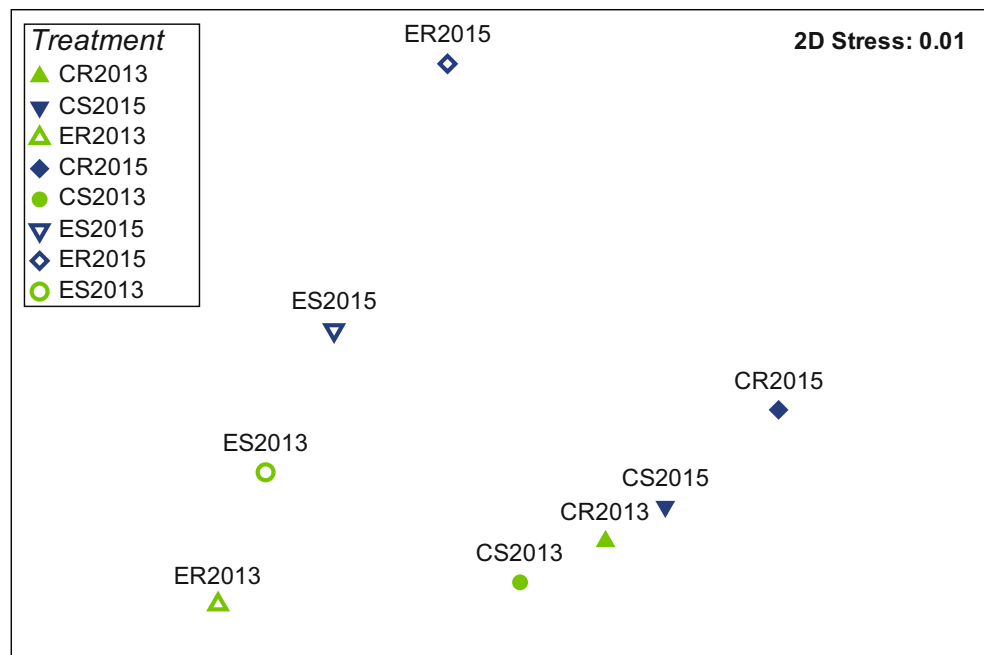
Results

Community composition

Non-metric MDS ordinations (Fig. 1) gave an excellent representation of calcareous community assemblages (2-D stress = 0.01) with groups separating out by both orientation (upwards or downwards) and period of submersion (11 or 34 months).

ANOSIM tests showed significant differences in community composition over time (with submersion period, orientation and tile topography set as independent variables; Global $R = 0.372$, $p = 0.001$). Exposed plates were characterised by a greater abundance of calcareous worms after 34 months than plates submerged for 11 months. Downwards-facing cryptic plates that were submerged for longer time were characterised by a greater abundance of coral recruits (< 1 cm) and calcareous worms. No effect of fine-scale surface topography (ridged vs smooth) was apparent at the macro scale (entire tile) (Figs. 1, 2a–d; full details in ESM Table S1).

Fig. 1 Multidimensional scaling ordinations of PERMANOVA distance from centroid matrices constructed from the benthic cover (%) of calcareous organisms. Green symbols represent 11 months of growth; blue symbols represent 34 months of growth. Downwards-facing, cryptic plates (C) are represented by filled-in symbols; and upwards-facing, exposed plates are represented by unfilled symbols. The letters R and S are for ridged and smooth plates, respectively



Coral recruitment

When the entire surface area of plates was scanned, a total of 370 coral recruits < 1 cm diameter were observed growing on plates after 11 months (Fig. 2d). Of these, 98.6% were attached to cryptic settlement plates (365 individuals) with the remainder (5 individuals, or 1.4%) growing on exposed settlement plates. As the majority of coral recruits were observed on cryptic tiles data, the following analysis is based on cryptic tile data.

A total of 105 coral recruits were randomly subsampled on cryptic settlement plates, 78 on ridged plates and 27 on smooth plates. Coral recruit data were normally distributed in cryptic tile treatments. There was no significant difference in the total number of recruits on ridged versus smooth plates ($p > 0.05$) at the macro scale.

Of 78 coral recruits growing on ridged plates (complex micro-habitat), 71 (91%) recruited to coralline algae and 7 (9%) to uncolonised portions of settlement plates, with 91% also preferentially recruiting to grooves instead of ridges (82% on coralline algae in grooves, 9% on bare sections of the groove; Fig. 3). Of the 27 coral recruits on smooth plates (low habitat complexity), 26 (96%) recruited to patches of crustose coralline algae and one recruited (4%) to a section of bare plate (ESM Fig. S1).

Sclerobiont micro scale analyses: ridges and grooves

Ridges and grooves on ridged plates were analysed at the micro scale (mm) after 11 months to assess if there were micro scale differences in sclerobiont (both encruster and

coral) recruitment. On cryptic plates, grooves had significantly higher sclerobiont recruitment (Mann–Whitney U test: median_{cryptic grooves} = 0.3 cm⁻¹, median_{cryptic ridges} = 0.07 cm⁻¹, $U = 46$, $p < 0.001$). On exposed plates, despite lower numbers of recruits, similar patterns were observed with organisms displaying a settlement preference for grooves over ridges ($U = 265.5$, $p < 0.05$; Fig. 4; Table 1; ESM Table S1).

Carbonate production

The mean rate of growth, averaged across all treatments, was 374 ± 154 g CaCO₃ m⁻² yr⁻¹ (Fig. 4; Table 2). GLM indicated significant differences in rates of carbonate production between treatments ($p = 0.000$). Post hoc Bonferroni tests (ESM Table S2) revealed significant differences between ridged and smooth tiles ($p \leq 0.005$), with ridged tiles characterised by greater rates of carbonate production (mean ± SE 421 ± 18 and 348 ± 19 g CaCO₃ m⁻² yr⁻¹, respectively). There were also significant differences between cryptic and exposed surfaces ($p \leq 0.002$; 344 ± 18 and 425 ± 18 g CaCO₃ m⁻² yr⁻¹, respectively). Finally, the combined effect of orientation and immersion period had a significant impact ($p = 0.000$). Cryptic plates showed increasing rates of production as the deployment period increased from 11 to 34 months of submersion (301 ± 31 and 386 ± 19 g CaCO₃ m⁻² yr⁻¹, respectively). In contrast, exposed plates displayed the opposite pattern, with rates of production falling between 11 and 34 months of deployment (513 ± 32 and 336 ± 18 g CaCO₃ m⁻² yr⁻¹, respectively) (Fig. 5).

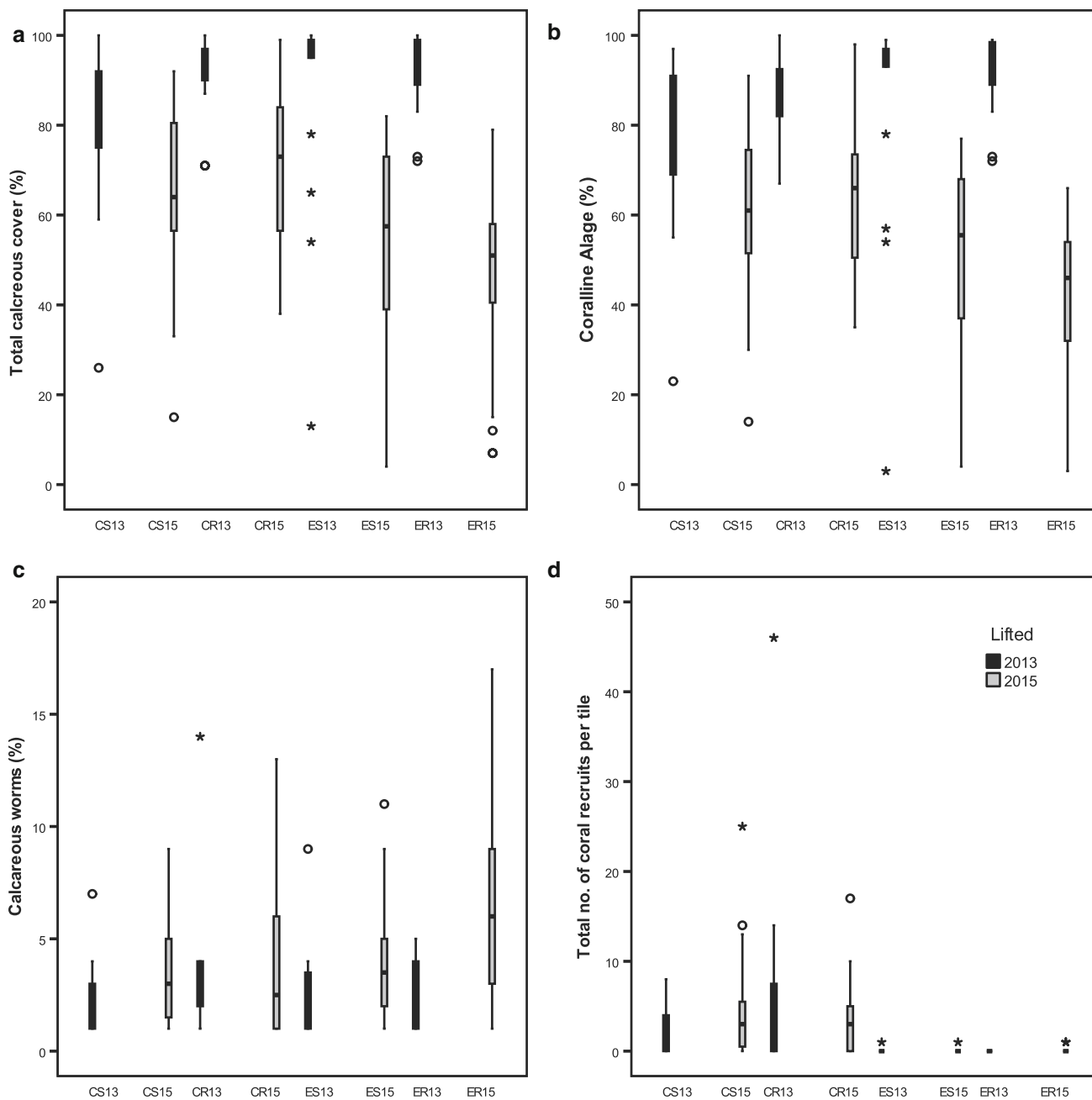


Fig. 2 Benthic cover (%) of **a** total calcareous organisms, **b** coralline algae, **c** calcareous worms and **d** the number of coral recruits (< 1 cm) per tile. *C* cryptic, *E* exposed, *R* ridged, *S* smooth, 13: lifted

after 11 months in 2013, 15: lifted after 34 months in 2015. Note different y axis scales. Circles indicate outliers ($> \times 1.5$ interquartile, IQ, range) and stars indicate extremes ($> 3 \times$ IQ range)

Parrotfish and urchin community composition

The parrotfish population in this study was dominated by small individuals. A total of 197 parrotfish were observed with 93% of individuals < 16 cm total length (0–5 cm: 45%, 6–10 cm 38%, 11–15 cm: 10%). *Chlorurus spilurus* made up 43% of all observed individuals; 12% were *Scarus rivulatus*; 2% were *C. microrhinos*, and 43% of

observations were of ‘other parrotfish’ (Table 3). No urchins were observed along any transects.

Discussion

This study investigated the micro scale (mm) and macro scale (cm) effects of fine-scale substrate topography, specifically the presence or absence of (micro) ridges and

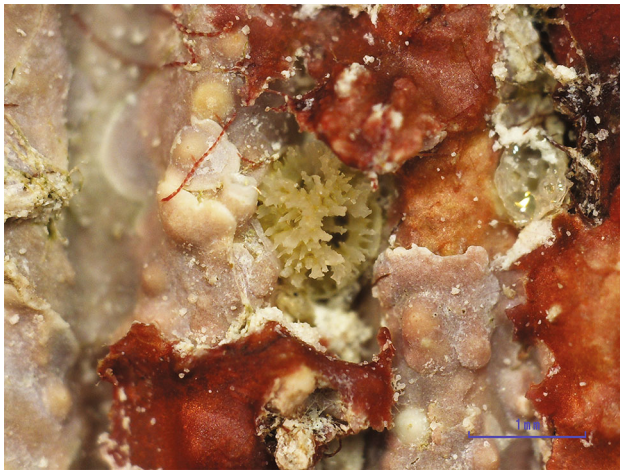


Fig. 3 A coral recruit growing in a groove on a cryptic plate. Image taken after 11 months of submersion in 2013. Scale bar 1 mm

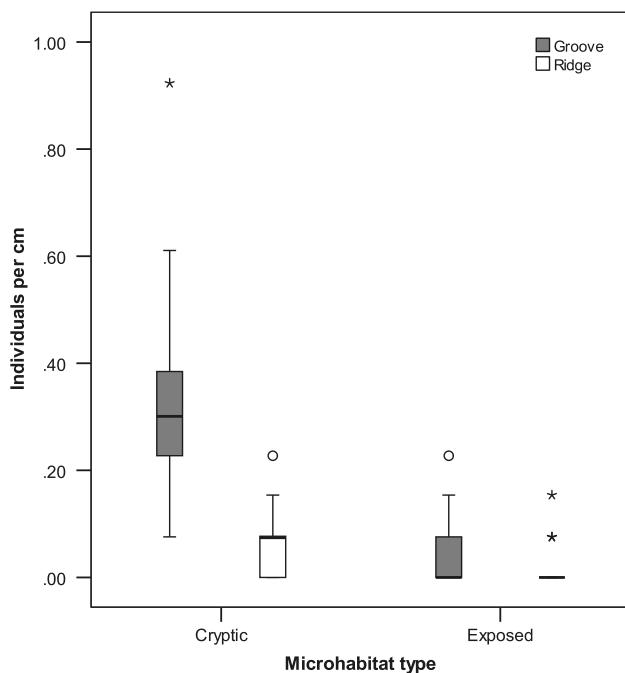


Fig. 4 Number of individuals cm^{-2} of solitary encrusters (solitary bryozoans, coral recruits, calcareous worms, bivalves, other) on ridges (white) and in grooves (grey) on corrugated plates in upwards-facing (exposed) and downwards-facing (cryptic) reef settings. Circles indicate outliers (> 1.5 interquartile, IQ, range) and stars indicate extremes ($> 3 \times$ IQ range)

grooves, on community composition, recruitment by reef-building sclerobionts (coral and encrusters) and macro scale carbonate production. On ridged substrates, all calcareous organisms, encrusters and corals, showed a preference for recruiting to grooves rather than ridges. Interestingly, at the macro scale (entire plate), no significant differences in recruitment or community composition were apparent when the community composition of ridged

substrates was compared with smooth plates; all plates were dominated by crustose coralline algae. The majority of coral recruits were observed on cryptically orientated ridged and smooth plates, and the majority ($> 90\%$) were observed to be overgrowing crustose coralline algae. Rates of carbonate production were significantly greater on ridged plates ($421 \pm 18 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) than on smooth plates ($348 \pm 26 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), and on exposed plates ($425 \pm 18 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) than on cryptic plates ($343 \pm 18 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). There were also clear interactions between substrate orientation (cryptic vs exposed) and the period of deployment (11 vs 34 months); rates of production increased on cryptic plates but decreased on exposed plates over time.

Community composition and sclerobiont recruitment

In this study, recruitment by calcareous reef-building organisms varied markedly at the micro scale with sclerobionts occurring more often in grooves than on ridges. These findings confirm earlier work which highlights the rugophilic (i.e. flourishing on rough surfaces or in small surface depressions) nature of encrusting organisms (e.g. Taylor 1990) and coral recruits (Carleton and Sammarco 1987; Harriott and Fisk 1987; Brandl et al. 2014; Doropoulos et al. 2016). At the larger, macro scale, community composition was similar between ridged and smooth plates. This contrasts with findings in Japan (Nozawa et al. 2011) on high-latitude, shallow reefs (5 m depth). Nozawa et al. (2011) found that settlement plates with micro-crevices were characterised by higher numbers of calcareous, benthic invertebrates (e.g. bryozoans, barnacles, calcareous worms) than smooth plates without micro-crevices. However, this difference may be due to the larger size of micro-structure used in the Japanese experiment and/or the abundance of urchins and parrotfish. The shape of micro-crevices is also likely to be an important variable (Brandl and Bellwood 2016). Nozawa et al. (2011) used a circular micro-structure, wider (5-mm diameter) and deeper (3–4 mm deep) than the shallow (1.1 mm deep), parallel grooves and ridges (1.3-mm spacing) used in this study.

Previous work has found that crevices promote coral recruitment, enabling the survival of recruits under high grazing (external abrasion) pressure from urchins and fish (Brock 1979; Sammarco 1980; Nozawa 2008; Edmunds et al. 2014; Brandl and Bellwood 2016; Gallagher and Doropoulos 2017). Interestingly, species-specific studies in Japan noted how coral growth rates may influence the importance of micro-crevices, with fast-growing corals (e.g. *Acropora* sp.) less dependent on micro-crevices to protect them from grazer activity as they are able to attain a larger size more rapidly making them less vulnerable to

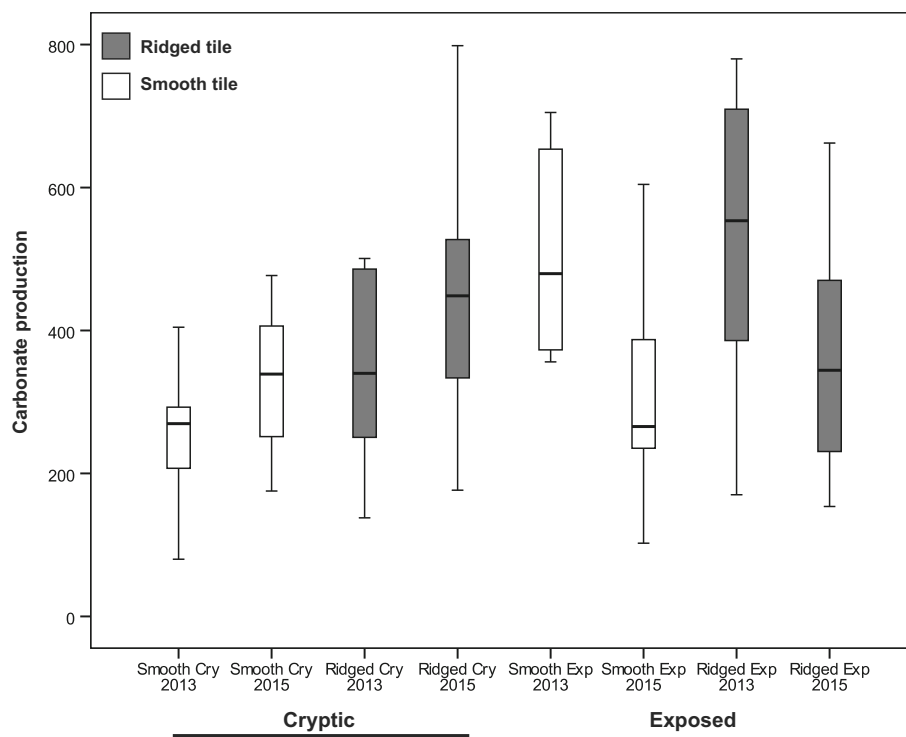
Table 1 Percentage cover (SD) of dominant calcareous organisms on belt transects from subsampled ridges and grooves on settlement plates. Data presented according to location (groove or ridge) and orientation (cryptic vs exposed)

Micro-habitat	Calcareous worms	Bryozoa	Coral recruits	Bivalves
Cryptic groove	51.8 ± 45.7	3.2 ± 7.6	6.4 ± 16.6	0 ± 0
Cryptic ridge	35.0 ± 47.6	6.7 ± 21.8	0 ± 0	0 ± 0
Exposed groove	19.1 ± 37.8	0 ± 0	0 ± 0	0 ± 0
Exposed ridge	5.6 ± 21.2	1.9 ± 9.6	0 ± 0	0 ± 0

Table 2 Carbonate production (g CaCO₃ m⁻² yr⁻¹) on smooth or ridged, cryptic or exposed settlement plates after 11 or 34 months of submersion

Plate treatment	Duration (months)	N	Mean	SD	SE	Minimum	Maximum
Smooth-cryptic	11	9	255.04	89.08	29.69	80.01	404.59
	34	24	332.63	91.03	18.58	175.44	476.96
Ridged-cryptic	11	10	348.33	133.30	42.15	137.94	500.80
	34	27	438.90	149.46	28.76	176.53	798.52
Smooth-exposed	11	9	502.28	140.19	46.73	356.02	704.98
	34	26	301.28	117.08	22.96	102.39	604.39
Ridged-exposed	11	9	523.94	221.09	73.70	170.26	780.04
	34	30	370.96	158.18	28.88	153.82	662.29
Total		144	373.68	153.93	12.83	80.01	798.52

SD standard deviation, *SE* standard error

Fig. 5 Carbonate production by coral recruits and encrusters in four different treatments: ridged substrates (dark grey) or smooth substrates (white) in cryptic (Cry) or exposed (Exp) orientation after 11 months (2013) or 34 months (2015) of deployment

grazing activity (Nozawa 2010). One Tree lagoon is characterised by very limited external bioerosion (this study; Kiene 1988a). During this study, no urchins were observed within the experimental areas and juvenile

parrotfish dominated, typically < 10 cm total length and hence with limited gape size/bioeroding capabilities (Bruggemann et al. 1996; Bonaldo et al. 2014). Micro-crevice studies in Japan have been conducted in locations

Table 3 Mean number of parrotfish (SD) in 5-cm size classes per 30 × 5 × 5 m belt transect ($n = 9$)

Species	Common name	Size class				
		0–5	6–10	11–15	16–20	21–25
<i>Cetoscarus bicolor</i>	Bicolour parrotfish	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Chlorurus bleekeri</i>	Bleekers parrotfish	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Bolbometopon muricatum</i>	Bumphead parrotfish	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Chlorurus spilurus</i>	Bullethead parrotfish	5.33 ± 2.78	3.33 ± 2.87	0.44 ± 0.73	0.22 ± 0.67	0.00 ± 0.00
<i>Chlorurus japanensis</i>	Japanese parrotfish	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Chlorurus microrhinos</i>	Steephead parrotfish	0.44 ± 0.73	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Scarus rivulatus</i>	Surf parrotfish	0.33 ± 0.50	0.67 ± 1.32	0.56 ± 1.01	0.56 ± 1.13	0.56 ± 0.73
<i>Scarus</i> spp.		3.78 ± 2.82	4.22 ± 2.49	1.22 ± 1.79	0.22 ± 0.44	0.00 ± 0.00

with abundant grazers and therefore attribute high mortality on flat substrates to chronic grazing activity, in particular by urchins, and the subsequent abrasion of encrusters and coral recruits (Nozawa 2008; Nozawa et al. 2011). In contrast, experiments in Palau investigating the effects of artificially excluding fish using cages found that maximum recruitment occurred in crevices in uncaged treatments (Doropoulos et al. 2016). It is suggested here that the small size of parrotfish and lack of urchins resulted in grazing of turf algae but limited external abrasion of sclerobionts within the lagoon system at One Tree Island. This resulted in domination of both smooth and ridged surfaces by crustose coralline algae and similar rates of encruster and coral recruitment at the macro scale. It should be noted that other external bioeroders (e.g. crabs and chitons) were not quantified in this study; however, they were not observed by scuba divers during the initial site selection.

Micro-structure and its effect on carbonate production

The continued and sustained recruitment of sclerobionts is critical to future reef growth and development. Despite this, there is remarkably little known about the role that micro-structure plays in facilitating and enabling reefal carbonate production over short (< 12 months) and longer (> 2 yr) time frames. This study demonstrates that micro-habitat features (grooves and ridges) on the underlying substrate enhance macro scale reef growth by increasing rates of carbonate production compared to smooth substrates. Carbonate production by both primary (corals) and secondary (encrusters) reef builders was 17% greater on ridged substrates. The presence of micro scale grooves and ridges may provide protection and refuge from physical and biological disturbances during early growth and calcification stages.

Asymptotic growth patterns are typically observed in most calcareous species; growth rates are initially high and then slow down as colonies mature and become larger (Martindale 1976). Interestingly, the exposed substrates in this study displayed this classic growth pattern with significant reductions in calcification over time. In contrast, carbonate production on cryptic substrates was initially slow, increased over time and had not yet plateaued after 34 months. It should be noted that no attempt was made to differentiate between rates of carbonate production of different calcifying organisms; this is an area that warrants future attention.

The study also investigated the effects of substrate orientation (cryptic or exposed) on carbonate production. Exposed plates had higher rates of carbonate production than cryptically oriented substrates. These findings are consistent with settlement-plate studies of encruster calcification on Caribbean fore-reefs in Tobago and at clear-water sites in Jamaica, which also demonstrated greater rates of carbonate production on exposed, well-illuminated substrates (Mallela 2007, 2013). Environmental conditions such as light penetration also influence encruster development, with higher growth rates and thicker calcareous crusts on more illuminated surfaces (Martindale 1992; Mallela and Perry 2007). As crustose coralline algae, a photosynthesising organism, dominated all substrates, it is perhaps unsurprising that these photophilic communities, growing on well-lit exposed substrates, initially calcified more rapidly than those recruiting to low-light, cryptic substrates.

Encruster carbonate production in shallow coral-reef lagoons

The mean rates of carbonate production recorded here fall within the lower range reported for One Tree lagoon from 1984 to 1986, which fluctuated from 0 to 1040 g CaCO₃

$\text{m}^{-2} \text{yr}^{-1}$ over the course of a two-year study of encruster growth on natural coral substrates (Kiene 1988b). The 2012–2015 One Tree Island production rates are consistent with other shallow lagoon settlement-plate studies which report mean rates of 358–476 $\text{g CaCO}_3 \text{m}^{-2} \text{yr}^{-1}$ in the back-reef lagoon (3 m depth) at Puerto Morelos, Mexico (2003–2004; Hepburn et al. 2015). Experiments on natural coral substrates in shallow atoll lagoons (1–2 m depth) in French Polynesia from 1990 to 1992 reported mean production rates ranging from 180 (± 190) to 1130 (± 540) $\text{g CaCO}_3 \text{m}^{-2} \text{yr}^{-1}$ (Pari et al. 1998). Interestingly, production rates at a mid-oceanic lagoon system in the Indian Ocean, Vabbinfaru, Maldives over 13 months (2010–2011) were much lower at $0.047 \pm 0.019 \text{ g CaCO}_3 \text{m}^{-2} \text{yr}^{-1}$ (Morgan and Kench 2014). Such differences could be attributed to differences in experimental substrate type as the Maldives study used PVC poles which can attract different encruster assemblages (Adey and Vassar 1975; Mallela et al. 2017), as opposed to settlement plates or natural coral substrates which have been reported to be characterised by similar assemblages (Martindale 1992; Mallela 2007). These tentative, initial multi-decadal comparisons of encruster carbonate production rates in shallow lagoons suggest that the maximum rates of calcification of encrusters observed in the 1980s and 1990s may be declining, warranting future attention.

External bioeroders: parrotfish and urchins

This study also provides an opportunity to consider the importance of micro-topography for reef accretion in a system characterised by low abundance of mature, externally bioeroding organisms. While bioeroding species (e.g. *Chlorurus spilurus*) were present, these predominantly small and usually juvenile fish were observed feeding on algal turf, sediment and rubble at the study site. This is consistent with historical observations within the One Tree lagoon which also note low levels of external bioerosion activity by parrotfish and urchins (Kiene 1988a). Parrotfish size has been positively correlated with their bioeroding capabilities (Bruggemann et al. 1996); the larger the mouth, the more carbonate substrate they can erode. The small gape size of most parrotfish within the One Tree lagoon clearly reduces their bioeroding capabilities. This study only considered the potential impact of parrotfish and urchins; other bioeroding organisms (e.g. chitons, trigger fish and surgeonfish), which may cause incidental mortality, were not considered. The small size of the resident parrotfish communities in the lagoon may limit their feeding to other food sources (e.g. algal turf and small clasts) (Clements et al. 2016), curtailing their ability to abrade or bioerode calcareous organisms recruiting to both flat and ridged surfaces.

Micro-topography of coral-reef substrates, particularly the presence of grooves, promoted the recruitment of reef-building organisms and subsequent reef development via carbonate production. Encruster and coral recruits primarily settled in micro-crevices when they were available. The presence of a biofilm such as crustose coralline algae was a clear driver of coral recruitment across all experimental substrates and habitats. Substrates that incorporated micro scale topography were also characterised by faster rates of carbonate production. Reef recovery and carbonate budget studies may benefit from also considering the role of micro-topography in facilitating future reef growth and carbonate production.

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