

# Spatial variation in mechanical properties of coral reef substrate and implications for coral colony integrity

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**Abstract** The physical structure of coral reefs plays a critical role as a barrier to storm waves and tsunamis and as a habitat for living reef-building and reef-associated organisms. However, the mechanical properties of reef substrate (i.e. the non-living benthos) are largely unknown, despite the fact that substrate properties may ultimately determine where organisms can persist. We used a geo-mechanical technique to measure substrate material density and strength over a reef hydrodynamic gradient. Contrary to expectation, we found a weak relationship between substrate strength and wave-induced water flow: flow rates decline sharply at the reef crest, whereas substrate properties are relatively constant over much of the reef before declining by almost an order of magnitude at the reef back. These gradients generate a novel hump-shaped pattern in resistance to mechanical disturbances for live corals, where colonies closer to the back reef are prone to dislodgement because of poorly cemented substrate. Our results help explain an intermediate zone of higher taxonomic and

morphological diversity bounded by lower diversity exposed reef crest and unstable reef back zones.

**Keywords** Reef substrate · Cementation · Scleractinian corals · Biomechanics

## Introduction

The mechanical integrity of the non-living component of the reef structure is of fundamental importance in coral reef ecosystems. This reef structure acts as a physical barrier to storm waves (Sheppard et al. 2005) and tsunamis (Fernando et al. 2005) and therefore provides protection for other marine habitats (e.g. lagoons, seagrass beds), coastal ecosystems and human populations (Wells et al. 2006). Meanwhile, the reef structure itself provides habitat for an enormous diversity of organisms, including reef-building species such as the scleractinian corals that in turn are the major source of carbonate material for reef maintenance and growth (Done 1983). The mechanical properties of the non-living reef are important determinants of habitat complexity and species distributions, both on top of the reef (Madin and Connolly 2006) and within the reef matrix (Highsmith 1981). For instance, the resistance of corals to dislodgement by waves explicitly depends on the strength of the reef substrate on which they recruit and grow (Madin 2005).

The mechanical integrity of reef substrate is determined by a variety of physical and biological processes. It begins with the supply of calcium carbonate from dead reef-building organisms. Wave agitation and water currents move these materials, aiding stabilisation and filling gaps in the reef with progressively smaller fragments (Rasser and Riegl 2002). Crustose coralline algae (CCA) grow over

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stabilised rubble and contribute to the initial binding process. However, it is the precipitation of secondary inorganic calcium carbonate ( $\text{CaCO}_3$ ), a process known as diagenetic reef cementation, that primarily binds framework components, fills interstitial pores and increases material density. Density and strength are strongly correlated in carbonate crystalline materials (Wainwright et al. 1982), and the degree of reef cementation is the main correlate of rigidity and stability of reef framework materials (Macintyre and Marshall 1988; Rasser and Riegl 2002; Perry and Hepburn 2008).

Many processes can influence reef cementation, which in turn contributes to the stability of the reef. Observations of reduced cementation in coral communities in the Galapagos, an area of lowered carbonate saturation state, suggest that cementation in coral reefs could decline as pH falls and stability may be threatened (Manzello et al. 2008). There is presently little understanding of baseline mechanical properties in a real reef system that would allow detection of changes in stability. Furthermore, despite a good and growing understanding of reef cementation processes, our understanding of how these processes translate into patterns of mechanical properties across the reef is poor. Therefore, our first objective was to measure the mechanical properties of reef substrate across a hydrodynamic reef gradient. For any given coral colony (i.e. size and shape) living at a given location over the reef gradient, vulnerability to dislodgement is determined by the maximum water velocity and the strength of the reef substrate to which it attaches (Madin and Connolly 2006). Therefore, our second objective was to utilise an existing long-term database of water motion to quantify how spatial patterns in reef substrate properties influence the mechanical vulnerability of reef corals to dislodgement.

## Materials and methods

Mechanical properties of coral reef surface substrate were estimated over a 120-m hydrodynamic gradient, from the exposed reef crest to the relatively benign reef back, at the south-east reef at Lizard Island, Australia. We chose a constant depth gradient, rather than the fore reef depth gradient, to avoid changes in irradiance and because it was more structurally comparable. Substrate properties were measured along two replicate transects, approximately 300 m apart, and at four locations on each transect (0 m: reef crest, 40 m: back crest, 80 m: reef flat and 120 m: back reef). We used a geo-mechanical technique called dynamic probing (Peck et al. 1974; Polous and Davies 1980; Bock 1984; Foruria 1984), which involves dropping a known mass a known distance down a pointed rod with known diameter. The resulting impact forces the rod into

the substrate, and various mechanical properties, such as density and strength, can be estimated based on correlations between these properties and the number of weight drops per penetration interval standardised by laboratory testing (Peck et al. 1974). We built a scaled-down version of the widely used dynamic cone penetrometer to focus on the surface substrate layer (upper 200 mm), given that this layer is of direct mechanical importance for coral colony integrity (Madin 2005). The cone diameter was 7.5 mm, and a 1,500 g weight was dropped 500 mm for each penetration. The scaled-down penetrometer could be easily operated by a single person, which enabled rapid collection of data and the high level of replication required to accurately capture the mechanical properties of the surface substrate, which were known a priori to be highly variable (Madin 2005).

At each of the four locations on each transect, ten haphazardly placed replicate vertical “depth transects” were taken into the hard, non-living (i.e. coral and algal) substrate (i.e. sand and rubble patches were avoided). Each depth transect consisted of ten sets of ten weight drops done at each of ten different points within the same immediate vicinity (approximately 10–20 cm maximum distance apart). Visible substrate fractures did not occur in the vicinity of the tests. Following each set of ten drops, the vertical depth of rod penetration into the substrate was recorded by a second person. The record of depth penetrated per ten drops was converted into drops per 10 mm penetrated. This 100-drop protocol for each depth transect meant that deeper measurements were not obtained in areas of reef with stronger surface substrate, which resulted in a lack of replication at depths greater than approximately 100 mm (Fig. 1a). We therefore grouped penetrometer measurements from the two transects and only calculated properties for 10-mm depth increments with four or more replicate measurements (Fig. 1a, above the dashed line).

Based on the specific energy required to displace a unit volume of material, the density of a carbonate material is proportional to the logarithm of the number of drops required to penetrate a given depth, and its strength is directly proportional to the number of drops (Polous and Davies 1980), which can be represented as follows:

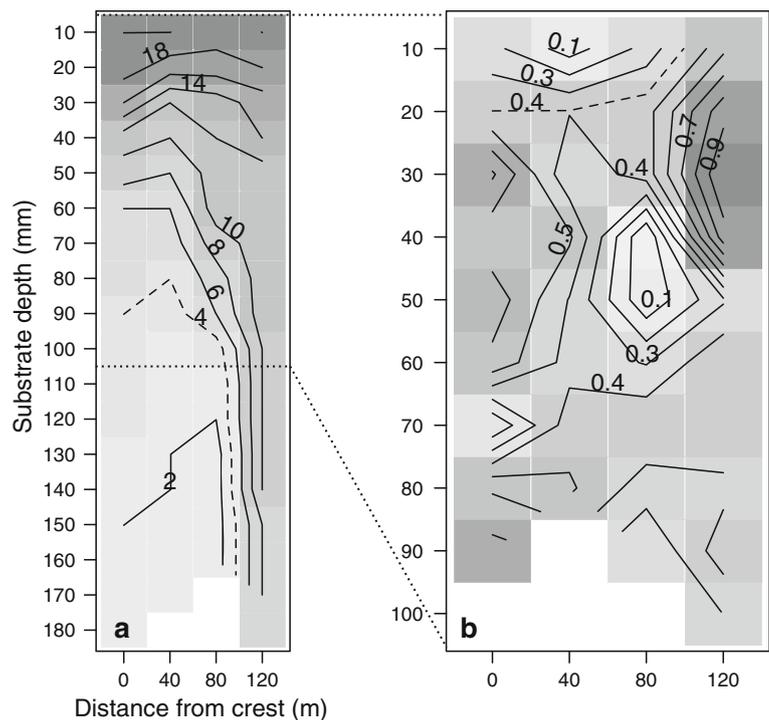
$$\rho = s_1 \log N + s_2 \quad (1)$$

$$\sigma_c = s_3 N \quad (2)$$

$$\sigma_t = s_4 N \quad (3)$$

where  $N$  is the number of drops to penetrate 10 mm,  $\rho$  is density,  $\sigma_c$  is compressive strength,  $\sigma_t$  is tensile strength and  $s_1$ – $s_4$  are laboratory-derived coefficients of proportionality. Coefficients of proportionality were calibrated in the laboratory by measuring the mechanical properties of 20 fist-sized substrate samples chiselled from the reef crest (0 m).

**Fig. 1** Contour plots showing **a** the number of penetrometer records and **b** standard deviation for number of drops per 10 mm depth increment for combinations of substrate depth and distance from the reef crest. Darker cells represent higher values. Substrate properties with fewer than 4 replicate measurements were not calculated (below dashed line in **a**), thereby limiting the study to the upper 100 mm of substrate. The dashed line in **b** highlights a general increase in substrate mechanical variability as a function of substrate depth and distance from the reef crest



Samples were soaked in a mild bleach solution to kill any epilithic organisms, blasted with water to remove dead tissue and then dried. The density of substrate samples was measured using Archimedes' Principle by first measuring the weight in air and then weight suspended in distilled water (density equals dry weight divided by dry minus immersed weight; Hughes 1987). Two cores were taken from all 20 substrate samples using a 12.5-mm-diameter diamond-tipped coring piece mounted into a standard drill press. We followed the same compressive and tensile strength testing procedure as outlined in Madin (2005). Tests were run until brittle failure, at which point strength was calculated by dividing the force of fracture by cross-sectional area. Given the difficulty of coring and testing heterogeneous substrate material, adequate mechanical measurements were only made for 11 of the original 20 substrate samples.

Coefficients of proportionality for each mechanical property were calculated by fitting the distribution of penetrometer measurements made at the reef crest (0 m) to the corresponding laboratory measurements (also made for the reef crest) using the *optim* function in the software package *R* (R Development Team 2012) (Fig. 2). Using these coefficients, material properties were estimated for all depth increments and locations over the reef gradient.

To examine how the interaction between substrate strength and wave-induced velocity influences the mechanical vulnerability of reef corals over the hydrodynamic gradient, we use the dimensionless dislodgement mechanical threshold (*DMT*) (Madin and Connolly 2006), which is expressed as follows:

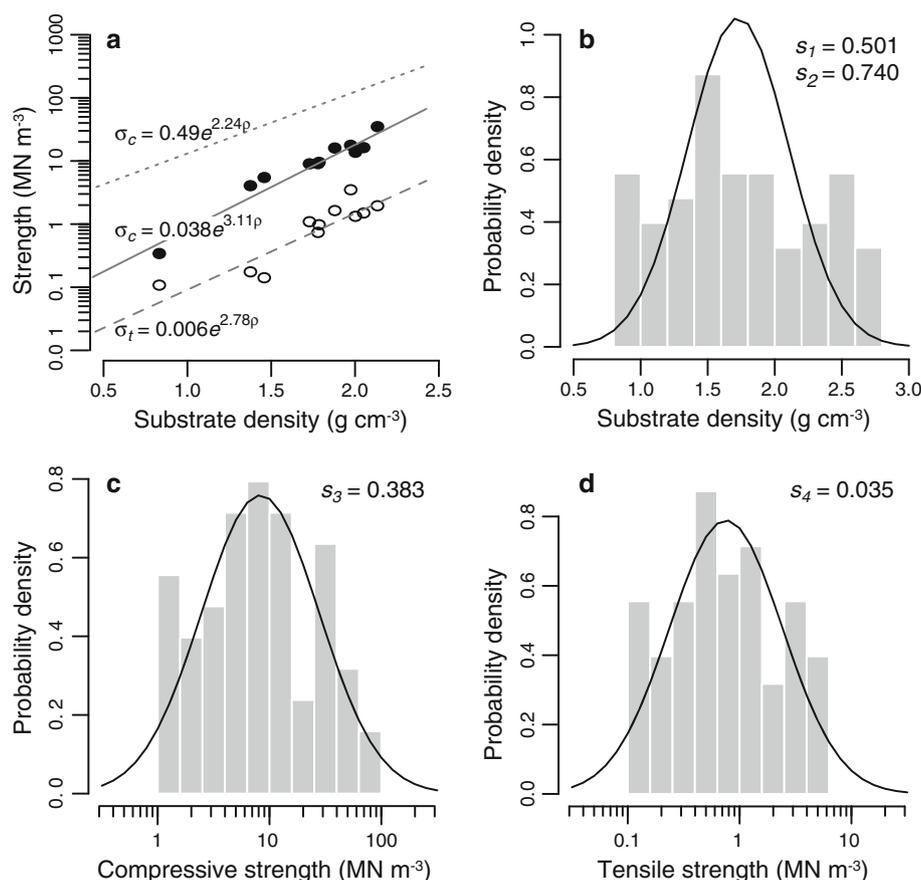
$$DMT = \frac{\sigma_t}{U^2 \rho_w} \quad (4)$$

where  $\sigma_t$  is the limiting material tensile strength (i.e. the reef substrate; Madin 2005),  $U$  is maximum water velocity and  $\rho_w$  is water density ( $\sim 1,025 \text{ kg m}^{-3}$ ). We used yearly maximum water velocities estimated at the reef substrate from a 37-year historical record estimated over the reef gradient at the study site (Madin et al. 2006). Given the fine spatial scale of the penetrometer cone and the variable nature of reef substrate, we assume that limiting substrate strength for a coral colony is best represented by the mean of the tensile strength for a replicate depth transect, resulting in ten means for each location across the hydrodynamic gradient. For each reef location, we used Monte Carlo simulations to randomly draw from the mean substrate strength and yearly maximum water velocity distributions to calculate the corresponding long-term *DMT* distribution (mean and standard deviation). However, we use mean yearly maximum water velocity to calculate variance in *DMT* over the gradient. Two-way nested ANOVAs and Tukey's honest significant differences were used to assess differences between locations over the hydrodynamic gradient (with depth transects nested within locations).

## Results and discussion

There is a clear exponential relationship between substrate density and strength for samples collected at the reef crest

**Fig. 2** **a** Laboratory substrate compressive (*solid points*) and tensile (*open points*) strength results as a function of density for reef crest samples (*solid and dashed lines* are best-fit linear models). *Dotted line* represents the relationship for coral skeleton compressive strength as a function of density from Madin et al. (2008). Best-fit penetrometer data (*grey bars*) with laboratory data (*black lines*) and corresponding coefficients of proportionality ( $s_1$ – $s_4$ ) for: **b** substrate density ( $\rho$ ) **c** compressive strength ( $\sigma_c$ ) and **d** tensile strength ( $\sigma_t$ )

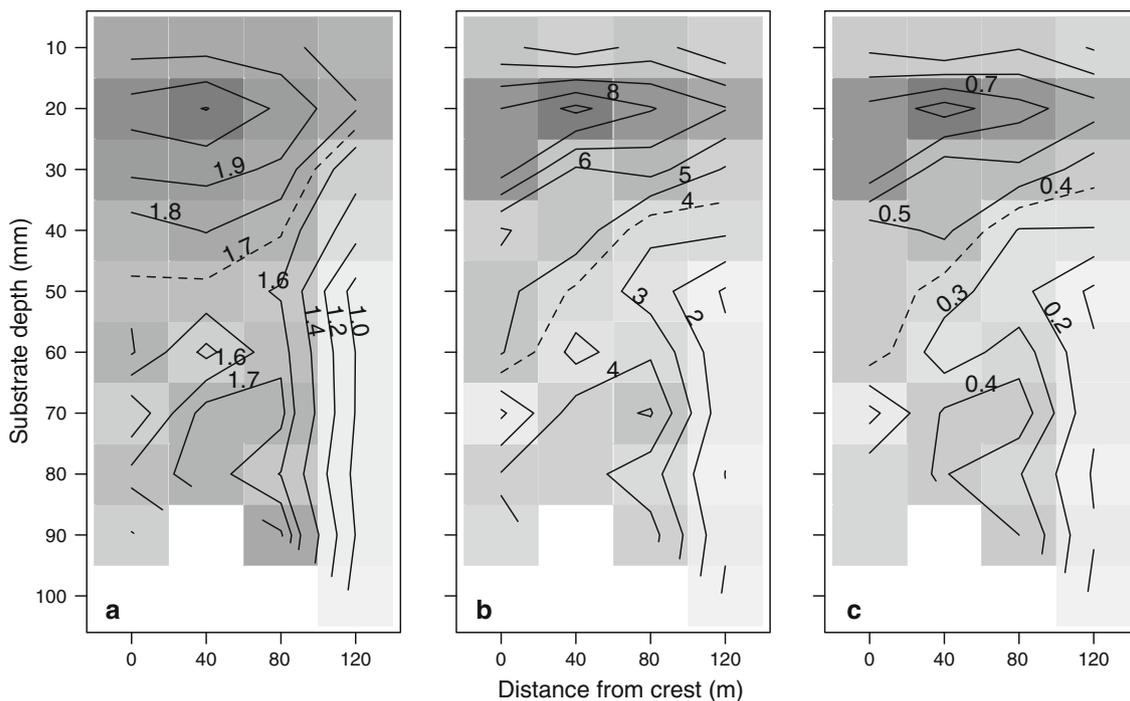


(Fig. 2a), similar to results for coral skeleton (Madin et al. 2008). Similar to other studies of crystalline materials, for a given material density, compressive strength is approximately an order of magnitude greater than tensile strength (Fig. 2a; Wainwright et al. 1982). Also in line with previous work, substrate strength is approximately an order of magnitude weaker than coral skeleton for a given density, presumably due to differences in biological and inorganic calcification processes (Fig. 2a; Macintyre and Marshall 1988).

Following the calibration of Eqs. 1 to 3 with the reef crest sample data (Fig. 2b, c), we found a marked reduction in substrate density and strength with increasing depth into the reef substrate and distance away from the reef crest (Fig. 3; Table 1). Dashed lines in the figure panels highlight the resulting wedge-shaped pattern in mechanical properties on the reef. Variability in mechanical properties showed the opposite pattern, where more variability was found in weaker, less-dense substrates (Fig. 1b). Maximum substrate density and strength were consistently observed just below the surface (10–20 mm). The weaker upper 10 mm of substrate may be related to partial diagenetic cementation at the substrate surface, weaker biological layers and crusts (e.g. CCA and algae) and/or greater amounts of bioerosion. Overall, mean substrate strength

remained relatively constant over the 80 m from the reef crest and then declined and became more variable towards the back reef (Figs. 3b, c, 4a). Surprisingly, this pattern was not strongly related to wave-induced water flow, which shows a characteristically different pattern across the reef (Fig. 4b). This suggests additional processes are acting to drive or contribute to differences in cementation across the reef (e.g. reef-scale  $\text{CaCO}_3$  saturation state gradient, biofacies, underlying substrate, alkalinity drawdown, tides and other currents). The decline in substrate strength at 80 m could indicate an upper limit to cementation or the commencement of substrate removal processes, for example, by bioeroders, or lagoon diurnal fluctuations to low pH (Santos et al. 2011) driving dissolution (Tynan and Opdyke 2011).

The 100-drop protocol created a bias where deeper substrate properties were only measured in weaker substrates. Consequently, material properties are likely to have been underestimated deeper into the substrate. For instance, it is difficult to know whether reductions in density and strength at greater substrate depths (Fig. 3) are a real pattern or simply the result of only measuring deeper layers in weaker substrates, which is more likely towards the reef crest. Furthermore, stronger substrate samples were easier to core and mechanically test in the laboratory,



**Fig. 3** Contour plots of mean substrate property estimates as a function of penetrometer substrate depth (to 100 mm) and distance from the reef crest. Panels are for **a** substrate density ( $\text{g cm}^{-3}$ ) and

**b** compressive strength and **c** tensile strength ( $\text{MN m}^{-2}$ ). Darker cells represent higher values. The dashed contour in each panel illustrates the tendency of material properties to be stronger and to permeate deeper towards the reef crest

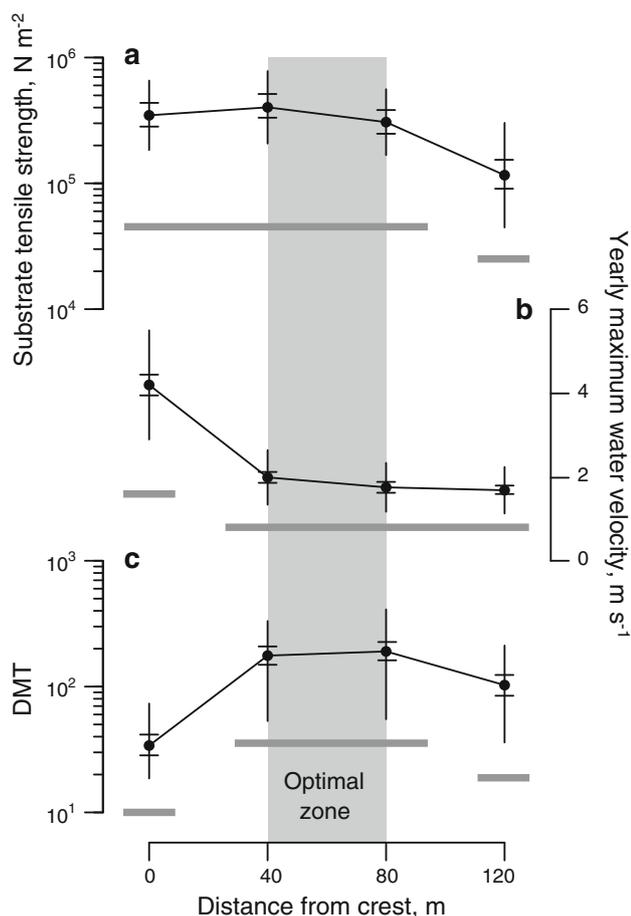
**Table 1** Two-way nested ANOVAs for a substrate density ( $\text{g cm}^{-3}$ ) and b compressive and tensile strength ( $\text{MN m}^{-2}$ ) and d *DMT* over the hydrodynamic reef gradient ( $n = 531$ )

	<i>Df</i>	<i>SS</i>	Mean squares	<i>F</i> value	$\text{Pr}(>F)$
<i>a. Substrate density</i>					
Site	3	52.06	17.354	60.57	$<2e-16$
Site:Depth	4	25.20	6.299	21.98	$<2e-16$
Residuals	523	149.85	0.287		
<i>b. Substrate strength</i>					
Site	3	39.28	13.093	60.57	$<2e-16$
Site:Depth	4	19.01	4.752	21.98	$<2e-16$
Residuals	523	113.05	0.216		
<i>c. Yearly maximum velocity</i>					
Site	3	159.93	53.31	77.14	$<2e-16$
Residuals	144	99.52	0.69		
<i>d. DMT</i>					
Site	3	48.06	16.019	74.11	$<2e-16$
Site:Depth	4	19.01	4.752	21.98	$<2e-16$
Residuals	523	113.05	0.216		

Depth transects were nested within gradient locations. One-way ANOVA for c yearly maximum water velocity over the hydrodynamic reef gradient ( $n = 37$ ). Because compressive and tensile strengths for a given penetration interval scale in the same way (Eqs. 3 and 4), the ANOVA table is the same for both strength types

resulting in a bias towards stronger samples being used to calibrate the penetrometer distributions (Fig. 2). While the absolute values of our results are largely consistent with other studies (Foruria 1984; Madin 2005), our protocol is therefore prone to overestimation of material properties. Nonetheless, these biases should act similarly over the hydrodynamic gradient and therefore not influence the broader patterns of substrate properties across the study reef. Finally, despite targeting visibly similar non-coral reef substrate at all locations over the reef gradient, we calibrated the specific energy equations (for all locations) with substrate from the reef crest, and therefore bias may arise if systematic differences in substrate composition occur over the gradient.

The characteristically different patterns in water flow and substrate strength attenuation across the reef result in a hump-shaped pattern of *DMT* (Fig. 4c). This occurs because at 40–80 m back from the reef crest, water velocity decreases markedly and substrate strength remains relatively high. This pattern suggests that rates of mechanical dislodgement are higher at the reef crest and reef back, resulting in a zone in between these and parallel to the crest that can support a wider range of colony shapes and sizes (or where for a given shape and size, dislodgement rates are predicted to be lower) (grey band in Fig. 4).



**Fig. 4** **a** Mean substrate strength, **b** mean yearly maximum water velocity and **c** dislodgement mechanical threshold (*DMT*), as a function of distance from the reef crest ( $\pm$  standard error [cap] and  $\pm 1$  standard deviation [no cap]). Grey horizontal bars summarise Tukey's honest significant differences. Shaded region highlights the zone with lowest risk of dislodgement for a given colony shape and size

Indeed, the integration of these environmental gradients into population models suggests an intermediate region across the reef where lifetime reproductive output of *Acropora hyacinthus* is greater (Madin et al. 2012). The hump-shaped *DMT* pattern also matches observed ecological patterns on the study reef (Madin pers obs) as well as general patterns—stunted colony forms on reef crests and the barren nature of many reef flats—across wave-exposed reef gradients (Done 1983).

Coral reef structures are the critical backbone of reef ecosystems and are vital for coastal protection. However, processes that act to stabilise and cement reef materials are sensitive to ocean acidification (Kuffner et al. 2008; Manzello et al. 2008), which is projected to rise with anthropogenic climate change (Kleypas et al. 1999). As a result, coral reef organisms are vulnerable not only from changes in their own structure and function, but also to change in the integrity of substrate to which they are

anchored or live within. It is therefore imperative for biologists to understand and quantify how these processes will affect coral distribution now and in the future. This study fills a gap in this understanding by measuring spatial variation in substrate properties and linking these patterns to the structural integrity of reef-building corals. Furthermore, our results demonstrate that baseline mechanical properties can be determined, thus allowing monitoring of reef stability as levels of atmospheric CO<sub>2</sub> rise.

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